EXAMINING SPECIES' RESPONSES TO CLIMATE CHANGE ACROSS MULTIPLE TAXONOMIC GROUPS

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Abstract

Many species are responding to anthropogenic climate change by shifting their ranges to higher latitudes. Understanding the factors that drive species' responses will help ecologists and conservationists develop strategies to avoid negative climate change impacts.

I investigated shifts at the northern (cool) range margins of 1573 southerly-distributed species from 21 animal groups in Great Britain, over the past four decades. My findings confirm continued polewards range shifts (18 km decade^{-1} over 1986-2010). I then concentrated on 347 British species from 14 invertebrate taxa, discovering considerable variation in the distances moved within each taxonomic group (but not between groups). I used land cover data and distribution records to determine each species' habitat specialism, and to quantify habitat availability. Habitat availability explained up to half of the range shift variation. I conclude that interactions between species' attributes and the environment are important determinants of range shifts.

Abundance data are used to study species' responses to environmental changes but, unlike distribution records, are not available for many taxa. Data from 33 British butterflies revealed a strong correlation between mean year-to-year changes in total number of distribution records and mean year-to-year change in abundance, suggesting that distribution data can be used to identify species' population variability, and ecologists can investigate the influence of climate change on species' populations without abundance data.

I conclude that rates of range shifting are highly variable among species, suggesting that understanding species-specific range shifts is necessary to assess species' responses to climate change. The availability of habitat at the range margin strongly influence rates of range shifting which suggests the need for habitat management aimed at facilitating species' dispersal and population establishment. Citizen science data have potential to assist ecologists in examining species' responses to climate change and in identifying, predicting and mitigating climate change impacts in the future.

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Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

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Chapter 1

General Introduction

In this thesis, I examine species responses to climate change. Redistribution of species under climate change has been observed globally, and has consequences for maintaining biodiversity and ecosystems. Climate change also has positive and negative impacts upon species population dynamics, which need to be examined to assess species' vulnerability. In this first chapter, I introduce the key topics of my thesis. First, I provide the context for my thesis, anthropogenic climate change (section 1.1). I discuss species associations with the climate (climatic niches), and how these associations can vary over space and time (section 1.2). I briefly discuss different evolutionary and ecological responses to climate change (section 1.3) and focus on range shifts, a response of interest (section 1.4). I consider the population changes that drive this response, before examining the impact of habitat availability upon species' rates of range shift (section 1.5). I present the biological records data used to measure range shifts and to create proxies for abundance in this thesis (section 1.6). Finally, I set out the research questions I address in this thesis and I provide an overview of each subsequent chapter (section 1.7).

1.1 Anthropogenic climate change

The global climate has always been changing, as evidenced by records of oxygen isotopes, pollen, and fossils (Shackleton, 1987; Jackson *et al.*, 2000; Davis & Shaw, 2001). Since the industrial revolution, there has been an increase in the rate of climatic warming (Karl & Trenberth, 2003), termed 'anthropogenic climate change', or climate change driven by human activity. This activity has been extensive, and the term 'Anthropocene' is used to describe the current epoch which has a range of proposed start dates, ranging from the 1800's (Steffen *et al.*, 2011) to the mid-20th Century (Waters *et al.*, 2016). Anthropogenic climate change is driven by greenhouse gases (GHGs), defined by the IPCC as "those gaseous constituents of the atmosphere, both natural and anthropogenic, that absorb and emit radiation at specific wavelengths within the spectrum of thermal infrared radiation emitted by the Earth's surface, the atmosphere itself, and by clouds" (IPCC, 2014). By absorbing radiation, GHSs act as an insulator, trapping heat and warming the earth. GHGs include water vapour, CO_2, CH_4, O_3 and N_2O. In 2011, CO_2 concentrations in the atmosphere were 40% higher than they were before the industrial revolution and CO_2, CH_4, and N_2O

concentrations were noted to “exceed the highest concentrations recorded in ice cores during the past 800,000 years” (IPCC, 2013). Human activities are contributing to GHG emissions through energy production, other industrial activities and land use change (Turner *et al.*, 1994; Ramankutty & Foley, 1999; Christidis *et al.*, 2013). There is a consensus in the literature that the global-scale warming trend since the mid 20th century has mainly been caused by anthropogenic emissions (Oreskes, 2005; Jenkins *et al.*, 2008; IPCC, 2013). The rapid proliferation of technology and exploitation of the Earth’s resources (e.g. fossil fuel energy) have led to increased GHG emissions. In future, human activities are likely to intensify as our rising population (now estimated globally at 7,550 million people: see United Nations report, 2017) demands an increasing supply of resources. As concentrations of atmospheric GHGs continue to rise, climatic conditions will change affecting the Earth’s ecosystems and the species that live there.

Atmospheric and oceanic temperature increases are a consequence of GHGs warming the planet by trapping radiation (Karl & Trenberth, 2003). At a worldwide scale, a globally averaged warming of 0.85°C has been observed from 1880 to 2012 for land and ocean surface temperatures combined (IPCC, 2013). Increases in the frequency of extreme events are predicted to occur under climate change (Easterling, 2000; Cai *et al.*, 2014). Extreme record-breaking temperatures are increasingly observed (Lhotka *et al.*, 2016), with 2017 being the second hottest year on record for the US (NOAA National Centers for Environmental Information, 2017). Warmer temperatures result in higher rates of evaporation from the Earth’s oceans, leading to greater incidence of heavy rainfall and flooding (Lenderink & van Meijgaard, 2008). However, in drier areas where there are fewer water bodies, increased temperatures may increase the risk of drought (IPCC, 2013). These extreme events are predicted to have detrimental impacts for ecosystems, causing population collapse in sensitive species (Oliver *et al.*, 2015) and reductions in habitat quality and availability (Ummenhofer & Meehl, 2017).

In this thesis, I study the responses of species in Britain to climate change. In the UK, the climate has been monitored for hundreds of years by volunteers and organisations such as the UK Met Office. Instrumental recording of monthly temperatures began with Central England Temperature (CET) data in 1600s (Parker *et al.*, 1992), and the longest continuously-active weather station has records since 1767 (Oxford University News, 2015). An analysis of UK climate changes show that all regions have experienced a trend of increased winter rainfall, the Central England Temperature (CET) has increased 1°C since the 1970s, and severe windstorms have become more frequent (Jenkins *et al.*, 2008). The UK Climate Projections science report (Murphy *et al.*, 2009) predicts that by 2080 the UK will experience increased daily temperatures by 5.4°C in summer and 2.8°C in winter (median emissions scenario, 50% probability). The projected impact of climate change on precipitation is less clear, but includes increased winter rainfall by up to 33% in the west of the UK, decreased summer rainfall by up to 40% in southern England, and an increased risk of flash-flooding (Kendon *et al.*, 2014). The potential consequences of these changes for biodiversity are a core area of ecological research, and in this thesis, I explore species' responses to climate change, in order to understand how and why species react to changes in their environment. These analyses will not only aid understanding of species' recent responses to climate, but also help inform conservation efforts to protect species in future. The results have implications beyond the UK, for example, informing on how different species types are likely to respond to climatic change in heavily human modified landscapes, as found in many countries globally.

1.2 Species' associations with climate

In order to understand the impacts of anthropogenic climate change on species and ecosystems, it is important to understand the relationships between species and climate. Fundamental niches constitute the multi-dimensional array of conditions (including climate) within which a species can exist (Hutchinson, 1957; Holt, 2009). However, species may be excluded from parts of their fundamental niches, due to interspecific interactions, such as predation, competition and parasitism. This new subset of their fundamental niche is called the 'realised' niche (Hutchinson, 1957). The range of climatic conditions where species are able to survive (measured within the realised niche) can be referred to as the 'climatic niche' (Bellard *et al.*, 2012). Extinctions can occur where climate becomes unsuitable, but species may colonise new areas that become habitable under climate change. These changes in species' distributions or 'range shifts' in response to climate change are a primary focus for my thesis, and I discuss them further below (section 1.4).

A suitable climate is a vital aspect of a species' niche, and species distributions and population sizes are commonly determined by climatic conditions (Stephens *et al.*, 2016). There are defined climatic regions across the world, and biodiversity is distributed non-randomly, peaking in moist, tropical regions. This pattern can be explained by the species-energy relationship (Gaston, 2000), which implies that more species will be able to persist where more energy (heat) and water is available (measured as temperature and/or evapotranspiration). This relationship is theorised to occur because higher energy availability will boost primary productivity, which in turn supports more primary consumers, with cascading impacts through the entire ecosystem. Alternatively, extreme dry or cold environments present limits to productivity, and fewer species can persist in such conditions (Araújo *et al.*, 2013). There are many interacting processes in biodiversity-rich regions, and understanding the extent to which different factors create and maintain diversity is complex (Brown, 2014).

Weather conditions influence populations by directly affecting fecundity and mortality rates, and by indirectly affecting interspecific relationships (i.e. abundance of predators or prey) and resources (e.g. host plant quantity and quality for herbivores). Temperature and rainfall are commonly examined in studies of population dynamics, because these variables are also metrics of climate change (WallisDeVries *et al.*, 2011). The impacts of these variables on species' biogeography have been studied for butterflies, a data-rich taxonomic group. Temperature is linked to fecundity in several butterfly species, because females rely on warm temperatures to seek out appropriate host plants (Kingsolver, 1989). Rainfall is beneficial for host plant growth, and some butterflies prefer moist conditions, although rainfall reduces dispersal (individuals' movement through the landscape) and may prevent foraging (Pollard, 1988). Roy *et al.* (2001) found that rainfall and temperature interacted to influence populations: the majority of butterfly species generally had positive associations with warmer summer temperatures, but for some species, droughts (caused by low rainfall) resulted in negative associations between abundance and warm summers in previous years. Given the heterogeneous impacts of weather conditions upon species populations, climate change is likely to have positive and negative impacts on populations. If temperatures rise, this may increase productivity, which will support larger populations for some species. Extreme climatic events can cause species' populations to severely decline (Oliver *et al.*, 2013) or increase in variability (Vázquez *et al.*, 2017). Increased variability in species abundances can increase risk of local extinctions (Wiens, 2016), and cause disappearances of species from larger areas (Parmesan, 2006; Stanton *et al.*, 2015). To summarise, species have strong associations with different climatic processes that directly and indirectly influence their vitality, fecundity and mortality. Until such details are known, the complexity of these interacting effects of weather on populations make it difficult to predict the longer-term impacts of climate change on species (Knape & de Valpine, 2011). However, some short-term impacts such as the effects of sudden and extreme climatic events have been observed and studied.

Climate change, in addition to impacting the persistence of species populations, may also affect species' climate associations. Under climate change, these associations may remain constant (niche conservatism), resulting in species shifting their ranges, or be altered (niche shifts) if species adapt *in situ* to changing climates (Holt, 2009). Under the assumption of conservatism, niches can be inferred from occupancy-environment relationships, whereby species persistence is determined by the suitability of its environment (Pearman *et al.*, 2008). In addition, conservatism rests on the assumption that species are in equilibrium with their environment, and will shift their ranges to track their climatic niche (La Sorte & Jetz, 2012). By contrast, niche shifts have been observed when species invade new areas and encounter new environmental conditions (Tingley *et al.*, 2014). While a species' realised niche can be used to predict whether that species might invade a new area, the niche can be inadequate for predicting future distributions (Broennimann *et al.*, 2007). Whether niches are conserved or altered over time is important for understanding whether the species will successfully shift its range and establish in new areas or not. For example, Yackulic *et al.* (2015) concluded that temporal variation in climatic conditions and colonisation and extinction events can result in species' occupancy-environment relationships changing over time. Most researchers consider that static occupancy-environment relationships, and the correlative models that utilise them, are over-simplistic for predicting species responses to climate change (Schurr *et al.*, 2012; Yackulic *et al.*, 2015). Species may not always be at equilibrium with their environment (such as at the edges of the range where exposure to changes in environmental conditions can make populations rapidly increase or decrease), and there may be delays or lags in response to climate change, but creating models that are reflective of the true occupancy-environment relationship of species is extremely challenging. In conclusion, species climate associations are not necessarily static; some species may contract or expand their realised and even fundamental niches over time, and thus adjust to climate change in different ways.

1.3 Species' responses to climate change

Across continents, a wide range of species' responses to climate change have been detected (Parmesan, 2006; Sutherland *et al.*, 2010). These are genetic, evolutionary responses (e.g. microevolution, (Parmesan, 2006; Bellard *et al.*, 2012; Vedder *et al.*, 2013), and ecological responses. Ecological responses include phenotypic plasticity, which is the ability of a genotype to express different phenotypes under different conditions, phenological changes, changes in population dynamics and range shifts (moving to new locations as species track suitable conditions), and while framed as species reactions to changes in the environment, these responses can have evolutionary bases (see below). In this section, I discuss the relationship between evolutionary and ecological responses, examples of genetic and phenotypical responses, and how population dynamics (e.g. changes in size) are used to monitor species' sensitivity to climate, before focussing on range shifts in more depth in the next section (1.4).

Understanding the mechanisms of species responses to climate change can be immensely difficult, as it is often unclear whether responses have a genetic underpinning, or are a result of phenotypic adaptations. Most studies of climate change responses do not test for genetic changes in species and populations (Gienapp *et al.*, 2008). Thus, evidence of evolutionary responses to climate change tends to be limited and many responses are inconclusively theorised to be evolutionary. Some phenotypic responses such as plasticity could be evolutionary responses to a changing environment (Vázquez *et al.*, 2017); alternatively, adaptations which are thought to be genetic may actually be driven by ecological processes (Gienapp *et al.*, 2008). Species may demonstrate both genetic and phenotypical adaptations under climate change. While these adaptations may enable species to respond to climate change, many studies do not explicitly identify climate as the selective driving force of the adaption (Gienapp *et al.*, 2008). With these issues in mind, I will now discuss case studies of evolutionary and ecological responses to climate change.

Evolutionary responses to climate change can facilitate species' successful colonisation of newly-suitable locations, or enable persistence of altered climate conditions *in situ* (Chevin & Hoffmann, 2016). For example, some British cricket species (*Concephalus discolor* and *Metrioptera roseii*) have short- and long-winged forms, and the longer-winged, more dispersive individuals have been observed more frequently in newly established populations (Thomas *et al.*, 2001; Simmons & Thomas, 2004). Temperature influences the form that individuals will mature into (as demonstrated by Sänger & Helfert, 1975), and climate change acts as a driving force for range expansion (Hochkirch & Damerau, 2009; also see below). Therefore, it is likely that climate has acted as a selective pressure to increase the proportion of the population with longer wings, because long distance dispersers are more likely to establish new populations in regions that have recently become climatically suitable for them. Once established, a costly dispersal strategy is unnecessary for individuals, and the incidence of long-winged forms declines over time; this demonstrates how evolutionary processes can cause short-lived changes in species' behaviour in response to climate change (Simmons & Thomas, 2004).

Another example of an evolutionary response to climate change is the changes observed in migration patterns of *Sylvia atricapilla*, the Eurasian blackcap. As temperatures increase, winters become warmer, changing the distribution of suitable areas where migrating birds can overwinter. Over the last 50 years, some German blackcap populations have evolved new migration patterns (Berthold *et al.*, 1992); while British populations migrate southwards, some German birds migrate westwards to Britain, where there are milder winters and an abundance of food resources in domestic gardens. Because of the closeness of this location to the species native range, birds overwintering in Britain can return to Germany sooner, and breed 2 weeks before individuals than overwinter in Africa and southern Europe. Because birds that return sooner breed with other birds do the same, there is genetic isolation between populations with different migration strategies which has enabled this rapid evolutionary change (Pulido, 2007). While there is much potential for evolutionary responses to climate change, many observed adaptations appear to be variations on normal behaviour and body size, and uniquely different phenotypes are not often observed. A lack of existing genetic variation, gene flow or new mutations may limit adaptations to climate change (Thomas, 2005).

The evidence base for adaptive responses to climate change is mostly comprised of phenotypic observations, which may be underpinned by genetic changes and/or by plasticity. Phenotypic plasticity is the phenomenon of changes in species' behaviour, thermal tolerances, physiology or other aspect of their phenotype. Climate change effects mediated through physiology can have positive or negative effects on individual fitness. For example, with regards to butterflies, warmer temperatures allow females more time to search for hostplants and to lay their eggs. Davies *et al.* (2006) studied the thermally-restricted silver spotted skipper butterfly (*Hesperia comma*), and found that warming climates had improved habitat availability, allowing the species to disperse and utilise a variety of hostplants beyond its traditional ones. As a result, egg-laying rates increased, which in turn may boost numbers of individuals. However, climate change can also lead to lowered fitness through heat stress (McCarty, 2001), or reduced foraging time for insects due to unsuitable conditions (Andrew *et al.*, 2013).

Phenotypic plasticity can help species survive in extreme and variable climates, and therefore is of interest to ecologists and conservationists (Chevin & Hoffmann, 2016). An example of phenotypic plasticity is phenological change. Alterations in phenology (the timings of seasonal events in species' lifecycles) are *in-situ* climate change responses, which are often prompted by temperature changes (Foden *et al.*, 2013; Dickinson *et al.*, 2014) and influenced by species' life histories (Forrest, 2016). As different species have different responses to climate change, changes in phenology can lead to either trophic matches, improving or creating interspecific interactions, or tropic mismatch, where ecological interactions between species are disrupted (Thackeray *et al.*, 2010; Schweiger *et al.*, 2012). Changes in phenology may allow species to track climate change and avoid mismatches. Without adaptations like this, populations may decline. One of the best examples of phenological responses to climate change is the interaction between great tits, *Parus major* and larvae of the winter moth, *Operophtera brumata* (Visser *et al.*, 2006). Great tits lay their eggs so that the hatching of their chicks coincides with the peak abundance of larvae (Noordwijk *et al.*, 1995), which in turn hatch during the bud burst of oak trees, to feed on new leaves. Larval growth and oak bud burst depends on temperature, and changing climates might have resulted in a mismatch between when larvae are abundant, and when the great tit eggs are laid. However, in Wytham Woods, great tits demonstrated plasticity, rather than microevolution, changing their nesting behaviour to track the emergence of the larvae (Charmantier *et al.*, 2008). Other phenological responses include changes in voltinism, the number of generations a species produces. Climate change has improved the prospects of Lepidoptera species in Europe, increasing the frequency of second and third broods in many species (Altermatt, 2010). Multiple generations per year may speed up evolutionary responses to climate change, and contribute to population growth.

Here, I briefly discuss climate effects on population size. Because climate can influence species fecundity and mortality, population metrics are often used to determine the risks of climate change to species. This responsiveness of populations to climate change (often termed vulnerability in the literature) to climate change is determined by two factors: sensitivity to climate and exposure (i.e. how much the climate has changed for species, see Williams *et al.*, 2008 and Huey *et al.*, 2012). Climate sensitivity is a metric that measures how populations respond to climate change, characterised as a species' ability to persist in changed environments or dependence on unaltered climate conditions (Dawson *et al.*, 2011; Foden *et al.*, 2013; Dickinson *et al.*, 2014). While much of the literature focuses on negative impacts of climate change, warm-associated species in Britain (which are the focus of my thesis) are set to benefit from climate change (Burns *et al.*, 2016). Populations may increase because of positive climate effects on fecundity and brood size, as stated above. Climate sensitivity is often assessed as the magnitude of changes in population size in response to climatic variables, and exposure reflects the degree of change of climate variables that the species is sensitive to (Foden *et al.*, 2013). The combined effects of sensitivity to different climatic variables and exposure to those climatic variables will determine how species respond to climatic change. The responsiveness of species populations to climate change must be measured in a clear and rigorous way (Wade *et al.*, 2017) so that ecologists can predict future outcomes for species and develop appropriate conservation management strategies (McMahon *et al.*, 2011). In this thesis, I explore a method to use distribution data to measure population variability where abundance data are lacking, potentially providing a key indicator of species responses to climate change (see section 1.6.2 below).

1.4 Range shifting in response to climate change

Naturalists and ecologists have observed the changing spatial distributions of species (Kaisila, 1962; Fuller et al., 1995; Brown et al., 1996). Range shifts are a well-studied response to climate change, and in this section, I discuss different patterns of range change and how they are measured, and the population processes that lead to range shifts. I finish this section by discussing the knowledge gaps that my thesis addresses.

Species responses to climate change are observed through changes in the size, shape or extent of species' ranges (Thuiller *et al.*, 2005), and changes in position of the range by latitude (Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Parmesan, 2006; Walther, 2010; Poloczanska *et al.*, 2013). Changes in the longitude (Gillings *et al.*, 2015; Lenoir & Svenning, 2015; Tayleur *et al.*, 2015) and elevation of ranges are also observed (Sekercioglu *et al.*, 2008; Chen *et al.*, 2009; Menéndez *et al.*, 2014). Shifts have been measured for many different species in different biomes, at different scales, both micro- and global. Latitudinal changes in a species' ranges are most often measured at the poleward (leading-edge) range margin, though they can also be measured by the shift of the centre point (centroid) of the whole distribution (Huntley *et al.*, 2008), or by measuring ranges shifts in other directions, e.g. north-westwards (Gillings *et al.*, 2015). In this thesis, I use measure latitudinal changes in the northern range margin of species, which is normally the leading-edge of the range in Britain for species which favour warmer climates.

1.4.1 Population and range shifts

Range shift is a distributional change underpinned by population processes, which are commonly driven by climate change. Distribution and abundance are both influenced by climate because the two are related (Brown, 1984), as reflected in the abundance-occupancy relationship (Gaston, 1996; Hartley, 1998; Roney *et al.*, 2015). This relationship is generally positive, but negative relationships can occur in situations where large populations of a species are highly aggregated (Webb *et al.*, 2012). Species ranges exist across geographical and climatic gradients, but none of these factors alone necessarily explains the spread of populations within ranges (Pironon *et al.*, 2015). Abundance within ranges is also influenced by inter- and intra-specific interactions, by species' ability to adapt to environmental change, and by human activity (Sagarin *et al.*, 2006).

As the climate warms, southern warm-adapted species in Britain experience range expansion. Species expand their distributions by colonisation, which involves individuals moving through landscapes (dispersal), and building populations in unoccupied habitats (establishment) at the leading-edge, (Hughes, 2000). At the leading-edge, abundance may limit colonisation of new areas (Mair *et al.*, 2014), where smaller populations produce few dispersing individuals. Some colonisations are undertaken by a few individuals over great distances, which can lead to founder effects, where the new population has low genetic diversity (Hill *et al.*, 2011). Reduced genetic variability, coupled with unfamiliar conditions, can threaten the success of the new populations by making species vulnerable to disease or extreme climatic conditions. The majority of population data on range shifts come from the leading-edge margins, and studies of periphery populations at the trailing-edge are relatively rare (Hampe & Petit, 2005). However, the population dynamics at this margin are important: this margin often contains older populations, with many genetic lineages (Hampe & Petit, 2005). These populations are sensitive to climate change, and retractions have been detected at the trailing edge margins (Franco *et al.*, 2006). Without local adaptation or population stability to enable persistence at the trailing edge, these populations may go extinct, causing the range to shift towards the leading-edge. The rate of population processes at the margins are not necessarily equal, and some species' leading-edges have been shown to expand faster than their trailing-edges contract (Chen *et al.*, 2011a).

1.4.2 Variation in range shifts amongst and within taxa

Species differ in their niches, thermal tolerances, and responses to climate change, and thus variation is expected in range shifts both within and between taxonomic groups (Parmesan & Yohe, 2003; Angert *et al.*, 2011). For example, tree and shrub species in Sweden have tracked climate change at different rates (Kullman, 2002); different species across a range of taxa show different latitudinal and elevational shifts over time (Chen *et al.*, 2011b); and British butterflies show heterogeneous distribution and abundance responses to climate change (Mair *et al.*, 2012).

Few studies examine variation in rates of range shifts across multiple taxonomic groups (Hickling *et al.*, 2006). It is important to study variation in range shifts across a wide range of groups because the range shifts of well-studied species and taxa may not be representative of shifts experienced by the full range of biodiversity. There may be differences (flight ability, body size, reproductive strategies) between groups, which could result in variable climate change responses. Within-group variation must also be assessed because apparently similar species may still exhibit a variety of climate associations and life histories. If phylogenetically similar species respond to climate change in similar ways, then (for example) one butterfly's range shift would be similar to another's. Where this is not the case, specific range shift measurements must be calculated for each species of interest.

While it is generally accepted that there is intra- and inter-taxon variation in range shifts, these types of variation are rarely assessed together. Detecting and understanding variation in range shifts across multiple taxonomic groups will help ecologists identify what types of species are likely to have limited colonisation abilities. By exploring which factors influence rates of range shift, targeted conservation strategies can be developed to help protect vulnerable species under climate change, and facilitate increases in other species. This thesis addresses the lack of multi-taxon analyses of range shifts by exploiting the rich data available for British taxa, collated by the UK Biological Records Centre.

1.5 Habitat factors in range shifts

In addition to specific climatic conditions, species are often associated with specific types of habitat. To respond to climate change, species require suitable habitats in order to persist, as 'stepping stones' so that they can move through landscapes, and for habitat to be available to colonise and establish populations in new regions. The presence of semi-natural (Papanikolaou et al., 2017), heterogeneous (Oliver et al., 2010), or intact (Eigenbrod et al., 2015) habitat can buffer species against negative effects of climate change by promoting population stability and providing refugia which faciliate range shifts. However, suitable habitat is not always available, as the world's biotopes are being converted, polluted, and fragmented by agricultural and industrial human activities (Vitousek *et al.*, 1997; Foley *et al.*, 2005). In this section, I discuss how climate and habitat factors interact to impact species populations and distributions (1.5.1), and then consider habitat availability within fragmented landscapes (1.5.2). I investigate the role of habitat availability in multi-taxon range shifts in Chapter 3.

1.5.1 Interactions between climate and habitat

Habitat is an important factor to consider when studying range shifts, because species require suitable habitats to establish new populations and track climate change. Attributing ecological changes (range expansions or contractions) to climate change, habitat availability, or both of these drivers is a challenge, as these drivers interact and other factors are also involved: life history traits, intraspecific competition and diseases (Oliver & Morecroft, 2014). The relationship between land use and climate change has different forms: additive, where the impacts of each driver can simply be summed, or interactive (Oliver *et al.*, 2016; Radinger *et al.*, 2016). Interactions between habitat and climate may be synergistic or antagonistic, where one factor amplifies or buffers (reduces) the effects of the other. For example, Bradbury *et al.* (2011) found that establishment of new populations of the Dartford Warbler in the UK was influenced by warmer climates improving the suitability of higher altitude, unoccupied and available habitats. This demonstrates a synergistic interaction between the amelioration of cold winters and habitat availability at higher altitudes. Because of the variety of impacts habitat change can have, it is important to control for habitat when studying climate change impacts (Clavero *et al.*, 2011).

Key examples of climate and habitat interactions include the altered habitat associations of butterflies, e.g. the silver spotted skipper, now increasingly utilises a wider variety of micro-habitats and northerly-facing habitat patches (Davies *et al.*, 2006). Pateman *et al.* (2012) examined the habitat associations of two British butterfly species, the brown argus *Aricia agestis* and the speckled wood *Pararge aegeria*. The brown argus butterfly is associated with two hostplants, rockrose and dove's-foot cranesbill. The rockrose is the favoured hostplant, supporting large, stable populations. In the 1980's, only 20% of this species population was found in cranesbill-only areas. However, warmer summers improved suitability of cranesbill habitat, promoting population growth. The cranesbill is much more abundant than the rockrose in Southern England, allowing the large numbers of individuals to expand over this area, and now over 40% of populations are found in cranesbill-only areas (Pateman *et al.*, 2012). The *Aricia agestis* case study is an example of niche constraints (climate) being relaxed, allowing the exploitation or less favoured hostplants. *Pararge aegeria* has also been shown to vary its broad habitat use under climate change. Giving this butterfly its name, the speckled wood butterfly is associated with deciduous and coniferous woodland. However, as winters and summers have warmed, and summer rainfall has increased, this species has been able to create and sustain new populations in open unsheltered grassland where chill and desiccation would have previously had negative impacts upon populations. Therefore, the degree to which species are specialised on different habitats may vary between populations and the climatic conditions those individuals experience (Suggitt *et al.*, 2012). While climate can impact species' habitat associations in this way, habitat structure can also impact the climate that species experience. For example, changes in habitat structure (e.g. vegetation height, cover and type) can influence microclimate. Various aspects of microclimate such as solar irradiation and moisture have been found to be a driver of species' occupancy, persistence and population dynamics (Suggitt *et al.*, 2015; Wilson *et al.*, 2015; Fourcade & Öckinger, 2017).

The combined impacts of land conversion and climate change may create negative impacts for some species such as range losses and extinctions, particularly in developing nations, as has been shown for birds (Jetz *et al.*, 2007), trees (García-Valdés *et al.*, 2015) and other groups including mammals, reptiles, and amphibians (Jantz *et al.*, 2015). Few studies have attempted to predict the extent of future negative impacts from the combined effects of habitat and climate on species (Titeux *et al.*, 2016). To form effective conservation strategies, ecologists need to identify drivers of distribution and population changes and understand how those drivers interact.

1.5.2 Habitat availability in anthropogenic landscapes

Species' habitats are embedded within landscapes, and global landscapes have been altered by land-use change. Thus, suitable habitat patches may become too far apart for species to move between them, creating barriers to dispersal (Hill *et al.*, 2001; Warren *et al.*, 2001; Menéndez *et al.*, 2006). For range expansion to occur, suitable habitat must be sufficient in size and quality to allow the establishment and persistence of species' populations (Mortelliti *et al.*, 2012), and species need to be able to access these habitats. The ability to traverse non-habitat areas is vital for species to successfully respond to climate change (Holyoak & Heath, 2016). Species that cannot do this may experience range collapses or extinction (Thomas, 2000).

Two metrics used to assess how species move through landscapes are structural connectivity, which is the spatial distribution of (single or multi-species) habitat types, and functional connectivity, which relates to the movement of (typically) individual species across a landscape (Tischendorf & Fahrig, 2000). Structural connectivity is often used as a proxy for functional connectivity, as the structure of a landscape relates to species movement. However, structural connectivity has limited value because it makes a single generalised assessment of connectivity for a landscape, but connectivity may be specific for different species in the same landscape (Tischendorf & Fahrig, 2000). Some species can disperse through habitats they would not establish in, demonstrating disparity between structural and functional connectivity (Keeley *et al.*, 2017). High functional connectivity is important for gene flow and diversity in species' populations, and synchrony between geographically-related populations can be used as a proxy for connectivity (Powney *et al.*, 2012). In this thesis, I examine species range expansions under climate change, which is the activity of individuals dispersing and establishing in new areas. Lawson *et al.* (2012) demonstrated how this activity was assisted by functional connectivity which allowed individuals to navigate through landscapes, and recommended connectivity-focussed conservation strategies to promote colonisations for the silver-spotted skipper butterfly. For example, protected areas provide 'stepping stone' habitats that may facilitate the range expansions of species (Thomas *et al.*, 2012). In my general discussion chapter, I consider connectivity issues further and what sorts of techniques, such as connecting habitat patches ('stepping stones' or 'corridors'), can best help species move through the landscape (Hodgson *et al.*, 2012, 2016).

The ability to shift across fragmented landscapes is influenced by species traits (Angert *et al.*, 2011; Reif & Flousek, 2012) such as habitat specificity. Habitat generalists generally have a greater ability to adjust to environmental change and are therefore more likely to track climate change than specialists, assuming their resources are widely available (Warren *et al.*, 2001; Hill *et al.*, 2002). Specialists have a smaller pool of resources that they can utilise, so these species are more likely to be threatened by habitat loss, unless they specialise on a particularly widespread habitat, or on human-modified environments. Accessing suitable habitat in fragmented landscapes is a key challenge for species. In this thesis, I examine how species traits and their landscapes interact to influence rates of range shift. While there are many studies examining habitat influences on species' persistence and range shifts, these studies are often restricted to a few species, and use specific resources (e.g. hostplants) to define habitats. In Chapter 3, I calculate detailed habitat associations and specialism scores for a wide range of species to explore the influence of habitat and species traits on rates of range shift.

1.6 Monitoring species' responses to climate change

To examine species' responses to climate change in this thesis, I use distribution data which are collected as species' presence records at a given time and location. Established in 1964, the UK Biological Records Centre (BRC) holds distribution records for many different taxonomic groups. Recording schemes are primarily volunteer-run organisations that collect these records. Over 80 schemes share their data with the BRC, making it a valuable source of biogeographical data containing millions of records, in some instances dating back from the 16th century (Roy *et al.*, 2014). BRC data are the foundation of this thesis, accompanied by two other data sources. The British Trust for Ornithology (BTO) has gathered distribution data for UK birds since 1933, and I include these data in Chapter 2 to increase the number of taxonomic groups studied. In Chapter 4, I compare patterns in abundance and distribution data, and use abundance records from the UK Butterfly Monitoring scheme (UKBMS), which runs weekly transect walks to monitor butterfly populations across the UK. Abundance data are important to ecological studies, but are not nearly as widely available (compared to distributional data) among different taxa. In this section, I discuss how abundance data are used to measure responses to climate change and how distribution data may be used in similar ways when abundance data are lacking (1.6.1). Then, I discuss the biases in distribution records during data collection, and how these biases can be addressed (section 1.6.2).

1.6.1 Population responses to climate change

In order to measure responses to climate change, suitable data must be available, and here I consider the opportunities distribution data provide to measure population variability. I have previously discussed the sensitivity of species' population abundance to climate change, because species rely on suitable weather conditions to sustain their fecundity, dispersal and resource use. Changing these conditions may have positive and/or negative impacts on species population growth and variability (Vázquez *et al.*, 2017). This makes abundance data a valuable resource for monitoring climate change responses. Abundance is often monitored at fixed locations to enable comparability over time. For example, volunteers collect abundance data for butterflies in the UK by making counts along fixed transect routes, recording numbers once a week for 26 weeks in a year, when the adult butterflies will be flying, and when weather conditions are suitable. The UKBMS uses these data to produce research outputs, such as broad assessments of UK butterfly status (Fox *et al.*, 2015) and statistical metrics (indicators) to demonstrate fluctuations in population numbers (Brereton *et al.*, 2011). Changes in abundance give ecologists and conservationists an early warning that a species may expand its range, or that it may be at risk (Ehrlen & Morris, 2015), as populations can decline gradually over time under unsuitable conditions, prior to extinction. Distribution records do not do this: a species is either observed as present at a site, or not observed. Despite the value of abundance data, the majority of species in the UK (and in the world) do not have detailed abundance data. In order to monitor changes in species' abundances and assess impacts of environmental change on populations, ecologists are examining the potential for distribution data to fill in the abundance data gap.

Because abundance and distribution are related, and distribution data are readily available for many taxonomic groups, these data are increasingly employed to estimate metrics of species' population changes. Distribution data have been used to create composite trends of occupancy and abundance (Pagel *et al.*, 2014) or to assess population trends by measuring changes in occupancy (Maes *et al.*, 2015). In this thesis, I describe these uses further in Chapter 4. Distribution records have not commonly been used to measure inter-annual changes in species' populations, a metric used to explore population-level responses to environmental change. I address this knowledge gap by investigating the potential for year-to-year changes in distribution records to act as a proxy for year-to-year changes in abundance, and discuss the applications of this proxy. This is important because understanding how species populations vary under climate change and over time helps ecologists comprehend patterns in species' population dynamics and to determine species responses to climate change.

1.6.2 Biases in distribution records

Distribution data in the UK are a long-term, widespread and ubiquitous source of ecological information, which I use in this thesis to create metrics of range shift, habitat associations and population variability. However, in the collection of these data, species are sampled unevenly due to biases in the behaviour and distribution of recorders. This phenomenon is sometimes referred to as the 'recorder effort problem' (Prendergast *et al.*, 1993; Hill, 2012). Four main biases have been identified in species' records (Isaac *et al.*, 2014) that I discuss below: 1) temporal biases in recording effort, 2) spatial biases in recording, 3) irregular recording effort per site visit, and 4) uneven detectability of the taxa being studied. There are a wealth of studies in the literature, which aim to address these biases, so that they do not adversely influence studies of distribution change.

Temporal biases arise when the intensity of recording is inconsistent over time. Methods of identifying species have improved, for example, smartphones allow users to identify and/or submit species records quickly. More people have become involved in recording and distribution datasets have rapidly increased in size (Tulloch *et al.*, 2013). For example, macromoths experienced a sevenfold increase in records over four decades (see Chapter 2). As a result, comparison of species' occupancy over time is not straightforward, and increased records of species over time may not be indicative of more individuals or of expanding ranges.

Spatial bias is the manifestation of highly variable sampling coverage (observed in Britain and globally, see Boakes *et al.* 2010, and Amano *et al.* 2016). This bias is driven by accessibility: volunteers tend to record in short-distance, familiar areas, such as the places they live or close-by (Isaac & Pocock, 2015). Because of this, recording effort has been noted to be intensified around human infrastructure such as roads and cities, particularly where large numbers of casual participants are involved in schemes (Geldmann *et al.*, 2016). This means that while improvements in transport have helped recorders access different parts of the country, and GPS technologies facilitate the accurate recording of locations, these transport links may create intensification of recording, while less accessible and less urban areas remain unrecorded. Additionally, recorders can demonstrate spatial bias by focusing their attention on areas where rare or interesting species have been reported.

Another source of bias is irregular recording effort per site visit. The number of species recorded during a site visit depends on how many species are actually present, and the amount of effort used to find those species. Also, the number of individuals of a species that are present at a site depends on the interaction between population dynamics and resource availability, e.g., how many offspring are produced, immigration and emigration levels, emergence periods of species (their phenology), and how many individuals the site can sustain. By visiting a site, recorders collect observations of a sample of the total species richness at the site, rarely attempt to record all species at a site, but rather record on an ad-hoc basis or record a specific species. Therefore, the number of species recorded at a site will vary between visits and between different recorders due to irregular recording effort and different protocols.

Detectability is the fourth source of bias; different species are not equally easy to locate *in situ* and therefore some species require more effort to be detected. Large, colourful species are easier to detect than cryptic or small species. One visit to a site is unlikely to detect all species present: species accumulation curves demonstrate how many site visits are required for the species richness to plateau (Graham *et al.*, 2015). Recording range shifts becomes challenging if the presence of a species can go unnoticed (Lahoz-Monfort *et al.*, 2014), particularly at the edges of a species' range, where numbers of individuals are lower.

There are also differences in recording effort and detectability between different taxonomic groups. Well-recorded groups can have millions of records, where others only have a few thousands (Isaac & Pocock, 2015). Recording schemes have different methods for collecting data, which will produce different patterns in numbers and locations of records (Geldmann *et al.*, 2016). For example, grasshopper species can be identified by their calls; moth recorders use light traps to lure species to a location; aquatic molluscs are sampled by netting. These differences should be taken into consideration when assessing differences in species' responses to environmental change.

Statistical methods are necessary to account for temporal and spatial heterogeneity in sampling effort within and between taxa: without these methods, estimates of range shift may be under- or over-estimated (Kujala *et al.*, 2013). Various techniques have been developed to deal with the bias associated with the recorder effort problem. The Hickling method (Hickling *et al.*, 2005, 2006) uses thresholds to determine the extent of species' ranges. This is done by comparing the number of species recorded in a location in two time periods and selecting those locations where a sufficient number of species was recorded, i.e. where a sufficient amount of recording effort was applied, in both time periods. The Hickling methods have been improved upon in this thesis, to incorporate issues of spatial bias (Mason *et al.*, 2017). FRESCALO (FREquency SCAling LOcal) is a recent method developed for dealing with detectability problems (Hill, 2012). This method estimates the likelihood of a species' presence given the level of recording effort a grid cell has undergone. The level of recording effort is estimated from the number of locally relevant 'benchmark' species recorded at the site in question. FRESCALO has widely used to develop occupancy patterns and trends (Fox *et al.*, 2014; Woodcock *et al.*, 2014; Dyer *et al.*, 2017). In these methods, key issues are avoiding false negatives or positives (measuring species' presence or not when the opposite is true), and to maximise the data which can be analysed. In this thesis, I apply a methodology that also considers local species richness to account for recording effort differences in distribution data in each of my data chapters, and I discuss the future for recording schemes in the General Discussion (Chapter 5).

1.7 Thesis structure

Following this introduction, (**Chapter 1**), this thesis is constructed around three data chapters:

In Chapter 2 (*Geographical range margins of a wide range of taxonomic groups continue to shift polewards*), I quantify range margin shifts of southerly-distributed species over time. I calculate range shift as the change in the location of the northern range margin (in km per decade) for 21 taxonomic groups (1599 species), over two intervals. I expand upon the previous study by Hickling *et al.* (2006) by including more recent data, more taxonomic groups, and an improved method to deal with spatial and temporal variation in recorder effort. I explore variation in rates of range shift over time for four taxonomic groups (butterflies, moths, dragonflies and birds), and present evidence that Lepidoptera have shifted their ranges fastest over time. I conclude that range shifts vary both within and between taxonomic groups, and that the rates at which ranges shift may not be consistent over time.

In Chapter 3 (*The importance of habitat for climate-driven range shifts across multiple taxa*), I examine the role of specialism and habitat availability on rate of range shift for multiple taxonomic groups. Range shifts, specialism scores and a metric of habitat availability are calculated for species from 14 taxonomic groups. I quantify intra and inter-taxon variation within and between groups, and use mixed models to test the relationships between range shifts, specialism and habitat availability. I show that habitat availability is more strongly linked to variation in range shifts (explaining up to 36% of the variation) than is specialism. Habitat availability (an interaction with specialism and the landscape) is an important part of determining rate of range shift, and is likely to play an important role in predicting species' responses to future climate scenarios.

Chapter 4 (*Population variability of species can be deduced from opportunistic citizen science records: a case study using British butterflies*), assesses the potential for distribution data to be used as a proxy for abundance data, by quantifying relationships between year-to-year changes in distribution and abundance. I focus on butterflies as a study taxon, and I explore the importance of biogeographical attributes derived from distribution datasets (frequency of records, spatial aggregation of species, mean inter-annual changes in numbers of records, and spatial scale) on the strength of distribution-abundance relationships. I conclude that distribution data can provide information on year-to-year changes in abundance, for some species, but most importantly that mean year-to-year changes in distribution records are comparable to mean year-to-year changes in abundance for all butterfly species. Thus, distribution records do show potential to be used as proxies for metrics of abundance in some circumstances, for example in calculating population stability, which could be important to assessments of species' extinction risk.

Chapter 5 discusses the findings of Chapters 2-4 in the context of the wider scientific literature and the implications of my results for conservation ecology. I also consider limitations of the data, and suggest future avenues of research. I conclude that 1) there is substantial variation in range shifts both within and between high level taxa, but the majority of variation in range shifts is found within taxonomic groups (rather than between groups); 2) a significant portion of this variation is explained by species' habitat specificity within a landscape context; and 3) distribution records have potential to act as proxies for abundance metrics, where abundance data are lacking.

Chapter 2

Geographical range margins of a wide range of taxonomic groups continue to shift polewards

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2.1 Abstract

Many species are extending their leading-edge (cool) range margins polewards in response to recent climate change. Here, we investigated range margin changes at the northern (cool) range margins of 1599 southerly-distributed species from 21 animal groups in Britain over the past four decades of climate change, updating previous work. Depending on data availability, range margin changes were examined over two time intervals during the past four decades. For four groups (birds, butterflies, macromoths, and dragonflies and damselflies), there were sufficient data to examine range margin changes over both time intervals. We found that most taxa shifted their northern range margins polewards and this finding was not greatly influenced by changes in recorder effort. The mean northwards range margin change in the first time interval was 24 km decade^{-1} (n=13 taxonomic groups), and in the second interval was 18 km decade^{-1} (n=16 taxonomic groups), during periods when the British climate warmed by 0.21°C and 0.28°C per decade, respectively. For the four taxa examined over both intervals, there was evidence for higher rate of range margin change in the more recent time interval in the two Lepidoptera groups. Our analyses confirm continued range margin shift polewards in a wide range of taxonomic groups.

2.2 Introduction

In recent years, ecological responses to climate change have been observed in global fauna and flora as species have responded and adapted to new environmental conditions (Parmesan 2006; IPCC 2014a). Species responses encompass genetic, physiological, phenological and biogeographical changes, and these responses by species may have implications for ecosystem functioning and structure (Bellard *et al.* 2012). One commonly observed response to climate change in a wide range of terrestrial and aquatic ecosystems is the polewards extension of species' distributions (Parmesan & Yohe 2003; Poloczanska *et al.* 2013).

Climate influences the distribution of species, often acting as a limiting factor on the extent and location of species' range margins (Hill & Preston 2015). Historical data have demonstrated how species' distributions have changed over time (Hill *et al.* 2002), extending their ranges at leading-edge 'cool' margins when climates become more favourable for these species (Chen *et al.* 2011a). Some species have shifted their ranges at rates reflecting local rates of climate warming (Parmesan *et al.* 1999; Chen *et al.* 2011a), whereas other species have lagged behind climate changes (Menéndez *et al.* 2006; Devictor *et al.* 2008; Valladares *et al.* 2014). Considering the wide variety of habitats, pre-warming ranges, life histories, resource requirements, dispersal behaviours and opportunities available to different taxonomic groups, the expectation has been for responses to climate change to vary between taxonomic groups (Angert *et al.* 2011). Indeed, studies have reported large inter- and intra-specific variation in the responses of taxonomic groups to climate change (Thomas *et al.* 2004; Hickling *et al.* 2006; Rapacciuolo *et al.* 2014). For example, butterflies have demonstrated idiosyncratic responses to climate change (Mair *et al.* 2012), with inter-specific variation partly explained by trends in abundance and habitat availability (Mair *et al.* 2014). The availability of large data sets for a wide range of taxonomic groups in Britain held by the UK National Biodiversity Network and other organisations, provides an excellent opportunity to explore the responses of different taxonomic groups to recent climate change.

Many species reach their leading-edge 'cool' range margins in Britain, and hence might be expected to shift their range northwards under recent climate warming. There are some single-taxon studies that have examined range changes in Britain (Hill *et al.* 2002; Hickling *et al.* 2005), but not all taxonomic groups may respond in the same way to climate warming. Hickling *et al*. (2006) studied range margin changes in 16 taxa that reach a leading-edge range margin in Britain, and here we update and build upon this earlier study by analysing 21 taxonomic groups, containing 1599 species monitored over four decades of climate warming. We also examine range margin changes over two time intervals, thereby investigating changes in response rates over time, as well as being able to compare range margin changes across more taxonomic groups than previously examined.

2.3 Materials and methods

2.3.1 Species data sets

We analysed British data gathered mainly by volunteer naturalists through recording schemes (see acknowledgements) overseen by the UK Biological Records Centre (www.brc.ac.uk), British Trust for Ornithology (BTO, www.bto.org) and Butterfly Conservation (www.butterfly-conservation.org). We categorised each observation (recorded presence) of individual species according to its location (Ordnance Survey 10km x 10km grid square; hereafter termed 'hectad') and the time period it was recorded in (see below). Most observations were for a specific day, but some recording schemes collate observations into date ranges spanning several years. In this study, we excluded observations with date ranges that fell outside our time periods (see below). Species were grouped into taxonomic groups, determined primarily by the recording schemes that collated records for that group. A total of 21 taxonomic groups had sufficient data for range margin changes to be calculated for at least one interval (the groups accepted or rejected for study are listed in Table A2.1). Four taxonomic groups (birds, butterflies, macromoths, and dragonflies and damselflies) had sufficient data for range margin changes to be calculated for both intervals.

Our analysis focussed on southerly-distributed species that reach a northern (leading-edge) range margin in GB. The study area was the British mainland, including islands connected to the mainland according to the contiguous distribution of hectads (2566 hectads in total). Hence, near-shore islands were included, but off-shore islands were not. Montane species (defined as species with a mean elevation ≥200m across their British range) were excluded from the analyses because latitudinal range changes by these species would be confounded by elevational shifts. We also excluded ubiquitous species (defined as those occurring in more than 90% of the study area), as well as species with a northern range margin in the first time period less than 100km from the north coast of mainland GB, because these species would have little opportunity for polewards range shifts. Species were also excluded if they were listed in the GB Non-native Species Information Portal (Roy *et al.*

2014b), because range changes by introduced species are likely to involve human-assisted dispersal and range filling unrelated to climate change. We also excluded observations where the identification of the species was uncertain (e.g. record listed as several possible species). Species listed with a sub-species trinomial were grouped to the species level (e.g. for the Dingy skipper butterfly, *Erynnis tages* subsp*. tages* was grouped with *Erynnis tages*), and different subspecies of the same species were grouped together.

2.3.2 Time periods of analysis

With the exception of birds, data were collated into three time periods (1966-1975; 1986-1995; 2001-2010), defining the northern range margin of each species in a given period. Range margin changes were analysed over two time intervals corresponding to range margin changes between the first and second periods (interval 1, 1966-1975 to 1986-1995) and between the second and third periods (interval 2, 1986-1995 to 2001-2010). We imposed gaps between time periods to provide opportunities over which range margin changes could occur. Bird data were analysed over slightly different time periods and intervals (interval 1, 1968-72 to 1988-1991; interval 2, 1988-1991 to 2008-2011) corresponding to bird atlas recording periods (Sharrock 1976; Gibbons, Reid & Chapman 1993; Balmer *et al.* 2014). We standardised the time periods as far as possible across the different taxonomic groups to ensure all species were studied over similar periods, and hence experienced similar climatic changes. A preliminary analysis using the slightly different time periods analysed by Hickling *et al*. (2006) produced qualitatively similar results to the standardised dates used in this study.

2.3.3 Controlling for variation in recorder effort

The intensity of recorder effort in GB has varied over time and space, as well as within and between taxonomic groups. Thus for each time interval and taxonomic group we controlled for variation in recording effort by selecting hectads with a minimum threshold of recording effort based on observed local species richness relative to the regional species richness pool. First, for each focal hectad, We identified the nearest 100 hectads (sufficient for the regional pool size of species to asymptote) where at least one species from that taxonomic group was recorded in both time periods (i.e. 1966-1975 and 1986-1995 for analyses of interval 1, or 1986-1995 and 2001-2010 for analyses of interval 2; or equivalents for birds). Second, the species richness of these neighbouring hectads was calculated from the total number of unique species recorded in both time periods. Focal hectads were included in analyses according to the level of recording effort they experienced, and hectads were termed 'recorded', 'well-recorded' and 'heavily-recorded' as follows. 'Recorded' hectads contained at least one species in both time periods, 'well-recorded' hectads contained at least 10% of the species richness of the surrounding hectads in both time periods, and 'heavily-recorded' hectads contained at least 25% of the species richness of the surrounding hectads in both time periods. This method for accounting for recorder effort was broadly similar to that used by Hickling *et al*. (2006) except that we used local species richness rather than the richness of all species in Britain when selecting hectads for inclusion. This new method is likely to be more sensitive in accounting for recorder effort, because it takes better account of underlying spatial variation in species richness across Britain.

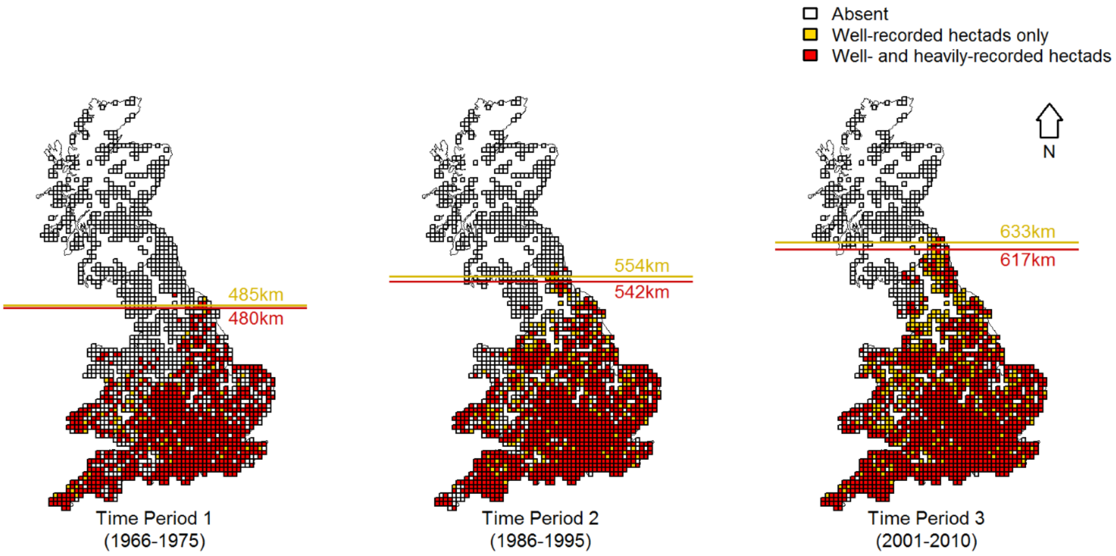
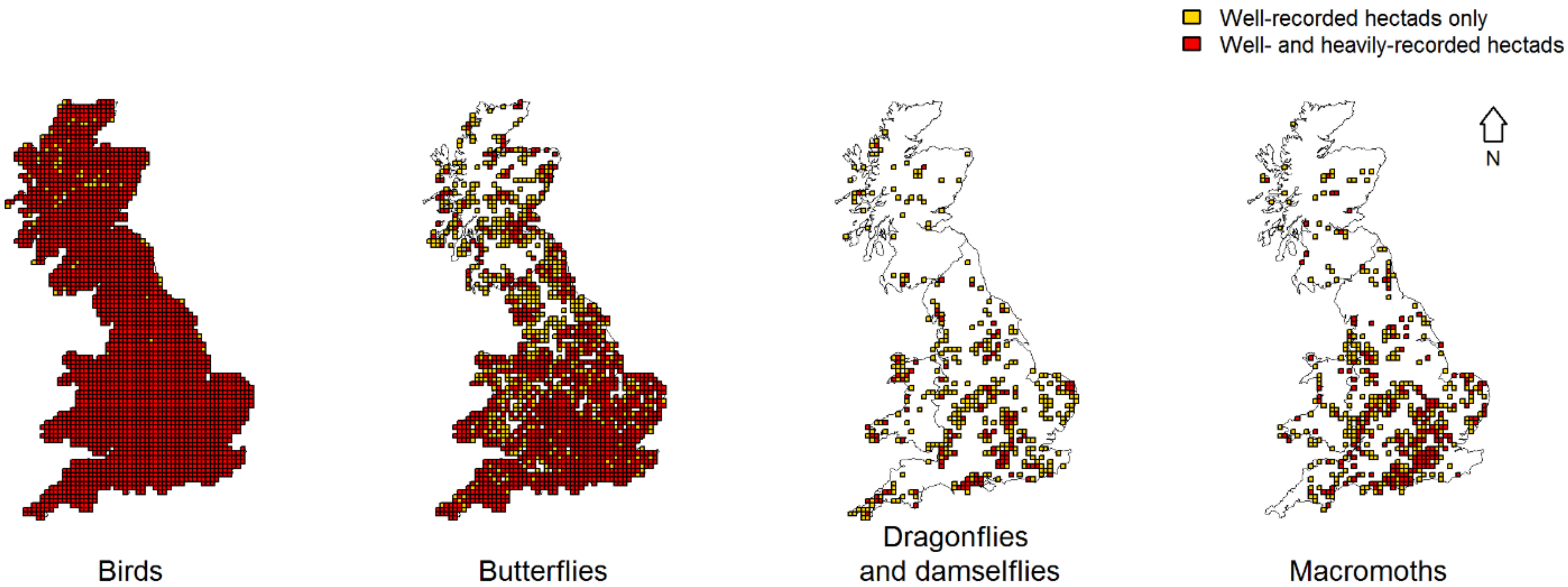


Figure 2.1. Locations of northern range margins calculated for different thresholds of recording effort control in each of three time periods of study (1966-75, 1986-95 and 2001-10) for the small skipper butterfly (*Thymelicus sylvestris*). This exemplar species was selected for illustration because it has extended its range northwards in recent years. Maps show species presence in well-recorded and heavily-recorded grid squares (10 km x 10 km), and (apparent) absence (hollow squares) where butterflies were observed, but not *Thymelicus sylvestris*. Labelled lines indicate range margin locations from analyses of well- and heavily-recorded hectads in each time period.

Our analyses of range margin changes were repeated for each of the three levels of recorder effort control. For the four taxonomic groups (birds, butterflies, macromoths, and dragonflies and damselflies) studied over both time intervals, northern range margins were calculated in a second analysis (see methods below) that used a subset of well-recorded and heavily-recorded hectads from both intervals that were common to all three time periods. Figure 2.1 shows how analysing well-recorded or heavily-recorded squares affected the calculation of the range margin location for an exemplar butterfly species, *Thymelicus sylvestris*. Compared with the other taxa studied, recorder effort variation is far less in birds than other taxonomic groups. For example, macromoths experienced a more than sixfold increase in the number of observations over the study period (294,951 and 1,474,592 unique year-location observations of species in GB hectads during time periods 1 and 3 respectively), such that hectads were more likely to have been intensively surveyed in the later time periods. By contrast, bird data are collated systematically for each atlas and so there is less change in the number of records of birds over time. Figure 2.2 shows the locations of well-recorded and heavily-recorded hectads for birds, butterflies, dragonflies and damselflies, and macromoths.

Figure 2.2.



Distribution of well-recorded and heavily-recorded hectads across both time intervals, for the four taxonomic groups analysed in Figure 2.4. Sample sizes for well-recorded hectads are 2561, 1729, 477 and 414 for birds, butterflies, macromoths and dragonflies and damselflies respectively. Sample sizes for heavily-recorded hectads are 2500, 1218, 205 and 119 for the respective group

2.3.4 Minimum data requirements for taxonomic groups and species

Each taxonomic group was selected for study if it occupied at least 20 well-recorded hectads during interval 1 or interval 2, and contained more than one species for which range margin changes could be calculated. Taxonomic groups without their own formal recording scheme (which apply various quality control measures, e.g. to avoid misidentifications) were rejected. Those taxonomic groups which had data from multiple sources (and hence no uniform quality control measures) were also rejected. Criteria for selecting taxonomic groups analysed over both intervals were stricter, given the more statistically challenging task of trying to identify not only range margin changes but also whether rates had changed over time. Thus taxonomic groups needed at least 20 heavily-recorded hectads which were common to all three time periods to qualify for inclusion, and also had to contain five or more species for which a range margin could be calculated (see below) based on heavily-recorded hectads. These criteria resulted in four taxonomic groups being studied (birds, butterflies, macromoths, and dragonflies and damselflies).

For each time period, the range margin of each species was calculated for each level of recording effort control. We excluded species from a time period if they were observed in fewer than 20 hectads, for a given level of recording effort control, because estimates for the locations of range margins would be subject to high recording error. Once northern range margins were calculated (see methods below), species which had fewer than 10 hectads of the necessary level of recording effort within 100km to the north and to the south of their range margin in the first time period were excluded. This excluded species whose estimates of potential range margin changes northwards or southwards would be biased by poor recording effort.

2.3.5 Calculating northern range margin changes

The locations of northern range margins were calculated in each of the three time periods. For each species that was included, the location of its northern range margin was computed as the mean northing (in km north, from the Ordnance Survey GB grid) of the species' 10 most northerly occupied hectads in that time period. For each taxonomic group and time interval, mean rate of change (plus 95% confidence intervals) in northern range margin was then calculated as the distance moved in km decade^{-1} (based on the number of years between the mid-points of each time period), with positive rate values indicating northward shifts, and negative values indicating southward shifts. These analyses were carried out for each of the three levels of recording effort. We used ANOVA and one-sample t-tests to examine differences in rates of range margin change among the taxonomic groups in each time interval, and whether rates of range margin change were significantly different from zero.

We examined if rates of range margin change differed between time intervals 1 and 2 in the four selected taxonomic groups (birds, butterflies, macromoths and dragonflies and damselflies). We generated linear mixed models using *lme4* package in R (Bates *et al.* 2013) with rate of range margin change (km decade^{-1}) as the response variable, time interval and taxonomic group as explanatory variables and species identity as a random effect. We fitted models with all possible combinations of explanatory variables and their interaction term and examined the goodness of fit of each model using Akaike information criterion (AIC) values, and models where ΔAIC was < 2 were assumed to be equally good at explaining the data (Burnham & Anderson 2002). Additionally, rates of range margin change in the two time intervals in each taxon were compared using paired t-tests, and one-sample t tests were used to examine if rates of range margin change in each interval were significantly different from zero. All statistical analyses were performed in R, v3.0.2 (R Core Team 2013).

2.3.6 Temperature variation across the study period

Mean seasonal temperature data from the Hadley Centre Central England Temperature (HadCET) series were downloaded from the UK Met Office (www.metoffice.gov.uk/hadobs). Over the study period (1966-2010), annual mean temperature was computed from the mean value of each of the four seasons (i.e. annual temperature was measured from December through to the following November). Descriptive analyses were undertaken to describe changes in temperature over the years included in interval 1 (1966-95) and interval 2 (1986-2010), and between these two intervals. We used regression analysis to examine changes in mean seasonal and annual temperatures within each time interval, and ANCOVA to determine if there was a difference in the rate of temperature change between the two time intervals.

2.4 Results

2.4.1 Northern range margin changes

Here, we focus primarily on describing the results for well-recorded hectads because we consider this level of recorder effort control to be the best compromise between robustness of data analysis and retaining large numbers of species and taxonomic groups in our analyses; although we also report full statistical results for the other two levels of recording effort control in appendices (Tables A2.2, A2.3). The locations of the northern range margins of all species during each time period are provided in Tables A2.4 (interval 1) and A2.5 (interval 2). Generally, most taxonomic groups shifted northwards for all levels of recording effort for which they could be analysed (Figure 2.3). The mean overall rate of range margin change, calculated from each taxonomic groups' mean rate of range margin change, was 24.1 km decade^{-1} (standard error [SE] = 5.5; n = 13 taxa) in time interval 1 and 18.0 km decade^{-1} in interval 2 (SE = 4.0; n = 16 taxa).

Eight of the 13 groups in interval 1 (butterflies, centipedes, dragonflies and damselflies, hoverflies, macromoths, millipedes, spiders, woodlice) and seven of the 16 groups in interval 2 (aquatic bugs, bees, butterflies, dragonflies and damselflies, hoverflies, macromoths, wasps) significantly extended their range margins northwards, for well-recorded hectads (Figure 2.3, Table A2.3). Qualitatively similar results were obtained for the other levels of recording (Figure 2.3); ten of the 13 groups analysed in interval 1, and eight out of 16 taxa in interval 2, showed significant northwards shifts for one or more levels of recording effort (Figure 2.3; Table A2.3). Despite most taxa shifting their range margins northwards in both time intervals, three taxa (ground beetles, hoverflies, solderflies and allies) demonstrated significant southwards retractions in interval 2, although the significance of the change depended on levels of recorder effort control (Figure 2.3, Table A2.2, A2.3). For taxonomic groups which occurred in both time periods (i.e. panels B and D in Figure 2.3), their rates of range margin change are not directly comparable between the two intervals because different sets of hectads and species were used to calculate rate of range margin change in each interval. Taxonomic groups differed in their rates of range margin change, and this was evident in both time intervals (ANOVA, interval 1, $F_{12, 560} = 4.41$, $p < 0.001$; interval 2, $F_{15, 868} = 9.64$, $p < 0.001$), and this finding was insensitive to the level of recorder effort control (Table A2.2). Mean annual temperature generally increased in Britain during the study period (on average by 0.21°C decade^{-1} during interval 1 and 0.28°C decade^{-1} during interval 2), with mean spring (March-May) temperature increasing significantly during interval 1, and mean autumn (September - November) temperatures increasing significantly in interval 2 (Table A2.6).

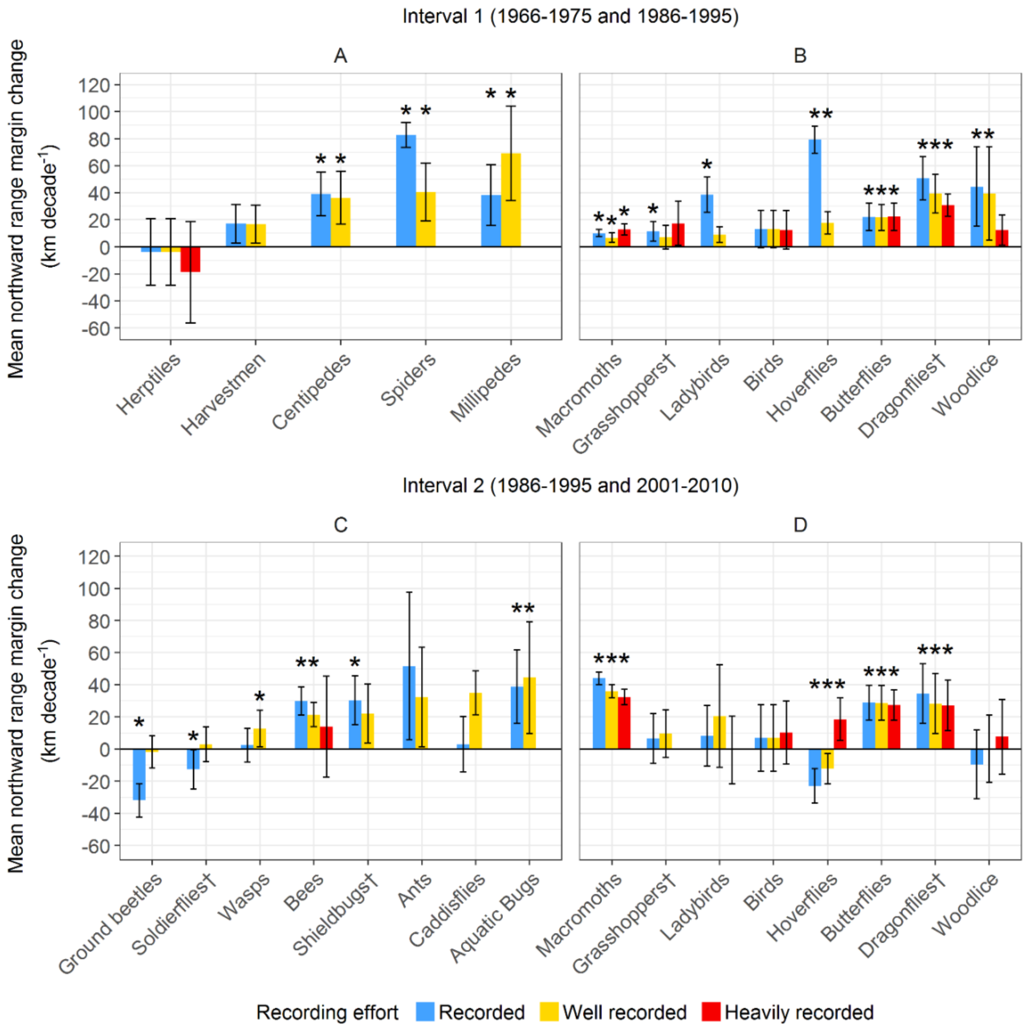


Figure 2.3. Mean rates of northern range margin changes of species in 21 taxonomic groups over interval 1 (upper panels) and interval 2 (lower panels); for each level of recording effort control. Panels A and C show range margin changes for taxonomic groups studied over one time interval only (13 taxa) and panels B and D show taxa studied in both intervals (8 taxa). Error bars represent 95% confidence intervals of the mean. Asterisks above bars indicate range changes that were significantly different from zero (one-sample t-test). In panels A-C, the bars are ordered along the x-axis by magnitude of range margin changes according to analyses of well-recorded hectads; panel D is ordered according to panel B's order. The number of species per taxonomic group varied among groups, recording effort control levels and intervals (see Table A2.3). Heavily-recorded bars are absent for some taxa because this level of analysis was not possible. For taxonomic groups studied in both

intervals, there were different species compositions in each interval and different sets of recorded, well-recorded and heavily-recorded grid squares. Thus differences in rates of range change between time intervals may be a result of differences in the species included and locations recorded, and so comparisons should be made with caution. Taxonomic group names accompanied by a dagger symbol indicate that the group contains allied species (See Table A2.1).

2.4.2 Changes in rates of range margin change over time

We examined if rates of range margin change were similar in the two time intervals for four taxonomic groups (birds, butterflies, macromoths, and dragonflies and damselflies) with sufficient data to analyse the same hectads across all three time periods. The estimates of rates of range margin change from this subset of hectads generated comparable estimates to those from the larger set of hectads used to calculate rates of change separately for intervals 1 and 2 (Figure A2.1). All four taxonomic groups shifted northwards in both intervals (Figure 2.4), and macromoths and butterflies showed significantly faster rates of range margin change in interval 2 compared with interval 1 (Table A2.7; macromoths paired t-test, t_{131} = -5.77, p = <0.001; butterflies t_{34} =-2.26, p = 0.03).The locations of the northern range margins of all species during all three time periods are provided in Table A2.8.

The most parsimonious statistical model of rate of range margin change for these four groups included the interaction term between taxonomic group and interval (Table 2.1). The interaction occurred primarily because macromoths tripled their rates of polewards range margin change between intervals 1 and 2 (interval 1 = 11.4km decade^{-1}, interval 2 = 31.2km decade^{-1}) and rates for butterflies nearly doubled (interval 1 = 18.3km decade^{-1}, interval 2 = 30.3km decade^{-1}). However, rates of rates of range margin change of birds and dragonflies and damselflies did not significantly differ over time (Table A2.7). This conclusion was not dependent on the inclusion of any single taxonomic group, and serial omission of each group (and of all Lepidoptera, i.e. butterflies and macromoths) consistently found that a mixed model with the interaction term between taxon and interval had the lowest AIC value (i.e. was the best model; Table A2.9). This apparently faster rate of range margin change in Lepidoptera in interval 2 was evident despite the fact that the rate of temperature warming was similar between interval 1 (1966 to 1995) and interval 2 (1986 to 2010; Table A2.10) for most measures of temperature. However, mean autumn temperature increased significantly between interval 1 and 2 (Table A2.10).

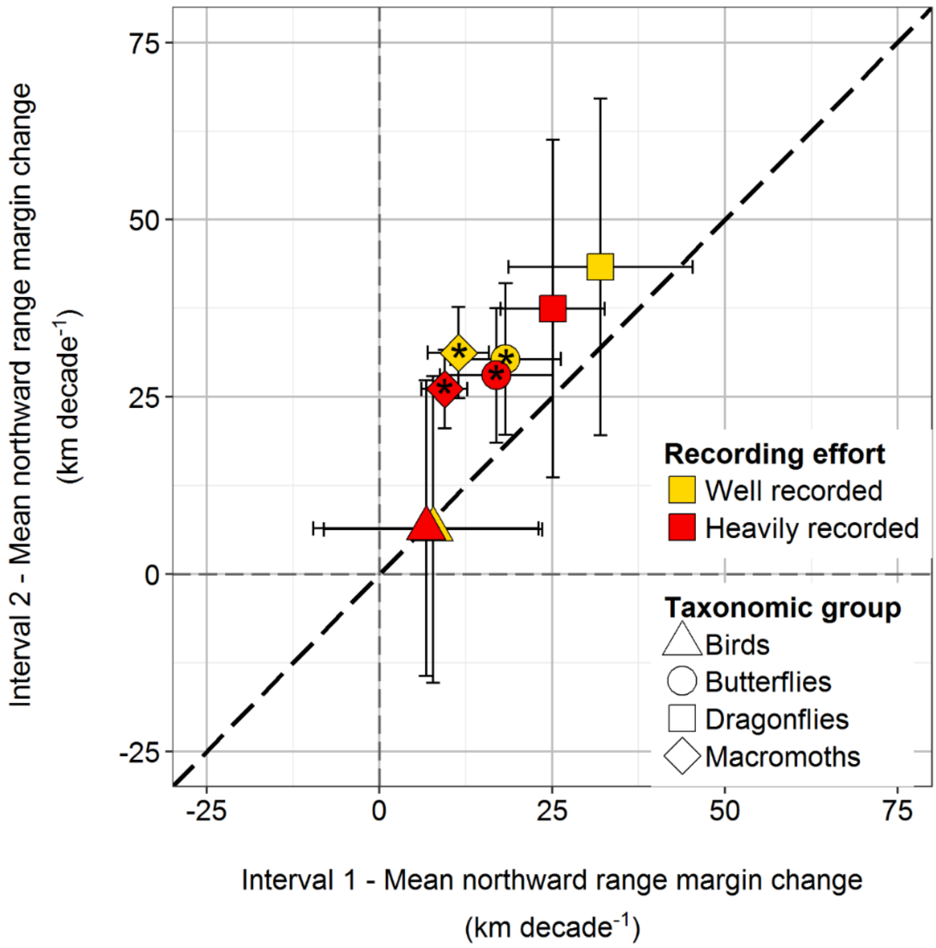


Figure 2.4. Comparison of rates of northern range margin change for four taxonomic groups across two time intervals (see main text for time interval dates). Taxonomic groups are as follows: birds (31 species), butterflies (35 species), dragonflies and damselflies (7 species) and macromoths (132 species). These estimates of rate of range margin change differ slightly from those in Figure 2.3, because only those hectads that were well-recorded in all three time periods were included. Asterisks indicate groups where range margin changes differed over time (two-tailed paired t-test, P≤0.05, see Table A2.7). 'Dragonflies' represents all Odonata, including damselflies.

Table 2.1. Linear mixed effects models for rate of northern range margin change (response variable, in km decade^{-1}) in well-recorded hectads, between two time intervals (spanning 1966-2010), for the four most heavily-recorded taxonomic groups (N = 205 species in total). All models included species identity as a random factor. For fixed effects, the most complex model included time interval and species group as predictor variables, as well as the interaction term. Shown for each model is the difference in AIC (ΔAIC) from the most parsimonious model (model 5). The four right hand columns provide information on the individual coefficients expressed as the difference relative to the intercept term.

Model	Fixed effects	ΔAIC	Fixed effects (breakdown)	Coefficient	SE	t
1	1	74.3	Intercept	20.2	1.8	11.09
2	Group	43	Intercept (Birds)	7	5	1.413
			Group (Butterflies)	17.3	6.8	2.525
			Group (Dragonflies*)	30.6	11.6	2.642
			Group (Macromoths)	14.3	5.5	2.586
3	Interval	41.2	Intercept (Interval 1)	-2.2	5.1	-0.431
			Interval (2)	15	3.2	4.722
4	Interval + Group	19.6	Intercept (Interval 1, Birds)	-15.4	6.9	-2.24
			Interval (2)	15	3.2	4.722
			Group (Butterflies)	17.3	6.8	2.526
			Group (Dragonflies*)	30.6	11.6	2.643
			Group (Macromoths)	14.3	5.5	2.586
5	Interval + Group + Interval : Group	0	Intercept (Interval 1, Birds)	9.2	13.1	0.698
			Interval (2)	-1.4	8.1	-0.176
			Group (Butterflies)	-3	18	-0.165
			Group (Dragonflies*)	11.5	30.6	0.376
			Group (Macromoths)	-17.5	14.6	-1.2
			Interval: Group (Butterflies)	13.5	11.1	1.214
			Interval: Group (Dragonflies*)	12.8	18.9	0.676
			Interval: Group (Macromoths)	21.2	9	2.357

2.5 Discussion

We analysed rates of range margin change in 1599 southerly-distributed species from 21 animal groups in two time intervals. Overall, the majority of taxonomic groups in our study shifted their range margins northwards in both time intervals (23.2km decade^{-1} in interval 1, 18.0km decade^{-1} in interval 2), supporting the findings of Hickling *et al.* (2006). Rates of range margin change varied between taxonomic groups and, for some groups, over time. For the four groups with sufficient data to undertake robust analyses of whether these rates have changed over time, there was evidence that recent rates of range margin change have been faster for macromoths and butterflies. These findings were relatively insensitive to recorder effort control, although increasingly strict recorder effort control reduced the number of hectads that could be analysed.

2.5.1 Controlling for variation in recorder effort

Variation in levels of recording effort across spatial and temporal scales can present problems to ecologists wishing to quantify range shifts (Tingley & Beissinger 2009; Isaac *et al.* 2014). Our results showed that the majority of taxa studied have shifted their range margins northwards for all levels of recording effort that we considered. However, there were some taxonomic groups where the shift in the northern range margin was qualitatively different according to the level of recorder effort control. For example, northern range margins of hoverflies apparently retracted southwards in interval 2 if recorded and well-recorded grid squares were analysed, but extended northwards according to analysis of heavily-recorded squares (Figure 2.3D). As the control for recorder effort became stricter, the number of hectads included was reduced, and so the number of species included was also reduced. Hence 137 and 131 species of hoverfly were included in analyses of 'recorded' and 'well-recorded' hectads respectively, but only 21 species for heavily-recorded hectads. If recorded and well-recorded hectads were assessed for just these 21 species, the recorded range margin shift (9km decade^{-1} southwards) was smaller than when all available species were analysed, and the well-recorded range margin shift changed to a northwards direction (8km decade^{-1} northwards). Thus, the reported range margin changes are a function of both the hectads included in the analyses as well as the identity of species included. Using the most thoroughly surveyed (heavily-recorded) subset of data, the observed trend was for 13 out of 14 measured changes (taxon by interval combinations) to show a northwards margin shift (Figure 2.3), and the overall data showed significant northwards trends across all taxa in both periods for all three levels of recording effort (Table A2.2). Thus, our qualitative findings appear robust to variation in recorder effort (at least for the three control methods assessed), although the quantified rate of change depends on the level of recorder effort control.

Our approach to filtering data for analysis represents an assessment of the sensitivity of our conclusions to variation in recording effort, rather than a true measure of 'control' for recording effort, given that the true recorder effort is unknown. We adopted the same general approach as Hill (2012), and assumed that any species that might potentially be recorded in a particular location (hectad) would be drawn from the pool of species found in the surrounding region (which we defined here as the nearest 100 hectads with any records for the taxon). The distribution of species richness in Britain does not change greatly from one hectad to the next (Fox *et al.* 2011; Balmer *et al.* 2014), and so the percentage of the regional species pool recorded as present in a hectad represents a first approximation for the relative level of recording effort. However, the percentage of species actually recorded in a hectad depends on the actual number of species present (which itself depends on local environmental conditions), as well as on the level of recording that has taken place. Hence we adopted an approach whereby we used thresholds (>0%, 10%, 25% of the regional species pool) rather than a continuous metric of species recorded.

Recorder effort has changed over time and the number of records of species in Britain has increased rapidly. However, if increased recording effort through time is primarily responsible for generating the erroneous impression of range margin changes, we would expect the recorded rate of range margin changes of common species to be less rapid than the rate of range margin changes of all species taken together, because rare species are more likely to go unnoticed during lower intensity surveys (Bates *et al.* 2014). In fact, we found few differences when we repeated our analyses to include only common species (defined as the top 50% of species ranked by number of presences in heavily recorded hectads). Analysing only common species, the estimated rate of range margin change decreased for common birds (despite little or no increase in recording effort), was largely unaffected for macromoths (which showed the greatest increase in recording effort), and increased for butterflies (Figure A2.2). If sampling effort was having an important influence, we would also expect higher levels of recording effort to generate markedly reduced estimates of range margin change, which we did not observe. Poor recorder effort may be an issue in interval 1, but analysis of well-recorded and heavily-recorded hectads in interval 2 produced higher estimates of northwards range margin change than data from recorded hectads, suggesting that northwards range margin changes are not primarily artefacts of recorder effort changes, at least since 1986-95. Examination of the rate of range margin changes of individual species (e.g. Figure 2.1) and differences in the distribution changes of northern and southern species also indicate that the polewards range margin shifts we report here are real (Warren *et al.* 2001; Hickling *et al.* 2005; Fox *et al.* 2013, 2014; Cham *et al.* 2014).

2.5.2 Variation over time and between taxonomic groups

Our results suggest that some taxa differed in their rates of range margin change over time, and that Lepidoptera apparently spread northwards more rapidly in the more recent time period, during a period when autumn temperatures significantly increased. The faster rate of range margin change more recently in Lepidoptera does not obviously align with any major morphological, habitat-use or other features of this group, and trait-based analyses have rarely explained very much of the variation in rates of range shift among species within taxonomic groups (Angert *et al.* 2011). Species may vary in their sensitivity to different aspects of climate, and responses of species may also reflect the amount of warming as well as habitat availability (Hill *et al.* 2001), which may contribute to these differences among taxa. We only compared four taxonomic groups, two of which were Lepidoptera, which is too few to draw any firm conclusions. In addition, the considerable variation that is exhibited between species within individual taxonomic groups (Chen *et al.* 2011a) and over time (Mair *et al.* 2012) suggests that there may be no simple explanation for variation among taxa in their responses to climate change.

Climate change is driving many species to extend their ranges northwards (Chen *et al.* 2011a) and the majority of taxonomic groups studied here supported that finding. However we found variation in rates of range margin change amongst the animal taxa studied. Taxa may vary in their response to temperature at different time of the year, and to different aspects of climate (Araújo, Thuiller & Pearson, 2006; Jiguet, Brotons & Devictor, 2011; Schweiger *et al.*, 2012). Taxa may also vary in the extent to which they occupy their climate niche (Sunday, Bates & Dulvy, 2012), and hence non-climatic constraints could account for differences in the rate of range margin changes we observe between groups. For example, Fox *et al.* (2013) suggested that the range extension of footman moths in Britain could be related to increased availability of larval hosts (algae and lichens), which in turn could be benefitting from changes in air quality and nutrient availability, as well as climate change (Morecroft *et al.* 2009; Pescott *et al.* 2015). In addition, evolutionary changes in dispersal ability and ecological changes in habitat associations may contribute to variation in rates of range change (Thomas *et al.*, 2001; Hill, Griffiths & Thomas, 2011; Pateman *et al.*, 2012). However, whilst resource and habitat availability are important for individual species, it is not clear whether they and many other range-determining factors (e.g. natural enemies, competing species) are important causes of the differences that we have observed between broader taxonomic groups.

2.5.3 Conclusion

Our study provides further support that the majority of taxonomic groups have shifted their leading-edge margins northwards. We also have evidence that rates of range margin change vary over time and between taxonomic groups, just as they vary between species within each taxonomic group. Hence conservation planning and habitat management strategies should be aware that rates of species' range changes in response to environmental change are highly variable. Our analyses have benefitted from the extensive data sets that exist for a large number of taxa in Britain, recording changes in distributions over the past four decades. Such recording schemes are vital for understanding biodiversity changes in human-dominated landscapes. Establishing robust monitoring systems that build on those that already exist will increase our capacity to detect, understand, and manage these changes (Pescott 2015).

Chapter 3

Habitat explains variation in climate-driven range shifts across multiple taxa

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This chapter has been submitted for publication in *Science*, and is reproduced here in its submitted form with minor alterations to the data and formatting.

Please find Supplementary Methods to accompany the text on page 51.

3.1 Abstract

It is not understood why individual species vary so greatly in the rates at which their ranges are shifting in response to climate warming. Using 40 years of distribution data, for 347 species from 14 invertebrate taxa in Britain, we show that habitat availability explains up to half of the variation in range boundary shifts. Habitat availability depends on habitat specificity of species, whether species are specialised on rare or widespread habitats, and the mixture of habitats in any given landscape. Hence, interactions between species' attributes and the environment are important determinants of variation in range shifts. Understanding this variation across multiple taxa leads us to conclude that better-connected landscapes could facilitate polewards shifts for the subset of species that are habitat constrained, whereas other species will successfully track the climate without intervention, or face barriers that cannot be circumvented.

3.2 Introduction and Methods

On average, species are shifting polewards and to higher elevations in response to climate warming, but there is extremely large variation in the rates at which the range boundaries of individual species are moving (Parmesan & Yohe, 2003; Lenoir *et al.*, 2010; Crimmins *et al.*, 2011). This variation could arise from species-specific climatic or habitat requirements, population growth rates, dispersal or biotic interactions (Hill *et al.*, 2001; Warren *et al.*, 2001; Mair *et al.*, 2014; Carroll *et al.*, 2015; Liang *et al.*, 2017). Yet, none of these factors has been shown to explain a large proportion of the between-species variation across multiple taxonomic groups (Angert *et al.*, 2011; MacLean & Beissinger, 2017). Here, we evaluate the degree to which species-specific habitat associations underlie the observed variation in range shifts. Our results help explain why responses to climate change appear individualistic, and provide insight into how we might facilitate species' responses to climate change.

We examined 347 non-migratory, native invertebrate species in mainland Britain, drawn from 14 taxonomic groups: aquatic bugs, bees, butterflies, dragonflies and damselflies, grasshoppers and allies, ground beetles, hoverflies, macromoths, non-marine molluscs, shieldbugs and allies, soldierflies and allies, spiders, wasps, and woodlice (Table A3.1). Each species reaches its northern (poleward) range margin in Britain and might, therefore, be expected to shift northwards during a period of sustained regional warming. We measured range shifts (latitudinal changes in the ten-northernmost occupied 10-km squares) between 1976-1990 and 2001-2015. The median observed range shift was 33 km (1.3 km y^{-1}, mean = 1.8 km y^{-1}) indicating significant poleward expansions (Wilcoxon signed rank, $P < 10^{-30}$, N = 347) in response to 0.8 °C of regional warming over the same time period (Hollis & McCarthy, 2017). There was considerable variation among species (Figure 3.1); one in five species retracted its range margin southward, and the interquartile range spanned twice the median shift (Table A3.2). Nearly all (91%) of this variation between species occurred within, rather than among, taxonomic groups (R^2 = 0.09 in a linear model of range shift *vs*. taxonomic group). The lack of a strong 'group effect' suggests that major trait differences among groups cannot be responsible for the variation in range shifts. In contrast, individualistic attributes of species and/or location-specific constraints, such as habitat factors, could still make strong contributions.

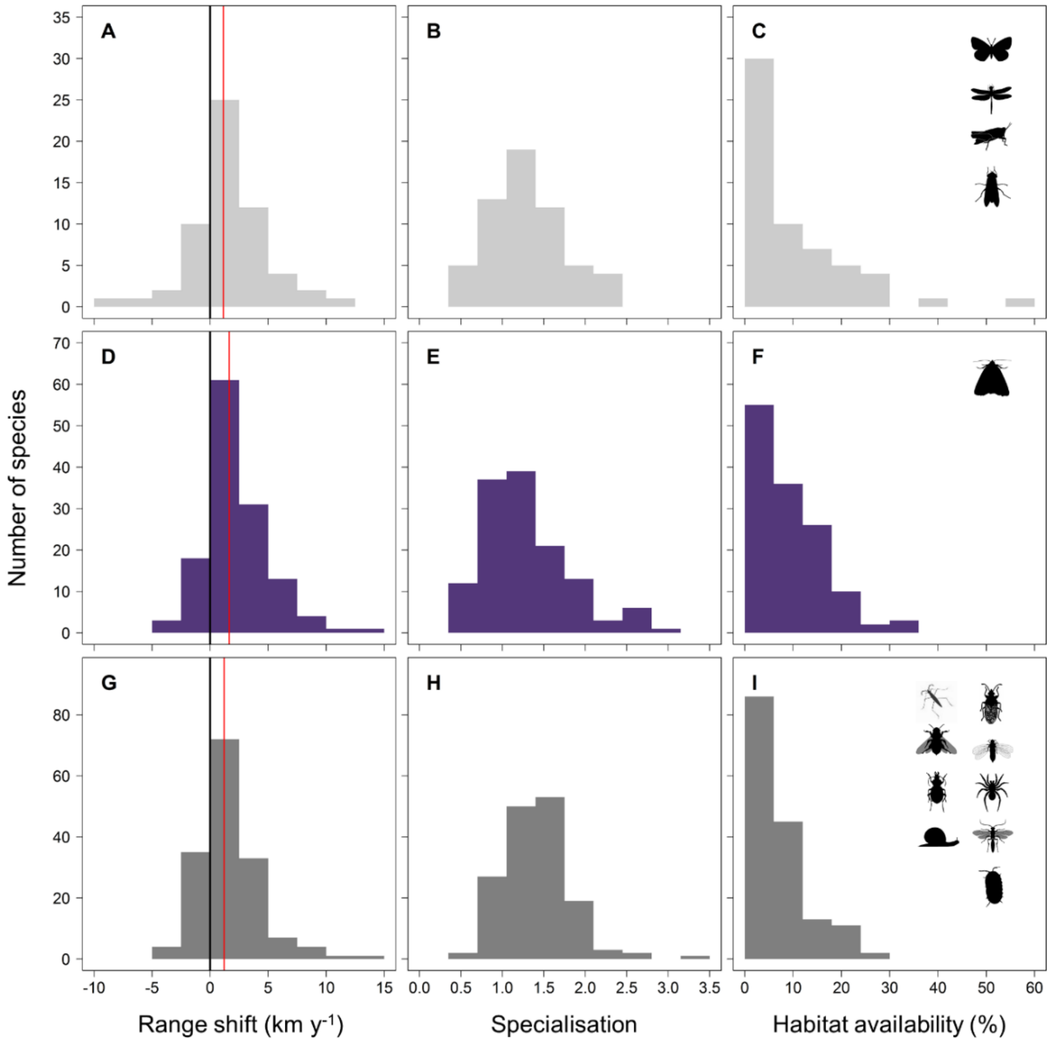


Figure 3.1. Variation in latitudinal range shifts over 25 years, habitat specialisation, and habitat availability at geographic range margins for 347 invertebrate species in Britain. (A-C) Four taxonomic groups with high levels of recording (butterflies, dragonflies and damselflies, grasshoppers and allies, and hoverflies; *N* = 58). (D-F) Macromoths (different recording method, *N* = 132 species). (G-I) Nine groups with lower levels of recording (*N* = 157; Table A3.1). In A, D and G: black lines show zero shift and red lines show median observed shift.

Hence, we quantified habitat associations, habitat specialisation and habitat availability (in range-margin landscapes) for the 347 species. We developed logistic regression models to quantify habitat associations, using 100-m resolution presence-absence records of study species in 18 satellite-derived habitat classes (Morton *et al.*, 2011). Species' specialisation indices (SSIs) were defined as the coefficient of variation (SD/mean) in the probability of occurrence across the 18 habitat classes (Julliard *et al.*, 2006), and ranged from SSI = 0.36 for the Gatekeeper butterfly *Pyronia tithonus*, a generalist present at varying densities in 17 of the 18 habitat classes, to SSI = 3.22 for the woodlouse *Ligidium hypnorum*, a broadleaved-woodland specialist. We estimated habitat availability by projecting probabilities of occurrence on to the land cover map at 25-m resolution, and averaging over the range-margin landscape (50-km buffer around the northernmost 10-km squares occupied by the species in 1976-1990). Habitat availability ranged from 0.4% for the heathland-associated Small Grass Emerald moth *Chlorissa viridata*, to over half of the landscape (56%) for *P. tithonus* butterfly. Again, this variation was mainly a feature of differences between individual species (93% for specialisation, 85% for habitat availability), rather than between taxonomic groups (tables A3.3- A3.4). Habitat specialisation and availability are inevitably related to one another, but they are not interchangeable (Figure 3.2): availability depends on whether a species is specialised on common or rare habitats, and on the absolute (rather than relative) probabilities of occurrence within those habitat classes. For more methods details, please refer to the Supplementary Methods on page 51.

3.3 Results and Discussion

Generalist species expanded northwards faster than specialists (Pearson correlation coefficient [*r*] of range shift *vs*. SSI = -0.22, $P < 10^{-4}$, $N = 347$). In a linear mixed-effects model, with taxonomic group as the grouping variable, the marginal R^2 (fixed SSI effect, R^2_m) was 0.04 and the conditional R^2 (fixed and group effects, R^2_c) was 0.13. The explanatory power of SSI was weak compared to the random effect of taxonomic group (Table A3.6). This echoes previous studies in which generalists (and species with traits potentially linked to generalism) have been found to track climate significantly better than specialists but where effect sizes are small, inconsistent in time and/or space, or not consistent between taxonomic groups (Angert *et al.*, 2011; MacLean & Beissinger, 2017). In contrast, we found that $\log_{10}$-habitat availability was more strongly correlated with range shifts ($r = 0.38$, $P < 10^{-12}$) and, in a mixed model, explained four times more variation ($R^2_m = 0.17$, $R^2_c = 0.21$). Habitat availability rather than specialism *per se* provides a stronger explanation for the observed variation in range shifts (*cf*. SSI model: ΔAIC = 35, ΔcAIC = 35; Table A3.6).

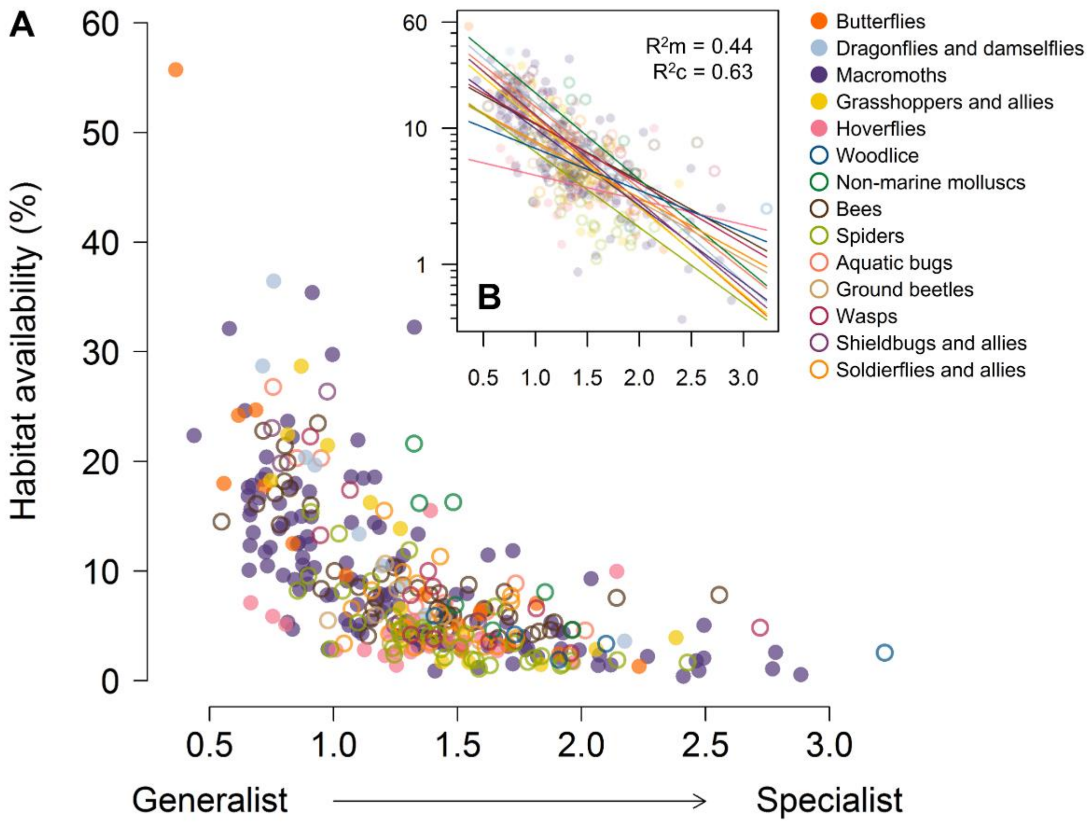
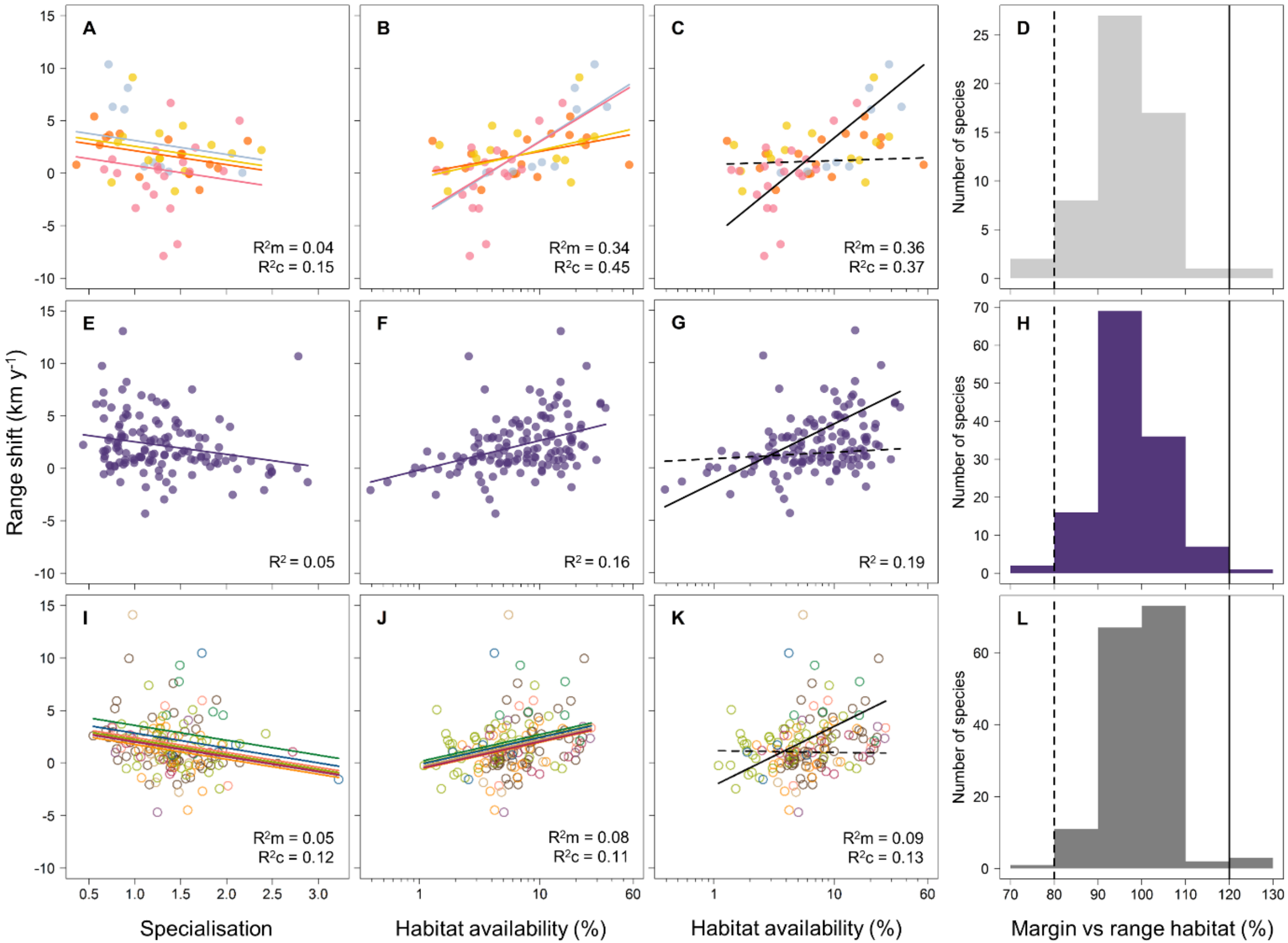


Figure 3.2. Relationship between habitat availability at the range margin and the degree of habitat specialisation, for 347 invertebrate species in 14 taxonomic groups. Plotted on untransformed axes (A) and with log-linear scaling (B). Lines in (B) show the effect of taxonomic group in a linear mixed-effects model, with intercepts and slopes conditional on taxonomic group. In the colour key, groups are listed in descending order of geographic coverage of citizen-science recording: solid symbols show five groups with the highest levels of recording, open symbols show nine groups with lower levels of recording.

Individual species also differ in the threshold amount of habitat required for metapopulations to persist or expand at the range margin (Hanski, 1999); on average, species have less habitat available in range-margin landscapes than in their distribution cores (Figure 3.3, D, H and L; species with less *vs*. more habitat at the margin, $\chi^2 = 10.03$, 1 df, $P < 0.002$, $N = 347$). We discovered that species with below-average habitat availability at the range margin (relative to availability in the entire range) have failed to expand northwards (dashed lines in Figure 3.3, C, G and K), most likely because those landscapes fall below their species-specific habitat requirements (dashed lines in Figure 3.3, D, H and L). Habitat availability (as a main effect) and our metric of relative range-margin habitat availability (as an interaction) provided the most parsimonious explanation of species' range shifts (*cf*. habitat model with random slopes for each group separately: ΔAIC = 8, ΔcAIC = 4; Table A3.6). The explanatory power of this model is likely to be driven by the combined effects of increased breeding success in landscapes with greater habitat availability, and more successful dispersal in landscapes where the distances between habitats patches are reduced (Wilson *et al.*, 2009; Hodgson *et al.*, 2012).

The distribution data for our study species come from citizen-science schemes, and so recorder effort varies among taxa (e.g., 20 million macromoth records were available, compared with 30 thousand records for shieldbugs and allies). Therefore, we tested the sensitivity of our findings to recording effort (we also analysed macromoths separately because light trapping may attract individuals from adjacent habitat types).


A
B
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R²m = 0.04
R²c = 0.15
R²m = 0.34
R²c = 0.45
R²m = 0.36
R²c = 0.37
R² = 0.05
R² = 0.16
R² = 0.19
R²m = 0.05
R²c = 0.12
R²m = 0.08
R²c = 0.11
R²m = 0.09
R²c = 0.13
Range shift (km y⁻¹)
Number of species
Specialisation
Habitat availability (%)
Habitat availability (%)
Margin vs range habitat (%)

Figure 3.3. Models of species' range-margin shift as a function of habitat specialisation and log_{10}-habitat availability at the range margin, for 14 taxonomic groups (indicated by different coloured points). (A-D) Butterflies, dragonflies and damselflies, grasshoppers and allies, and hoverflies. (E-H) Macromoths. (I-L) Nine taxonomic groups with lower levels of recording (Table A3.1). In the first two columns, different coloured lines show the random effect of taxonomic group (Table A3.6). In the third column, group-specific slopes are not shown but rather the effect of habitat is varied (as an interaction term) by the relative habitat availability at the range margin as compared to the whole range (calculated as a percentage of the range-wide average). Dashed and solid black lines illustrate the interaction term using two exemplars: below-average habitat in range-margin landscapes (dashed, 80% of a species' range-wide average) and above-average habitat in range-margin landscapes (solid, 120%). In the fourth column (D, H and L), the frequencies of different range-margin habitat availability are displayed in histograms for each set of taxonomic groups, with the same dashed and solid lines used as in the previous column.

The habitat interaction model explained over a third of the variation in range shifts for the best-recorded groups (R^2_m = 0.36, Figure 3.3C), 19% of the variation for macromoths (R^2 = 0.19, Figure 3.3G), and 9% for nine groups with reduced levels of recording (R^2_m = 0.09, Figure 3.3K). More generally, we found that the greater the level of biological recording (i.e., ranking groups by geographic coverage of recording across both time periods), the more variation in range shifts could be explained by habitat factors (r = 0.97, $P < 10^{-6}$, N = 10). Extrapolating to assume universal geographic recording for all study taxa implies that habitat availability could explain up to half of the variation in species' range shifts (Figure 3.4). This is extremely high, given that there are additional sources of variation in the data: satellite-derived habitat classes do not provide a full species-eye view of 'habitat', land cover may change over time (although minimal for our study region/period), species' habitat associations may vary geographically, and evolutionary changes in resource use can take place during range expansion (Thomas *et al.*, 2001; Oliver *et al.*, 2009, 2012; Hanski & Mononen, 2011; Pateman *et al.*, 2012, 2016; Weiss-Lehman *et al.*, 2017). The remaining variation between species may be explained by species-specific sensitivities to different elements of the climate, and hence their exposure to climate change (Palmer *et al.*, 2017), other phylogenetic variation which has not yet been tested, and perhaps also by the accidental or deliberate transportation of individuals to otherwise unreachable locations (Auffret *et al.*, 2014).

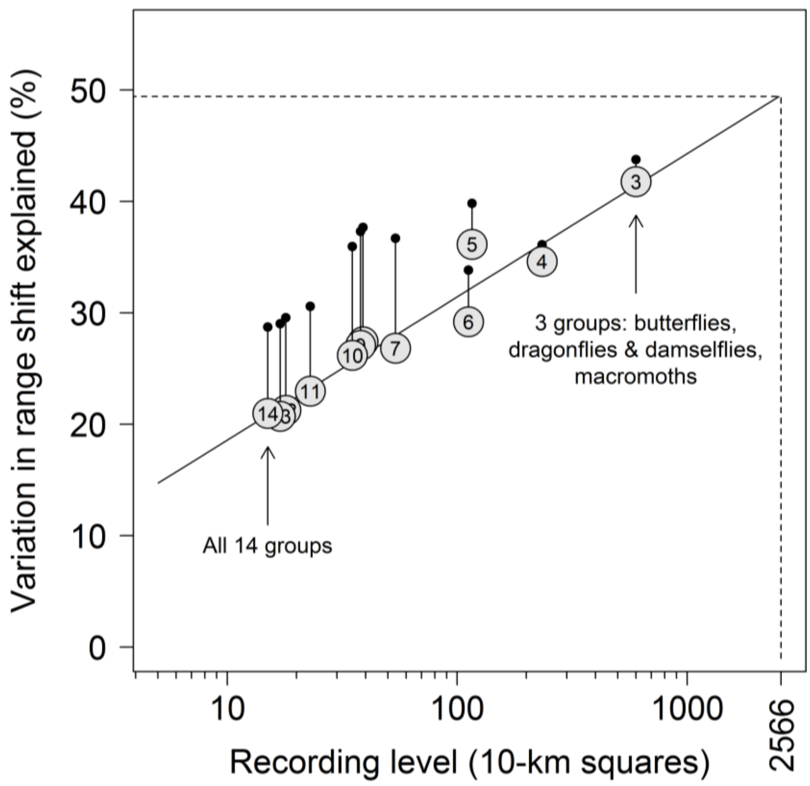

Figure 3.4. Variation explained by habitat in range-shift models, as a function of the geographic coverage of citizen-science biological recording. Recording level is the number of 10-km squares where at least 25% of the regional species richness was recorded in both time periods (up to a maximum of 2566 in Britain). Vertical lines extend from marginal R^2 (grey circles, fixed effects of habitat) to conditional R^2 (black dots, random intercept conditional on taxonomic group). The fixed effects are log10-habitat availability at the range margin, interacting with margin habitat as a percentage of the range-wide average. Each pair of points was generated over 10,000 randomised draws of 30 species from any three qualifying groups, with the pool of groups decreasing from left to right as fewer met the required level of recording. The higher the recording level, the greater the explanatory power of habitat, up to a possible 49% (dashed lines, assuming complete geographic recording for all study taxa).

3.4 Conclusions

We conclude that range boundary dynamics vary greatly among species, and that up to half of this variation depends on the interplay between species' habitat associations and the landscapes they encounter during range expansion. This has important consequences for facilitating species' responses to climate change: (i) a subset of species will successfully track climate polewards without intervention, because their species-specific habitat requirements are already exceeded in range-margin landscapes; (ii) some species may be assisted by the provision of better-connected landscapes that contain high quality habitats for these species; whereas (iii) location-specific natural or human-related barriers may make it impractical to achieve sufficient connectivity for others (Hoegh-Guldberg *et al.*, 2008; Robillard *et al.*, 2015). Landscape management and restoration strategies need to target habitats required by species in the second category, because these are the interventions that can increase the rates at which species' distributions are able to spread polewards.

3.5 Supplementary Methods

We conducted all statistical analyses and created figures using R version 3.3.3 (R Core Team, 2017). In additional to base R functions, we used several contributed packages, detailed in Table A3.7.

3.5.1 Study region and observed warming

The study region encompassed 2566 Ordnance Survey 10 km × 10 km grid squares (hectads) covering the British mainland plus any near-shore islands connected to the mainland by the contiguous spread of hectads. We calculated annual mean temperatures for the study region using gridded data from the UK Meteorological Office (Hollis & McCarthy, 2017). During the first recording period (1976-1990), the mean temperature was 8.5 °C, increasing to 9.3 °C during the second recording period (2001-2015). The level of warming was therefore 0.8 °C (0.03 °C y^{-1}) across the 25-year interval between the midpoints of the two recording periods.

3.5.2 Species occurrence records

Great Britain has one of the highest concentrations of volunteer naturalist biological recorders (citizen scientists) in the world (Sutherland *et al.*, 2015), supported by various recording schemes and societies, whose data are housed by the UK Biological Records Centre (BRC, http://www.brc.ac.uk).

We considered all animal groups held in the BRC database, and included any group that contained at least five species meeting our inclusion criteria, and for which range-margin shifts and habitat associations could be calculated (see sections below). We identified 14 taxonomic groups with sufficient data for inclusion: aquatic bugs, bees, butterflies, dragonflies and damselflies, grasshoppers and allies, ground beetles, hoverflies, macromoths, non-marine molluscs, shieldbugs and allies, soldierflies and allies, spiders, wasps, and woodlice. These are all invertebrate groups, and therefore share some commonality, but they are also diverse in many respects. They include carnivores, herbivores and omnivores, aquatic and terrestrial taxa, groups that disperse in the soil, by walking, by ballooning and by active flight, and span orders of magnitude in body mass.

Each of these groups was covered by a formal recording scheme (Table A3.1). The data were mainly collected by citizen scientist recorders, before being collated and cleaned by experts in the group/region to filter out possible errors. We retained the taxonomic distinctions and groupings used by these recording schemes (e.g. butterflies and macromoths were treated as separate groups, whereas dragonflies and damselflies were aggregated). It should be noted that any 'group effect' may reflect differences in the recording schemes as well as the effects of taxonomic group *per se*.

Each biological record represents a unique location × date observation of species presence. We removed records with ambiguous taxonomy (*sensu lato*, *sensu auct*, naming multiple species or identified only to genus). Species listed with a sub-species trinomial, with the label *sensu stricto*, with variants or different morphs were aggregated at the species level. When analysing range shifts, we used all records with at least hectad-level spatial accuracy that could be unambiguously assigned to one of the two recording periods (1976-1990 and 2001-2015). For habitat associations, we used day-specific records accurate to 100-m resolution (for the 347 species included in the final analysis, 74% of records had this level of precision).

3.5.3 Criteria for species inclusion

We selected non-migratory species that reach their northern (cool) range boundaries in southern/lowland Britain. We defined these species as having 90% of their 1976-1990 distribution in the warmest 50% of the study region (using gridded temperature data from the UK Meteorological Office (Hollis & McCarthy, 2017), averaged over the same time window). Since these species have historically been concentrated in the warmer half of Britain, it is reasonable to postulate that they might be favoured by climate warming. As non-migrants, any expansion should represent the establishment of new, persistent populations, which ought to be evident in the distribution record from the second recording period (2001-2015).

We excluded species classified as non-native, alien-native hybrid, unknown origin, and those that are dependent on non-native species, as defined by the BRC and the GB Non-native Species Information Portal (Roy *et al.*, 2014). We also excluded vagrants and species thought to be extinct from the study region, including species that have been reintroduced following extinction (e.g. Large Blue butterfly *Maculinea arion*). Many such species are not at equilibrium with the climate (e.g. following (re)introduction), and so recent changes in their distributions cannot be reliably linked with changes in temperature. Other exclusions were made only if species' distribution data were insufficient for range-shift or habitat calculations.

3.5.4 Range-shift calculations

To calculate range shifts, we first controlled for changes in recorder effort over time (1976-1990 to 2001-2015). We restricted distribution data to hectads for which at least 10% of the regional species pool for a group was recorded present in both recording periods (Hickling *et al.*, 2006). For each group × hectad, we defined the regional species pool as the total number of species recorded in the nearest 100 hectads (Mason *et al.*, 2015), using all species in the database for a given taxonomic group (i.e. regardless of the above inclusion criteria).

For all species occupying at least 20 such hectads in both recording periods, we calculated northern (cool) range margins as the mean latitude of the ten-northernmost occupied hectads. We checked that species had sufficient area to expand or retreat from their 1976-1990 range margins: we excluded any species with fewer than ten hectads reaching the 10% criterion within 100 km to the north, and ten such hectads within 100 km to the south of the range margin (Mason *et al.*, 2015). For the remaining species, we defined range shifts as the latitudinal change (km) in range margins between 1976-1990 and 2001-2015. We converted latitudinal changes to annual rates (km y^{-1}) by dividing by the interval between the midpoints of the two recording periods (25 years). Results are summarised by group in Table A3.2, and are reported for individual species in Table A3.8.

3.5.5 Habitat classes

To identify habitat classes, we used a 25-m land cover map for Great Britain (LCM2007). This map was created by the NERC Centre for Ecology and Hydrology (Morton *et al.*, 2011), using combined summer and winter satellite data (Landsat-TM5, IRS-LISS3, SPOT-4 and SPOT-5 sensors, pixel size of 20-30 m), enhanced with extensive cartographical information (e.g. Ordnance Survey data, soil types, agricultural census boundaries and urban extents). The classification was trained and validated using a large network of habitat surveys and ground reference points, producing an overall accuracy of 83%. Out of 23 habitat classes identified in LCM2007, we discarded one (saltwater), retained 14 as originally mapped, and created four aggregate classes from the remaining eight: 'heather' and 'heather grassland' became 'dwarf shrub heath'; 'supra-littoral rock' and 'littoral rock' became 'coastal rock'; 'supra-littoral sediment' and 'littoral sediment' became 'coastal sediment'; 'suburban' and 'urban' became 'built-up and gardens'. This resulted in a total of 18 habitat classes (Table A3.9).

Habitat, as we use the term here (we could alternatively have referred to ecotype or biotype), reflects a combination of the physiognomy of the vegetation and land management, and does not imply any particular mechanism of association; i.e. we take a resource-based view of habitat (Dennis, 2010), recognising that a species occupies particular habitat classes because certain resources (e.g., host plants, prey, mutualists), structural elements (e.g., that enable spider webs to be built), or micro-environments (e.g., sheltered microclimates) are present somewhere within that class, and/or because negative influences (e.g., natural enemies, disruptive land management) are absent. For example, hedgerow species can be positively associated with arable and improved grassland (albeit at low frequencies), which is a true reflection of where many of these species live, given that field boundaries are demarcated by hedgerows, and that such linear features are nested within the grain size of satellite imagery.

3.5.6 Habitat associations

We identified habitat associations using logistic regression of species presence or absence (binary response) overlaid on the 18 habitat classes (categorical predictor). The regression equation for each species was used to estimate its probability of occurrence in each habitat class, under the assumption of equal availability of all habitat classes (i.e., as close as is possible to a 'species characteristic'). We defined levels of habitat specialisation to be the coefficient of variation across these 18 probabilities (13), producing a species' specialisation index (SSI) which, for our dataset, ranged from SSI = 0.36 (generalist) to SSI = 3.22 (highly specialised). Results are summarised by group in Table A3.3, and are reported for individual species in Table A3.8.

Given the finer grain of the land-cover map (25 m), compared with species records (100 m), individual species records could potentially be associated with up to 16 different habitat classes. To reduce the number of false positive associations, we removed mixed pixels at 100-m resolution (so that each species record was associated with exactly one habitat class). We further restricted the spatial extent for analysis to a 50-km buffer around presence records for the target species, excluding landscapes that were occupied during only one recording period. We did this to reduce the number of absences that might be caused by unsuitable climate or dispersal limitation (i.e., a pixel contains suitable habitat for a species, but lies outside its climate niche or dispersal radius in one or both recording periods).

We took all recorded presences to be 'true' for the purposes of modelling, and included in the final analysis all species with at least 50 such records (mean = 787, median = 197, maximum = 44 580). Inferring absence data from presence-only datasets is inherently more difficult. Further to the spatial filters described above, we applied the following criteria to minimise the number of false absences in the models. First, we only included as potential absences those pixels that had been visited by recorders of the same recording scheme (as deduced from records of other species within the same recording scheme). Second, we filtered absences according to time of year, for example to avoid treating late summer data as absences if the target species' flight period is in spring. We did this by fitting a smooth phenology curve to the frequency of records for the target species, as a function of the Julian day of observation. Any potential absences with record dates in the tails of this distribution (lower or upper 10% area under the curve) were excluded.

The remaining absences were from pixels visited under the same recording scheme as the target species, in landscapes where (or near where) the target species occurred and within the appropriate phenological time window(s). The absences still varied in reliability, however, because some qualifying pixels had only been visited once, whereas others had been visited multiple times. Third, therefore, we weighted absence data by the probability of recording the target species if it was present, given the number times (t) the absence pixel was visited:

$$\frac{1}{n}\sum_{s=1..n} 1-(1-p_s)^t$$

That is, one minus the probability of failing to detect the species on every occasion, where the ps are probabilities of detection across n known presence sites for the target species (these were calculated as the number of times the species was recorded in pixel s divided by the number of times s was visited).

3.5.7 Habitat availability

We obtained spatial estimates of habitat availability by projecting each species' regression model back on the land cover map at 25-m resolution (so that all pixels, including mixed pixels at the 1-ha scale, were included), using the same 50-km buffer as we used for model calibration. Range-wide habitat availability for each study species was calculated as the mean value across all of these pixels, indicative of the amount of habitat typically accessible to a species across its British distribution.

Habitat availability at the range margin was defined as the mean value across all land cover pixels in a 50-km buffer around the ten (or more) northernmost hectads that were used to define the range margin in the first recording period (1976-1990); i.e. landscapes across which the species had potential to expand (or retract) over time. Habitat availability for individual species at the range margin ranged from 0.4% (very little of the landscape could be colonised) to 56% of the landscape (ample opportunity for expansion, given suitable climate; Table A3.4 and Table A3.8).

To assess the relative suitability of the range-margin landscape, compared to what a species experiences on average across its range, we divided the mean habitat availability in range-margin landscapes by the range-wide average. Significantly more species had reduced habitat availability in their range-margin landscapes ($\chi^2 = 10.03$, 1 df, $P < 0.002$, $N = 347$). The size of the effect was small on average, but correlated positively with higher levels of recording ($r = 0.54$, $P < 0.05$; reduction in margin habitat *vs*. number of hectads where at least 25% of the regional species richness was recorded in both time periods).

3.5.8 Models of range shift

We modelled range shifts (km y^{-1}) as linear functions of habitat specialisation, and $\log_{10}$-transformed habitat availability at the range margin. Habitat specialisation and $\log_{10}$-habitat availability are highly correlated ($r = -0.70$; see Figure 3.1B), and so we did not include both predictors in the same model. Rather, we tested the hypothesis that habitat availability provides a stronger explanation for the observed variation in species' range shifts, compared to specialisation.

To account for phylogenetic relatedness and methodological differences in recording between taxonomic groups (i.e. across recording schemes), we used linear mixed-effects models fitted via maximum likelihood (Bates *et al.*, 2014), with taxonomic group specified as a random intercept term. We included random slopes of the predictor variable, with respect to taxonomic group identity, if this lowered the conditional AIC (Greven & Kneib, 2010) when all 347 species were included in the model, considering both a correlated or uncorrelated random slope and intercept for the random effect grouping variable.

For all random effects structures, habitat availability was a stronger predictor of range shifts than was specialisation (Table A3.6). For range shifts modelled against specialisation, the top model included a random intercept term but not random slopes (model 1); for range shifts against habitat availability, the top model included (uncorrelated) random intercept and random slope terms (model 2). Next, we extended model 2 by including an interaction between $\log_{10}$-habitat availability, and margin habitat as a percentage of the range-wide average. This model had lower AIC and cAIC, compared with single-predictor models. The top model included the interaction term plus random intercept with respect to group (model 3).

3.5.9 Sensitivity to recording level

We ranked the 14 taxonomic groups by descending geographic coverage of citizen-science recording, defined by the number of hectads where there has been sufficient recording for at least 25% of the regional species richness (considering the nearest 100 hectads) to have been sampled in both time periods (Table A3.1). In Figure 3.3 of the main text, we plotted models 1-3 separately for: (i) four groups with the highest levels of recording, minus macromoths; (ii) macromoths; and (iii) nine groups with lower levels of recording. We plotted macromoths separately because, unlike other groups, moth recording used attractant methods (light traps at night) so that the areas sampled – and thus habitat associations – were more uncertain.

The proportion of variation in range shift that could be explained was higher for taxonomic groups with higher recording coverage. The slopes of the relationships were, however, similar (Figure 3.3 and Table A3.6), demonstrating that the patterns we report are qualitatively robust to recorder effort. In Figure 3.4, we systematically varied the threshold of recording coverage, above which species are included in the model. For example, when the recording threshold is very low, all groups are eligible for inclusion; when the threshold is very high, only the best-recorded groups are included. For consistency across different levels of group inclusion, each pair of points (R^2_m and R^2_c) in Figure 3.4 was generated by averaging over 10,000 randomised draws of 30 species from three qualifying groups. This analysis revealed a log-linear relationship between the geographic coverage of citizen-science recording, and the proportion of variation in range shifts that could be explained. Extrapolating the fitted line to assume complete geographic coverage (2566 hectads) for all groups in the study, we infer that approximately half (49%) of the variation in range shift could be explained by habitat availability.

Chapter 4

Population variability of species can be deduced from opportunistic citizen science records: a case study using British butterflies.

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Keywords: Abundance, biogeography, biological records, inter-annual varia- tion, population size, range extent.

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Abstract

Abundance data are the foundation for many ecological and conservation projects, but are only available for a few taxonomic groups. In contrast, distribution records (georeferenced presence records) are more widely available. Here we examine whether year-to-year changes in numbers of distribution records, collated over a large spatial scale, can provide a measure of species' population variability, and hence act as a metric of abundance changes. We used 33 British butterfly species to test this possibility, using distribution and abundance data (transect counts) from 1976-2012. Comparing across species, we found a strong correlation between mean year-to-year changes in total number of distribution records and mean year-to-year change in abundance (N = 33 species; R^2 = 0.66). This suggests that annual distribution data can be used to identify species with low versus high population variability. For individual species, there was considerable variation in the strength of relationships between year-to-year changes in total number of distribution records and abundance. Between-year changes in abundance can be identified from distribution records most accurately for species whose populations are most variable (i.e. have high annual variation in numbers of records). We conclude that year-to-year changes in distribution records can indicate overall population variability within a taxon, and are a reasonable proxy for year-to-year changes in abundance for some types of species. This finding opens up more opportunities to inform ecological and conservation studies about population variability, based on the wealth of citizen science distribution records that are available for other taxa.

4.2 Introduction

The long term monitoring of population dynamics is an important aspect of ecology, and allows examination of factors driving species' abundance trends, such as the effects of weather (Roy *et al.* 2001), habitat availability and land use (Lemoine *et al.* 2007), disease (Daszak, Cunningham & Hyatt 2003), and human impacts (Lewis & Vandewoude 2015). Monitoring abundance trends of species thus helps to identify species at risk, develop conservation strategies to halt population declines (Brown, Mehlman & Stevens 1995), and identify increasing populations of pests to implement control strategies (Petrovskii, Petrovskaya & Bearup 2014). Measuring population variability is essential to explore the influence of environmental factors, such as climatic cycles or food availability, on population dynamics (van Schaik & van Noordwijk 1985; Lynam, Hay & Brierley 2004). In addition, population variability may be an important determinant of the likelihood that populations will survive in habitat fragments, and variability may indicate the sensitivity of populations to climatic fluctuations (Pimm, Jones & Diamond 1998; Vucetich *et al.* 2000; Oliver *et al.* 2012). However, collecting abundance data may be time-consuming and expensive, and thus many taxonomic groups lack information on abundance trends and population dynamics. By contrast, many more species have large datasets of distribution records (i.e. unique records of the presence of species at a given location and date). Such data are available for a wide range of taxonomic groups, tend to cover wide areas, span many years, and are often collected as part of 'citizen science' projects (Devictor, Whittaker & Beltrame 2010; Pocock *et al.* 2015).

It is well known that there is a positive relationship between species' abundances and distributions (Brown 1984; Gaston *et al.* 2000) and very abundant species tend to have larger ranges (Holt *et al.* 1997). Abundance-distribution relationships are general patterns in ecology, but there are many forms of the relationship (Gaston 1996), and these relationships are not necessarily linear (Hartley 1998). In spite of this complexity, strong relationships have been found between distribution and abundance, which are evident over time, large spatial scales and different taxonomic groups (Zuckerberg, Porter & Corwin 2009; Roney, Kuparinen & Hutchings 2015). These relationships allow occupancy changes (changes in the likelihood of a species' presence) to be used to estimate population trends (Tempel & Gutiérrez 2013), broad biodiversity changes to be assessed across multiple taxonomic groups (Oliver *et al.* 2015a), and long-term trends in the frequency of species' occurrences to be modelled (Pearce & Boyce 2006). These long-term occurrence trends have been shown to be reasonable proxies for abundance trends for both birds (Kamp *et al.*

2016) and butterflies (Warren *et al.* 2001; Oliver *et al.* 2015a). However, there is little information on the capacity of distribution data to describe other aspects of population dynamics, such as population variability, which is an important factor affecting extinction risk (Inchausti & Halley 2003; Mace *et al.* 2008).

A challenge for ecologists is deriving an accurate measure of population variability when standardised abundance estimates are lacking. The positive associations between distribution size and abundance suggest that distribution records could potentially be used in analyses inferring species' population dynamics, by acting as proxies for abundance data. If there are strong and predictable relationships between year-to-year changes in abundance and year-to-year changes in distribution records, then distribution records could provide a useful metric for ecologists to study the factors affecting population variability in a much wider range of taxa than is currently possible.

In this study, we examine the relationships between abundance and distribution to assess whether year-to-year changes in the number of distribution records are strongly related to year-to-year changes in abundance. We study British butterflies because there are long-term and fine-scale data on both distribution and abundance, allowing robust testing of these relationships. We predict that year-to-year changes in abundance will be strongly positively related to year-to-year changes in distribution records, because increasing numbers of individuals would be expected to result in an increased likelihood of a species being recorded. In addition, as a population increases in size, density-dependent dispersal would be expected to result in individuals moving away from areas of high population density, thereby increasing the number of sites where species can be observed (Gaston *et al.* 2000).

Within this broad topic, we examine three issues. The first is whether it is possible to identify species with higher or lower population variability using distribution data – a between-species comparison. We do this by calculating average between-year changes in the numbers of distribution records over time, and comparing these estimates with measures of variability that are based on fixed-transect population count data. Secondly, we assess whether distribution records can be used as proxies for inter-annual changes in abundance in each species separately – a within-species analysis. Finally, we identify the characteristics of species for which distribution data provide a proxy for abundance, concentrating on three attributes that can be deduced from the distribution records themselves (i.e. not requiring additional ecological or population dynamic data, which are lacking for many taxa). We selected these metrics because they are likely to be linked to our statistical capacity to detect year-to-year variation in abundance from distribution records: (1) the total number of distribution records for a species, (2) how aggregated these records are in space (using a metric of 'fractal dimension' of distribution records), and (3) the average size of the year-to-year changes in distribution records (i.e. how much annual variation there is in distribution records for a species). We refer to these metrics as 'biogeographical attributes', but recognise that they are also influenced by variation in recording intensity across species and over time. We also examine the effect of the spatial scale of the study area on the relationship between year-to-year changes in distribution records and year-to-year changes in abundance, by comparing data analysed at national (UK study area, 302,800 km^2) and regional (county study area, 440 km^2) levels, given that population fluctuations may be synchronous in their dynamics at one spatial scale but not others (Sutcliffe, Thomas & Moss 1996).

4.3 Materials and methods

4.3.1 Study species

We studied 33 species of British butterfly (See Table 4.1), including northern and southern species, and resident and migrant species, over the period 1976 to 2012. This study period was selected to maximise the geographic coverage of data, the length of the time-series of data analysed, and the number of species analysed. We excluded species without 37 years of abundance and distribution data. Species that were subject to targeted, intensive surveying effort during certain years of the study period were also excluded (*Hesperia comma*; Thomas & Jones, 1993, *Boloria euphrosyne*; Brereton, 1998, and *Satyrium w-album*; Thomas, 2010), because large differences in the level of recording effort between years could bias results.

4.3.2 Distribution records

We computed year-to-year changes in distribution records based on data collected by volunteers for the Butterflies for the New Millennium (BNM) recording scheme, surveying sites in the study area (see below) on an opportunistic basis using unstructured sampling (Fox *et al.* 2015). A distribution record is an observation (recorded presence) of an individual species at a location on a particular date. Recording efforts are generally unstructured (there are no fixed or assigned times, places or methods for recording) and opportunistic, with little to no guidance given to recorders as to how, when and where to record, meaning that recording is influenced heavily by recorder behaviour (Boakes et al., 2010; Isaac & Pocock, 2015). Recorder behaviour can vary due to encouragement to record in under-represented regions for the purposes of atlas creation or other targeted survey efforts. Despite these attempts to encourage, spatial and temporal variation in opportunistic recording effort remains high. Due to increased recruitment of recorders over time numbers of distribution records have increased (see Figure A4.2), which is why we de-trended the data prior to analysis. The spatial and temporal resolution of BNM distribution records varies; we excluded records with spatial resolution coarser than a 10 km x 10 km grid square or with date ranges which fell outside the study period. The study area was the UK, Isle of Man and Channel Islands (3028 hectads in total). We analysed a total of 5,873,182 distribution records from 1976 to 2012, after all filtering processes (see below). The majority of distribution records are independent of abundance data (UK Butterfly Monitoring Scheme (UKBMS) transect), but the distribution dataset did contain some records sourced from transects. Therefore, distribution records were excluded if they occurred within the 1 km grid cell that contained a UKBMS transect (based on the centroid of the digitised transect route). This led to 1604 1km cells being excluded; approximately 5.3% of the UK land area and 26.2% (2,089,886) of records. Year-to-year changes in $\log_{10}$ distribution records were calculated for each study species over the 37-year study period by subtracting the number of distribution records ($\log_{10}$-transformed) in year *t-1* from the number of records in year *t*.

4.3.3 Abundance data

We analysed abundance data from the UKBMS national collated index (www.ukbms.org). The UKBMS calculates their index from counts from weekly transect walks along fixed routes undertaken during the recording period (April-September) every year since 1976 (see http://www.ukbms.org/Methods.aspx for full details). Counts are taken from sites in Great Britain and Northern Ireland (1854 transect sites in total). Counts for missing weeks are estimated by the UKBMS by considering the area of a GAM curve fitted to observed weekly count data throughout the year (Rothery & Roy 2001). The UKBMS national collated index from 1976-2012 is created using a log-linear model, with a transect site and year effect (Brereton *et al.* 2011), as shown below:

$$\log_{10}(c_{ij}) = x_i + y_j$$

Where c is the expected count for site *i* in year *j*, and where x_i and y_j give the means for the *i*th site and the *j*th year. The index is then scaled to a mean of 2, for the purposes of comparing abundance trends across species. This produces a $\log_{10}$-transformed abundance index, which we used in our calculation of population variability. We computed year-to-year changes in $\log_{10}$ abundance by subtracting the abundance index value ($\log_{10}$-transformed) for year *t-1* from the value for year *t*.

4.3.4 Accounting for phylogeny

The butterfly species studied here are phylogenetically related, and this must be taken into account when analysing species together in models. All multi-species analyses conducted in this study accounted for the non-independence of species using phylogenetically-informed linear models with estimated Pagel's λ, using the *pgls* function of the caper package in R (Pagel, 1999; Orme et al., 2013), and a recently-published butterfly phylogeny (please see Brooks *et al.* 2016 for full details of how the phylogeny was constructed). These models are interpreted by lambda P values (distinct from the P values produced by the model estimates) indicating the difference between the phylogenetic correlation λ value (estimated using maximum likelihood) and the upper and lower bounds: 1 (indicating phylogenetic dependence) and 0 (indicating phylogenetic independence). In all our analyses, the phylogenetic correlation was not significantly different from the lower bound, indicating that there was little evidence of phylogenetic signal in our models.

4.3.5 Examining relationships between abundance and distribution records

First, we explored whether mean yearly changes in $\log_{10}$ distribution records (as above) were correlated with mean yearly changes in $\log_{10}$ abundance (as above) over the 37-year study period, in a multi-species analysis with a control for phylogenetic independence (see section above). In both cases (distribution-record and abundance changes), we calculated the average absolute magnitude of the year-to-year changes, rather than directional changes (positive or negative). This analysis tests whether species with high population variability (on transects) also have high variability in terms of numbers of distribution records.

Secondly, we examined each species separately. We calculated the strength of the relationships between year-to-year changes in $\log_{10}$ distribution records and changes in $\log_{10}$ abundance using R^2 values from least squares regressions. This relationship is hereafter termed the inter-annual distribution-abundance relationship and, for each study species, it reflects the extent to which yearly changes in $\log_{10}$ numbers of distribution records can be used to predict population size changes (from transect data). We analysed year-to-year changes rather than absolute numbers each year to de-trend the data, and to remove any temporal trends in recording effort.

Thirdly, we examined the influence of three independent biogeographical attributes on these inter-annual distribution-abundance relationships to identify species for which distribution records were adequate proxies for population change. These attributes were: total number of distribution records; fractal dimension of a species' range; and overall variability in distribution records. We computed the total number of distribution records collected at any spatial resolution (10 m to 10 km grid) for a species during the study period (1976-2012). Fractal dimension is a metric of how 'well-filled' a species' range is, based on the proportion of 10km grid cells with records within each occupied 100km grid cell (Wilson *et al.* 2004). For each species, we calculated the total area of all occupied 10 km and 100 km grid cells, and regressed these values against the length of the grid cells (10 km and 100 km respectively; all values $\log_{10}$ transformed).The slope of the regression gives a measure (fractal dimension) of how 'well-filled' a species range is at 10km scale, where a slope of 0 indicates a completely-filled range, and a slope of 2 indicates a minimally-filled range (see Figure A4.1 for two exemplar species; *Thymelicus sylvestris,* with the most well-filled range and *Hipparchia semele* with the most minimally-filled range). For overall variability in distribution records we used the mean year-to-year change in $\log_{10}$ distribution records over the study period.

A phylogenetic multivariate regression was then fitted with the three biogeographical attributes as explanatory variables and the R^2 value of each species' inter-annual distribution-abundance relationship as the response variable. We fitted a fourth term to the model, the quadratic term of mean year-to-year change in $\log_{10}$ distribution records, to account for its apparent non-linear relationship with goodness-of-fit (R^2) values when relationships were visually inspected by plotting the data. We tested a full model, then removed non-significant terms using a stepwise deletion approach.

Autoecological information may be limited for other taxonomic groups, but the biogeographical attributes tested in this paper can be easily derived from distribution datasets for many different taxa. Because butterflies do have detailed autoecological information, we tested the influence of dispersal ability on the inter-annual distribution-abundance relationship in PGLS models, using two metrics: dispersal rankings based on expert opinion (Cowley et al., 2001) and a mobility score calculated from indices of ecological information (Dennis et al., 2004). We found no significant relationship between dispersal ability and the strength of the inter-annual distribution-abundance relationship (see Supplementary Table 4.2).

4.3.6 Comparison of national and regional inter-annual distribution-abundance relationships

To investigate whether the goodness of fit of the inter-annual distribution-abundance relationships varied with spatial scale, we repeated our analysis of this relationship at a regional level, for the county of Dorset. We compared r^2 values from national and regional inter-annual distribution-abundance relationships for a sub-set of 23 butterfly species for the period 1983-2009 (maximum time period containing abundance data for species in Dorset). Dorset was selected because of its extensive history of surveying butterflies (Robertson, Woodburn & Hill 1988; Thomas *et al.* 2001).

4.4 Results

4.4.1 Relationship between variability in abundance and distribution records across species

Across the 33 study species, there was a strong positive relationship between the mean year-to-year changes in $\log_{10}$ distribution records and mean year-to-year changes in $\log_{10}$ abundance (Figure 4.1a, PGLS, λ = 0, R^2: 0.95, $F_{1,31}$ = 623.8, P = <0.001), even when two outlier species were removed (Figure 4.1b, λ = 0.059, PGLS, R^2: 0.66, $F_{1,29}$ = 55.35, P = <0.001). Thus, species that show high variability in abundance also have high variability in distribution records, and there was little evidence for any phylogenetic signal (i.e. results were not significantly different between models based on estimated λ, and where λ was set to 0).

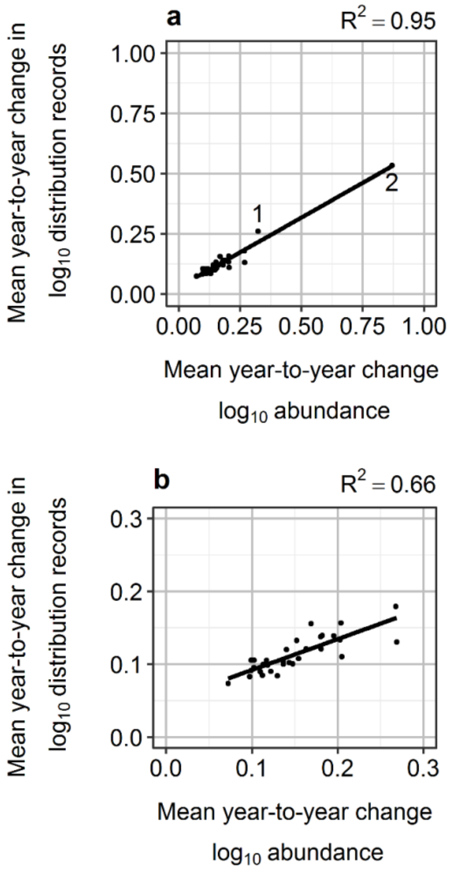

Figure 4.1. Regressions of the mean year-to-year change in $\log_{10}$ distribution records against the mean year-to-year change in $\log_{10}$ abundance: a) including all 33 species, with two outlier species labelled as follows: *Celastrina argiolus* (1) and *Vanessa cardui* (2); and b) for 31 species, excluding these outlier species.

4.4.2 Measuring inter-annual distribution-abundance relationships within species

For each of our 33 study species, the relationships between year-to-year changes in $\log_{10}$ distribution records and year-to-year changes in $\log_{10}$ abundance produced an overall mean R^2 value of 0.36, indicating that year-to year changes in distribution records of UK butterflies provide a moderate proxy for year-to-year abundance changes. Eight butterfly species had $R^2 > 0.5$, showing that distribution records were particularly informative in approximately 25% of study species. However, there was considerable variation among species, with r^2 values varying between 0.03 and 0.92 (Table 4.1). Figure 4.2 highlights two exemplar species, where the relationship was strong (Holly blue, *Celastrina argiolus,* R^2 = 0.85) and one where the relationship was very weak (Marbled White, *Melanargia galathea,* R^2 = 0.16).

Table 4.1. Goodness of fit of the inter-annual distribution-abundance relationships for 33 butterflies. Latin names with an asterisk (*) indicate migratory species. Presented are the Pearson's R^2 values of the relationship between year-to-year $\log_{10}$ change in abundance and year-to-year $\log_{10}$ change in total number of distribution records. We checked r values and found them to all be positive, indicating that the relationships below were always positive. Biogeographical attribute values are also included for each species: total number of distribution records (ΣD), mean absolute year-to-year change in $\log_{10}$ distribution records, fractal dimension (Fractal D).

Species	R^2	ΣD	Mean $\lvert \Delta D \rvert$	Fractal D
Aglais io	0.36	407408	0.10	0.338
Aglais urticae	0.60	442648	0.13	0.322
Anthocharis cardamines	0.22	220768	0.11	0.302
Aphantopus hyperantus	0.18	177673	0.08	0.300
Argynnis aglaja	0.37	28184	0.10	0.468
Argynnis paphia	0.27	31324	0.13	0.516
Aricia agestis	0.65	44785	0.16	0.441
Boloria selene	0.03	20723	0.11	0.480
Callophrys rubi	0.25	31394	0.12	0.448
Celastrina argiolus	0.85	165545	0.26	0.365
Coenonympha pamphilus	0.35	144788	0.08	0.311
Erynnis tages	0.39	31119	0.10	0.543
Favonius quercus	0.07	30622	0.14	0.413
Gonepteryx rhamni	0.34	184215	0.11	0.390
Hipparchia semele	0.18	22647	0.09	0.716
Lasiommata megera	0.43	87900	0.11	0.384
Limenitis camilla	0.48	17988	0.16	0.520
Lycaena phlaeas	0.66	150387	0.14	0.332
Maniola jurtina	0.11	459084	0.07	0.309
Melanargia galathea	0.16	66946	0.10	0.479
Ochlodes sylvanus	0.29	135278	0.09	0.276
Pararge aegeria	0.10	400596	0.10	0.375
Pieris brassicae	0.44	458225	0.13	0.353
Pieris napi	0.25	399295	0.10	0.303
Pieris rapae	0.32	474880	0.11	0.370
Polygonia c-album	0.58	223318	0.14	0.353
Polyommatus coridon	0.47	17523	0.10	0.669
Polyommatus icarus	0.55	226639	0.12	0.328
Pyrgus malvae	0.28	17215	0.12	0.577
Pyronia tithonus	0.13	278385	0.08	0.331
Thymelicus sylvestris	0.11	134606	0.09	0.257
*Vanessa atalanta**	0.62	384283	0.18	0.338
*Vanessa cardui**	0.92	183430	0.53	0.342

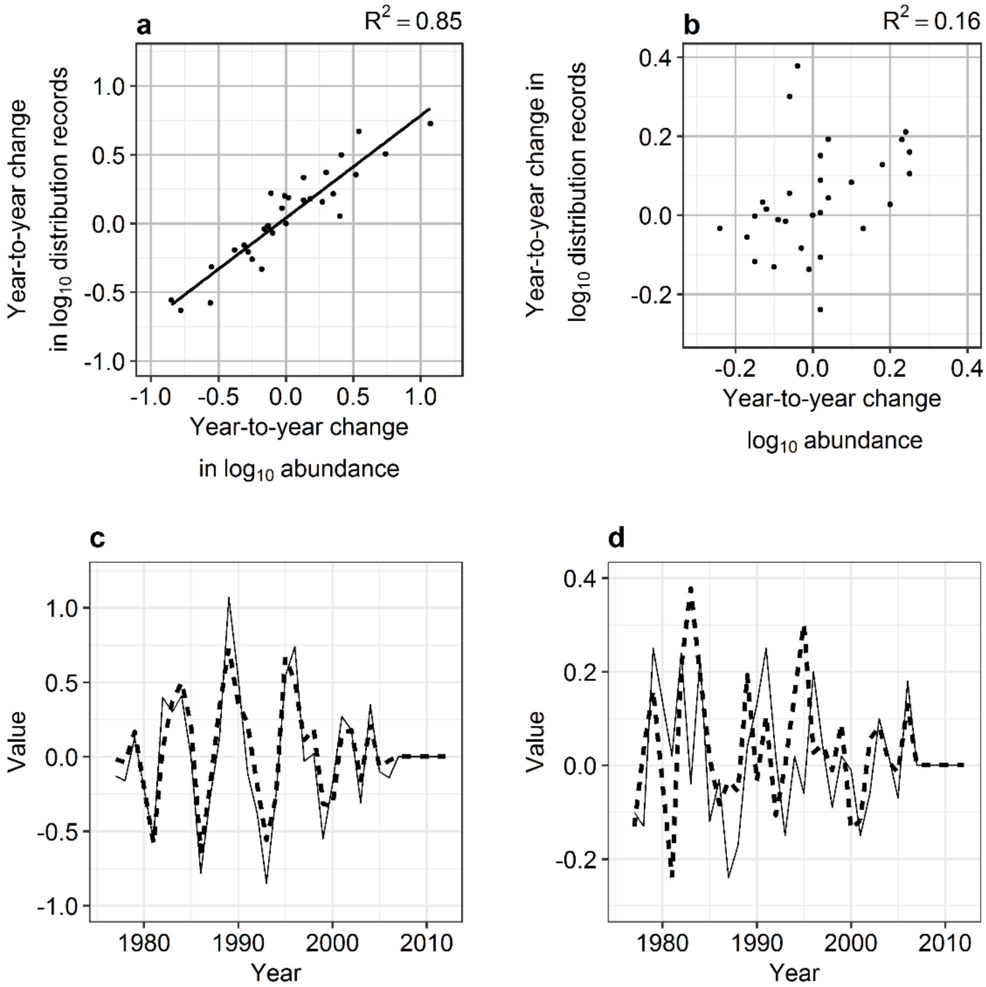

Figure 4.2. Inter-annual distribution-abundance relationships for two exemplar species. Plots show year-to-year changes in log_{10} distribution records and year-to-year change in log_{10} abundance for *Celastrina argiolus* (a, c; left panels) and *Melanargia galathea* (b, d; right panels). Panels a and b show regressions (each point represents the change between a given pair of years), and panels c and d plot the same data together in a time series (solid lines indicate year-to-year changes in log_{10} abundance, dashed line year-to-year changes in log_{10} distribution records).

4.4.3 Influence of biogeographical attributes

The R^2 value for each species' inter-annual distribution-abundance relationship (i.e. relationships between year-to year changes in log_{10} distribution records and year-to-year changes in log_{10} abundance; as in Figure 4.2) was then analysed in relation to the biogeographical attributes of each species, which are provided in Table 4.1. We tested all these variables in a full model (PGLS, λ = 0, R^2 = 0.64, $F_{4,28}$ = 12.58, AIC = -30.43, P = <0.001; Table 4.2a). Only mean absolute year-to-year changes in distribution records and its quadratic term significantly influenced inter-annual distribution-abundance relationships: total number of distribution records and fractal dimension did not, and were consequently dropped during model simplification. The best and most parsimonious model (PGLS, λ = 0, R^2 = 0.63, $F_{2,30}$ = 26.02, AIC = -33.70, P = <0.001; Table 4.2b) revealed that the strength of the relationship (R^2 value) increased with overall variability in distribution records (Figure 4.3). Thus, the results show that species with greater fluctuations in distribution records over time had stronger inter-annual distribution-abundance relationships (although the effect of variability in records was non-linear and asymptoted at roughly 0.8; Figure 4.3). Two species (*Celastrina argiolus* and *Vanessa cardui*) potentially had strong effects on the analyses (Figure 4.3c), but excluding these two species did not alter our conclusions (Table A4.1).

Table 4.2a and 4.2b. The influence of species attributes on the goodness of fit (R^2 value) of the inter-annual distribution-abundance relationships, which is the response variable. Table 4.2a shows the first, full model with the following explanatory variables: mean absolute year- to-year change in distribution records, total number of species records, and fractal dimension. The model summary statistics were: $\lambda = 0$, $R^2 = 0.64$, $F_{4,28} = 12.58$, AIC = -30.43, P = <0.001. Table 4.2b shows the best model with only one explanatory variable: mean absolute year-to-year change in distribution records. Model summary statistics: $\lambda = 0$, $R^2 = 0.63$, $F_{2,30} = 26.02$, AIC = -33.70, P = <0.001. In both models, the quadratic term of the mean absolute year-to-year change in distribution records was included to account for the non-linear nature of the relationship, and model results with estimated λ were not significantly different from a model with λ set to 0 (Fig. 3).

Coefficients	Estimate	Std. Error	t value	P
a)				
Intercept	-0.333	0.193	-1.724	0.096
Mean year-to-year change in log_{10} distribution records	6.756	1.385	4.879	<0.001
Quadratic mean year-to-year change in log_{10} distribution records	-8.307	2.310	-3.597	0.001
Total number of species records	<0.001	<0.001	0.570	0.573
Fractal dimension	-0.025	0.290	-0.086	0.932
b)				
Intercept	-0.317	0.128	-2.481	0.019
Mean year-to-year change in log_{10} distribution records	6.701	1.351	4.961	<0.001
Quadratic mean year-to-year change in log_{10} distribution records	-8.214	2.250	-3.660	<0.001

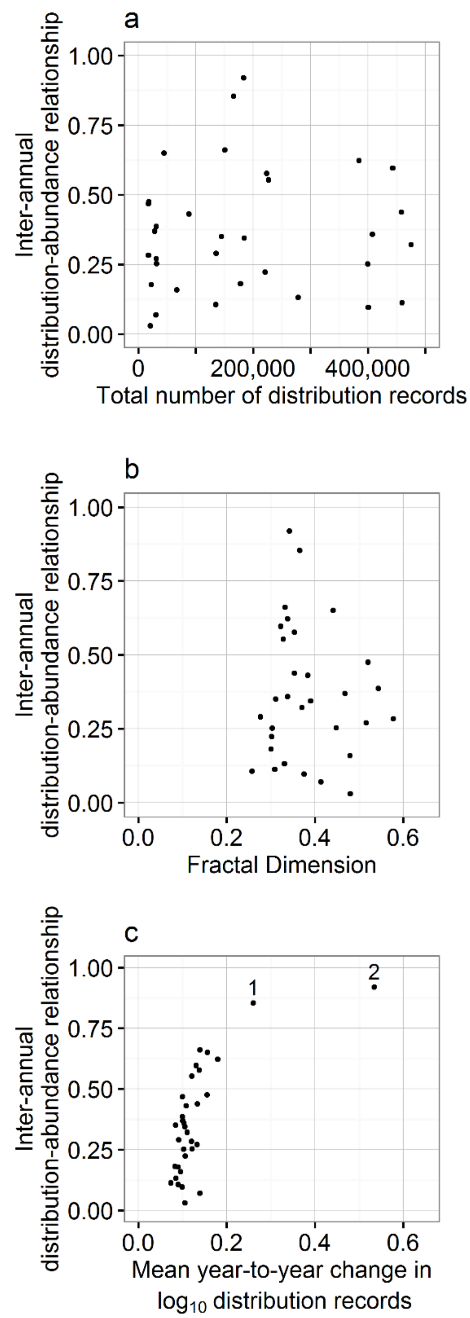

Figure 4.3. Inter-annual distribution-abundance relationship and three biogeographical attributes of the species: a) total number of distribution records (PGLS, $\lambda = 0.907$, $R^2 = <0.01$ $F_{1,31} = 0.09$, $P = 0.76$); b) fractal dimension (PGLS, $\lambda = 0.928$, $R^2 = 0.02$, $F_{1,31} = 0.61$, $P = 0.44$), and c) mean absolute year-to-year change in $\log_{10}$ distribution records (PGLS, $\lambda = 0$, $R^2 = 0.63$, $F_{2,30} = 26.02$, $P = <0.001$). Each dot represents a species; the numbered data points on panel (c) are *Celastrina argiolus* (1) and *Vanessa cardui* (2).

4.4.4 Comparison of national and regional inter-annual distribution-abundance relationships

The strength of inter-annual distribution-abundance relationships computed for species at a regional level (Dorset) were strongly positively correlated with those computed at the national level, PGLS, $\lambda = 0.562$, $R^2 = 0.53$, $F_{1,21} = 23.25$, $P = <0.001$; Figure 4.4). This is despite the fact that the average value of the inter-annual distribution-abundance relationships was higher at the national level (Mean, National = 0.41 Regional = 0.19; SD, National = 0.24 Regional = 0.24). Therefore, we conclude that any differences in population synchrony between national and regional scales had little influence on the strength of inter-annual distribution-abundance relationships for butterfly species.

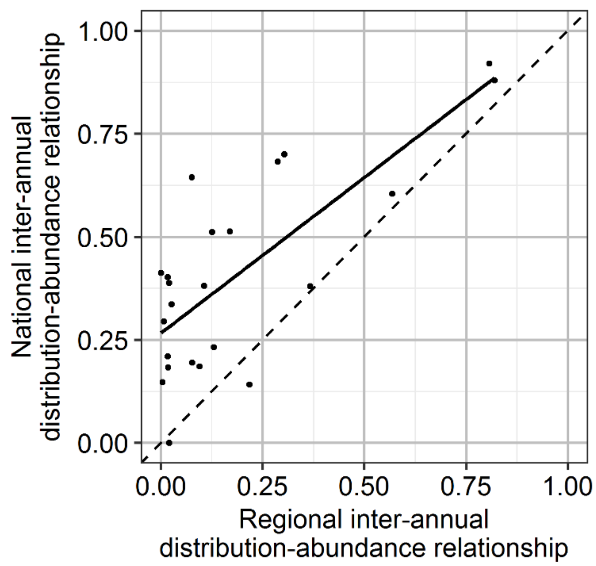

Figure 4.4. National inter-annual distribution-abundance relationship regressed against a regional inter-annual distribution-abundance relationship (region = county of Dorset) calculated for 23 butterfly species, indicated by the solid black line. The dashed line indicates the 1:1 line.

4.5 Discussion

We found that citizen-collected distribution data can be used to extract information about population variability, in the absence of bespoke abundance monitoring programmes. In particular, mean year-to-year changes in distribution records were positively related to mean year-to-year changes in abundance (with outlier species removed, R^2 value: 0.66; Figure 4.1). Thus, we were able to identify species with low and high between-year population variability quite accurately, using distribution data. This result supports the ability of unstructured citizen science data to reflect population-dynamic patterns found in long-term abundance data, and hence citizen science data may be useful in multi-species studies for which it is necessary have an overall measure of population variability (Robertson *et al.* 2015; Gandiwa *et al.* 2016) where abundance data are lacking. The ability to recognise species with the highest levels of population variability may help identify species that are at greatest risk of stochastic extinction following habitat fragmentation (Pimm, Jones & Diamond 1998; Vucetich *et al.* 2000; Oliver *et al.* 2012), and the most variable species may potentially be the most responsive to yearly variation in climatic conditions (Maclean *et al.* 2008; Howard *et al.* 2015) and to parasitoids or other natural enemies (Robertson *et al.* 2015). The findings from these analyses imply that information from citizen science data can provide useful input to landscape-scale conservation planning and to climate-change risk assessments.

When we considered each species in turn, there was considerable variation in the strength of relationships between year-to-year changes in distribution records and abundance among the study species; although these associations were always positive, averaging an R^2 of 0.36 across all species (Table 4.1). These relationships suggest that there is also some potential to use the distribution records of individual species to infer their population dynamics in greater detail (rather than as one metric for overall variability of the time-series). However, this is only feasible for some species: only eight out of 33 species having ‘strong’ relationships ($R^2 > 0.5$) between year-to-year abundance and distribution changes. Thus it should not be presumed that distribution records can be used as a substitute for population data in the assessment of inter-annual change for all species.

4.5.1 Inferring abundance change from distribution data

Many species are declining or facing range retractions (Hayhow *et al.* 2016), and it is important to monitor their population trends. Species with highly variable population dynamics tend to be at high risk of extinction (Pimm, Jones & Diamond 1998; Vucetich *et al.* 2000; Oliver *et al.* 2012) and thus our measure of variability in distribution records has ecological value, with the potential to assist conservation assessments by helping to identify species at risk of extinction or habitats in need of management (Meyer *et al.* 2015; Sánchez-Hernández, Cobo & Amundsen 2015). Our multi-species analysis (Figure 4.1) indicates that it is possible to derive robust estimates of population variability using distribution data alone.

Despite the promising results, there are two caveats that we should highlight. In this study, we examined only one taxonomic group with a high level of recording effort by citizen scientists. We also included only species with data in every year of the study period, excluding rare/less well-studied species. The value of other distribution datasets with lower recording effort may not be so informative. Kamp et al. (2016) found that reducing the number of distribution records resulted in poorer abundance trend estimates for Danish birds. Even without reducing the sample size, population trends were misclassified for 50% of the species they considered. Thus, using distribution data to infer population changes may require quite mature citizen science schemes, with substantial numbers of distribution records. Given that butterflies are a data-rich taxonomic group in the UK it is unknown whether other groups will have sufficient data to replicate these results. Datasets which may have sufficient data for this method are butterflies in other countries, or other taxa in the UK, for which standardised abundance monitoring schemes are lacking, e.g. dragonflies.

The second caveat is that more detailed population-dynamic interpretations of distribution data only seem possible for some species. Our finding that citizen science distribution data explain an average of only 34% of the year-to-year variation in abundance is unlikely to be sufficient to build meaningful models for examining the sensitivity of populations to environmental drivers, such as specific climate variables. For example, Malinowska *et al.* (2014) were unable to detect impacts of extreme weather events on populations of ectothermic species from distribution records, despite evidence of these impacts from population data (e.g. Oliver *et al.*, 2015b). In addition, while we have removed species which have unusually high levels of recording effort due to species-specific surveys, not all species are necessary reliably monitored by UKBMS, which could result in poor year-to-year distribution-abundance relationships. For example, the purple hairstreak butterfly (*Favonius quercus*) occurs in tree canopies, and is therefore difficult to monitor from ground-based surveys. Other species may suffer from limited recording for other reasons, such as occurring in restricted locations or not being identified correctly due to confusion with other morphologically similar species.

4.5.2 Biogeographical attributes

Despite the above caveats, we conclude that year-to-year changes in distribution records represented an adequate proxy for abundance change in species with large fluctuations in their occurrence from year to year (Figure 4.3, Table 4.1). Species with large year-to-year fluctuations in their occurrences, such as migrants, may offer the greatest statistical power to deduce population changes from distribution data. Even though two migrant species and the holly blue butterfly *Celastrina argiolus* demonstrate the strongest inter-annual distribution-abundance relationships, the mean year-to-year change in distribution records was also an important variable in predicting the strength of the year-to-year distribution-abundance relationship for other species. Therefore, mean year-to-year change in distribution records may help to identify non-butterfly species where citizen science distribution data could be used as a 'replacement' for direct population data. We found that total numbers of records and fractal dimension did not significantly influence the inter-annual distribution-abundance relationship. The most parsimonious explanation for this is that these variables are not important, and that our hypotheses, that the statistical capacity to detect year-to-year variation in abundance from distribution records was linked to the total number of distribution records, and fractal dimension, were wrong. We had predicted that a large total number of records would mean greater statistical power to find the inter-annual distribution-abundance relationship. The lack of a significant relationship between the inter-annual distribution-abundance relationship and total number of distribution records could be because patterns of year-to-year change in distribution records can be similar those in abundance even when numbers of observations are low. Recorder behaviour may have biased our results, as recorders may not record widespread common species on an ad hoc basis instead favouring notable records (e.g. rare species), this contrasts the abundance data that were collected following a structured survey design where all species seen are recorded. This could lead to mismatch in abundance and distribution patterns even for inter-annual changes, as recording effort varies temporally. Finally, the lowest total number of distribution records in this study was quite high (see Table 4.1), therefore the concerns with low sample size were not an issue here. However, the issue may be important to other more poorly recorded taxonomic groups.

Fractal dimension of species' distribution also did not impact the inter-annual distribution-abundance relationship. This might be because even if a range is fragmented, distribution recorders and transect volunteers still find and document species in those locations. In addition, if a species is known to be fragmented (which usually indicates rareness or being at risk of extinction), there may be a recording bias towards it (Isaac & Pocock 2015), which results in good information for that species. Therefore, species with a high fractal dimension may still have a positive inter-annual distribution-abundance relationship. However, it should be noted that species which are very poorly studied, and therefore likely rare and in fragmented habitats, were not been included due to the selection criteria. The study species also had ranges which were relatively well-filled, with fractal dimension scores ranging from 0.257 to 0.716 (maximum possible value is 2). It is possible that fractal dimension is an important factor for highly fragmented species, and there may have been insufficient variation in this attribute to be important to the inter-annual distribution-abundance relationship. Similarly we found no relationship between the inter-annual distribution-abundance relationship and dispersal for butterflies (Table A4.2). If these variables lack significant explanatory power even for a well-studied taxon, then this suggests that they will have limited use for identifying species in other taxa for which our method may be appropriate.

4.5.3 Population synchrony and inter-annual distribution-abundance relationships

The success of year-to-year changes in distribution records mirroring abundance changes in migratory species suggests that population synchrony over large areas may play a role, and so we examined the impact of scale on the inter-annual distribution-abundance relationship by comparing national and county-level analyses. Weak relationships at the national level may occur if species' population dynamics are asynchronous, such that abundances and distributions may be closely linked locally, but a 'good year' in one region might occur when it is a 'bad year' in another region, obscuring any overall pattern at a national scale. However, when we repeated the national-scale analysis for a much smaller region (the county of Dorset), the results were similar: goodness of fit scores across species for the inter-annual distribution-abundance relationship for Dorset were correlated with those for the same species at the national level (Figure 4.4). The majority of species had lower R^2 values for the regional analyses, probably due to reduced data quantity. The spatial scales at which abundance and distribution changes are linked deserve more attention, but our preliminary conclusion is that reducing the extent of the study region considered does not improve the inter-annual distribution-abundance relationship.

4.5.4 Conclusions

The key finding that (mean year-to-year changes in) citizen-collected distribution data can provide useful information on population variability suggests that it may be possible to expand these methods to other taxonomic groups, or to populations of butterflies in countries that do not have standardised population monitoring schemes. Such measures of variability can inform habitat, landscape and regional conservation decision-making. The use of distribution data for more detailed analyses of inter-annual population change is only likely to be possible, however, for species that have highly variable numbers of records between years. For these species, it may be possible to analyse year-to-year population changes across much longer time periods than are covered by transect data and hence identify how populations are influenced by the effects of specific weather variables, density dependence, and any other process that operates at a large geographic and temporal scale. Further investigation is required, however, in the feasibility of extending these methods to other taxonomic groups without abundance data (e.g. grasshoppers, dragonflies).

Chapter 5

General Discussion

5.1 Synthesis

The overall aim of my thesis was to explore species' responses to climate change, quantifying rates of range shifts for multiple taxonomic groups and testing the influence of species' attributes and landscapes on these shifts. I did this by utilising British species' occurrence records and land cover maps derived from satellite and cartographic data. My results demonstrated that species are, on average, shifting their ranges northwards, and habitat specialism and the availability of suitable habitats influences the rate of species' range expansion. Quantifying species' habitat availability can help conservationists determine appropriate actions to facilitate range shifts. In addition, I investigated the potential for distribution data to be used as a proxy for abundance patterns. Environmental changes affect species' populations, making it valuable to find ways to make deductions about changes to species' populations in circumstances when abundance data are lacking. I found that the mean year-to-year change in distribution records and the mean year-to-year change in abundance matched well across all species, suggesting that distribution records may be applied to ecological studies in place of abundance change metrics. Below, I briefly review the content and results of each of my chapters, before discussing my results and their implications for ecology, conservation and species monitoring.

Chapter 1 is a General Introduction to my thesis, and provides an overview of the impacts of climate change on biodiversity, explaining the need to understand how species are responding to climate change, and clarifying how citizen science data facilitate the exploration of patterns in species' range shifts.

In **Chapter 2**, I investigated the variation in rates of range shifting among 21 taxa, using citizen science data to measure changes in northern leading-edge range boundaries from 1966 to 2010. For the analyses, I examined range shifts across two intervals: interval 1 was 1966 to 1995, and interval 2 was 1986 to 2010. In this chapter, I investigated variation in range shifting rates among taxa and over time. I found that taxonomic groups studied experienced a mean northwards range shift of 24 km decade^{-1} over interval 1 (13 taxa), and 18 km decade^{-1} over interval 2 (16 taxa). At least half of the taxonomic groups studied underwent significant northwards shifts for at least one level of recording effort. The different levels of recorder effort were: 'recorded', for which range shift calculations incorporated data for all cells where at least one species was recorded in both time periods of one interval; 'well recorded', which included all cells where at least 10% of a regional species richness was recorded in both time periods; and 'heavily recorded', with cells including 25% of a regional species richness. There were significant differences in rates of range shifting among taxonomic groups at every level of recording effort ($P<0.05$), and confidence intervals indicate high levels of variation in range shifts within groups. I also investigated changes in the rate of range shift over time for four taxa (dragonflies and damselflies, birds, butterflies and macromoths), and found that the Lepidoptera appeared to have accelerated their range expansions over interval 2. I concluded that species are responding to environmental change through range shifts, that there is variation in rates of shift within and between taxa, and that these rates may not be constant over time.

In **Chapter 3**, I tested the influence of habitat and traits on rates of range shifting for 347 species (from 14 taxa) over four decades (1976-1990 to 2001-2015). I investigated the relative importance of habitat specialism (a single score indicating how strongly a species was associated with 18 habitat classes) and habitat availability (the probability of species being observed in those habitats) on range shift, measured as the distance in kilometres that a species' northern range margin moved per year. I used species-specific values for all metrics. Using linear regression, I found that there appears to be more variation in range shifts among species within taxonomic groups (91%) than between taxonomic groups (9%). I tested the hypothesis that habitat availability provides a stronger explanation for the observed variation in species' range shifts, compared to specialisation. Both specialism (4%) and habitat availability (17%) significantly explained variation in rates of range shifting (linear mixed-effects model, $P<0.01$). Next, I included an interaction term in my linear model that compared habitat availability across the whole range with availability at the northern margin for each species. Those species with less habitat availability at the margin were less likely to shift their northern range margins polewards. The amount of variation explained by the covariates depended on the level of recording effort (defined as the number of heavily recorded grid cells, as described in Chapter 2 and above). For well-recorded groups, covariates explained 36% of variation in rates of range shifting. If all 2566 hectads in the study region had been heavily recorded for all taxa groups, I estimated that the influence of habitat and traits could explain up to half of the variation in species' range shifts. I concluded that variation in species' range shifts is driven substantially by the habitat availability of species, which is the interplay between species' level of specialisation, the types of habitats species are specialised to, and the accessibility of habitat within the landscape. By increasing connectivity and the amount of habitat in the landscape for species with low habitat availability, conservationists can facilitate range expansions that may not otherwise occur (see 'Conservation Management' section below).

In **Chapter 4**, I examined the potential of distribution data to act as a proxy for changes in species' abundance. Using 33 British butterflies in both between- and within-species analyses, I explored whether there were relationships between inter-annual changes in abundance and inter-annual changes in distribution records. A multi-species analysis demonstrated that the relationship between mean year-to-year changes in abundance and mean year-to-year changes in numbers of distribution records was positive and strong (PGLS, R^2= 0.95, $F_{1,31}$ = 623.8, P = <0.001). This relationship was maintained when two outlier species were removed from the analysis (PGLS, R^2= 0.66, $F_{1,29}$ = 55.35, P = <0.001). Next, I performed a species-specific analysis of the relationship between year-to-year changes in abundance and year-to-year changes in distribution records. My findings demonstrated that the strength of the relationship varied among species (min R^2= 0.03 for *Boloria selene*, max R^2= 0.92 for *Vanessa cardui*, mean R^2= 0.36), implying that using distribution data to monitor inter-annual population changes is limited to certain types of species. I investigated species-specific biogeography attributes that could explain variation in R^2 values. I found that species that had large mean year-to-year changes in distribution records showed strong inter-annual abundance-distribution relationships (R^2 >0.5). In other words, it is feasible to use year-to-year changes in distribution records to estimate abundance changes for species such as *Vanessa cardui* and *Celastrina argiolus*, which have high levels of inter-annual population variability. I concluded that distribution records have potential to be used to measure population variability and long-term changes in year-to-year abundance.

In my data chapters, I found that variation in species' range shifts is influenced by the species' traits and habitat availability. However, much of this variation remains unexplained. I also found that distribution data has potential to be used as a proxy for abundance patterns, which is important because abundance data is lacking for many species. In the remainder of this chapter, I discuss the implications of these findings, their relationship to the wider literature, constraints of my studies and future opportunities for research. I then discuss the overall contribution of my findings for conservation of species under climate change, the future for citizen science recording schemes, and my final conclusions.

5.2 Exploring variation in range shifts

The results indicate that many species from a wide variety of taxonomic groups are shifting the leading-edges of their ranges polewards in response to climate change. This finding provides further evidence to support the evidence in the current literature, which shows species are shifting polewards (Parmesan & Yohe, 2003; Chen *et al.*, 2011a; Lenoir & Svenning, 2015). I quantified variation in range shifts within and between taxonomic groups in this thesis, and I discuss this below.

One of my primary goals was to explore variation in range shifts within and between taxonomic groups, and I found that, while there are significant differences in mean range shifts among different taxonomic groups (Chapter 2), linear regressions revealed that there is more variation within groups than between groups (Chapter 3). This is new evidence; previous studies that have assessed rates of range shifting have not previously analysed this variation. Chen *et al.* (2011a) examined rates of shift between different taxonomic groups and concluded that groups showed similar averages, but contained species with variable rates of range shift, and did not explicitly test variation within- and between-groups. My findings indicate that closely-related species within a single taxon may not necessarily have similar responses to climate change. In an ecological context, this conclusion is perhaps unsurprising as single taxonomic groups contain species with a variety of niches, life histories, reproductive strategies, habitat specialisations, and climate sensitivities, and therefore would be expected to vary in their rates of range shift. My results indicate that species within taxonomic groups should be investigated individually to quantify specific responses to climate change. Variation in range shift within taxonomic groups may be driven by a few species, where most species are responding in a similar manner, but a few make large retractions or expansions, which has been observed in grasshoppers and crickets (Beckmann *et al.*, 2015). Therefore, average range shifts should be taken as general observations about groups of species, and these average shifts may not be indicative of rates of individual species' range shifts.

Another discovery of my research is that some taxonomic groups appear to be increasing their rates of range shifting over time. For example, butterflies and macromoths shifted their northern range margins faster in interval 2, compared to interval 1 (Chapter 2). Past changes in rates of range shift have been measured over coarse spatial and temporal scales (Jackson *et al.*, 2000; Davis & Shaw, 2001), and few studies have considered changes in rates of range shifts over recent time scales. One example is the work of Mair *et al.* (2012), who measured range shifts in British butterflies from 1970 to 2009. They noted that species had faster rates of shifting in the second time interval (1.29 km yr^{-1} on average; 1995-1999 to 2005-2009) than the first (-0.17 km yr^{-1} on average, 1970-1982 to 1995-1999), despite a smaller increase in warming in the second time period (0.03 °C yr^{-1} vs. 0.01 °C yr^{-1}). In my study, I did not observe a statistically significant change in mean annual temperature between intervals. It is possible that the statistically significant increase in autumn (September, October, November) temperatures over interval 2 (0.46 °C $decade^{-1}$) contributed to increases in rates of range shift in Lepidoptera, given that this was when most warming was detected (Chapter 2, Figure 2.4, Table A2.6). Warm autumn temperatures may delay insect diapause, allowing individuals to remain active for longer periods, potentially dispersing further. However, in spite of the many ecological processes that occur in autumn, the impacts of changing autumn temperatures on species is relatively unknown (Gallinat *et al.*, 2015), and warrants further study.

In Chapters 2 and 3, I examined rates of range shift and found that while the majority of species are shifting northward, some species have not shifted far or have retracted their ranges southwards (e.g. 20% of species' range margins retracted southwards in Chapter 3). This is consistent with other studies; slower rates or lags in response to climate change have been noted in a variety of taxa including birds (Devictor *et al.*, 2008), fish (Comte & Grenouillet, 2013) and butterflies (Devictor *et al.*, 2012). Invertebrates, which most of my study species were, tend to have rapid generation times and high fecundities, giving them an advantage in tracking climate change. However, some invertebrate species may be delayed in responding immediately to climate change due to limited dispersal capabilities, or there may be physical barriers such as mountains or coastlines, or regions of intensive agriculture, that prevent them from doing so (Parmesan & Yohe, 2003). Retractions at leading-edge range margins are a result of local extinctions, and for warm-adapted species in the UK, indicate that unfavourable climatic conditions (Thomas *et al.*, 2006) or other, non-climatic factors such as habitat loss are probably influencing species occupancy of these sites. Habitat, species' traits, climate and biotic interactions have all been suggested as being important to range shifts, and hence I discuss them in the following sections.

5.3 Habitat and trait drivers of range shift variation

In Chapter 3, I found that habitat availability, which arises from the interplay with species' attributes and the environment, affected rates of range shifting in multiple taxonomic groups. Whilst habitat is commonly assumed to be important to species' range shifts, this idea is rarely directly tested among different taxa, and those tests that do exist often use methodological simplification, such as expert opinion (Warren *et al.*, 2001). One of my key findings was that species' attributes (habitat specialism) did not explain much variation in range shifting when studied alone (only ~4% across 347 species). In contrast, but when habitat associations were combined with a landscape context (i.e. the amount and distribution of suitable habitat), the explanatory power was much higher (up to 36%, and as much as 49% under an assumption of extensive recording). Thus, I conclude that whilst species' attributes may be influential to rates of range shift, it is the context of the landscape where species are found that determines the impacts of species' traits on range shifting, as species can only utilise habitat that is accessible to them. These results are of general importance, both for the fundamental ecological understanding of species' range dynamics, and to identify effective habitat management and restoration strategies, which can facilitate range expansions of species for which habitat availability is limiting (for example, Great Crested Newts experiencing southwards retractions, which is likely caused by the absence of suitable breeding ponds, see Rannap et al., 2009). In this next section, I discuss the impacts of habitat availability and species' traits on variation in range shifting, and then discuss other potential drivers of variation in range shifting in the next section.

The impacts of species' traits on rates of range shifting have been investigated many times in recent years. In a key study, Angert *et al.* (2011) tested the influence of different species' traits (e.g. dispersal rates, physiology and habitat specialism) on rates of range shifting for four taxonomic groups (mammals, birds, dragonflies and alpine plants). They found only weak associations between traits and rates of shift, with only 3-6% of range shift variation explained by traits. Because there are many species' attributes, and different methods to measure them, understanding the role of species' characteristics on range shifts is not a simple task. MacLean & Beissinger (2017) published a recent review and meta-analysis of trait studies across multiple taxa, including more species than Angert *et al.*, and analysed the effect sizes of different traits on variation in range shifts. Habitat breadth (the number of habitats a species occupies) in some studies had significant positive impacts, so that generalists moved further than specialists. However, an important point noted by these authors is that effect sizes of habitat specificity varied across studies, and they suggested that this may be due to differences in the methods used to calculate specialism metrics. Coverage and quantity of data available may also contribute to differences in trait effect sizes, as my findings in Chapter 3 indicated that recording effort influenced the amount of variation explained by my models. While habitat specialism does appear to be important does appear to be an important influence on range shifts, many traits remain untested or have insufficient evidence to determine whether they impact range expansion (MacLean & Beissinger, 2017).

As part of my analysis on the influence of habitat availability on species' rates of range expansion, I used a metric which assessed specialism based on a species distribution modelling (SDM) approach (Julliard *et al.*, 2006). By using a logistic regression with a detailed, fine-scaled land cover map and long-term species presence data, I determined the likelihood of species' presences in different habitats. The species' specialism index (SSI) was the coefficient of variation calculated from these likelihoods. This methodology for quantifying habitat associations of species can potentially be applied to any species that has sufficient occurrence data (at least 50 occurrence records found in 100m cells containing one land use or habitat type), and where habitat data are present. Previous methods of measuring habitat specialisation of species have relied on expert opinion (Reif *et al.*, 2010), or on creating composite scores of ecological values (Oliver *et al.*, 2009), or on counting the number of habitats where a species is present (MacLean & Beissinger, 2017). Measuring habitat specificity objectively is difficult and many methods of calculation do not allow ecologists to compare across different taxa (Lawton, 1993; McGeoch & Latombe, 2016). The method I use addresses some of these issues, by providing a way of investigating species' habitat associations that is quantitative, comparable across taxa, and does not require in-depth ecological knowledge of species.

In my investigation on the impacts of habitat availability on range shift, I found that habitat availability at the northern range margin (relative to the whole range) had a significant effect on rates of range shift. In the UK, the quantity of upland and montane habitat increases with latitude, and southern species that are specialised to lowland habitats may be less likely to have as much suitable habitat in the north of the country. Habitat generalists, utilising many habitats, and habitat specialists, that utilise montane and upland habitat, will be able to expand through these areas (excepting any non-habitat barriers). Therefore, habitat availability at the leading-edge margin, as determined by species' specialism, may be a critical barrier to British species' ability to track climate and expand their ranges. This has implications for conservation efforts, which can implement techniques to assist species to overcome problems caused by low habitat availability, which I discuss further below in Section 5.4.

5.4 Climate change and other drivers of range shifting

Habitat and species' specialism explained up to 36% of variation in range shifts (Chapter 3), yet much of the variation in rates of range shifting remained unexplained. Range shifts were examined as a response to climate change, however the degree to which climate drives variation in range shifts for multiple taxonomic groups (as opposed to other drivers such as habitat and species' traits) is largely unknown. A lack of abundance data or detailed understanding of population trends for most species meant that investigating species' sensitivity to climate, as a driver of range shift variation, was not possible in my thesis. I found that range shifts, as well as habitat specialism and availability, are species-specific. This implies that the degree to which climate impacts species' rates of range shift may also be individualistic, an idea which is supported in the literature (Davis and Shaw, 2001, Parmesan *et al.* 2006), who suggest that past and present range shifts may be linked to species' climatic tolerances. The majority of studies focus on single dimensions of climate i.e. mean temperature changes, although species are likely to respond to several different aspects of the climate, such as rainfall and seasonal temperatures. Variability and declines in species' populations as a response to climatic extremes have also been shown to be highly individualistic (Palmer *et al.*, 2017), which is why proxy metrics for population variability would be beneficial to ecologists wishing to assess species' status under climate change. I discuss my attempts to produce a proxy measure of abundance changes below (section 5.6.1)

Because different environmental processes impact species' responses to climate change, there is much uncertainty around the extent to which these factors interact. Many biotic factors influence range shifts, such as interspecific competition, population dynamics and predation (Van der Putten *et al.*, 2010). Mair *et al.* (2014) found that the importance of habitat availability (measured as the proportion of a butterfly's breeding habitat in the landscape) was moderated by species' population trends. Population growth was a key predictor of range margin shift, because stable and increasing population produce individuals which can disperse and establish further populations. This suggests that habitat creation and restoration to improve availability will not help declining species unless these conservation practices also have positive effects on population trends. Abundance trend data were not available for most of my study species, and so I could not test the importance of population trends on range shifting in my study, but further research could investigate whether habitat availability as measured in this thesis also interacts with abundance to influence range expansion.

5.5 Conservation management

Under climate change, species may respond to altered environmental conditions by exhibiting phenotypic plasticity, adapting *in situ*, moving to environments that are more suitable, or by going extinct. My findings suggest that while some species are able to shift their ranges to track climate change, other species are shifting their ranges at a slower rate or not at all. The failure of species to shift their ranges in response to environmental change may result in local or, eventually, global extinction. Therefore, conservation strategies can be implemented to facilitate range shifting for these at-risk species. Several techniques are available to do this, by tackling different constraints that limit dispersal and the colonisation of new habitats. These include the role of protected areas, habitat connectivity, and human movement of species (through reintroductions and translocations). I will introduce each of these techniques and their advantages and disadvantages.

5.5.1 Protected areas and connectivity

This thesis demonstrates that habitat availability is important for species' range shifts, and so conservation could aim to maintain the quantity and quality of suitable habitat, which will act to both provide breeding habitats for species to establish populations, and suitable habitats which will help species move through landscapes (Thomas & Gillingham, 2015). Protected areas (PAs) are a longstanding method for conserving species where a specific area of land is afforded special status, forbidding certain human activities in it and/or promoting beneficial management. Over 18% of land in the European Union is protected under the Natura 2000 network (European Environment Agency, 2015), and the UK has many types of PA, depending on the conservation need. These areas are designated by governmental and public bodies, and include National Nature Reserves, Sites of Special Scientific Interest, and Special Areas of Conservation.

As species are shifting their ranges under climate change, there has been concern that species currently protected by PAs, would shift outside of these regions, reducing conservation protection of vulnerable species and therefore the conservation value of PAs. Thomas and Gillingham (2015) reviewed the impacts of protected areas for species under climate change and found that while some species shifted their ranges out of protected areas, others persisted or colonised PAs as they shifted polewards. Thus, one benefit of PAs is that they may act as breeding sites for colonising species, and hence help facilitate range shifts (Thomas *et al.*, 2012). PAs have also been referred to as 'landing mats' and 'stepping stones' due to their role in allowing species to establish populations and move polewards beyond PA borders (Thomas & Gillingham, 2015). In addition, PAs support retracting species, which have showed increased persistence within protected regions (Gillingham *et al.*, 2015). PAs benefit species and their range shifts by maintaining the amount of available habitat in the landscape through management and protection, and conservation efforts should maintain these areas for species.

Protected areas can also provide connectivity benefits, which are key management strategies for facilitating species' range shifts (Saura *et al.*, 2014). As the climate changes, functional connectivity is important for many southern species in the UK, so they can disperse across landscapes and colonise climatically-suitable habitats. Enhancing habitat connectivity is done through the (re)creation and maintenance of new or existing habitat. Computer modelling studies have been used to assess how species will move through landscapes (Hodgson *et al.*, 2012), identifying colonisation routes through different landscape structures (Hodgson *et al.*, 2016a) and suitable sites to create and restore habitats. Being able to identify how species move through landscapes, and therefore which habitat patches, corridors and conservation techniques are associated with high levels of dispersal and range expansion is a vital tool for conservationists to implement evidence-based management for range shifting species (Baguette *et al.*, 2013). Connectivity measures can be variable in their success, for example, wildlife road tunnels, designed to allow species such as great crested newt (*Triturus cristatus*) to transverse underneath, are often not utilised by individuals (Matos et al., 2017). These results suggest that careful monitoring is required to check the success rate of connectivity measures, with reassessment of conservation strategies based on the latest evidence.

5.5.2 Reintroductions and translocations

My results demonstrate that species with less habitat availability at their northern range margins will be less likely to shift northwards into newly climatically suitable areas. Creating new habitat or linking habitats together is not always feasible, and so conservationists transport species to new areas, bypassing barriers to species' dispersal that prevent re-colonisations. Reintroduction is the practice of moving individuals of a species to establish a new population, in a location where the species was previously present but became locally extinct. Translocation involves the same actions, but species are moved to locations where they are not know to have existed previously, but where conditions are now suitable.

Reintroductions are undertaken in order to rebuild populations where they are known to have been established in the past. The motivations for doing so may be to protect species from extinction, return ecosystems to a 'traditional' state, or to reap ecosystem service benefits from the reintroduction. A case study is the reintroduction of the large blue butterfly (*Maculinea arion*) to England, after total extinction in the UK in 1979 (Thomas, 1995). The large blue is an endangered species, with a globally declining population. The extinction of this species in Britain is thought to have been driven by changes in agricultural practises, coupled with specific needs to support a complex life cycle. Reintroductions have taken place at several locations, and the butterfly has been successfully re-established in England, 33 years after the first reintroduction in 1984. This example demonstrates that reintroductions can benefit endangered species that have become locally extinct. However, if climate change makes an environment unsuitable for a species, then there is no logic in reintroduction (Seddon, 2010), as re-establishment sites must meet the species' requirements for long-term persistence. Conservationists must consider not only how suitable a potential habitat is now, but also how suitable it will be in the future as the climate continues to change. In 2013, the IUCN released guidelines on releasing species to indigenous and non-indigenous habitats, emphasising that for reintroductions, the causes of extinction must be removed or sufficiently reduced before any action is taken (IUCN/SSC, 2013). This is why translocations should be preferred in cases where climate-driven extinctions occur (Thomas, 2011): species can be moved outside their indigenous ranges, and ecosystems which lose species of important functional groups can acquire different non-indigenous species which fulfil those roles. Certain types of habitat are becoming climatically unsuitable for the species which traditionally dwelt there, such as montane habitat (Hoegh-Guldberg *et al.*, 2008). Species have been noted to shift to higher elevations under climate change (Hickling *et al.*, 2006; Chen *et al.*, 2011b), and translocations to higher regions outside of species' indigenous ranges (if possible) may be the only option for conservation beyond committing species to extinction. Translocations can assist species that have barriers to dispersal (e.g. physical barriers such as mountains, or threats to population growth such as disease, competition or predation) and are restricted to isolated habitats. Where habitat has become unsuitable, careful management and restoration can make conditions suitable for reintroductions. In order to help species respond to climate change, these activities are likely to become a vital part of conservation management.

Human movement of species has many benefits but it also comes with risks. Dealing with the logistics of capturing individuals, moving them, monitoring their progress, costs time and money, and can have legal constraints, especially if these actions occur over country borders (Hoegh-Guldberg *et al.*, 2008). Many introduction attempts fail, which can reduce species' populations; all such projects require careful planning and management (IUCN/SSC, 2013). When species are introduced to new areas, there is always uncertainty of how species will fit in the pre-existing ecological networks. A famously disastrous example is the release of the cane toad *Bufo marinus* into Australia to act as biocontrol for beetles that fed upon sugar cane crops, whereupon the toads became invasive pests. To prevent similar problems occurring, conservation actions that involve moving species must be carefully planned.

To summarise, there are effective conservation strategies available to assist species under climate change. Conservation management practices tend to be undertaken by conservation charities or government agencies which either target taxonomic groups (e.g. in the UK the charity Butterfly Conservation) or geographic areas (e.g. National Park Authorities and Wildlife Trusts). These groups need to manage habitats to support the general ecological requirements of species according to their rates of range shift, helping maintain breeding habitats to support populations, improving connectivity to facilitate range expansions, and moving species to establish populations in suitable locations when necessary and appropriate.

5.6 Recording species: applications and future prospects

Throughout this thesis, I stress the importance of measuring biogeographical responses to climate change across multiple taxonomic groups. My results endorse the value of citizen science data for measuring these responses, using these data to estimate range shifting rates, and factors affecting range shifts, including habitat availability. Data derived from citizen science schemes can address many ecological questions. In this thesis, I have focussed on occurrence data from citizen science schemes, but other sorts of data can be derived from voluntary mass participation activities such as Zooniverse, where members of the public extract scientific information from images, e.g. population sizes from pictures of penguin colonies (Simpson *et al.*, 2014). Here I discuss how I have used occurrence records to estimate population trends and my thoughts on the future of recording for ecological research.

5.6.1 Measuring population variability

In my thesis, I decided to take a different approach in Chapter 4, and explored the potential for distribution data to act as a proxy for abundance data, as abundance is a valuable metric that can be used to measure species' responses to environmental change. By doing this, I provided new evidence that population variability information could be obtained from distribution data for some British butterfly species, particularly species with highly-fluctuating populations. Inter-annual fluctuations in population are often linked to weather variation, with climate change causing positive or negative impacts depending on species' climatic tolerances. Martay *et al.* (2016) used inter-annual variation in abundance to assess the impacts of climate change on mammal, bird, aphid, and Lepidoptera species, and concluded that climate change is causing population declines in many species, while promoting increase in other species. McCain *et al.* (2016) carried out simulations to test the impacts of population variability on estimates of population trends and range shifts. They found that when abundances were low, but highly variable, there was a 50% chance of detecting local extinctions where none occurred, and moderate to high variability in abundance produced a bias towards detecting false range expansions and contractions. This means that population variability influences detections of range shifts and other responses to climate change. To accurately measure these responses, ecologists need to develop methods to estimate these abundance patterns for species without detailed population data.

There are several avenues for further research after my exploration of a potential abundance proxy; firstly, whether other groups with abundance data (macromoths and birds) demonstrate similar relationships between abundance and distribution metrics, as my research as only examined butterflies. The second question would be whether this abundance and distribution relationship is observed in other groups, most of which have no abundance data. This is an interesting and important question because taxonomic groups that are lacking in detailed abundance information would benefit most from an accurate proxy metric, providing new data on how the populations of those species change and respond to changes in their environment, particularly climate change. To explore this question, I would investigate the how reducing the level of recording intensity would impact the relationship between year-to-year changes in abundance and numbers of distribution records. My study was focussed on a taxonomic group (butterflies) with widespread intensive recording effort, however this level of recording effort is not common across all taxonomic groups (Chapter 2, Figure 2.2). Using the butterfly distribution data, subsampling methods would be applied to test how recording intensity (and variation in recording effort in time and space) affects the capability of occurrence records to measure population variability. These additional investigations further explore the potential for citizen science data to provide metrics of population dynamics.

5.6.2 Future of recording

As the trajectory of climate change and habitat loss, and consequently their impacts, are set to continue (Frishkoff *et al.*, 2016), and ecologists should explore methods for encouraging widespread species monitoring, to provide data to examine these impacts. One of the main concerns for recording species' responses to climate change is encouraging the monitoring of a wide array of species, so that ecologists can observe responses in different types of species in different environments. While I have demonstrated the heterogeneity of responses across multiple species and groups in this thesis, the majority of species that are included belong to invertebrate families. Invertebrates are only one part of biodiversity, though a large one. It is important that other taxa such as mammals, fish, plants, fungi and others are studied to examine how these species are responding to climate change. Some groups are not included in this thesis because I focused upon groups with the best data availability. For example, Hickling *et al.* (2006) included fish in their analyses, but data from this scheme were insufficient for my study. The National Amphibian and Reptile Recording Scheme (NARRS) has experienced a decline in recording effort in recent years, although work has been done to engage more volunteers in herptile recording activities. It is important that schemes are maintained because many taxonomic groups suffer from a recording deficit. Groups like bryophytes, fungi and reptiles each contribute roughly 1% to the Global Biodiversity Information Facility (GBIF) records dataset, whereas birds make up over 50% (Chandler *et al.*, 2017). These numbers do not reflect the true global biodiversity of these groups, of which bryophytes (0.0008%), reptiles (0.0004%), and birds (0.0005%) comprise only a small proportion, and fungi contain a larger share (5.2%, all percentages calculated from Chapman, 2009). To get a full picture of ecosystem-wide responses to climate change, we need to encourage recording of species across the tree of life, and one of the problems that ecologists face is how to encourage recording of cryptic and uncharismatic species, which may be of ecological importance.

Species monitoring benefits from new technologies, as many improvements are made to assist and speed up the recording process. This includes apps that help the identification of species, geolocation on smart devices which pinpoint the location to fine-scale accuracy, and internet connections which allows instant submission of records. Apps also allow rapid responses to the detection of invasive species, for example, the Asian Hornet Watch app was created in response to a sighting of an Asian hornet in Gloucestershire in 2015, to help people distinguish between European and Asian hornets. The iGrasshopper app uses acoustic identification to detect species by their calls, with no visual identification required. eDNA and barcoding techniques can be used to classify species by their genetic material. Drones flying on fixed routes can survey sites for species (Hodgson *et al.*, 2016b), and this has been accomplished for bat surveys in Oxfordshire. Hence spatial and temporal coverage of species records has greatly increased, improving ecologists’ ability to monitor species and their responses to climate change.

5.7 Conclusion

By examining species' responses to climate change, my study has highlighted the variation in range shifts that is present within and between taxonomic groups. For the first time, within and between group variation has been compared and my findings demonstrate that differences in range shifts are larger within taxonomic groups than between groups, supporting previous work which has inferred this result (Chen *et al.*, 2011a). While the causes of this variation are uncertain, my research points to a substantial proportion (up to a third) being explained by species' traits that affect habitat use and habitat availability. My findings have broad implications for conservation management, which can identify species that cannot access suitable habitats, and take steps to facilitate range expansion or support population sizes. My investigations were only possible due to the enormous amount of data held in citizen science schemes, and in this thesis I also demonstrated how occurrence records derived from such schemes have the potential to show patterns of population variability where abundance data are lacking. The creation and maintenance of these schemes should be encouraged, so that a greater variety of species' responses to climate change can be explored in future.

Appendix Chapter 2

In Chapter 2's appendices, group names with asterisks (*) indicate that those groups contain allied species, i.e. species which are phylogenetically related, such as dragonflies and damselflies.

Table A2.1. List of taxonomic groups considered for analysis: the number of species (not all of which qualify for analysis) and observations (records) across all time periods for all species for each taxonomic group that was analysed. Taxonomic groups were either accepted or rejected for analysis in interval 1, interval 2 or over both intervals according to whether they met the selection criteria (see methods in main text).

Taxonomic group	Number of species	Number of observations	Interval 1	Interval 2	Both intervals
Birds	243	~ 2,000,000	Accepted	Accepted	Accepted
Butterflies	59	5225574	Accepted	Accepted	Accepted
Dragonflies*	53	523899	Accepted	Accepted	Accepted
Macromoths	831	10454592	Accepted	Accepted	Accepted
Grasshoppers*	68	102088	Accepted	Accepted	Rejected
Hoverflies	268	542823	Accepted	Accepted	Rejected
Ladybirds	53	112481	Accepted	Accepted	Rejected
Woodlice	47	133413	Accepted	Accepted	Rejected
Centipedes	55	40757	Accepted	Accepted	Rejected
Harvestmen	25	20109	Accepted	Rejected	Rejected
Herptiles	16	38511	Accepted	Rejected	Rejected
Millipedes	60	42203	Accepted	Rejected	Rejected
Spiders	602	339375	Accepted	Rejected	Rejected
Ants	50	33398	Rejected	Accepted	Rejected
Aquatic bugs	92	77811	Rejected	Accepted	Rejected
Bees	235	278431	Rejected	Accepted	Rejected
Caddisflies	26	32245	Rejected	Accepted	Rejected
Ground beetles	356	189104	Rejected	Accepted	Rejected
Shieldbugs	64	24359	Rejected	Accepted	Rejected
Soldierflies*	152	57259	Rejected	Accepted	Rejected
Wasps	213	103398	Rejected	Accepted	Rejected

Groups rejected from all analyses were: auchenorrhyncha, click beetles, craneflies, fleas, gelechiid moths, jewelled beetles, lacewings, long horned beetles, mayflies, non-marine molluscs, plantbugs and allies, plume moths, predaceous diving beetles, soldier beetles*, ticks, and water scavenger beetles

Table A2.2. Overall mean rate of range margin changes (and SEs) across taxonomic groups, calculated for interval 1 and interval 2, and for each level of recording effort control. Means were calculated by taking the average of the mean rate of range margin change of all taxonomic groups included. With the number of groups is the number of those (in parentheses) which are significantly expanding northwards (see Table A2.3). Total numbers of species included in each estimate are shown. The ANOVAs compare mean rate of range margin changes across the groups, for each level of recording effort control in each interval; significant results indicate that taxonomic groups differ in northwards range shifts.

Summary statistics of overall rate of northern range margin shifts, averaged across taxonomic groups						Test of whether taxonomic groups differ from one another in range shift rates		
Interval	Recording effort control	Mean northwards range shift (km decade^{-1})	Standard error	Number of taxonomic groups	Number of species	F statistic	df	p value
1	Recorded	34.1	7.3	13 (10)	975	46.81	12, 962	<0.001
1	Well recorded	24.1	5.5	13 (8)	573	4.41	12, 560	<0.001
1	Heavily recorded	12.8	5.8	7 (3)	260	2.20	6, 253	0.043
2	Recorded	13.1	6.2	16 (6)	1231	26.04	15, 1215	<0.001
2	Well recorded	18.0	4.0	16 (6)	884	9.64	15, 868	<0.001
2	Heavily recorded	17.1	4.0	8 (4)	428	2.58	7, 420	0.013

Table A2.3. Summary table and statistics for Figure 3: mean rate of range shift and 95% confidence interval (CI) for each taxonomic group, for each interval, and for each level of recording effort. Numbers of hectads (No. hectads), the number of species per group (No. spp), and results of one-sample t-tests to assess whether shifts for each group differ from zero (significant p values in bold) are also given.

Group	Level of recording effort	Mean range shift (km decade^{-1})	95% CI	No. hectads	No. spp	One-sample t test		
						df	t	P value
Interval 1								
Birds	Recorded	13.2	13.9	2566	41	40	1.9	0.069
Birds	Well recorded	13.2	13.9	2561	41	40	1.9	0.069
Birds	Heavily recorded	12.5	14.2	2500	41	40	1.7	0.093
Butterflies	Recorded	22.2	10.1	2095	39	38	4.3	**<0.001**
Butterflies	Well recorded	21.8	9.6	1735	42	41	4.4	**<0.001**
Butterflies	Heavily recorded	22.3	10.1	1230	41	40	4.3	**<0.001**
Centipedes	Recorded	39.2	16.2	337	14	13	4.7	**<0.001**
Centipedes	Well recorded	36.4	19.5	132	7	6	3.6	**0.011**
Dragonflies*	Recorded	50.6	15.9	936	25	24	6.2	**<0.001**
Dragonflies*	Well recorded	39.3	14.2	514	22	21	5.4	**<0.001**
Dragonflies*	Heavily recorded	30.9	8.3	173	15	14	7.2	**<0.001**
Grasshoppers*	Recorded	11.4	7.4	869	22	21	3	**0.006**
Grasshoppers*	Well recorded	7.2	8.8	459	20	19	1.6	0.126
Grasshoppers*	Heavily recorded	17.3	16.4	87	5	4	2.1	0.107
Harvestmen	Recorded	17.2	14.2	153	3	2	2.4	0.142
Harvestmen	Well recorded	16.8	14.2	89	2	1	2.3	0.26
Herptiles	Recorded	-3.9	24.7	997	7	6	-0.3	0.766
Herptiles	Well recorded	-3.9	24.7	989	7	6	-0.3	0.766
Herptiles	Heavily recorded	-18.7	37.6	392	5	4	-1	0.384
Hoverflies	Recorded	79.2	10.1	875	99	98	15.4	**<0.001**
Hoverflies	Well recorded	17.8	8.2	110	19	18	4.2	**<0.001**
Ladybirds	Recorded	38.6	13.2	382	11	10	5.7	**<0.001**
Ladybirds	Well recorded	9	5.9	77	3	2	3	0.096
Macromoths	Recorded	10.1	2.7	1492	526	525	7.2	**<0.001**
Macromoths	Well recorded	6.8	3.4	504	389	388	3.8	**<0.001**
Macromoths	Heavily recorded	13	4.1	217	150	149	6.2	**<0.001**
Millipedes	Recorded	38.3	22.5	369	11	10	3.3	**0.008**
Millipedes	Well recorded	69.3	35	129	4	3	3.9	**0.03**
Spiders	Recorded	82.8	9.2	451	164	163	17.7	**<0.001**
Spiders	Well recorded	40.6	21.5	53	6	5	3.7	**0.014**
Woodlice	Recorded	44.6	29.5	972	13	12	3	**0.012**
Woodlice	Well recorded	39.5	34.6	511	11	10	2.2	**0.049**
Woodlice	Heavily recorded	12.3	11.1	55	3	2	2.2	0.16

Interval 2								
Ants	Recorded	51.8	46	415	12	11	2.2	0.05
Ants	Well recorded	32.4	30.9	123	3	2	2.1	0.176
Aquatic Bugs	Recorded	38.9	22.8	549	21	20	3.3	**0.003**
Aquatic Bugs	Well recorded	44.4	34.7	156	11	10	2.5	**0.031**
Bees	Recorded	29.9	8.7	1003	140	139	6.7	**<0.001**
Bees	Well recorded	21.5	7.4	207	90	89	5.7	**<0.001**
Bees	Heavily recorded	14	31.4	58	2	1	0.9	0.542
Birds	Recorded	7	20.7	2566	44	43	0.7	0.508
Birds	Well recorded	7	20.7	2562	44	43	0.7	0.508
Birds	Heavily recorded	10.4	19.7	2504	43	42	1	0.308
Butterflies	Recorded	28.9	10.8	2318	34	33	5.2	**<0.001**
Butterflies	Well recorded	28.7	10.8	2075	34	33	5.2	**<0.001**
Butterflies	Heavily recorded	27.4	9.5	1715	37	36	5.7	**<0.001**
Caddisflies	Recorded	3.1	17.1	142	5	4	0.4	0.743
Caddisflies	Well recorded	35	13.7	82	2	1	5	0.126
Dragonflies*	Recorded	34.6	18.6	1663	23	22	3.6	**0.001**
Dragonflies*	Well recorded	28.4	18.7	1226	23	22	3	**0.007**
Dragonflies*	Heavily recorded	27.2	15.8	720	22	21	3.4	**0.003**
Grasshoppers*	Recorded	6.6	15.4	1028	25	24	0.8	0.411
Grasshoppers*	Well recorded	9.6	14.8	671	23	22	1.3	0.216
Ground beetles	Recorded	-31.9	10.5	797	132	131	-6	**<0.001**
Ground beetles	Well recorded	-1.7	10.1	95	24	23	-0.3	0.74
Hoverflies	Recorded	-22.9	10.8	1783	137	136	-4.2	**<0.001**
Hoverflies	Well recorded	-12.1	9.6	582	131	130	-2.5	**0.014**
Hoverflies	Heavily recorded	18.6	13.3	130	21	20	2.7	**0.013**
Ladybirds	Recorded	8.3	19	925	21	20	0.9	0.403
Ladybirds	Well recorded	20.6	31.9	415	13	12	1.3	0.229
Ladybirds	Heavily recorded	-0.5	21.1	97	13	12	0	0.963
Macromoths	Recorded	44.1	3.9	1754	454	453	22.3	**<0.001**
Macromoths	Well recorded	36.1	4	839	411	410	17.6	**<0.001**
Macromoths	Heavily recorded	32.4	4.8	502	286	285	13.2	**<0.001**
Shieldbugs*	Recorded	30.3	15.2	462	18	17	3.9	**0.001**
Shieldbugs*	Well recorded	22.1	18.3	96	5	4	2.4	0.077
Soldierflies*	Recorded	-12.6	12.2	680	52	51	-2	**0.048**
Soldierflies*	Well recorded	3	10.8	113	19	18	0.5	0.591
Wasps	Recorded	2.5	10.4	579	96	95	0.5	0.64
Wasps	Well recorded	12.8	11.4	99	39	38	2.2	**0.033**
Woodlice	Recorded	-9.5	21.4	1120	17	16	-0.9	0.398
Woodlice	Well recorded	0.3	20.8	523	12	11	0	0.98
Woodlice	Heavily recorded	7.7	23.2	89	4	3	0.6	0.564

Table A2.4. Northern range margin locations (in metres, on the GB Ordnance Survey Grid) during interval 1 of all species included in Figure 3, for each time period, T1 (1966-75) or T2 (1986-1995), and for each level of recording effort control (Recorded, Well Recorded or Heavily Recorded). For bird species, the time period years are 1968-72 for T1 and 1988-1991 for T2. Margin values which are denoted as 'C' indicate confidential data. Note that for species which also qualify for analysis in interval 2, the calculation of range margin locations for 1986-1995 in interval 2 (in Table A2.5) will differ from values for 1986-1995 in interval 1 due to a different set of hectads being analysed.

Taxonomic group	Species	Recorded T1	Recorded T2	Well recorded T1	Well recorded T2	Heavily recorded T1	Heavily recorded T2
Birds	*Acrocephalus palustris*	228000	197000	228000	197000	228000	197000
Birds	*Acrocephalus scirpaceus*	533000	648000	533000	648000	533000	648000
Birds	*Alcedo atthis*	774000	822000	774000	822000	774000	822000
Birds	*Anas querquedula*	569000	757000	569000	757000	569000	757000
Birds	*Anas strepera*	739000	915000	739000	915000	739000	915000
Birds	*Aythya ferina*	873000	911000	873000	911000	873000	911000
Birds	*Botaurus stellaris*	405000	333000	405000	333000	405000	333000
Birds	*Burhinus oedicnemus*	327000	303000	327000	303000	327000	303000
Birds	*Caprimulgus europaeus*	829000	654000	829000	654000	829000	654000
Birds	*Carduelis carduelis*	864000	943000	864000	943000	864000	943000
Birds	*Charadrius dubius*	566000	601000	566000	601000	566000	601000
Birds	*Circus aeruginosus*	466000	683000	466000	683000	466000	683000
Birds	*Circus pygargus*	C	C	C	C	C	C
Birds	*Coccothraustes coccothraustes*	733000	747000	733000	747000	733000	747000
Birds	*Coturnix coturnix*	856000	937000	856000	937000	856000	937000
Birds	*Dendrocopos minor*	511000	542000	511000	542000	511000	542000
Birds	*Emberiza cirlus*	253000	133000	253000	133000	253000	133000
Birds	*Falco subbuteo*	528000	599000	528000	599000	528000	599000
Birds	*Garrulus glandarius*	798000	839000	798000	839000	798000	839000
Birds	*Lanius collurio*	C	C	C	C	C	C
Birds	*Limosa limosa*	621000	762000	621000	762000	621000	762000
Birds	*Lullula arborea*	335000	310000	335000	310000	335000	310000
Birds	*Luscinia megarhynchos*	413000	391000	413000	391000	413000	391000
Birds	*Motacilla flava*	692000	673000	692000	673000	692000	673000

Birds	*Panurus biarmicus*	384000	388000	384000	388000	384000	388000
Birds	*Phoenicurus ochruros*	347000	448000	347000	448000	347000	448000
Birds	*Pica pica*	869000	896000	869000	896000	869000	896000
Birds	*Picus viridis*	782000	851000	782000	851000	782000	851000
Birds	*Podiceps cristatus*	798000	813000	798000	813000	798000	813000
Birds	*Poecile montana*	733000	655000	733000	655000	733000	655000
Birds	*Poecile palustris*	645000	659000	645000	659000	645000	658000
Birds	*Porzana porzana*	784000	823000	784000	823000	784000	823000
Birds	*Puffinus puffinus*	797000	864000	797000	864000	797000	864000
Birds	*Pyrrhocorax pyrrhocorax*	679000	682000	679000	682000	679000	674000
Birds	*Rallus aquaticus*	878000	890000	878000	890000	878000	890000
Birds	*Sitta europaea*	614000	626000	614000	626000	614000	626000
Birds	*Sterna dougallii*	774000	676000	774000	676000	774000	658000
Birds	*Streptopelia turtur*	777000	679000	777000	679000	777000	645000
Birds	*Sylvia curruca*	775000	834000	775000	834000	775000	834000
Birds	*Sylvia undata*	115000	147000	115000	147000	115000	147000
Birds	*Tyto alba*	864000	871000	864000	871000	864000	871000
Butterflies	*Aglais polychloros*	337000	366000	337000	366000	337000	286000
Butterflies	*Anthocharis cardamines*	837000	866000	831000	860000	732000	833000
Butterflies	*Apatura iris*	208000	235000	208000	235000	208000	216000
Butterflies	*Aphantopus hyperantus*	741000	853000	734000	849000	722000	823000
Butterflies	*Argynnis adippe*	405000	430000	405000	407000	403000	407000
Butterflies	*Argynnis paphia*	325000	411000	323000	411000	320000	411000
Butterflies	*Aricia agestis*	380000	421000	380000	421000	378000	420000
Butterflies	*Aricia artaxerxes*	810000	821000	799000	812000	773000	776000
Butterflies	*Boloria euphrosyne*	827000	839000	822000	816000	746000	785000
Butterflies	*Boloria selene*	878000	918000	871000	901000	846000	873000
Butterflies	*Callophrys rubi*	807000	846000	805000	843000	798000	816000
Butterflies	*Celastrina argiolus*	563000	580000	563000	580000	542000	575000
Butterflies	*Colias croceus*	629000	950000	603000	930000	564000	875000
Butterflies	*Cupido minimus*	850000	887000	829000	885000	725000	875000
Butterflies	*Erynnis tages*	733000	845000	676000	793000	647000	734000
Butterflies	*Euphydryas aurinia*	750000	726000	750000	723000	694000	645000
Butterflies	*Gonepteryx rhamni*	493000	508000	487000	508000	487000	507000
Butterflies	*Hamearis lucina*	390000	471000	390000	464000	390000	430000
Butterflies	*Hesperia comma*	175000	168000	175000	168000	175000	168000
Butterflies	*Hipparchia semele*	NA	NA	879000	873000	NA	NA
Butterflies	*Inachis io*	805000	801000	782000	784000	768000	780000
Butterflies	*Lasiommata megera*	651000	629000	620000	625000	560000	606000
Butterflies	*Leptidea sinapis*	278000	318000	278000	318000	278000	283000
Butterflies	*Limenitis camilla*	308000	371000	308000	371000	308000	369000
Butterflies	*Lycaena phlaeas*	862000	872000	862000	872000	855000	856000
Butterflies	*Lysandra bellargus*	176000	179000	176000	179000	176000	172000

Butterflies	*Lysandra coridon*	275000	274000	275000	274000	274000	272000
Butterflies	*Melanargia galathea*	361000	484000	361000	484000	361000	482000
Butterflies	*Neozephyrus quercus*	576000	624000	551000	610000	494000	555000
Butterflies	*Ochlodes faunus*	562000	615000	562000	609000	562000	601000
Butterflies	*Pararge aegeria*	831000	891000	817000	891000	777000	875000
Butterflies	*Plebejus argus*	366000	374000	366000	374000	366000	367000
Butterflies	*Polygonia c-album*	396000	573000	396000	573000	396000	561000
Butterflies	*Pyrgus malvae*	428000	377000	428000	377000	428000	371000
Butterflies	*Pyronia tithonus*	477000	499000	477000	499000	469000	493000
Butterflies	*Satyrium pruni*	286000	274000	286000	274000	286000	274000
Butterflies	*Satyrium w-album*	413000	516000	413000	512000	411000	494000
Butterflies	*Thecla betulae*	306000	296000	306000	296000	306000	296000
Butterflies	*Thymelicus lineola*	330000	382000	330000	382000	329000	382000
Butterflies	*Thymelicus sylvestris*	485000	554000	485000	554000	480000	542000
Butterflies	*Vanessa atalanta*	NA	NA	872000	932000	831000	898000
Butterflies	*Vanessa cardui*	NA	NA	848000	859000	806000	851000
Centipedes	*Cryptops hortensis*	259000	407000	245000	361000	NA	NA
Centipedes	*Geophilus carpophagus*	564000	665000	NA	NA	NA	NA
Centipedes	*Geophilus flavus*	458000	614000	450000	541000	NA	NA
Centipedes	*Geophilus insculptus*	530000	647000	NA	NA	NA	NA
Centipedes	*Geophilus truncorum*	617000	632000	NA	NA	NA	NA
Centipedes	*Lithobius borealis*	358000	418000	NA	NA	NA	NA
Centipedes	*Lithobius calcaratus*	468000	590000	NA	NA	NA	NA
Centipedes	*Lithobius melanops*	603000	639000	447000	481000	NA	NA
Centipedes	*Lithobius microps*	413000	510000	375000	478000	NA	NA
Centipedes	*Lithobius variegatus*	501000	518000	NA	NA	NA	NA
Centipedes	*Schendyla nemorensis*	304000	477000	273000	392000	NA	NA
Centipedes	*Stigmatogaster subterranea*	417000	492000	376000	449000	NA	NA
Centipedes	*Strigamia acuminata*	403000	394000	403000	376000	NA	NA
Centipedes	*Strigamia crassipes*	258000	247000	NA	NA	NA	NA
Dragonflies*	*Aeshna cyanea*	524000	582000	505000	571000	NA	NA
Dragonflies*	*Aeshna grandis*	532000	478000	512000	470000	NA	NA
Dragonflies*	*Aeshna juncea*	848000	894000	827000	867000	NA	NA
Dragonflies*	*Aeshna mixta*	347000	411000	343000	396000	301000	327000
Dragonflies*	*Anax imperator*	294000	428000	290000	418000	269000	340000
Dragonflies*	*Brachytron pratense*	343000	545000	343000	410000	313000	346000
Dragonflies*	*Calopteryx splendens*	420000	552000	389000	508000	369000	442000
Dragonflies*	*Calopteryx virgo*	529000	645000	459000	567000	319000	418000
Dragonflies*	*Ceriagrion tenellum*	225000	286000	225000	259000	190000	221000
Dragonflies*	*Coenagrion puella*	540000	689000	504000	636000	458000	529000
Dragonflies*	*Coenagrion pulchellum*	400000	514000	377000	443000	347000	360000
Dragonflies*	*Cordulegaster boltonii*	856000	879000	826000	843000	NA	NA
Dragonflies*	*Cordulia aenea*	273000	586000	273000	430000	200000	297000

Dragonflies*	*Enallagma cyathigerum*	831000	886000	NA	NA	NA	NA
Dragonflies*	*Erythromma najas*	372000	389000	371000	386000	282000	351000
Dragonflies*	*Ischnura elegans*	761000	894000	NA	NA	NA	NA
Dragonflies*	*Lestes sponsa*	774000	863000	760000	848000	NA	NA
Dragonflies*	*Libellula depressa*	358000	413000	355000	400000	295000	326000
Dragonflies*	*Libellula quadrimaculata*	817000	882000	817000	858000	NA	NA
Dragonflies*	*Orthetrum cancellatum*	288000	382000	286000	363000	276000	330000
Dragonflies*	*Orthetrum coerulescens*	385000	693000	366000	667000	307000	419000
Dragonflies*	*Platycnemis pennipes*	261000	307000	261000	302000	240000	274000
Dragonflies*	*Sympetrum danae*	806000	885000	800000	850000	NA	NA
Dragonflies*	*Sympetrum sanguineum*	326000	456000	324000	448000	264000	376000
Dragonflies*	*Sympetrum striolatum*	788000	887000	NA	NA	NA	NA
Grasshoppers*	*Acheta domesticus*	391000	345000	377000	289000	NA	NA
Grasshoppers*	*Chorthippus albomarginatus*	385000	383000	368000	361000	NA	NA
Grasshoppers*	*Chorthippus brunneus*	738000	748000	733000	748000	NA	NA
Grasshoppers*	*Chorthippus parallelus*	713000	782000	713000	782000	NA	NA
Grasshoppers*	*Conocephalus dorsalis*	353000	346000	341000	346000	260000	255000
Grasshoppers*	*Ectobius lapponicus*	153000	208000	153000	180000	NA	NA
Grasshoppers*	*Ectobius pallidus*	165000	205000	165000	205000	NA	NA
Grasshoppers*	*Ectobius panzeri*	157000	198000	NA	NA	NA	NA
Grasshoppers*	*Gomphocerippus rufus*	166000	179000	NA	NA	NA	NA
Grasshoppers*	*Leptophyes punctatissima*	402000	394000	398000	367000	NA	NA
Grasshoppers*	*Meconema thalassinum*	388000	401000	351000	362000	258000	293000
Grasshoppers*	*Metrioptera brachyptera*	393000	465000	378000	448000	NA	NA
Grasshoppers*	*Metrioptera roeselii*	306000	277000	292000	274000	NA	NA
Grasshoppers*	*Myrmeleotettix maculatus*	758000	792000	758000	792000	NA	NA
Grasshoppers*	*Omocestus rufipes*	163000	191000	163000	182000	NA	NA
Grasshoppers*	*Omocestus viridulus*	797000	813000	797000	813000	NA	NA
Grasshoppers*	*Pholidoptera griseoaptera*	363000	421000	363000	386000	NA	NA
Grasshoppers*	*Platycleis albopunctata*	171000	191000	162000	185000	NA	NA
Grasshoppers*	*Stenobothrus lineatus*	270000	285000	270000	280000	189000	198000
Grasshoppers*	*Tetrix subulata*	282000	386000	265000	361000	188000	280000
Grasshoppers*	*Tetrix undulata*	664000	646000	647000	618000	NA	NA
Grasshoppers*	*Tettigonia viridissima*	234000	258000	234000	235000	157000	199000

Harvestmen	*Lacinius ephippiatus*	449000	455000	NA	NA	NA	NA
Harvestmen	*Leiobunum blackwalli*	366000	409000	325000	344000	NA	NA
Harvestmen	*Leiobunum rotundum*	470000	524000	434000	482000	NA	NA
Herptiles	*Anguis fragilis*	766000	847000	766000	847000	710000	813000
Herptiles	*Lacerta vivipara*	836000	875000	836000	875000	NA	NA
Herptiles	*Natrix natrix*	472000	439000	472000	439000	457000	415000
Herptiles	*Triturus cristatus*	675000	589000	675000	589000	626000	531000
Herptiles	*Triturus helveticus*	804000	784000	804000	784000	753000	717000
Herptiles	*Triturus vulgaris*	736000	649000	736000	649000	644000	527000
Herptiles	*Vipera berus*	825000	876000	825000	876000	NA	NA
Hoverflies	*Anasimyia lineata*	484000	696000	NA	NA	NA	NA
Hoverflies	*Arctophila superbiens*	755000	662000	NA	NA	NA	NA
Hoverflies	*Baccha elongata*	603000	783000	NA	NA	NA	NA
Hoverflies	*Brachyopa scutellaris*	297000	510000	NA	NA	NA	NA
Hoverflies	*Chalcosyrphus nemorum*	341000	654000	NA	NA	NA	NA
Hoverflies	*Cheilosia albitarsis*	494000	809000	389000	465000	NA	NA
Hoverflies	*Cheilosia antiqua*	525000	758000	NA	NA	NA	NA
Hoverflies	*Cheilosia bergenstammi*	647000	820000	NA	NA	NA	NA
Hoverflies	*Cheilosia fraterna*	592000	797000	NA	NA	NA	NA
Hoverflies	*Cheilosia grossa*	501000	605000	NA	NA	NA	NA
Hoverflies	*Cheilosia illustrata*	814000	844000	NA	NA	NA	NA
Hoverflies	*Cheilosia impressa*	333000	577000	NA	NA	NA	NA
Hoverflies	*Cheilosia lasiopa*	395000	524000	NA	NA	NA	NA
Hoverflies	*Cheilosia pagana*	457000	779000	NA	NA	NA	NA
Hoverflies	*Cheilosia proxima*	509000	525000	NA	NA	NA	NA
Hoverflies	*Cheilosia scutellata*	417000	542000	NA	NA	NA	NA
Hoverflies	*Cheilosia variabilis*	432000	763000	377000	432000	NA	NA
Hoverflies	*Cheilosia vernalis*	472000	572000	NA	NA	NA	NA
Hoverflies	*Chrysogaster solstitialis*	501000	744000	400000	384000	NA	NA
Hoverflies	*Chrysotoxum arcuatum*	685000	815000	NA	NA	NA	NA
Hoverflies	*Chrysotoxum bicinctum*	569000	762000	346000	432000	NA	NA
Hoverflies	*Chrysotoxum cautum*	279000	289000	NA	NA	NA	NA
Hoverflies	*Chrysotoxum festivum*	390000	462000	NA	NA	NA	NA
Hoverflies	*Chrysotoxum verralli*	288000	317000	NA	NA	NA	NA
Hoverflies	*Criorhina berberina*	468000	514000	369000	351000	NA	NA
Hoverflies	*Criorhina floccosa*	450000	560000	384000	385000	NA	NA
Hoverflies	*Dasysyrphus albostriatus*	516000	753000	NA	NA	NA	NA
Hoverflies	*Dasysyrphus pinastri*	527000	797000	NA	NA	NA	NA
Hoverflies	*Dasysyrphus tricinctus*	552000	805000	NA	NA	NA	NA
Hoverflies	*Dasysyrphus venustus*	542000	805000	NA	NA	NA	NA

Hoverflies	*Epistrophe eligans*	485000	669000	NA	NA	NA	NA
Hoverflies	*Epistrophe grossulariae*	616000	786000	NA	NA	NA	NA
Hoverflies	*Episyrphus balteatus*	686000	913000	NA	NA	NA	NA
Hoverflies	*Eristalinus aeneus*	553000	633000	NA	NA	NA	NA
Hoverflies	*Eristalinus sepulchralis*	499000	476000	383000	387000	NA	NA
Hoverflies	*Eristalis arbustorum*	739000	876000	NA	NA	NA	NA
Hoverflies	*Eristalis horticola*	736000	816000	NA	NA	NA	NA
Hoverflies	*Eristalis intricaria*	708000	876000	NA	NA	NA	NA
Hoverflies	*Eristalis pertinax*	797000	890000	NA	NA	NA	NA
Hoverflies	*Eristalis tenax*	786000	837000	NA	NA	NA	NA
Hoverflies	*Eumerus strigatus*	428000	430000	350000	351000	NA	NA
Hoverflies	*Eupeodes corollae*	553000	877000	NA	NA	NA	NA
Hoverflies	*Eupeodes latifasciatus*	421000	612000	NA	NA	NA	NA
Hoverflies	*Eupeodes luniger*	525000	816000	NA	NA	NA	NA
Hoverflies	*Ferdinandea cuprea*	410000	687000	381000	423000	NA	NA
Hoverflies	*Helophilus hybridus*	471000	745000	374000	375000	NA	NA
Hoverflies	*Helophilus pendulus*	801000	907000	NA	NA	NA	NA
Hoverflies	*Helophilus trivittatus*	440000	532000	NA	NA	NA	NA
Hoverflies	*Lejogaster metallina*	566000	799000	380000	440000	NA	NA
Hoverflies	*Leucozona glaucia*	690000	802000	369000	434000	NA	NA
Hoverflies	*Leucozona laternaria*	661000	688000	NA	NA	NA	NA
Hoverflies	*Leucozona lucorum*	680000	838000	NA	NA	NA	NA
Hoverflies	*Melangyna cincta*	421000	789000	NA	NA	NA	NA
Hoverflies	*Melangyna labiatarum*	483000	768000	NA	NA	NA	NA
Hoverflies	*Melangyna lasiophthalma*	578000	803000	NA	NA	NA	NA
Hoverflies	*Melangyna umbellatarum*	355000	579000	NA	NA	NA	NA
Hoverflies	*Melanogaster hirtella*	705000	832000	NA	NA	NA	NA
Hoverflies	*Melanostoma mellinum*	806000	869000	NA	NA	NA	NA
Hoverflies	*Meliscaeva auricollis*	464000	752000	356000	423000	NA	NA
Hoverflies	*Meliscaeva cinctella*	655000	809000	NA	NA	NA	NA
Hoverflies	*Myathropa florea*	632000	803000	NA	NA	NA	NA
Hoverflies	*Neoascia podagrica*	652000	817000	NA	NA	NA	NA
Hoverflies	*Neoascia tenur*	566000	810000	NA	NA	NA	NA
Hoverflies	*Parasyrphus punctulatus*	459000	777000	NA	NA	NA	NA
Hoverflies	*Parhelophilus frutetorum*	310000	410000	NA	NA	NA	NA
Hoverflies	*Parhelophilus versicolor*	406000	478000	NA	NA	NA	NA
Hoverflies	*Pipiza austriaca*	376000	507000	NA	NA	NA	NA
Hoverflies	*Pipiza fenestrata*	320000	377000	NA	NA	NA	NA
Hoverflies	*Pipiza luteitarsis*	420000	448000	NA	NA	NA	NA

Hoverflies	*Pipiza noctiluca*	389000	660000	366000	386000	NA	NA
Hoverflies	*Pipizella viduata*	360000	796000	NA	NA	NA	NA
Hoverflies	*Platycheirus albimanus*	807000	910000	NA	NA	NA	NA
Hoverflies	*Platycheirus angustatus*	702000	843000	NA	NA	NA	NA
Hoverflies	*Platycheirus fulviventris*	384000	744000	NA	NA	NA	NA
Hoverflies	*Platycheirus granditarsus*	602000	810000	NA	NA	NA	NA
Hoverflies	*Platycheirus manicatus*	815000	922000	NA	NA	NA	NA
Hoverflies	*Platycheirus rosarum*	509000	751000	391000	446000	NA	NA
Hoverflies	*Platycheirus scambus*	645000	811000	NA	NA	NA	NA
Hoverflies	*Platycheirus scutatus*	613000	817000	NA	NA	NA	NA
Hoverflies	*Portevinia maculata*	500000	525000	NA	NA	NA	NA
Hoverflies	*Rhingia campestris*	751000	848000	NA	NA	NA	NA
Hoverflies	*Riponnensia splendens*	444000	516000	376000	384000	NA	NA
Hoverflies	*Scaeva pyrastri*	636000	867000	NA	NA	NA	NA
Hoverflies	*Sphaerophoria interrupta*	790000	803000	NA	NA	NA	NA
Hoverflies	*Sphaerophoria scripta*	446000	652000	NA	NA	NA	NA
Hoverflies	*Sphegina clunipes*	759000	815000	NA	NA	NA	NA
Hoverflies	*Sphegina elegans*	525000	670000	NA	NA	NA	NA
Hoverflies	*Syritta pipiens*	687000	831000	NA	NA	NA	NA
Hoverflies	*Syrphus ribesii*	794000	865000	NA	NA	NA	NA
Hoverflies	*Syrphus torvus*	660000	810000	NA	NA	NA	NA
Hoverflies	*Syrphus vitripennis*	636000	828000	NA	NA	NA	NA
Hoverflies	*Tropidia scita*	462000	482000	325000	356000	NA	NA
Hoverflies	*Volucella pellucens*	726000	818000	NA	NA	NA	NA
Hoverflies	*Volucella zonaria*	184000	186000	NA	NA	NA	NA
Hoverflies	*Xanthogramma citrofasciatum*	233000	409000	NA	NA	NA	NA
Hoverflies	*Xanthogramma pedissequum*	279000	458000	240000	349000	NA	NA
Hoverflies	*Xylota segnis*	623000	812000	NA	NA	NA	NA
Hoverflies	*Xylota sylvarum*	534000	661000	366000	395000	NA	NA
Hoverflies	*Xylota xanthocnema*	342000	310000	NA	NA	NA	NA
Ladybirds	*Adalia bipunctata*	486000	511000	NA	NA	NA	NA
Ladybirds	*Adalia decempunctata*	452000	585000	405000	416000	NA	NA
Ladybirds	*Anisosticta novemdecimpunctata*	395000	428000	NA	NA	NA	NA
Ladybirds	*Calvia quattuordecimguttata*	477000	586000	408000	421000	NA	NA
Ladybirds	*Chilocorus renipustulatus*	337000	480000	NA	NA	NA	NA
Ladybirds	*Coccidula rufa*	400000	460000	NA	NA	NA	NA

Ladybirds	*Coccinella undecimpunctata*	428000	474000	NA	NA	NA	NA
Ladybirds	*Propylea quattuordecimpunctata*	446000	498000	NA	NA	NA	NA
Ladybirds	*Psyllobora vigintiduopunctata*	412000	469000	395000	425000	NA	NA
Ladybirds	*Rhyzobius litura*	317000	457000	NA	NA	NA	NA
Ladybirds	*Subcoccinella vigintiquattuorpunctata*	352000	403000	NA	NA	NA	NA
Macromoths	*Abraxas grossulariata*	868000	884000	746000	767000	NA	NA
Macromoths	*Abraxas sylvata*	555000	592000	509000	568000	NA	NA
Macromoths	*Abrostola tripartita*	842000	919000	NA	NA	NA	NA
Macromoths	*Acasis viretata*	675000	720000	494000	660000	NA	NA
Macromoths	*Acherontia atropos*	556000	536000	461000	426000	349000	388000
Macromoths	*Achlya flavicornis*	838000	869000	NA	NA	NA	NA
Macromoths	*Acronicta aceris*	320000	363000	304000	341000	281000	337000
Macromoths	*Acronicta alni*	434000	512000	415000	460000	385000	431000
Macromoths	*Acronicta leporina*	804000	705000	670000	681000	NA	NA
Macromoths	*Acronicta megacephala*	743000	720000	594000	586000	NA	NA
Macromoths	*Acronicta psi*	811000	801000	789000	738000	NA	NA
Macromoths	*Acronicta rumicis*	815000	857000	791000	784000	NA	NA
Macromoths	*Acronicta tridens*	465000	428000	408000	376000	394000	351000
Macromoths	*Adscita geryon*	401000	416000	NA	NA	NA	NA
Macromoths	*Adscita statices*	475000	503000	361000	354000	NA	NA
Macromoths	*Aethalura punctulata*	604000	711000	491000	579000	NA	NA
Macromoths	*Agriopis aurantiaria*	822000	881000	NA	NA	NA	NA
Macromoths	*Agriopis leucophaearia*	690000	647000	603000	560000	NA	NA
Macromoths	*Agriopis marginaria*	818000	885000	NA	NA	NA	NA
Macromoths	*Agrius convolvuli*	679000	889000	642000	647000	NA	NA
Macromoths	*Agrochola circellaris*	817000	867000	777000	792000	NA	NA
Macromoths	*Agrochola helvola*	794000	780000	717000	658000	NA	NA
Macromoths	*Agrochola litura*	815000	821000	755000	786000	NA	NA
Macromoths	*Agrochola lota*	843000	856000	NA	NA	NA	NA
Macromoths	*Agrochola lychnidis*	646000	563000	610000	511000	NA	NA
Macromoths	*Agrochola macilenta*	828000	876000	798000	804000	NA	NA
Macromoths	*Agrotis cinerea*	391000	271000	261000	248000	237000	187000
Macromoths	*Agrotis clavis*	646000	551000	641000	454000	NA	NA
Macromoths	*Agrotis exclamationis*	827000	843000	NA	NA	NA	NA
Macromoths	*Agrotis ipsilon*	825000	856000	785000	754000	NA	NA
Macromoths	*Agrotis puta*	488000	457000	474000	450000	NA	NA
Macromoths	*Agrotis ripae*	514000	504000	NA	NA	NA	NA
Macromoths	*Agrotis segetum*	792000	733000	728000	723000	NA	NA
Macromoths	*Agrotis vestigialis*	824000	838000	773000	714000	NA	NA
Macromoths	*Alcis jubata*	796000	820000	727000	797000	NA	NA
Macromoths	*Alcis repandata*	866000	890000	NA	NA	NA	NA
Macromoths	*Allophyes oxyacanthae*	835000	864000	NA	NA	NA	NA

Macromoths	*Alsophila aescularia*	799000	807000	755000	757000	NA	NA
Macromoths	*Amphipoea fucosa*	427000	675000	409000	447000	NA	NA
Macromoths	*Amphipoea lucens*	830000	899000	NA	NA	NA	NA
Macromoths	*Amphipoea oculea*	848000	842000	NA	NA	NA	NA
Macromoths	*Amphipyra tragopoginis*	849000	843000	NA	NA	NA	NA
Macromoths	*Anaplectoides prasina*	836000	853000	NA	NA	NA	NA
Macromoths	*Anarta myrtilli*	824000	796000	720000	620000	372000	348000
Macromoths	*Angerona prunaria*	276000	266000	248000	250000	238000	240000
Macromoths	*Anticlea badiata*	819000	831000	773000	802000	NA	NA
Macromoths	*Anticlea derivata*	811000	864000	792000	810000	NA	NA
Macromoths	*Antitype chi*	856000	902000	NA	NA	NA	NA
Macromoths	*Apamea anceps*	362000	328000	328000	328000	324000	322000
Macromoths	*Apamea crenata*	859000	919000	NA	NA	NA	NA
Macromoths	*Apamea epomidion*	740000	579000	568000	496000	NA	NA
Macromoths	*Apamea furva*	838000	783000	767000	575000	NA	NA
Macromoths	*Apamea lithoxylaea*	862000	878000	NA	NA	NA	NA
Macromoths	*Apamea oblonga*	408000	387000	403000	342000	NA	NA
Macromoths	*Apamea ophiogramma*	601000	640000	545000	604000	NA	NA
Macromoths	*Apamea remissa*	843000	901000	NA	NA	NA	NA
Macromoths	*Apamea scolopacina*	497000	513000	418000	467000	380000	424000
Macromoths	*Apamea sordens*	835000	829000	NA	NA	NA	NA
Macromoths	*Apamea sublustris*	303000	318000	254000	291000	248000	249000
Macromoths	*Apamea unanimis*	693000	740000	631000	704000	NA	NA
Macromoths	*Apeira syringaria*	508000	599000	469000	535000	408000	516000
Macromoths	*Aplocera efformata*	335000	542000	317000	463000	305000	336000
Macromoths	*Aplocera plagiata*	860000	886000	NA	NA	NA	NA
Macromoths	*Apocheima hispidaria*	365000	387000	330000	318000	317000	284000
Macromoths	*Apoda limacodes*	200000	280000	200000	209000	NA	NA
Macromoths	*Aporophyla nigra*	863000	906000	NA	NA	NA	NA
Macromoths	*Archanara dissoluta*	358000	361000	350000	338000	339000	322000
Macromoths	*Archanara geminipuncta*	314000	343000	307000	339000	291000	323000
Macromoths	*Archanara sparganii*	208000	280000	NA	NA	NA	NA
Macromoths	*Archiearis parthenias*	809000	695000	680000	629000	NA	NA
Macromoths	*Arctia villica*	242000	258000	242000	246000	232000	230000
Macromoths	*Arenostola phragmitidis*	427000	449000	417000	438000	380000	402000
Macromoths	*Asteroscopus sphinx*	491000	507000	386000	465000	385000	374000
Macromoths	*Asthena albulata*	479000	619000	444000	546000	422000	488000
Macromoths	*Atethmia centrago*	787000	728000	702000	676000	NA	NA
Macromoths	*Atolmis rubricollis*	356000	436000	275000	396000	NA	NA
Macromoths	*Autographa jota*	839000	783000	NA	NA	NA	NA
Macromoths	*Axylia putris*	690000	697000	638000	646000	NA	NA
Macromoths	*Bena bicolorana*	358000	435000	334000	424000	320000	384000
Macromoths	*Biston betularia*	832000	852000	NA	NA	NA	NA

Macromoths	*Biston strataria*	654000	606000	529000	516000	NA	NA
Macromoths	*Blepharita adusta*	864000	905000	NA	NA	NA	NA
Macromoths	*Brachylomia viminalis*	848000	885000	NA	NA	NA	NA
Macromoths	*Bupalus piniaria*	838000	851000	NA	NA	NA	NA
Macromoths	*Cabera exanthemata*	839000	887000	NA	NA	NA	NA
Macromoths	*Cabera pusaria*	866000	883000	NA	NA	NA	NA
Macromoths	*Callimorpha dominula*	230000	280000	202000	253000	NA	NA
Macromoths	*Callistege mi*	759000	773000	595000	690000	392000	526000
Macromoths	*Calliteara pudibunda*	502000	487000	448000	464000	429000	440000
Macromoths	*Campaea margaritata*	856000	914000	NA	NA	NA	NA
Macromoths	*Camptogramma bilineata*	879000	897000	NA	NA	NA	NA
Macromoths	*Caradrina morpheus*	807000	767000	746000	709000	NA	NA
Macromoths	*Catarhoe cuculata*	307000	359000	293000	261000	NA	NA
Macromoths	*Catarhoe rubidata*	315000	248000	296000	234000	276000	207000
Macromoths	*Catocala nupta*	405000	487000	368000	447000	326000	435000
Macromoths	*Celaena leucostigma*	826000	866000	789000	720000	NA	NA
Macromoths	*Cepphis advenaria*	211000	204000	197000	202000	183000	195000
Macromoths	*Cerastis leucographa*	312000	376000	295000	309000	284000	303000
Macromoths	*Cerastis rubricosa*	854000	919000	NA	NA	NA	NA
Macromoths	*Cerura vinula*	844000	833000	798000	753000	NA	NA
Macromoths	*Charanyca trigrammica*	439000	440000	422000	407000	385000	373000
Macromoths	*Charissa obscurata*	617000	587000	314000	417000	260000	285000
Macromoths	*Chesias legatella*	837000	878000	787000	790000	NA	NA
Macromoths	*Chesias rufata*	824000	757000	591000	659000	NA	NA
Macromoths	*Chiasmia clathrata*	736000	724000	674000	693000	NA	NA
Macromoths	*Chilodes maritimus*	332000	426000	314000	395000	312000	346000
Macromoths	*Chloroclysta citrata*	869000	914000	NA	NA	NA	NA
Macromoths	*Chloroclysta miata*	841000	898000	NA	NA	NA	NA
Macromoths	*Chloroclysta siterata*	818000	890000	794000	822000	NA	NA
Macromoths	*Chloroclysta truncata*	869000	906000	NA	NA	NA	NA
Macromoths	*Chloroclystis v-ata*	503000	662000	463000	635000	NA	NA
Macromoths	*Chortodes pygmina*	838000	926000	NA	NA	NA	NA
Macromoths	*Cidaria fulvata*	869000	918000	NA	NA	NA	NA
Macromoths	*Cilix glaucata*	622000	634000	573000	618000	NA	NA
Macromoths	*Cleorodes lichenaria*	726000	761000	608000	618000	424000	407000
Macromoths	*Clostera curtula*	325000	330000	312000	324000	302000	323000
Macromoths	*Clostera pigra*	634000	654000	NA	NA	NA	NA
Macromoths	*Coenobia rufa*	439000	390000	394000	383000	384000	358000
Macromoths	*Colocasia coryli*	851000	868000	NA	NA	NA	NA
Macromoths	*Colostygia multistrigaria*	839000	919000	NA	NA	NA	NA
Macromoths	*Colotois pennaria*	838000	861000	791000	818000	NA	NA
Macromoths	*Comibaena bajularia*	380000	422000	348000	406000	348000	355000
Macromoths	*Conistra ligula*	571000	557000	549000	458000	NA	NA

Macromoths	*Conistra rubiginea*	188000	204000	NA	NA	NA	NA
Macromoths	*Conistra vaccinii*	829000	864000	NA	NA	NA	NA
Macromoths	*Cosmia affinis*	375000	359000	349000	312000	306000	290000
Macromoths	*Cosmia pyralina*	313000	331000	312000	326000	304000	320000
Macromoths	*Cosmia trapezina*	820000	824000	NA	NA	NA	NA
Macromoths	*Cosmorhoe ocellata*	878000	925000	NA	NA	NA	NA
Macromoths	*Cossus cossus*	463000	386000	333000	257000	NA	NA
Macromoths	*Craniophora ligustri*	636000	696000	476000	620000	405000	473000
Macromoths	*Crocallis elinguaria*	865000	890000	NA	NA	NA	NA
Macromoths	*Cryphia domestica*	778000	744000	673000	691000	NA	NA
Macromoths	*Cryphia muralis*	228000	218000	203000	209000	164000	189000
Macromoths	*Cucullia absinthii*	368000	388000	NA	NA	NA	NA
Macromoths	*Cucullia asteris*	320000	338000	313000	303000	NA	NA
Macromoths	*Cucullia chamomillae*	560000	554000	531000	545000	NA	NA
Macromoths	*Cucullia umbratica*	850000	812000	654000	675000	NA	NA
Macromoths	*Cybosia mesomella*	737000	728000	638000	651000	NA	NA
Macromoths	*Cyclophora albipunctata*	828000	825000	627000	676000	NA	NA
Macromoths	*Cyclophora annularia*	247000	205000	224000	205000	208000	185000
Macromoths	*Cyclophora linearia*	316000	385000	272000	347000	265000	331000
Macromoths	*Cyclophora porata*	307000	271000	NA	NA	NA	NA
Macromoths	*Cyclophora punctaria*	351000	366000	310000	315000	287000	287000
Macromoths	*Cymatophorima diluta*	368000	387000	331000	306000	298000	284000
Macromoths	*Dasypolia templi*	827000	919000	NA	NA	NA	NA
Macromoths	*Deilephila elpenor*	658000	781000	583000	712000	NA	NA
Macromoths	*Deilephila porcellus*	616000	694000	489000	594000	408000	478000
Macromoths	*Deileptenia ribeata*	418000	662000	320000	567000	314000	521000
Macromoths	*Deltote uncula*	549000	692000	442000	436000	393000	360000
Macromoths	*Diacrisia sannio*	782000	771000	768000	732000	NA	NA
Macromoths	*Diaphora mendica*	547000	636000	497000	541000	NA	NA
Macromoths	*Diarsia brunnea*	859000	888000	NA	NA	NA	NA
Macromoths	*Diarsia dahlii*	834000	905000	NA	NA	NA	NA
Macromoths	*Dicallomera fascelina*	806000	783000	732000	670000	NA	NA
Macromoths	*Dichonia aprilina*	777000	745000	773000	679000	NA	NA
Macromoths	*Diloba caeruleocephala*	653000	611000	633000	587000	NA	NA
Macromoths	*Discestra trifolii*	676000	581000	562000	512000	NA	NA
Macromoths	*Discoloxia blomeri*	427000	455000	318000	391000	298000	340000
Macromoths	*Drepana falcataria*	810000	809000	771000	752000	NA	NA
Macromoths	*Drymonia dodonaea*	592000	615000	490000	528000	366000	384000
Macromoths	*Drymonia ruficornis*	699000	637000	538000	616000	NA	NA
Macromoths	*Dryobotodes eremita*	692000	777000	609000	746000	NA	NA
Macromoths	*Dypterygia scabriuscula*	343000	395000	343000	380000	340000	359000
Macromoths	*Dyscia fagaria*	834000	822000	786000	749000	NA	NA
Macromoths	*Earias clorana*	338000	389000	301000	338000	NA	NA

Macromoths	*Ecliptopera silaceata*	839000	890000	763000	803000	NA	NA
Macromoths	*Ectropis bistortata*	833000	859000	NA	NA	NA	NA
Macromoths	*Ectropis crepuscularia*	596000	519000	561000	476000	NA	NA
Macromoths	*Eilema complana*	361000	392000	340000	364000	323000	352000
Macromoths	*Eilema depressa*	304000	348000	290000	327000	269000	322000
Macromoths	*Eilema griseola*	354000	375000	332000	359000	308000	347000
Macromoths	*Eilema lurideola*	797000	709000	609000	611000	NA	NA
Macromoths	*Eilema sororcula*	175000	288000	NA	NA	NA	NA
Macromoths	*Elaphria venustula*	171000	235000	164000	195000	NA	NA
Macromoths	*Electrophaes corylata*	834000	863000	NA	NA	NA	NA
Macromoths	*Ematurga atomaria*	842000	831000	NA	NA	NA	NA
Macromoths	*Enargia paleacea*	774000	831000	613000	673000	NA	NA
Macromoths	*Ennomos alniaria*	851000	834000	NA	NA	NA	NA
Macromoths	*Ennomos autumnaria*	284000	303000	265000	296000	NA	NA
Macromoths	*Ennomos erosaria*	668000	627000	621000	579000	NA	NA
Macromoths	*Ennomos fuscantaria*	471000	469000	463000	438000	NA	NA
Macromoths	*Ennomos quercinaria*	485000	469000	453000	414000	424000	363000
Macromoths	*Epione repandaria*	827000	862000	792000	799000	NA	NA
Macromoths	*Epirrhoe alternata*	872000	908000	NA	NA	NA	NA
Macromoths	*Epirrhoe galiata*	575000	515000	463000	426000	360000	415000
Macromoths	*Epirrhoe rivata*	376000	383000	363000	381000	353000	351000
Macromoths	*Epirrita autumnata*	822000	869000	785000	817000	NA	NA
Macromoths	*Epirrita christyi*	716000	771000	689000	725000	NA	NA
Macromoths	*Epirrita dilutata*	820000	861000	786000	796000	NA	NA
Macromoths	*Erannis defoliaria*	821000	877000	793000	806000	NA	NA
Macromoths	*Eremobia ochroleuca*	400000	459000	382000	433000	366000	387000
Macromoths	*Euchoeca nebulata*	442000	663000	393000	508000	357000	466000
Macromoths	*Euclidia glyphica*	534000	488000	410000	461000	376000	376000
Macromoths	*Eulithis mellinata*	803000	717000	740000	670000	NA	NA
Macromoths	*Eulithis prunata*	803000	801000	777000	739000	NA	NA
Macromoths	*Eulithis pyraliata*	822000	896000	795000	813000	NA	NA
Macromoths	*Eulithis testata*	870000	926000	NA	NA	NA	NA
Macromoths	*Euphyia biangulata*	266000	277000	243000	257000	224000	247000
Macromoths	*Euphyia unangulata*	352000	318000	335000	314000	316000	282000
Macromoths	*Eupithecia abbreviata*	749000	823000	695000	812000	NA	NA
Macromoths	*Eupithecia absinthiata*	823000	874000	766000	777000	NA	NA
Macromoths	*Eupithecia assimilata*	817000	881000	765000	765000	NA	NA
Macromoths	*Eupithecia centaureata*	698000	683000	664000	654000	NA	NA
Macromoths	*Eupithecia dodoneata*	310000	498000	295000	461000	275000	429000
Macromoths	*Eupithecia exiguata*	680000	713000	550000	676000	NA	NA
Macromoths	*Eupithecia expallidata*	365000	404000	319000	280000	NA	NA
Macromoths	*Eupithecia haworthiata*	350000	334000	284000	288000	263000	278000
Macromoths	*Eupithecia icterata*	849000	850000	NA	NA	NA	NA
Macromoths	*Eupithecia indigata*	799000	821000	702000	745000	NA	NA

Macromoths	*Eupithecia innotata*	615000	369000	NA	NA	NA	NA
Macromoths	*Eupithecia inturbata*	393000	421000	321000	364000	286000	348000
Macromoths	*Eupithecia linariata*	624000	592000	584000	535000	NA	NA
Macromoths	*Eupithecia nanata*	865000	907000	NA	NA	NA	NA
Macromoths	*Eupithecia pimpinellata*	318000	312000	NA	NA	NA	NA
Macromoths	*Eupithecia plumbeolata*	350000	360000	287000	311000	NA	NA
Macromoths	*Eupithecia pulchellata*	833000	880000	NA	NA	NA	NA
Macromoths	*Eupithecia pusillata*	836000	873000	NA	NA	NA	NA
Macromoths	*Eupithecia simpliciata*	388000	461000	368000	412000	284000	351000
Macromoths	*Eupithecia subfuscata*	812000	875000	752000	804000	NA	NA
Macromoths	*Eupithecia subumbrata*	464000	429000	420000	342000	330000	314000
Macromoths	*Eupithecia succenturiata*	636000	661000	636000	636000	NA	NA
Macromoths	*Eupithecia tantillaria*	784000	804000	629000	743000	NA	NA
Macromoths	*Eupithecia tenuiata*	729000	776000	608000	744000	NA	NA
Macromoths	*Eupithecia tripunctaria*	609000	768000	537000	718000	NA	NA
Macromoths	*Eupithecia trisignaria*	369000	600000	NA	NA	NA	NA
Macromoths	*Eupithecia valerianata*	534000	703000	NA	NA	NA	NA
Macromoths	*Eupithecia venosata*	598000	644000	524000	540000	NA	NA
Macromoths	*Eupithecia virgaureata*	572000	840000	NA	NA	NA	NA
Macromoths	*Eupithecia vulgata*	836000	894000	794000	817000	NA	NA
Macromoths	*Euplexia lucipara*	853000	880000	NA	NA	NA	NA
Macromoths	*Euproctis chrysorrhoea*	331000	475000	296000	427000	254000	344000
Macromoths	*Euproctis similis*	566000	533000	508000	509000	NA	NA
Macromoths	*Eupsilia transversa*	780000	816000	712000	758000	NA	NA
Macromoths	*Eurois occulta*	821000	797000	NA	NA	NA	NA
Macromoths	*Euthrix potatoria*	821000	854000	765000	777000	NA	NA
Macromoths	*Euxoa cursoria*	843000	773000	NA	NA	NA	NA
Macromoths	*Euxoa nigricans*	828000	827000	787000	741000	NA	NA
Macromoths	*Euxoa tritici*	863000	844000	NA	NA	NA	NA
Macromoths	*Falcaria lacertinaria*	843000	860000	NA	NA	NA	NA
Macromoths	*Furcula bicuspis*	336000	417000	304000	393000	NA	NA
Macromoths	*Furcula bifida*	445000	461000	439000	429000	375000	409000
Macromoths	*Furcula furcula*	832000	809000	795000	785000	NA	NA
Macromoths	*Gastropacha quercifolia*	342000	322000	327000	312000	309000	308000
Macromoths	*Geometra papilionaria*	834000	864000	NA	NA	NA	NA
Macromoths	*Gortyna flavago*	796000	818000	734000	766000	NA	NA
Macromoths	*Graphiphora augur*	858000	898000	NA	NA	NA	NA
Macromoths	*Gymnoscelis rufifasciata*	826000	861000	800000	766000	NA	NA
Macromoths	*Habrosyne pyritoides*	481000	541000	461000	497000	NA	NA
Macromoths	*Hada plebeja*	832000	916000	793000	803000	NA	NA
Macromoths	*Hadena bicruris*	822000	813000	755000	733000	NA	NA

Macromoths	*Hadena confusa*	755000	794000	642000	733000	NA	NA
Macromoths	*Hadena perplexa*	524000	581000	524000	534000	NA	NA
Macromoths	*Hadena rivularis*	848000	856000	796000	711000	NA	NA
Macromoths	*Hecatera bicolorata*	687000	690000	577000	626000	NA	NA
Macromoths	*Helicoverpa armigera*	323000	373000	NA	NA	NA	NA
Macromoths	*Heliothis peltigera*	270000	510000	263000	423000	NA	NA
Macromoths	*Hemistola chrysoprasaria*	353000	336000	336000	333000	324000	328000
Macromoths	*Hemithea aestivaria*	450000	466000	450000	460000	429000	442000
Macromoths	*Hepialus fusconebulosa*	850000	910000	NA	NA	NA	NA
Macromoths	*Hepialus hecta*	828000	845000	784000	801000	NA	NA
Macromoths	*Hepialus humuli*	863000	896000	779000	793000	NA	NA
Macromoths	*Hepialus lupulinus*	720000	699000	678000	678000	NA	NA
Macromoths	*Hepialus sylvina*	786000	804000	695000	715000	NA	NA
Macromoths	*Herminia grisealis*	795000	821000	762000	763000	NA	NA
Macromoths	*Hoplodrina alsines*	691000	665000	645000	603000	NA	NA
Macromoths	*Hoplodrina ambigua*	248000	340000	238000	339000	238000	327000
Macromoths	*Hoplodrina blanda*	797000	758000	741000	708000	NA	NA
Macromoths	*Horisme tersata*	315000	323000	299000	315000	298000	292000
Macromoths	*Horisme vitalbata*	273000	300000	265000	282000	259000	280000
Macromoths	*Hydraecia petasitis*	571000	547000	538000	459000	NA	NA
Macromoths	*Hydrelia flammeolaria*	437000	641000	421000	608000	409000	558000
Macromoths	*Hydrelia sylvata*	302000	258000	NA	NA	NA	NA
Macromoths	*Hydriomena impluviata*	820000	873000	771000	806000	NA	NA
Macromoths	*Hydriomena ruberata*	780000	865000	677000	706000	NA	NA
Macromoths	*Hylaea fasciaria*	858000	916000	NA	NA	NA	NA
Macromoths	*Hyles gallii*	725000	515000	646000	426000	NA	NA
Macromoths	*Hyloicus pinastri*	253000	342000	235000	334000	211000	328000
Macromoths	*Hypena crassalis*	347000	334000	311000	321000	242000	271000
Macromoths	*Hypena rostralis*	258000	264000	240000	219000	NA	NA
Macromoths	*Hypenodes humidalis*	374000	576000	359000	452000	NA	NA
Macromoths	*Hypomecis punctinalis*	282000	326000	282000	325000	263000	309000
Macromoths	*Hypomecis roboraria*	264000	309000	237000	260000	233000	247000
Macromoths	*Idaea aversata*	853000	855000	NA	NA	NA	NA
Macromoths	*Idaea biselata*	851000	876000	797000	817000	NA	NA
Macromoths	*Idaea dimidiata*	624000	662000	616000	627000	NA	NA
Macromoths	*Idaea emarginata*	391000	366000	354000	363000	337000	355000
Macromoths	*Idaea fuscovenosa*	362000	396000	328000	386000	314000	362000
Macromoths	*Idaea muricata*	319000	374000	NA	NA	NA	NA
Macromoths	*Idaea seriata*	753000	823000	641000	694000	NA	NA
Macromoths	*Idaea straminata*	817000	842000	771000	780000	NA	NA
Macromoths	*Idaea subsericeata*	445000	412000	419000	343000	338000	342000
Macromoths	*Idaea sylvestraria*	300000	234000	280000	177000	264000	177000
Macromoths	*Idaea trigeminata*	288000	325000	286000	324000	285000	303000

Macromoths	*Ipimorpha retusa*	332000	339000	286000	278000	NA	NA
Macromoths	*Ipimorpha subtusa*	562000	560000	475000	491000	426000	440000
Macromoths	*Jodis lactearia*	553000	575000	547000	439000	NA	NA
Macromoths	*Lacanobia contigua*	778000	783000	726000	753000	425000	527000
Macromoths	*Lacanobia oleracea*	853000	889000	NA	NA	NA	NA
Macromoths	*Lacanobia suasa*	470000	506000	407000	454000	350000	362000
Macromoths	*Lacanobia thalassina*	848000	888000	NA	NA	NA	NA
Macromoths	*Lacanobia w-latinum*	342000	349000	308000	338000	276000	320000
Macromoths	*Lampropteryx otregiata*	290000	337000	NA	NA	NA	NA
Macromoths	*Lampropteryx suffumata*	853000	898000	NA	NA	NA	NA
Macromoths	*Laothoe populi*	879000	896000	NA	NA	NA	NA
Macromoths	*Larentia clavaria*	469000	431000	438000	395000	387000	357000
Macromoths	*Lasiocampa quercus*	NA	NA	787000	798000	NA	NA
Macromoths	*Laspeyria flexula*	339000	359000	324000	356000	307000	343000
Macromoths	*Leucoma salicis*	427000	455000	422000	426000	371000	405000
Macromoths	*Ligdia adustata*	383000	419000	329000	341000	329000	325000
Macromoths	*Lithophane hepatica*	316000	382000	257000	357000	194000	329000
Macromoths	*Lithophane ornitopus*	351000	365000	324000	365000	304000	343000
Macromoths	*Lithophane semibrunnea*	336000	390000	318000	372000	289000	343000
Macromoths	*Lithosia quadra*	363000	209000	NA	NA	NA	NA
Macromoths	*Lobophora halterata*	813000	810000	723000	791000	NA	NA
Macromoths	*Lomaspilis marginata*	833000	849000	756000	806000	NA	NA
Macromoths	*Lomographa bimaculata*	368000	407000	350000	370000	331000	357000
Macromoths	*Lomographa temerata*	616000	701000	595000	674000	NA	NA
Macromoths	*Luperina testacea*	824000	820000	763000	721000	NA	NA
Macromoths	*Lycia hirtaria*	813000	828000	793000	788000	NA	NA
Macromoths	*Lycophotia porphyrea*	866000	928000	NA	NA	NA	NA
Macromoths	*Lygephila pastinum*	446000	393000	376000	375000	336000	332000
Macromoths	*Lymantria monacha*	321000	326000	321000	323000	299000	309000
Macromoths	*Macaria alternata*	350000	348000	282000	302000	282000	273000
Macromoths	*Macaria liturata*	827000	832000	788000	783000	NA	NA
Macromoths	*Macaria notata*	820000	854000	718000	784000	NA	NA
Macromoths	*Macaria wauaria*	784000	686000	726000	655000	NA	NA
Macromoths	*Macrochilo cribrumalis*	296000	319000	NA	NA	NA	NA
Macromoths	*Macroglossum stellatarum*	626000	637000	390000	508000	365000	455000
Macromoths	*Macrothylacia rubi*	875000	887000	NA	NA	NA	NA
Macromoths	*Malacosoma neustria*	421000	473000	371000	437000	342000	407000
Macromoths	*Mamestra brassicae*	814000	801000	749000	709000	NA	NA
Macromoths	*Meganola albula*	215000	265000	NA	NA	NA	NA
Macromoths	*Melanchra persicariae*	562000	545000	549000	520000	NA	NA
Macromoths	*Melanchra pisi*	847000	869000	NA	NA	NA	NA

Macromoths	*Mesoleuca albicillata*	640000	785000	592000	685000	NA	NA
Macromoths	*Mesoligia furuncula*	719000	670000	711000	668000	NA	NA
Macromoths	*Mesoligia literosa*	831000	853000	744000	683000	NA	NA
Macromoths	*Miltochrista miniata*	335000	331000	327000	329000	313000	307000
Macromoths	*Mimas tiliae*	399000	450000	390000	432000	377000	406000
Macromoths	*Minoa murinata*	256000	250000	NA	NA	NA	NA
Macromoths	*Mormo maura*	655000	652000	538000	543000	418000	466000
Macromoths	*Mythimna comma*	761000	809000	663000	754000	NA	NA
Macromoths	*Mythimna ferrago*	841000	836000	NA	NA	NA	NA
Macromoths	*Mythimna l-album*	123000	108000	122000	108000	NA	NA
Macromoths	*Mythimna litoralis*	494000	433000	427000	393000	NA	NA
Macromoths	*Mythimna obsoleta*	366000	419000	339000	392000	NA	NA
Macromoths	*Mythimna pallens*	822000	796000	795000	727000	NA	NA
Macromoths	*Mythimna pudorina*	412000	366000	386000	357000	365000	356000
Macromoths	*Mythimna straminea*	416000	427000	375000	411000	359000	384000
Macromoths	*Mythimna turca*	294000	226000	NA	NA	NA	NA
Macromoths	*Mythimna unipuncta*	363000	240000	228000	208000	NA	NA
Macromoths	*Mythimna vitellina*	173000	389000	NA	NA	NA	NA
Macromoths	*Naenia typica*	847000	789000	771000	700000	NA	NA
Macromoths	*Noctua fimbriata*	791000	806000	686000	719000	NA	NA
Macromoths	*Noctua interjecta*	503000	529000	462000	507000	NA	NA
Macromoths	*Nola confusalis*	697000	813000	563000	750000	NA	NA
Macromoths	*Nola cucullatella*	482000	532000	461000	492000	NA	NA
Macromoths	*Nonagria typhae*	664000	752000	535000	602000	NA	NA
Macromoths	*Notodonta dromedarius*	848000	875000	NA	NA	NA	NA
Macromoths	*Notodonta ziczac*	835000	837000	NA	NA	NA	NA
Macromoths	*Nudaria mundana*	800000	798000	743000	746000	NA	NA
Macromoths	*Nycteola revayana*	654000	688000	341000	578000	329000	538000
Macromoths	*Ochropacha duplaris*	844000	863000	NA	NA	NA	NA
Macromoths	*Ochropleura plecta*	872000	922000	NA	NA	NA	NA
Macromoths	*Odezia atrata*	819000	815000	782000	732000	NA	NA
Macromoths	*Odontopera bidentata*	833000	898000	793000	821000	NA	NA
Macromoths	*Odontosia carmelita*	797000	821000	703000	749000	NA	NA
Macromoths	*Oligia fasciuncula*	866000	925000	NA	NA	NA	NA
Macromoths	*Oligia latruncula*	735000	551000	639000	474000	NA	NA
Macromoths	*Oligia strigilis*	827000	816000	NA	NA	NA	NA
Macromoths	*Oligia versicolor*	668000	639000	541000	580000	NA	NA
Macromoths	*Omphaloscelis lunosa*	765000	741000	717000	675000	NA	NA
Macromoths	*Operophtera brumata*	820000	894000	792000	790000	NA	NA
Macromoths	*Operophtera fagata*	819000	833000	790000	784000	NA	NA
Macromoths	*Orgyia antiqua*	817000	769000	760000	638000	NA	NA
Macromoths	*Orthonama obstipata*	534000	452000	494000	365000	NA	NA
Macromoths	*Orthonama vittata*	833000	848000	751000	789000	NA	NA
Macromoths	*Orthosia cerasi*	837000	903000	NA	NA	NA	NA
Macromoths	*Orthosia cruda*	757000	772000	717000	732000	NA	NA

Macromoths	*Orthosia gothica*	843000	919000	NA	NA	NA	NA
Macromoths	*Orthosia gracilis*	835000	804000	NA	NA	NA	NA
Macromoths	*Orthosia incerta*	837000	888000	NA	NA	NA	NA
Macromoths	*Orthosia miniosa*	338000	329000	283000	318000	263000	300000
Macromoths	*Orthosia munda*	618000	651000	517000	620000	NA	NA
Macromoths	*Orthosia opima*	560000	463000	446000	348000	NA	NA
Macromoths	*Orthosia populeti*	775000	639000	737000	549000	NA	NA
Macromoths	*Ourapteryx sambucaria*	690000	680000	669000	639000	NA	NA
Macromoths	*Pachycnemia hippocastanaria*	240000	146000	227000	146000	225000	144000
Macromoths	*Panemeria tenebrata*	462000	492000	404000	476000	376000	468000
Macromoths	*Panolis flammea*	825000	854000	794000	755000	NA	NA
Macromoths	*Papestra biren*	843000	849000	NA	NA	NA	NA
Macromoths	*Paradarisa consonaria*	332000	289000	309000	274000	287000	245000
Macromoths	*Paradrina clavipalpis*	869000	812000	NA	NA	NA	NA
Macromoths	*Parascotia fuliginaria*	234000	298000	229000	276000	214000	253000
Macromoths	*Parasemia plantaginis*	829000	839000	699000	681000	NA	NA
Macromoths	*Parastichtis suspecta*	794000	807000	742000	733000	NA	NA
Macromoths	*Parastichtis ypsillon*	575000	600000	560000	553000	NA	NA
Macromoths	*Parectropis similaria*	268000	313000	268000	304000	263000	278000
Macromoths	*Pasiphila rectangulata*	802000	854000	750000	763000	NA	NA
Macromoths	*Pelurga comitata*	654000	740000	588000	623000	NA	NA
Macromoths	*Perconia strigillaria*	678000	534000	486000	373000	312000	263000
Macromoths	*Peribatodes rhomboidaria*	855000	787000	788000	718000	NA	NA
Macromoths	*Peridea anceps*	430000	471000	368000	407000	351000	359000
Macromoths	*Peridroma saucia*	691000	540000	599000	478000	NA	NA
Macromoths	*Perizoma affinitata*	785000	820000	722000	756000	NA	NA
Macromoths	*Perizoma albulata*	871000	871000	NA	NA	NA	NA
Macromoths	*Perizoma alchemillata*	864000	894000	NA	NA	NA	NA
Macromoths	*Perizoma bifaciata*	575000	577000	500000	485000	NA	NA
Macromoths	*Perizoma flavofasciata*	708000	835000	702000	750000	NA	NA
Macromoths	*Petrophora chlorosata*	833000	878000	NA	NA	NA	NA
Macromoths	*Phalera bucephala*	836000	834000	784000	781000	NA	NA
Macromoths	*Pheosia gnoma*	860000	878000	NA	NA	NA	NA
Macromoths	*Pheosia tremula*	812000	827000	NA	NA	NA	NA
Macromoths	*Phibalapteryx virgata*	271000	284000	NA	NA	NA	NA
Macromoths	*Phigalia pilosaria*	839000	849000	NA	NA	NA	NA
Macromoths	*Philereme transversata*	409000	413000	356000	344000	354000	343000
Macromoths	*Philereme vetulata*	348000	356000	313000	334000	312000	318000
Macromoths	*Phlogophora meticulosa*	839000	892000	781000	813000	NA	NA
Macromoths	*Photedes minima*	841000	915000	NA	NA	NA	NA
Macromoths	*Phragmatobia fuliginosa*	834000	828000	799000	784000	NA	NA

Macromoths	*Phytometra viridaria*	790000	795000	613000	590000	297000	373000
Macromoths	*Plagodis dolabraria*	611000	665000	565000	599000	NA	NA
Macromoths	*Plagodis pulveraria*	755000	725000	631000	651000	NA	NA
Macromoths	*Plemyria rubiginata*	823000	801000	747000	710000	NA	NA
Macromoths	*Plusia festucae*	860000	892000	NA	NA	NA	NA
Macromoths	*Plusia putnami*	649000	733000	607000	701000	NA	NA
Macromoths	*Poecilocampa populi*	831000	860000	793000	815000	NA	NA
Macromoths	*Polia bombycina*	370000	278000	NA	NA	NA	NA
Macromoths	*Polia nebulosa*	804000	771000	781000	691000	NA	NA
Macromoths	*Polia trimaculosa*	805000	644000	782000	445000	NA	NA
Macromoths	*Polychrysia moneta*	550000	531000	542000	510000	NA	NA
Macromoths	*Polymixis flavicincta*	392000	366000	356000	348000	353000	344000
Macromoths	*Polymixis lichenea*	474000	488000	443000	481000	421000	442000
Macromoths	*Polyploca ridens*	348000	336000	307000	321000	291000	299000
Macromoths	*Protodeltote pygarga*	332000	346000	318000	342000	302000	337000
Macromoths	*Pseudoips prasinana*	604000	703000	554000	522000	NA	NA
Macromoths	*Pseudopanthera macularia*	774000	791000	431000	581000	326000	404000
Macromoths	*Pseudoterpna pruinata*	564000	615000	529000	570000	NA	NA
Macromoths	*Pterapherapteryx sexalata*	351000	405000	312000	359000	295000	302000
Macromoths	*Pterostoma palpina*	706000	834000	606000	805000	NA	NA
Macromoths	*Ptilodon capucina*	864000	888000	NA	NA	NA	NA
Macromoths	*Ptilodon cucullina*	304000	323000	300000	322000	296000	316000
Macromoths	*Pyrrhia umbra*	448000	546000	448000	487000	403000	353000
Macromoths	*Rheumaptera cervinalis*	325000	413000	280000	302000	252000	280000
Macromoths	*Rheumaptera hastata*	809000	772000	500000	530000	NA	NA
Macromoths	*Rheumaptera undulata*	422000	494000	362000	454000	351000	386000
Macromoths	*Rhizedra lutosa*	746000	756000	711000	648000	NA	NA
Macromoths	*Rhodometra sacraria*	480000	570000	430000	557000	376000	393000
Macromoths	*Rhyacia simulans*	492000	705000	373000	631000	NA	NA
Macromoths	*Rivula sericealis*	752000	816000	705000	698000	NA	NA
Macromoths	*Rusina ferruginea*	857000	893000	NA	NA	NA	NA
Macromoths	*Schrankia costaestrigalis*	604000	759000	495000	638000	378000	483000
Macromoths	*Schrankia taenialis*	222000	201000	206000	187000	NA	NA
Macromoths	*Scoliopteryx libatrix*	795000	829000	768000	719000	NA	NA
Macromoths	*Scopula emutaria*	308000	324000	299000	292000	NA	NA
Macromoths	*Scopula floslactata*	732000	767000	589000	623000	NA	NA
Macromoths	*Scopula imitaria*	430000	444000	420000	424000	371000	395000
Macromoths	*Scopula immutata*	413000	427000	352000	395000	349000	356000
Macromoths	*Scopula marginepunctata*	416000	394000	303000	322000	272000	283000

Macromoths	*Scotopteryx bipunctaria*	389000	334000	253000	197000	NA	NA
Macromoths	*Scotopteryx chenopodiata*	870000	877000	NA	NA	NA	NA
Macromoths	*Scotopteryx luridata*	829000	708000	NA	NA	NA	NA
Macromoths	*Scotopteryx mucronata*	810000	781000	753000	624000	NA	NA
Macromoths	*Selenia dentaria*	831000	898000	NA	NA	NA	NA
Macromoths	*Selenia lunularia*	799000	874000	748000	799000	NA	NA
Macromoths	*Selenia tetralunaria*	737000	766000	737000	705000	NA	NA
Macromoths	*Semiaspilates ochrearia*	303000	341000	282000	297000	223000	271000
Macromoths	*Sesia bembeciformis*	453000	716000	NA	NA	NA	NA
Macromoths	*Shargacucullia verbasci*	451000	453000	440000	417000	400000	371000
Macromoths	*Sideridis albicolon*	413000	458000	330000	348000	NA	NA
Macromoths	*Smerinthus ocellata*	473000	480000	448000	463000	425000	421000
Macromoths	*Spaelotis ravida*	439000	419000	418000	408000	402000	323000
Macromoths	*Sphinx ligustri*	373000	396000	368000	328000	353000	323000
Macromoths	*Spilosoma lubricipeda*	852000	915000	NA	NA	NA	NA
Macromoths	*Spilosoma luteum*	798000	773000	734000	680000	NA	NA
Macromoths	*Spodoptera exigua*	355000	403000	285000	361000	231000	318000
Macromoths	*Standfussiana lucernea*	868000	643000	NA	NA	NA	NA
Macromoths	*Stauropus fagi*	350000	331000	310000	326000	290000	306000
Macromoths	*Stilbia anomala*	873000	884000	NA	NA	NA	NA
Macromoths	*Tethea ocularis*	444000	553000	439000	496000	425000	491000
Macromoths	*Tethea or*	813000	834000	522000	811000	408000	608000
Macromoths	*Tetheella fluctuosa*	336000	428000	280000	380000	238000	297000
Macromoths	*Thalpophila matura*	772000	733000	582000	612000	NA	NA
Macromoths	*Thera firmata*	823000	861000	792000	829000	NA	NA
Macromoths	*Thera juniperata*	815000	832000	794000	805000	NA	NA
Macromoths	*Thera obeliscata*	844000	904000	NA	NA	NA	NA
Macromoths	*Theria primaria*	656000	637000	618000	594000	NA	NA
Macromoths	*Tholera cespitis*	797000	657000	711000	516000	NA	NA
Macromoths	*Tholera decimalis*	673000	641000	602000	611000	NA	NA
Macromoths	*Thumatha senex*	416000	489000	365000	446000	357000	356000
Macromoths	*Thyatira batis*	778000	800000	773000	773000	NA	NA
Macromoths	*Timandra comae*	504000	555000	493000	509000	NA	NA
Macromoths	*Trichiura crataegi*	860000	885000	NA	NA	NA	NA
Macromoths	*Trichopteryx carpinata*	835000	883000	NA	NA	NA	NA
Macromoths	*Triphosa dubitata*	459000	460000	429000	410000	374000	345000
Macromoths	*Tyria jacobaeae*	715000	659000	605000	618000	NA	NA
Macromoths	*Watsonalla binaria*	430000	470000	420000	458000	402000	420000
Macromoths	*Watsonalla cultraria*	337000	354000	306000	318000	285000	297000
Macromoths	*Xanthia aurago*	445000	441000	384000	400000	333000	384000

Macromoths	*Xanthia citrago*	767000	734000	656000	715000	NA	NA
Macromoths	*Xanthia gilvago*	572000	618000	507000	578000	NA	NA
Macromoths	*Xanthia icteritia*	843000	904000	NA	NA	NA	NA
Macromoths	*Xanthia togata*	835000	904000	799000	833000	NA	NA
Macromoths	*Xanthorhoe designata*	853000	905000	NA	NA	NA	NA
Macromoths	*Xanthorhoe ferrugata*	802000	707000	775000	668000	NA	NA
Macromoths	*Xanthorhoe fluctuata*	865000	917000	NA	NA	NA	NA
Macromoths	*Xanthorhoe quadrifasiata*	370000	441000	347000	402000	337000	365000
Macromoths	*Xanthorhoe spadicearia*	815000	852000	790000	801000	NA	NA
Macromoths	*Xestia agathina*	844000	910000	NA	NA	NA	NA
Macromoths	*Xestia baja*	847000	899000	NA	NA	NA	NA
Macromoths	*Xestia c-nigrum*	856000	903000	NA	NA	NA	NA
Macromoths	*Xestia castanea*	872000	856000	NA	NA	NA	NA
Macromoths	*Xestia ditrapezium*	784000	753000	719000	589000	NA	NA
Macromoths	*Xestia rhomboidea*	538000	471000	425000	377000	NA	NA
Macromoths	*Xestia sexstrigata*	872000	915000	NA	NA	NA	NA
Macromoths	*Xestia triangulum*	834000	869000	NA	NA	NA	NA
Macromoths	*Xylena vetusta*	822000	883000	NA	NA	NA	NA
Macromoths	*Xylocampa areola*	781000	742000	672000	648000	NA	NA
Macromoths	*Zanclognatha tarsipennalis*	664000	667000	636000	638000	NA	NA
Macromoths	*Zeuzera pyrina*	400000	436000	371000	412000	337000	384000
Macromoths	*Zygaena filipendulae*	823000	873000	629000	741000	NA	NA
Macromoths	*Zygaena lonicerae*	602000	615000	521000	548000	NA	NA
Macromoths	*Zygaena trifolii*	414000	322000	347000	300000	320000	265000
Millipedes	*Blaniulus guttulatus*	435000	587000	336000	525000	NA	NA
Millipedes	*Brachydesmus superus*	457000	677000	457000	558000	NA	NA
Millipedes	*Cylindroiulus latestriatus*	456000	645000	NA	NA	NA	NA
Millipedes	*Glomeris marginata*	552000	552000	NA	NA	NA	NA
Millipedes	*Julus scandinavius*	737000	795000	NA	NA	NA	NA
Millipedes	*Nemasoma varicorne*	552000	607000	440000	497000	NA	NA
Millipedes	*Ommatoiulus sabulosus*	736000	743000	NA	NA	NA	NA
Millipedes	*Ophyiulus pilosus*	NA	NA	454000	661000	NA	NA
Millipedes	*Polydesmus angustus*	738000	751000	NA	NA	NA	NA
Millipedes	*Polydesmus coriaceus*	349000	392000	NA	NA	NA	NA
Millipedes	*Polydesmus denticulatus*	461000	489000	NA	NA	NA	NA
Millipedes	*Polydesmus inconstans*	404000	482000	NA	NA	NA	NA
Spiders	*Agelena labyrinthica*	289000	355000	NA	NA	NA	NA
Spiders	*Agroeca brunnea*	306000	322000	NA	NA	NA	NA
Spiders	*Agroeca proxima*	378000	717000	NA	NA	NA	NA
Spiders	*Agyneta conigera*	361000	688000	NA	NA	NA	NA

Spiders	*Agyneta subtilis*	469000	619000	NA	NA	NA	NA
Spiders	*Alopecosa barbipes*	279000	371000	NA	NA	NA	NA
Spiders	*Alopecosa pulverulenta*	666000	816000	NA	NA	NA	NA
Spiders	*Amaurobius fenestralis*	756000	798000	NA	NA	NA	NA
Spiders	*Anelosimus vittatus*	288000	478000	NA	NA	NA	NA
Spiders	*Antistea elegans*	538000	720000	NA	NA	NA	NA
Spiders	*Aphileta misera*	513000	507000	NA	NA	NA	NA
Spiders	*Araeoncus humilis*	541000	522000	NA	NA	NA	NA
Spiders	*Araneus quadratus*	321000	781000	NA	NA	NA	NA
Spiders	*Arctosa perita*	358000	551000	NA	NA	NA	NA
Spiders	*Bathyphantes approximatus*	528000	598000	NA	NA	NA	NA
Spiders	*Bathyphantes gracilis*	685000	806000	NA	NA	NA	NA
Spiders	*Bathyphantes nigrinus*	581000	695000	NA	NA	NA	NA
Spiders	*Bathyphantes parvulus*	518000	626000	NA	NA	NA	NA
Spiders	*Centromerita bicolor*	570000	787000	NA	NA	NA	NA
Spiders	*Centromerita concinna*	681000	830000	NA	NA	NA	NA
Spiders	*Centromerus dilutus*	514000	772000	NA	NA	NA	NA
Spiders	*Centromerus sylvaticus*	493000	756000	NA	NA	NA	NA
Spiders	*Ceratinella brevipes*	785000	840000	NA	NA	NA	NA
Spiders	*Ceratinella brevis*	430000	668000	NA	NA	NA	NA
Spiders	*Clubiona comta*	497000	732000	NA	NA	NA	NA
Spiders	*Clubiona corticalis*	300000	357000	NA	NA	NA	NA
Spiders	*Clubiona diversa*	610000	756000	NA	NA	NA	NA
Spiders	*Clubiona lutescens*	416000	679000	NA	NA	NA	NA
Spiders	*Clubiona phragmitis*	399000	501000	301000	348000	NA	NA
Spiders	*Clubiona reclusa*	409000	798000	303000	486000	NA	NA
Spiders	*Clubiona stagnatilis*	394000	494000	NA	NA	NA	NA
Spiders	*Clubiona subtilis*	334000	329000	NA	NA	NA	NA
Spiders	*Clubiona terrestris*	419000	584000	307000	375000	NA	NA
Spiders	*Cnephalocotes obscurus*	575000	683000	NA	NA	NA	NA
Spiders	*Crustulina guttata*	351000	338000	NA	NA	NA	NA
Spiders	*Dictyna arundinacea*	611000	718000	NA	NA	NA	NA
Spiders	*Dicymbium nigrum*	743000	696000	NA	NA	NA	NA
Spiders	*Diplocephalus cristatus*	563000	730000	NA	NA	NA	NA
Spiders	*Diplocephalus latifrons*	504000	779000	NA	NA	NA	NA
Spiders	*Diplocephalus permixtus*	627000	788000	NA	NA	NA	NA
Spiders	*Diplocephalus picinus*	428000	736000	NA	NA	NA	NA
Spiders	*Diplostyla concolor*	615000	735000	NA	NA	NA	NA
Spiders	*Dismodicus bifrons*	674000	776000	NA	NA	NA	NA
Spiders	*Drapetisca socialis*	339000	737000	NA	NA	NA	NA
Spiders	*Drassodes cupreus*	399000	784000	NA	NA	NA	NA
Spiders	*Drassodes lapidosus*	541000	386000	NA	NA	NA	NA

Spiders	*Enoplognatha thoracica*	220000	443000	NA	NA	NA	NA
Spiders	*Episinus angulatus*	377000	408000	NA	NA	NA	NA
Spiders	*Erigone atra*	517000	817000	NA	NA	NA	NA
Spiders	*Erigone dentipalpis*	618000	838000	NA	NA	NA	NA
Spiders	*Erigonella hiemalis*	493000	776000	NA	NA	NA	NA
Spiders	*Ero cambridgei*	356000	679000	NA	NA	NA	NA
Spiders	*Ero furcata*	360000	677000	NA	NA	NA	NA
Spiders	*Euophrys frontalis*	400000	501000	NA	NA	NA	NA
Spiders	*Evarcha falcata*	364000	419000	NA	NA	NA	NA
Spiders	*Floronia bucculenta*	309000	442000	NA	NA	NA	NA
Spiders	*Gnathonarium dentatum*	481000	629000	NA	NA	NA	NA
Spiders	*Gonatium rubellum*	379000	778000	NA	NA	NA	NA
Spiders	*Gonatium rubens*	771000	796000	NA	NA	NA	NA
Spiders	*Gongylidiellum vivum*	476000	731000	NA	NA	NA	NA
Spiders	*Gongylidium rufipes*	436000	676000	NA	NA	NA	NA
Spiders	*Hahnia helveola*	387000	481000	NA	NA	NA	NA
Spiders	*Hahnia montana*	589000	769000	NA	NA	NA	NA
Spiders	*Hahnia nava*	414000	587000	NA	NA	NA	NA
Spiders	*Haplodrassus signifer*	320000	784000	NA	NA	NA	NA
Spiders	*Harpactea hombergi*	372000	548000	NA	NA	NA	NA
Spiders	*Heliophanus cupreus*	283000	302000	NA	NA	NA	NA
Spiders	*Heliophanus flavipes*	275000	549000	NA	NA	NA	NA
Spiders	*Helophora insignis*	389000	734000	NA	NA	NA	NA
Spiders	*Hypomma bituberculatum*	590000	741000	NA	NA	NA	NA
Spiders	*Hypselistes jacksoni*	447000	509000	NA	NA	NA	NA
Spiders	*Hypsosinga pygmaea*	395000	369000	NA	NA	NA	NA
Spiders	*Kaestneria pullata*	471000	568000	NA	NA	NA	NA
Spiders	*Labulla thoracica*	509000	761000	NA	NA	NA	NA
Spiders	*Larinioides cornutus*	388000	835000	NA	NA	NA	NA
Spiders	*Lathys humilis*	221000	341000	NA	NA	NA	NA
Spiders	*Lepthyphantes alacris*	727000	776000	NA	NA	NA	NA
Spiders	*Lepthyphantes cristatus*	617000	752000	NA	NA	NA	NA
Spiders	*Lepthyphantes ericaeus*	795000	848000	NA	NA	NA	NA
Spiders	*Lepthyphantes flavipes*	360000	727000	308000	341000	NA	NA
Spiders	*Lepthyphantes minutus*	411000	776000	NA	NA	NA	NA
Spiders	*Lepthyphantes obscurus*	518000	779000	NA	NA	NA	NA
Spiders	*Lepthyphantes pallidus*	629000	744000	NA	NA	NA	NA
Spiders	*Lepthyphantes tenuis*	757000	861000	NA	NA	NA	NA

Spiders	*Lepthyphantes zimmermanni*	831000	871000	NA	NA	NA	NA
Spiders	*Leptorhoptrum robustum*	422000	675000	NA	NA	NA	NA
Spiders	*Linyphia hortensis*	306000	578000	NA	NA	NA	NA
Spiders	*Linyphia triangularis*	496000	793000	NA	NA	NA	NA
Spiders	*Lophomma punctatum*	548000	692000	NA	NA	NA	NA
Spiders	*Macrargus rufus*	476000	728000	NA	NA	NA	NA
Spiders	*Maso sundevalli*	532000	729000	NA	NA	NA	NA
Spiders	*Meioneta rurestris*	408000	672000	307000	400000	NA	NA
Spiders	*Metellina mengei*	725000	821000	NA	NA	NA	NA
Spiders	*Metellina merianae*	800000	835000	NA	NA	NA	NA
Spiders	*Metopobactrus prominulus*	496000	503000	NA	NA	NA	NA
Spiders	*Micaria pulicaria*	433000	616000	NA	NA	NA	NA
Spiders	*Microlinyphia impigra*	307000	328000	NA	NA	NA	NA
Spiders	*Microlinyphia pusilla*	594000	809000	NA	NA	NA	NA
Spiders	*Microneta viaria*	486000	743000	NA	NA	NA	NA
Spiders	*Monocephalus fuscipes*	748000	825000	NA	NA	NA	NA
Spiders	*Neon reticulatus*	541000	683000	NA	NA	NA	NA
Spiders	*Neriene clathrata*	572000	733000	NA	NA	NA	NA
Spiders	*Neriene montana*	348000	676000	NA	NA	NA	NA
Spiders	*Neriene peltata*	400000	762000	NA	NA	NA	NA
Spiders	*Nuctenea umbratica*	476000	789000	NA	NA	NA	NA
Spiders	*Oedothorax fuscus*	491000	840000	NA	NA	NA	NA
Spiders	*Oedothorax gibbosus*	641000	816000	NA	NA	NA	NA
Spiders	*Oedothorax retusus*	558000	758000	NA	NA	NA	NA
Spiders	*Ozyptila atomaria*	482000	475000	NA	NA	NA	NA
Spiders	*Ozyptila trux*	472000	778000	NA	NA	NA	NA
Spiders	*Pachygnatha clercki*	562000	791000	NA	NA	NA	NA
Spiders	*Pachygnatha degeeri*	725000	741000	NA	NA	NA	NA
Spiders	*Pardosa amentata*	767000	806000	NA	NA	NA	NA
Spiders	*Pardosa monticola*	314000	439000	NA	NA	NA	NA
Spiders	*Pardosa nigriceps*	531000	819000	NA	NA	NA	NA
Spiders	*Pardosa palustris*	584000	766000	NA	NA	NA	NA
Spiders	*Pardosa prativaga*	365000	479000	NA	NA	NA	NA
Spiders	*Peponocranium ludicrum*	698000	667000	NA	NA	NA	NA
Spiders	*Philodromus aureolus*	444000	781000	NA	NA	NA	NA
Spiders	*Philodromus cespitum*	356000	706000	NA	NA	NA	NA
Spiders	*Philodromus dispar*	283000	392000	NA	NA	NA	NA
Spiders	*Pholcomma gibbum*	582000	783000	NA	NA	NA	NA
Spiders	*Phrurolithus festivus*	262000	322000	NA	NA	NA	NA
Spiders	*Pirata hygrophilus*	408000	533000	NA	NA	NA	NA
Spiders	*Pirata latitans*	367000	350000	NA	NA	NA	NA

Spiders	*Pirata piraticus*	630000	822000	NA	NA	NA	NA
Spiders	*Pirata uliginosus*	453000	557000	NA	NA	NA	NA
Spiders	*Pisaura mirabilis*	348000	483000	298000	361000	NA	NA
Spiders	*Pocadicnemis juncea*	367000	474000	NA	NA	NA	NA
Spiders	*Porrhomma pygmaeum*	517000	703000	NA	NA	NA	NA
Spiders	*Robertus lividus*	839000	873000	NA	NA	NA	NA
Spiders	*Saaristoa abnormis*	705000	826000	NA	NA	NA	NA
Spiders	*Salticus scenicus*	317000	543000	NA	NA	NA	NA
Spiders	*Segestria senoculata*	755000	810000	NA	NA	NA	NA
Spiders	*Steatoda bipunctata*	300000	616000	NA	NA	NA	NA
Spiders	*Stemonyphantes lineatus*	559000	723000	NA	NA	NA	NA
Spiders	*Tallusia experta*	527000	496000	NA	NA	NA	NA
Spiders	*Tapinocyba praecox*	394000	423000	NA	NA	NA	NA
Spiders	*Tapinopa longidens*	573000	769000	NA	NA	NA	NA
Spiders	*Taranucnus setosus*	332000	348000	NA	NA	NA	NA
Spiders	*Tetragnatha extensa*	607000	838000	NA	NA	NA	NA
Spiders	*Tetragnatha montana*	470000	580000	NA	NA	NA	NA
Spiders	*Textrix denticulata*	749000	809000	NA	NA	NA	NA
Spiders	*Theridion sisyphium*	518000	770000	NA	NA	NA	NA
Spiders	*Theridion varians*	301000	660000	NA	NA	NA	NA
Spiders	*Tibellus oblongus*	365000	701000	NA	NA	NA	NA
Spiders	*Tiso vagans*	623000	725000	NA	NA	NA	NA
Spiders	*Trichopterna thorelli*	268000	539000	NA	NA	NA	NA
Spiders	*Trochosa ruricola*	437000	401000	NA	NA	NA	NA
Spiders	*Trochosa terricola*	665000	789000	NA	NA	NA	NA
Spiders	*Walckenaeria acuminata*	742000	870000	NA	NA	NA	NA
Spiders	*Walckenaeria antica*	513000	703000	NA	NA	NA	NA
Spiders	*Walckenaeria atrotibialis*	438000	402000	NA	NA	NA	NA
Spiders	*Walckenaeria cucullata*	345000	519000	NA	NA	NA	NA
Spiders	*Walckenaeria cuspidata*	661000	799000	NA	NA	NA	NA
Spiders	*Walckenaeria nudipalpis*	722000	822000	NA	NA	NA	NA
Spiders	*Walckenaeria unicornis*	399000	494000	NA	NA	NA	NA
Spiders	*Walckenaeria vigilax*	446000	470000	NA	NA	NA	NA
Spiders	*Xysticus cristatus*	753000	812000	NA	NA	NA	NA
Spiders	*Xysticus erraticus*	244000	482000	NA	NA	NA	NA
Spiders	*Zelotes latreillei*	322000	536000	NA	NA	NA	NA
Spiders	*Zora spinimana*	386000	585000	NA	NA	NA	NA
Spiders	*Zygiella atrica*	456000	625000	NA	NA	NA	NA

Spiders	*Zygiella x-notata*	439000	703000	NA	NA	NA	NA
Woodlice	*Androniscus dentiger*	511000	738000	505000	724000	379000	409000
Woodlice	*Armadillidium nasatum*	253000	283000	NA	NA	NA	NA
Woodlice	*Armadillidium vulgare*	525000	647000	525000	643000	NA	NA
Woodlice	*Asellus aquaticus*	669000	624000	616000	594000	379000	420000
Woodlice	*Haplophthalmus danicus*	284000	384000	284000	384000	NA	NA
Woodlice	*Ligidium hypnorum*	238000	288000	219000	260000	NA	NA
Woodlice	*Philoscia muscorum*	752000	887000	NA	NA	NA	NA
Woodlice	*Platyarthrus hoffmannseggii*	423000	467000	420000	452000	349000	352000
Woodlice	*Porcellio spinicornis*	540000	738000	540000	736000	NA	NA
Woodlice	*Porcellionides cingendus*	208000	275000	198000	265000	NA	NA
Woodlice	*Porcellionides pruinosus*	383000	495000	370000	436000	NA	NA
Woodlice	*Proasellus meridianus*	593000	454000	593000	416000	NA	NA
Woodlice	*Trichoniscus pygmaeus*	484000	743000	474000	702000	NA	NA

Table A2.5. Northern range margin locations (in metres, on the GB Ordnance Survey Grid) during interval 2 of all species included in Figure 3, for each time period T2 (1986-1995) or T3 (2001-2010) and for each level of recording effort control (Recorded, Well Recorded or Heavily Recorded). For bird species, the time period years are 1988-1991 for T2 and 2007-2011 for T3. Margin values which are denoted as 'C' indicate confidential data. Note that for species which also qualify for analysis in interval 1, the calculation of range margin locations for 1986-1995 in interval 1 (in Table A2.4) will differ from values for 1986-1995 in interval 2 due to a different set of hectads being analysed. Ground beetles are denoted by 'G beetles'.

Taxonomic group	Species	Recorded T1	Recorded T2	Well recorded T1	Well recorded T2	Heavily recorded T1	Heavily recorded T2
Ants	*Formica cunicularia*	235000	238000	188000	195000	NA	NA
Ants	*Formica fusca*	353000	417000	NA	NA	NA	NA
Ants	*Formica rufa*	298000	313000	NA	NA	NA	NA
Ants	*Formica sanguinea*	431000	571000	NA	NA	NA	NA
Ants	*Lasius brunneus*	203000	241000	NA	NA	NA	NA
Ants	*Lasius fuliginosus*	286000	319000	208000	258000	NA	NA
Ants	*Myrmecina graminicola*	192000	202000	NA	NA	NA	NA
Ants	*Myrmica scabrinodis*	416000	855000	NA	NA	NA	NA
Ants	*Myrmica schencki*	197000	236000	NA	NA	NA	NA
Ants	*Stenamma debile*	213000	246000	NA	NA	NA	NA
Ants	*Temnothorax nylanderi*	225000	224000	NA	NA	NA	NA
Ants	*Tetramorium caespitum*	256000	375000	195000	284000	NA	NA
Aquatic Bugs	*Corixa dentipes*	455000	626000	NA	NA	NA	NA
Aquatic Bugs	*Corixa panzeri*	370000	437000	355000	405000	NA	NA
Aquatic Bugs	*Cymatia coleoptrata*	389000	423000	387000	376000	NA	NA
Aquatic Bugs	*Gerris gibbifer*	403000	377000	NA	NA	NA	NA
Aquatic Bugs	*Gerris thoracicus*	493000	730000	410000	659000	NA	NA
Aquatic Bugs	*Hebrus ruficeps*	439000	385000	NA	NA	NA	NA
Aquatic Bugs	*Hesperocorixa castanea*	720000	695000	NA	NA	NA	NA
Aquatic Bugs	*Hesperocorixa linnaei*	NA	NA	394000	503000	NA	NA
Aquatic Bugs	*Hesperocorixa moesta*	255000	341000	NA	NA	NA	NA
Aquatic Bugs	*Hydrometra stagnorum*	485000	519000	NA	NA	NA	NA
Aquatic Bugs	*Ilyocoris cimicoides*	371000	447000	371000	407000	NA	NA
Aquatic Bugs	*Mesovelia furcata*	341000	322000	NA	NA	NA	NA
Aquatic Bugs	*Micronecta poweri*	488000	498000	NA	NA	NA	NA
Aquatic Bugs	*Micronecta scholtzi*	326000	412000	NA	NA	NA	NA

Aquatic Bugs	*Microvelia reticulata*	402000	596000	330000	502000	NA	NA
Aquatic Bugs	*Notonecta glauca*	722000	713000	NA	NA	NA	NA
Aquatic Bugs	*Notonecta maculata*	375000	462000	367000	372000	NA	NA
Aquatic Bugs	*Notonecta viridis*	344000	467000	344000	405000	NA	NA
Aquatic Bugs	*Plea minutissima*	407000	486000	387000	411000	NA	NA
Aquatic Bugs	*Ranatra linearis*	304000	425000	297000	400000	NA	NA
Aquatic Bugs	*Sigara falleni*	726000	711000	NA	NA	NA	NA
Aquatic Bugs	*Sigara stagnalis*	386000	355000	370000	305000	NA	NA
Bees	*Andrena angustior*	452000	333000	296000	250000	NA	NA
Bees	*Andrena argentata*	146000	161000	NA	NA	NA	NA
Bees	*Andrena barbilabris*	496000	623000	431000	499000	NA	NA
Bees	*Andrena bicolor*	494000	747000	NA	NA	NA	NA
Bees	*Andrena bimaculata*	227000	298000	221000	246000	NA	NA
Bees	*Andrena bucephala*	232000	231000	182000	213000	NA	NA
Bees	*Andrena carantonica*	746000	850000	NA	NA	NA	NA
Bees	*Andrena chrysosceles*	468000	476000	NA	NA	NA	NA
Bees	*Andrena cineraria*	490000	491000	421000	450000	NA	NA
Bees	*Andrena clarkella*	481000	771000	448000	580000	NA	NA
Bees	*Andrena coitana*	418000	489000	NA	NA	NA	NA
Bees	*Andrena denticulata*	402000	731000	351000	540000	NA	NA
Bees	*Andrena dorsata*	303000	331000	286000	302000	NA	NA
Bees	*Andrena flavipes*	221000	310000	182000	280000	170000	215000
Bees	*Andrena fucata*	705000	713000	NA	NA	NA	NA
Bees	*Andrena fulva*	492000	486000	NA	NA	NA	NA
Bees	*Andrena fuscipes*	447000	572000	385000	432000	NA	NA
Bees	*Andrena haemorrhoa*	802000	847000	NA	NA	NA	NA
Bees	*Andrena hattorfiana*	188000	248000	NA	NA	NA	NA
Bees	*Andrena helvola*	429000	423000	379000	381000	NA	NA
Bees	*Andrena humilis*	415000	452000	354000	371000	NA	NA
Bees	*Andrena labialis*	238000	245000	201000	203000	NA	NA
Bees	*Andrena labiata*	215000	280000	168000	224000	NA	NA
Bees	*Andrena lapponica*	807000	695000	NA	NA	NA	NA
Bees	*Andrena minutula*	463000	480000	397000	424000	NA	NA
Bees	*Andrena nigroaenea*	465000	511000	442000	490000	NA	NA
Bees	*Andrena nitida*	294000	324000	263000	302000	NA	NA
Bees	*Andrena ovatula*	309000	338000	219000	275000	NA	NA
Bees	*Andrena praecox*	328000	385000	278000	316000	NA	NA
Bees	*Andrena proxima*	196000	161000	NA	NA	NA	NA
Bees	*Andrena semilaevis*	478000	523000	NA	NA	NA	NA
Bees	*Andrena subopaca*	734000	830000	437000	609000	NA	NA
Bees	*Andrena synadelpha*	303000	375000	246000	335000	NA	NA
Bees	*Andrena tarsata*	547000	704000	NA	NA	NA	NA
Bees	*Andrena thoracica*	266000	293000	200000	240000	NA	NA
Bees	*Andrena tibialis*	321000	330000	274000	259000	NA	NA
Bees	*Andrena trimmerana*	243000	215000	226000	177000	NA	NA
Bees	*Andrena wilkella*	743000	602000	NA	NA	NA	NA

Bees	*Anthophora plumipes*	375000	429000	281000	337000	NA	NA
Bees	*Apis mellifera*	485000	559000	NA	NA	NA	NA
Bees	*Bombus barbutellus*	571000	473000	304000	310000	NA	NA
Bees	*Bombus bohemicus*	875000	880000	NA	NA	NA	NA
Bees	*Bombus campestris*	647000	577000	402000	459000	NA	NA
Bees	*Bombus humilis*	229000	213000	177000	209000	NA	NA
Bees	*Bombus lapidarius*	658000	858000	NA	NA	NA	NA
Bees	*Bombus muscorum*	842000	918000	NA	NA	NA	NA
Bees	*Bombus pratorum*	857000	867000	NA	NA	NA	NA
Bees	*Bombus ruderarius*	445000	418000	275000	262000	NA	NA
Bees	*Bombus rupestris*	205000	408000	NA	NA	NA	NA
Bees	*Bombus sylvestris*	775000	854000	NA	NA	NA	NA
Bees	*Bombus terrestris*	643000	852000	NA	NA	NA	NA
Bees	*Bombus vestalis*	555000	504000	419000	471000	NA	NA
Bees	*Chelostoma campanularum*	212000	288000	196000	231000	NA	NA
Bees	*Chelostoma florisomne*	415000	377000	308000	220000	NA	NA
Bees	*Coelioxys conoidea*	238000	249000	NA	NA	NA	NA
Bees	*Coelioxys elongata*	561000	396000	NA	NA	NA	NA
Bees	*Coelioxys rufescens*	257000	273000	250000	215000	NA	NA
Bees	*Colletes daviesanus*	483000	556000	NA	NA	NA	NA
Bees	*Colletes fodiens*	371000	402000	281000	339000	NA	NA
Bees	*Colletes similis*	240000	239000	188000	215000	NA	NA
Bees	*Colletes succinctus*	548000	906000	424000	535000	NA	NA
Bees	*Dasypoda hirtipes*	248000	278000	223000	236000	NA	NA
Bees	*Epeolus cruciger*	394000	432000	355000	393000	NA	NA
Bees	*Epeolus variegatus*	396000	401000	347000	370000	NA	NA
Bees	*Halictus rubicundus*	802000	857000	NA	NA	NA	NA
Bees	*Halictus tumulorum*	503000	604000	NA	NA	NA	NA
Bees	*Hoplitis claviventris*	303000	327000	274000	267000	NA	NA
Bees	*Hylaeus brevicornis*	408000	383000	353000	361000	NA	NA
Bees	*Hylaeus communis*	443000	485000	425000	431000	NA	NA
Bees	*Hylaeus confusus*	397000	444000	293000	274000	NA	NA
Bees	*Hylaeus cornutus*	193000	217000	174000	207000	NA	NA
Bees	*Hylaeus dilatatus*	267000	281000	240000	249000	NA	NA
Bees	*Hylaeus hyalinatus*	429000	456000	390000	366000	NA	NA
Bees	*Hylaeus signatus*	336000	384000	312000	339000	NA	NA
Bees	*Lasioglossum albipes*	621000	737000	NA	NA	NA	NA
Bees	*Lasioglossum calceatum*	766000	855000	NA	NA	NA	NA
Bees	*Lasioglossum cupromicans*	537000	542000	NA	NA	NA	NA
Bees	*Lasioglossum fratellum*	829000	850000	NA	NA	NA	NA
Bees	*Lasioglossum fulvicorne*	481000	448000	410000	306000	NA	NA
Bees	*Lasioglossum laevigatum*	223000	229000	200000	190000	NA	NA
Bees	*Lasioglossum lativentre*	189000	331000	166000	309000	NA	NA

Bees	*Lasioglossum leucopus*	779000	668000	NA	NA	NA	NA
Bees	*Lasioglossum leucozonium*	378000	437000	363000	398000	NA	NA
Bees	*Lasioglossum malachurum*	205000	278000	179000	257000	NA	NA
Bees	*Lasioglossum minutissimum*	292000	328000	265000	311000	NA	NA
Bees	*Lasioglossum morio*	367000	382000	340000	343000	NA	NA
Bees	*Lasioglossum parvulum*	333000	310000	263000	264000	NA	NA
Bees	*Lasioglossum pauxillum*	214000	288000	NA	NA	NA	NA
Bees	*Lasioglossum prasinum*	150000	155000	NA	NA	NA	NA
Bees	*Lasioglossum punctatissimum*	433000	417000	330000	371000	NA	NA
Bees	*Lasioglossum rufitarse*	648000	715000	NA	NA	NA	NA
Bees	*Lasioglossum smeathmanellum*	457000	484000	447000	441000	NA	NA
Bees	*Lasioglossum villosulum*	553000	496000	NA	NA	NA	NA
Bees	*Lasioglossum xanthopus*	207000	227000	NA	NA	NA	NA
Bees	*Lasioglossum zonulum*	184000	187000	166000	169000	158000	155000
Bees	*Macropis europaea*	212000	247000	NA	NA	NA	NA
Bees	*Megachile centuncularis*	508000	632000	NA	NA	NA	NA
Bees	*Megachile dorsalis*	256000	323000	NA	NA	NA	NA
Bees	*Megachile ligniseca*	294000	345000	250000	322000	NA	NA
Bees	*Megachile maritima*	288000	275000	211000	247000	NA	NA
Bees	*Megachile versicolor*	423000	457000	384000	425000	NA	NA
Bees	*Megachile willughbiella*	461000	561000	432000	516000	NA	NA
Bees	*Melecta albifrons*	224000	345000	NA	NA	NA	NA
Bees	*Melitta leporina*	252000	246000	217000	225000	NA	NA
Bees	*Melitta tricincta*	179000	173000	170000	162000	NA	NA
Bees	*Nomada fabriciana*	480000	492000	438000	470000	NA	NA
Bees	*Nomada flava*	371000	444000	345000	424000	NA	NA
Bees	*Nomada flavoguttata*	482000	604000	435000	523000	NA	NA
Bees	*Nomada flavopicta*	261000	275000	261000	240000	NA	NA
Bees	*Nomada fucata*	200000	260000	179000	229000	NA	NA
Bees	*Nomada fulvicornis*	263000	339000	NA	NA	NA	NA
Bees	*Nomada goodeniana*	474000	520000	NA	NA	NA	NA
Bees	*Nomada lathburiana*	451000	421000	NA	NA	NA	NA
Bees	*Nomada leucophthalma*	513000	642000	444000	453000	NA	NA
Bees	*Nomada marshamella*	606000	777000	NA	NA	NA	NA
Bees	*Nomada panzeri*	631000	668000	NA	NA	NA	NA
Bees	*Nomada ruficornis*	625000	635000	NA	NA	NA	NA
Bees	*Nomada rufipes*	426000	471000	404000	398000	NA	NA
Bees	*Nomada striata*	473000	479000	423000	406000	NA	NA
Bees	*Osmia aurulenta*	322000	299000	195000	210000	NA	NA
Bees	*Osmia bicolor*	261000	285000	225000	255000	NA	NA

Bees	*Osmia caerulescens*	397000	436000	357000	375000	NA	NA
Bees	*Osmia leaiana*	383000	374000	324000	344000	NA	NA
Bees	*Osmia spinulosa*	246000	302000	238000	274000	NA	NA
Bees	*Panurgus banksianus*	279000	287000	216000	229000	NA	NA
Bees	*Panurgus calcaratus*	201000	190000	165000	175000	NA	NA
Bees	*Sphecodes crassus*	371000	412000	339000	405000	NA	NA
Bees	*Sphecodes ephippius*	372000	458000	357000	437000	NA	NA
Bees	*Sphecodes ferruginatus*	280000	313000	NA	NA	NA	NA
Bees	*Sphecodes geoffrellus*	621000	811000	NA	NA	NA	NA
Bees	*Sphecodes gibbus*	462000	457000	432000	391000	NA	NA
Bees	*Sphecodes hyalinatus*	559000	583000	439000	336000	NA	NA
Bees	*Sphecodes monilicornis*	455000	615000	442000	559000	NA	NA
Bees	*Sphecodes pellucidus*	442000	464000	427000	403000	NA	NA
Bees	*Sphecodes puncticeps*	390000	423000	343000	387000	NA	NA
Bees	*Sphecodes reticulatus*	280000	364000	251000	340000	NA	NA
Birds	*Accipiter gentilis*	819000	867000	819000	867000	819000	867000
Birds	*Acrocephalus scirpaceus*	648000	712000	648000	712000	648000	710000
Birds	*Alcedo atthis*	822000	844000	822000	844000	822000	844000
Birds	*Anas acuta*	859000	757000	859000	757000	859000	757000
Birds	*Anas querquedula*	757000	727000	757000	727000	757000	727000
Birds	*Burhinus oedicnemus*	303000	306000	303000	306000	303000	306000
Birds	*Calidris pugnax*	673000	519000	673000	519000	673000	519000
Birds	*Caprimulgus europaeus*	654000	629000	654000	629000	654000	629000
Birds	*Cettia cetti*	309000	437000	309000	437000	309000	437000
Birds	*Charadrius dubius*	601000	797000	601000	797000	601000	797000
Birds	*Circus aeruginosus*	683000	841000	683000	841000	683000	841000
Birds	*Circus pygargus*	C	C	C	C	C	C
Birds	*Coccothraustes coccothraustes*	747000	681000	747000	681000	747000	681000
Birds	*Columba oenas*	864000	907000	864000	907000	864000	907000
Birds	*Dendrocopos minor*	542000	515000	542000	515000	542000	515000
Birds	*Emberiza cirlus*	133000	78000	133000	78000	133000	78000
Birds	*Falco subbuteo*	599000	768000	599000	768000	599000	768000
Birds	*Garrulus glandarius*	839000	861000	839000	861000	839000	861000
Birds	*Larus melanocephalus*	433000	686000	433000	686000	433000	686000
Birds	*Limosa limosa*	762000	452000	762000	452000	762000	452000
Birds	*Locustella luscinioides*	357000	329000	357000	329000	357000	329000
Birds	*Lullula arborea*	310000	423000	310000	423000	310000	423000
Birds	*Luscinia megarhynchos*	391000	417000	391000	417000	391000	417000
Birds	*Motacilla flava*	673000	658000	673000	658000	673000	657000
Birds	*Oriolus oriolus*	524000	377000	524000	377000	524000	377000
Birds	*Panurus biarmicus*	388000	590000	388000	590000	388000	590000
Birds	*Pernis apivorus*	C	C	C	C	C	C
Birds	*Phoenicurus ochruros*	448000	587000	448000	587000	448000	538000
Birds	*Picus viridis*	851000	824000	851000	824000	851000	824000
Birds	*Podiceps cristatus*	813000	788000	813000	788000	813000	788000

Birds	*Podiceps nigricollis*	710000	571000	710000	571000	710000	571000
Birds	*Poecile montana*	655000	623000	655000	623000	655000	623000
Birds	*Poecile palustris*	659000	647000	659000	647000	658000	647000
Birds	*Porzana porzana*	823000	755000	823000	755000	823000	755000
Birds	*Puffinus puffinus*	864000	607000	864000	607000	NA	NA
Birds	*Pyrrhocorax pyrrhocorax*	682000	668000	682000	668000	674000	668000
Birds	*Recurvirostra avosetta*	324000	524000	324000	524000	324000	524000
Birds	*Regulus ignicapilla*	321000	375000	321000	375000	321000	375000
Birds	*Sitta europaea*	626000	717000	626000	717000	626000	717000
Birds	*Sterna dougallii*	676000	416000	676000	416000	658000	416000
Birds	*Streptopelia turtur*	679000	525000	679000	525000	645000	525000
Birds	*Sylvia curruca*	834000	790000	834000	790000	834000	790000
Birds	*Sylvia undata*	147000	342000	147000	342000	147000	342000
Birds	*Tyto alba*	871000	959000	871000	959000	871000	959000
Butterflies	*Aglais polychloros*	387000	347000	387000	347000	387000	347000
Butterflies	*Anthocharis cardamines*	866000	924000	866000	924000	862000	909000
Butterflies	*Apatura iris*	235000	272000	235000	272000	235000	272000
Butterflies	*Aphantopus hyperantus*	855000	877000	854000	873000	839000	866000
Butterflies	*Argynnis adippe*	430000	479000	430000	479000	430000	479000
Butterflies	*Argynnis paphia*	411000	478000	411000	478000	411000	478000
Butterflies	*Aricia agestis*	421000	512000	421000	512000	421000	505000
Butterflies	*Boloria euphrosyne*	856000	877000	850000	877000	843000	852000
Butterflies	*Callophrys rubi*	855000	889000	855000	883000	848000	867000
Butterflies	*Celastrina argiolus*	580000	674000	580000	674000	580000	674000
Butterflies	*Erynnis tages*	853000	858000	853000	858000	818000	857000
Butterflies	*Euphydryas aurinia*	731000	751000	730000	744000	701000	739000
Butterflies	*Gonepteryx rhamni*	518000	571000	518000	561000	516000	561000
Butterflies	*Hamearis lucina*	471000	440000	471000	440000	471000	440000
Butterflies	*Hesperia comma*	168000	184000	168000	184000	168000	184000
Butterflies	*Hipparchia semele*	NA	NA	NA	NA	873000	897000
Butterflies	*Inachis io*	841000	959000	825000	956000	825000	943000
Butterflies	*Lasiommata megera*	635000	654000	635000	650000	629000	647000
Butterflies	*Leptidea sinapis*	318000	356000	318000	356000	318000	356000
Butterflies	*Limenitis camilla*	371000	406000	371000	406000	371000	406000
Butterflies	*Lycaena phlaeas*	NA	NA	NA	NA	878000	878000
Butterflies	*Lysandra bellargus*	179000	208000	179000	208000	179000	208000
Butterflies	*Lysandra coridon*	274000	292000	274000	292000	273000	292000
Butterflies	*Melanargia galathea*	484000	533000	484000	533000	482000	527000
Butterflies	*Neozephyrus quercus*	641000	745000	627000	745000	627000	737000
Butterflies	*Ochlodes faunus*	615000	636000	607000	633000	606000	625000
Butterflies	*Papilio machaon*	319000	410000	319000	410000	319000	410000
Butterflies	*Plebejus argus*	374000	377000	374000	377000	374000	377000
Butterflies	*Polygonia c-album*	573000	795000	573000	785000	573000	772000
Butterflies	*Pyrgus malvae*	377000	366000	377000	366000	377000	366000
Butterflies	*Pyronia tithonus*	499000	540000	499000	540000	497000	533000

Butterflies	*Satyrium pruni*	274000	297000	274000	297000	274000	297000
Butterflies	*Satyrium w-album*	516000	578000	516000	578000	516000	572000
Butterflies	*Thecla betulae*	296000	300000	296000	300000	296000	300000
Butterflies	*Thymelicus lineola*	385000	408000	385000	408000	385000	408000
Butterflies	*Thymelicus sylvestris*	554000	642000	554000	634000	550000	624000
Butterflies	*Vanessa cardui*	NA	NA	NA	NA	875000	945000
Caddisflies	*Leuctra fusca*	487000	504000	441000	504000	NA	NA
Caddisflies	*Leuctra hippopus*	480000	501000	446000	488000	NA	NA
Caddisflies	*Nemoura avicularis*	400000	428000	NA	NA	NA	NA
Caddisflies	*Nemoura cambrica*	421000	423000	NA	NA	NA	NA
Caddisflies	*Nemoura erratica*	475000	430000	NA	NA	NA	NA
Dragonflies*	*Aeshna cyanea*	719000	856000	718000	856000	717000	853000
Dragonflies*	*Aeshna grandis*	486000	497000	476000	470000	476000	466000
Dragonflies**	*Aeshna mixta*	432000	582000	424000	582000	414000	530000
Dragonflies*	*Anax imperator*	452000	663000	452000	663000	422000	597000
Dragonflies*	*Brachytron pratense*	582000	617000	580000	617000	580000	616000
Dragonflies*	*Calopteryx splendens*	558000	621000	531000	590000	483000	577000
Dragonflies*	*Calopteryx virgo*	745000	744000	743000	744000	713000	710000
Dragonflies*	*Ceriagrion tenellum*	289000	279000	289000	279000	277000	275000
Dragonflies*	*Coenagrion mercuriale*	209000	216000	209000	210000	NA	NA
Dragonflies*	*Coenagrion puella*	699000	717000	699000	711000	689000	701000
Dragonflies*	*Coenagrion pulchellum*	591000	595000	587000	564000	541000	548000
Dragonflies*	*Cordulia aenea*	658000	679000	657000	679000	609000	665000
Dragonflies*	*Erythromma najas*	392000	420000	392000	420000	392000	396000
Dragonflies*	*Gomphus vulgatissimus*	331000	334000	331000	334000	331000	334000
Dragonflies*	*Ischnura pumilio*	352000	380000	352000	335000	336000	334000
Dragonflies*	*Libellula depressa*	432000	570000	432000	528000	432000	483000
Dragonflies*	*Libellula fulva*	290000	300000	287000	300000	277000	300000
Dragonflies*	*Orthetrum cancellatum*	383000	552000	375000	541000	357000	487000
Dragonflies*	*Orthetrum coerulescens*	799000	752000	787000	746000	661000	628000
Dragonflies*	*Platycnemis pennipes*	308000	322000	308000	322000	308000	320000
Dragonflies*	*Somatochlora metallica*	548000	656000	548000	601000	546000	601000
Dragonflies*	*Sympetrum flaveolum*	458000	458000	446000	422000	420000	398000
Dragonflies*	*Sympetrum sanguineum*	446000	542000	446000	534000	445000	504000
Grasshoppers*	*Acheta domesticus*	405000	291000	357000	277000	NA	NA
Grasshoppers*	*Chorthippus albomarginatus*	380000	402000	361000	385000	NA	NA
Grasshoppers*	*Chorthippus brunneus*	775000	749000	NA	NA	NA	NA
Grasshoppers*	*Chorthippus parallelus*	868000	881000	868000	881000	NA	NA
Grasshoppers*	*Conocephalus discolor*	225000	351000	225000	342000	NA	NA
Grasshoppers*	*Conocephalus dorsalis*	339000	479000	339000	464000	NA	NA
Grasshoppers*	*Ectobius lapponicus*	200000	183000	190000	183000	NA	NA
Grasshoppers*	*Ectobius panzeri*	198000	156000	194000	143000	NA	NA
Grasshoppers*	*Forficula lesnei*	221000	228000	210000	228000	NA	NA
Grasshoppers*	*Gomphocerippus rufus*	183000	212000	183000	212000	NA	NA
Grasshoppers*	*Labia minor*	450000	322000	391000	295000	NA	NA

Grasshoppers*	*Leptophyes punctatissima*	372000	427000	359000	427000	NA	NA
Grasshoppers*	*Meconema thalassinum*	436000	450000	415000	429000	NA	NA
Grasshoppers*	*Metrioptera brachyptera*	489000	479000	489000	464000	NA	NA
Grasshoppers*	*Metrioptera roeselii*	299000	369000	299000	364000	NA	NA
Grasshoppers*	*Myrmeleotettix maculatus*	855000	851000	855000	851000	NA	NA
Grasshoppers*	*Omocestus rufipes*	194000	176000	194000	176000	NA	NA
Grasshoppers*	*Omocestus viridulus*	858000	861000	858000	861000	NA	NA
Grasshoppers*	*Pholidoptera griseoaptera*	407000	410000	386000	377000	NA	NA
Grasshoppers*	*Platycleis albopunctata*	191000	225000	156000	207000	NA	NA
Grasshoppers*	*Stenobothrus lineatus*	285000	340000	285000	338000	NA	NA
Grasshoppers*	*Tetrix ceperoi*	170000	168000	NA	NA	NA	NA
Grasshoppers*	*Tetrix subulata*	387000	444000	380000	438000	NA	NA
Grasshoppers*	*Tetrix undulata*	856000	827000	856000	827000	NA	NA
Grasshoppers*	*Tettigonia viridissima*	258000	267000	248000	260000	NA	NA
G. beetles	*Abax parallelepipedus*	662000	646000	NA	NA	NA	NA
G. beetles	*Acupalpus dubius*	420000	433000	366000	393000	NA	NA
G. beetles	*Acupalpus meridianus*	363000	315000	NA	NA	NA	NA
G. beetles	*Acupalpus parvulus*	385000	363000	NA	NA	NA	NA
G. beetles	*Agonum emarginatum*	495000	405000	356000	344000	NA	NA
G. beetles	*Agonum fuliginosum*	799000	837000	NA	NA	NA	NA
G. beetles	*Agonum gracile*	684000	747000	NA	NA	NA	NA
G. beetles	*Agonum marginatum*	528000	426000	NA	NA	NA	NA
G. beetles	*Agonum micans*	495000	359000	NA	NA	NA	NA
G. beetles	*Agonum muelleri*	813000	778000	NA	NA	NA	NA
G. beetles	*Agonum piceum*	508000	687000	NA	NA	NA	NA
G. beetles	*Agonum thoreyi*	477000	465000	337000	369000	NA	NA
G. beetles	*Agonum viduum*	0	357000	NA	NA	NA	NA
G. beetles	*Amara aenea*	634000	592000	NA	NA	NA	NA
G. beetles	*Amara apricaria*	620000	342000	NA	NA	NA	NA
G. beetles	*Amara bifrons*	598000	382000	NA	NA	NA	NA
G. beetles	*Amara communis*	658000	623000	NA	NA	NA	NA
G. beetles	*Amara convexior*	324000	371000	NA	NA	NA	NA
G. beetles	*Amara eurynota*	378000	289000	NA	NA	NA	NA
G. beetles	*Amara familiaris*	671000	602000	NA	NA	NA	NA
G. beetles	*Amara lunicollis*	730000	484000	NA	NA	NA	NA
G. beetles	*Amara ovata*	598000	628000	NA	NA	NA	NA
G. beetles	*Amara plebeja*	707000	672000	NA	NA	NA	NA
G. beetles	*Amara similata*	521000	488000	NA	NA	NA	NA
G. beetles	*Amara tibialis*	468000	415000	NA	NA	NA	NA
G. beetles	*Anchomenus dorsalis*	653000	645000	NA	NA	NA	NA
G. beetles	*Asaphidion curtum*	432000	481000	NA	NA	NA	NA
G. beetles	*Asaphidion stierlini*	338000	304000	NA	NA	NA	NA
G. beetles	*Badister bullatus*	574000	546000	NA	NA	NA	NA

G. beetles	*Bembidion aeneum*	653000	545000	NA	NA	NA	NA
G. beetles	*Bembidion articulatum*	345000	338000	308000	305000	NA	NA
G. beetles	*Bembidion assimile*	396000	399000	313000	353000	NA	NA
G. beetles	*Bembidion biguttatum*	520000	471000	NA	NA	NA	NA
G. beetles	*Bembidion clarkii*	367000	326000	NA	NA	NA	NA
G. beetles	*Bembidion deletum*	487000	448000	NA	NA	NA	NA
G. beetles	*Bembidion dentellum*	413000	409000	364000	367000	NA	NA
G. beetles	*Bembidion doris*	614000	705000	NA	NA	NA	NA
G. beetles	*Bembidion femoratum*	600000	605000	NA	NA	NA	NA
G. beetles	*Bembidion fumigatum*	345000	366000	NA	NA	NA	NA
G. beetles	*Bembidion gilvipes*	367000	312000	NA	NA	NA	NA
G. beetles	*Bembidion guttula*	633000	634000	NA	NA	NA	NA
G. beetles	*Bembidion illigeri*	438000	380000	354000	298000	NA	NA
G. beetles	*Bembidion iricolor*	335000	327000	NA	NA	NA	NA
G. beetles	*Bembidion lampros*	664000	632000	NA	NA	NA	NA
G. beetles	*Bembidion lunulatum*	418000	437000	NA	NA	NA	NA
G. beetles	*Bembidion mannerheimii*	606000	721000	NA	NA	NA	NA
G. beetles	*Bembidion minimum*	607000	431000	NA	NA	NA	NA
G. beetles	*Bembidion normannum*	382000	301000	NA	NA	NA	NA
G. beetles	*Bembidion obtusum*	453000	370000	357000	293000	NA	NA
G. beetles	*Bembidion properans*	464000	407000	NA	NA	NA	NA
G. beetles	*Bembidion punctulatum*	713000	613000	NA	NA	NA	NA
G. beetles	*Bembidion quadrimaculatum*	438000	468000	363000	316000	NA	NA
G. beetles	*Bembidion tetracolum*	831000	827000	NA	NA	NA	NA
G. beetles	*Bembidion varium*	423000	367000	311000	311000	NA	NA
G. beetles	*Bradycellus harpalinus*	758000	692000	NA	NA	NA	NA
G. beetles	*Bradycellus ruficollis*	594000	517000	NA	NA	NA	NA
G. beetles	*Bradycellus verbasci*	470000	448000	344000	308000	NA	NA
G. beetles	*Broscus cephalotes*	715000	419000	NA	NA	NA	NA
G. beetles	*Calathus ambiguus*	368000	294000	NA	NA	NA	NA
G. beetles	*Calathus cinctus*	386000	322000	NA	NA	NA	NA
G. beetles	*Calathus erratus*	703000	691000	NA	NA	NA	NA
G. beetles	*Calathus melanocephalus*	714000	754000	NA	NA	NA	NA
G. beetles	*Calathus mollis*	840000	482000	NA	NA	NA	NA
G. beetles	*Calathus rotundicollis*	672000	577000	364000	354000	NA	NA
G. beetles	*Calodromius spilotus*	420000	530000	NA	NA	NA	NA
G. beetles	*Carabus granulatus*	514000	476000	NA	NA	NA	NA
G. beetles	*Carabus nemoralis*	634000	556000	NA	NA	NA	NA
G. beetles	*Carabus violaceus*	852000	710000	NA	NA	NA	NA
G. beetles	*Chlaenius nigricornis*	329000	296000	NA	NA	NA	NA
G. beetles	*Chlaenius vestitus*	310000	341000	NA	NA	NA	NA
G. beetles	*Clivina collaris*	449000	409000	NA	NA	NA	NA
G. beetles	*Clivina fossor*	716000	655000	NA	NA	NA	NA

G. beetles	*Curtonotus aulicus*	646000	545000	NA	NA	NA	NA
G. beetles	*Curtonotus convexiusculus*	445000	276000	NA	NA	NA	NA
G. beetles	*Cychrus caraboides*	873000	850000	NA	NA	NA	NA
G. beetles	*Demetrias atricapillus*	412000	422000	361000	368000	NA	NA
G. beetles	*Demetrias imperialis*	275000	305000	NA	NA	NA	NA
G. beetles	*Dicheirotrichus gustavii*	690000	614000	NA	NA	NA	NA
G. beetles	*Dromius meridionalis*	352000	287000	NA	NA	NA	NA
G. beetles	*Dromius quadrimaculatus*	679000	480000	366000	373000	NA	NA
G. beetles	*Dyschirius aeneus*	347000	318000	NA	NA	NA	NA
G. beetles	*Dyschirius globosus*	640000	618000	NA	NA	NA	NA
G. beetles	*Dyschirius luedersi*	445000	354000	NA	NA	NA	NA
G. beetles	*Dyschirius salinus*	533000	421000	NA	NA	NA	NA
G. beetles	*Elaphrus riparius*	682000	604000	NA	NA	NA	NA
G. beetles	*Harpalus affinis*	654000	540000	NA	NA	NA	NA
G. beetles	*Harpalus anxius*	347000	326000	NA	NA	NA	NA
G. beetles	*Harpalus latus*	762000	574000	NA	NA	NA	NA
G. beetles	*Harpalus rubripes*	345000	398000	318000	326000	NA	NA
G. beetles	*Harpalus rufipalpis*	357000	202000	NA	NA	NA	NA
G. beetles	*Harpalus rufipes*	612000	508000	NA	NA	NA	NA
G. beetles	*Harpalus tardus*	490000	383000	347000	342000	NA	NA
G. beetles	*Leistus ferrugineus*	534000	474000	NA	NA	NA	NA
G. beetles	*Leistus fulvibarbis*	559000	521000	NA	NA	NA	NA
G. beetles	*Leistus rufomarginatus*	519000	407000	NA	NA	NA	NA
G. beetles	*Leistus spinibarbis*	428000	433000	348000	351000	NA	NA
G. beetles	*Leistus terminatus*	874000	744000	NA	NA	NA	NA
G. beetles	*Microlestes maurus*	341000	288000	NA	NA	NA	NA
G. beetles	*Nebria salina*	843000	787000	NA	NA	NA	NA
G. beetles	*Notiophilus aquaticus*	846000	820000	NA	NA	NA	NA
G. beetles	*Notiophilus germinyi*	614000	651000	NA	NA	NA	NA
G. beetles	*Notiophilus palustris*	597000	682000	371000	486000	NA	NA
G. beetles	*Notiophilus rufipes*	370000	322000	NA	NA	NA	NA
G. beetles	*Notiophilus substriatus*	621000	467000	NA	NA	NA	NA
G. beetles	*Ocys harpaloides*	521000	518000	NA	NA	NA	NA
G. beetles	*Olisthopus rotundatus*	706000	569000	NA	NA	NA	NA
G. beetles	*Ophonus rufibarbis*	480000	386000	NA	NA	NA	NA
G. beetles	*Oxypselaphus obscurus*	450000	420000	NA	NA	NA	NA
G. beetles	*Paradromius linearis*	683000	467000	NA	NA	NA	NA
G. beetles	*Patrobus atrorufus*	683000	469000	NA	NA	NA	NA
G. beetles	*Philorhizus melanocephalus*	475000	431000	335000	339000	NA	NA
G. beetles	*Platyderus depressus*	304000	326000	NA	NA	NA	NA
G. beetles	*Platynus assimilis*	658000	760000	NA	NA	NA	NA
G. beetles	*Poecilus cupreus*	370000	394000	311000	316000	NA	NA
G. beetles	*Poecilus versicolor*	537000	564000	NA	NA	NA	NA
G. beetles	*Pogonus chalceus*	415000	371000	NA	NA	NA	NA

G. beetles	*Pterostichus madidus*	866000	680000	NA	NA	NA	NA
G. beetles	*Pterostichus melanarius*	751000	618000	NA	NA	NA	NA
G. beetles	*Pterostichus minor*	647000	625000	NA	NA	NA	NA
G. beetles	*Pterostichus nigrita*	507000	815000	NA	NA	NA	NA
G. beetles	*Pterostichus rhaeticus*	715000	841000	NA	NA	NA	NA
G. beetles	*Pterostichus strenuus*	738000	798000	NA	NA	NA	NA
G. beetles	*Pterostichus vernalis*	592000	493000	368000	363000	NA	NA
G. beetles	*Stenolophus mixtus*	415000	402000	331000	339000	NA	NA
G. beetles	*Stomis pumicatus*	495000	370000	377000	308000	NA	NA
G. beetles	*Syntomus foveatus*	445000	378000	333000	319000	NA	NA
G. beetles	*Syntomus obscuroguttatus*	202000	267000	NA	NA	NA	NA
G. beetles	*Synuchus vivalis*	535000	404000	NA	NA	NA	NA
G. beetles	*Trechus obtusus*	867000	807000	NA	NA	NA	NA
G. beetles	*Trechus quadristriatus*	672000	647000	NA	NA	NA	NA
G. beetles	*Trichocellus placidus*	675000	466000	NA	NA	NA	NA
Hoverflies	*Anasimyia contracta*	628000	474000	507000	459000	NA	NA
Hoverflies	*Anasimyia lineata*	767000	718000	734000	619000	NA	NA
Hoverflies	*Anasimyia transfuga*	479000	379000	419000	374000	NA	NA
Hoverflies	*Arctophila superbiens*	809000	785000	719000	678000	NA	NA
Hoverflies	*Baccha elongata*	863000	845000	838000	827000	NA	NA
Hoverflies	*Brachyopa insensilis*	819000	458000	NA	NA	NA	NA
Hoverflies	*Brachyopa scutellaris*	655000	560000	576000	498000	347000	334000
Hoverflies	*Brachypalpoides lentus*	694000	520000	469000	477000	NA	NA
Hoverflies	*Brachypalpus laphriformis*	415000	441000	382000	417000	NA	NA
Hoverflies	*Callicera aurata*	214000	257000	NA	NA	NA	NA
Hoverflies	*Chalcosyrphus nemorum*	806000	809000	698000	739000	NA	NA
Hoverflies	*Cheilosia albipila*	738000	529000	509000	405000	NA	NA
Hoverflies	*Cheilosia albitarsis*	855000	850000	829000	831000	NA	NA
Hoverflies	*Cheilosia antiqua*	830000	777000	789000	660000	NA	NA
Hoverflies	*Cheilosia bergenstammi*	874000	858000	824000	828000	NA	NA
Hoverflies	*Cheilosia fraterna*	826000	836000	815000	708000	NA	NA
Hoverflies	*Cheilosia griseiventris*	447000	374000	425000	302000	NA	NA
Hoverflies	*Cheilosia grossa*	761000	803000	578000	746000	NA	NA
Hoverflies	*Cheilosia impressa*	653000	508000	465000	427000	NA	NA
Hoverflies	*Cheilosia lasiopa*	612000	516000	509000	510000	NA	NA
Hoverflies	*Cheilosia latifrons*	548000	676000	448000	524000	NA	NA
Hoverflies	*Cheilosia longula*	873000	854000	NA	NA	NA	NA
Hoverflies	*Cheilosia pagana*	872000	847000	822000	821000	NA	NA
Hoverflies	*Cheilosia proxima*	639000	767000	535000	660000	NA	NA
Hoverflies	*Cheilosia scutellata*	702000	662000	586000	560000	NA	NA
Hoverflies	*Cheilosia soror*	263000	300000	257000	292000	212000	244000
Hoverflies	*Cheilosia urbana*	522000	322000	NA	NA	NA	NA
Hoverflies	*Cheilosia variabilis*	839000	809000	750000	722000	NA	NA

Hoverflies	*Cheilosia vulpina*	346000	318000	307000	310000	209000	260000
Hoverflies	*Chrysogaster cemiteriorum*	668000	720000	467000	623000	360000	402000
Hoverflies	*Chrysogaster solstitialis*	851000	865000	841000	835000	NA	NA
Hoverflies	*Chrysogaster virescens*	838000	801000	801000	697000	NA	NA
Hoverflies	*Chrysotoxum bicinctum*	792000	821000	678000	680000	NA	NA
Hoverflies	*Chrysotoxum cautum*	296000	296000	291000	296000	267000	274000
Hoverflies	*Chrysotoxum elegans*	197000	232000	188000	218000	NA	NA
Hoverflies	*Chrysotoxum festivum*	501000	599000	407000	461000	NA	NA
Hoverflies	*Chrysotoxum verralli*	334000	319000	314000	316000	265000	307000
Hoverflies	*Criorhina asilica*	448000	394000	400000	372000	NA	NA
Hoverflies	*Criorhina berberina*	672000	660000	540000	553000	NA	NA
Hoverflies	*Criorhina floccosa*	650000	570000	495000	474000	362000	362000
Hoverflies	*Criorhina ranunculi*	539000	679000	472000	667000	353000	419000
Hoverflies	*Dasysyrphus albostriatus*	829000	853000	720000	817000	NA	NA
Hoverflies	*Dasysyrphus pinastri*	873000	825000	839000	743000	NA	NA
Hoverflies	*Dasysyrphus tricinctus*	837000	838000	831000	792000	NA	NA
Hoverflies	*Dasysyrphus venustus*	841000	839000	823000	766000	NA	NA
Hoverflies	*Didea fasciata*	739000	797000	677000	652000	NA	NA
Hoverflies	*Didea intermedia*	790000	834000	NA	NA	NA	NA
Hoverflies	*Epistrophe diaphana*	194000	284000	178000	262000	161000	221000
Hoverflies	*Epistrophe eligans*	748000	704000	641000	679000	NA	NA
Hoverflies	*Epistrophe grossulariae*	834000	889000	814000	854000	NA	NA
Hoverflies	*Epistrophe nitidicollis*	453000	372000	380000	372000	336000	338000
Hoverflies	*Eristalinus aeneus*	674000	751000	376000	413000	NA	NA
Hoverflies	*Eristalinus sepulchralis*	704000	569000	527000	501000	NA	NA
Hoverflies	*Eristalis abusiva*	760000	670000	693000	615000	NA	NA
Hoverflies	*Eristalis arbustorum*	NA	NA	841000	851000	NA	NA
Hoverflies	*Eristalis horticola*	866000	856000	828000	811000	NA	NA
Hoverflies	*Eristalis intricaria*	NA	NA	835000	832000	NA	NA
Hoverflies	*Eristalis tenax*	NA	NA	831000	849000	NA	NA
Hoverflies	*Eumerus ornatus*	351000	324000	336000	320000	203000	252000
Hoverflies	*Eumerus strigatus*	450000	425000	394000	381000	NA	NA
Hoverflies	*Eupeodes corollae*	NA	NA	827000	839000	NA	NA
Hoverflies	*Eupeodes latifasciatus*	786000	830000	618000	689000	NA	NA
Hoverflies	*Eupeodes luniger*	843000	846000	804000	819000	NA	NA
Hoverflies	*Ferdinandea cuprea*	798000	782000	741000	645000	NA	NA
Hoverflies	*Helophilus hybridus*	835000	793000	644000	730000	NA	NA
Hoverflies	*Helophilus trivittatus*	586000	761000	438000	503000	NA	NA
Hoverflies	*Heringia heringi*	418000	377000	411000	335000	NA	NA
Hoverflies	*Heringia vitripennis*	375000	394000	NA	NA	NA	NA
Hoverflies	*Lejogaster metallina*	857000	831000	807000	773000	NA	NA
Hoverflies	*Leucozona glaucia*	841000	878000	811000	860000	NA	NA
Hoverflies	*Leucozona laternaria*	822000	832000	716000	763000	NA	NA
Hoverflies	*Leucozona lucorum*	873000	870000	847000	849000	NA	NA
Hoverflies	*Melangyna cincta*	803000	783000	768000	680000	NA	NA

Hoverflies	*Melangyna compositarum*	833000	850000	791000	839000	NA	NA
Hoverflies	*Melangyna labiatarum*	851000	450000	707000	435000	NA	NA
Hoverflies	*Melangyna lasiophthalma*	855000	840000	825000	807000	NA	NA
Hoverflies	*Melangyna umbellatarum*	763000	639000	634000	598000	NA	NA
Hoverflies	*Melanogaster aerosa*	870000	641000	NA	NA	NA	NA
Hoverflies	*Meligramma trianguliferum*	453000	414000	372000	328000	NA	NA
Hoverflies	*Meliscaeva auricollis*	823000	872000	726000	822000	NA	NA
Hoverflies	*Meliscaeva cinctella*	864000	876000	845000	857000	NA	NA
Hoverflies	*Microdon mutabilis*	465000	368000	NA	NA	NA	NA
Hoverflies	*Myathropa florea*	879000	863000	848000	835000	NA	NA
Hoverflies	*Myolepta dubia*	206000	270000	NA	NA	NA	NA
Hoverflies	*Neoascia geniculata*	733000	595000	584000	521000	NA	NA
Hoverflies	*Neoascia meticulosa*	785000	781000	723000	760000	NA	NA
Hoverflies	*Neoascia obliqua*	718000	637000	NA	NA	NA	NA
Hoverflies	*Neoascia podagrica*	NA	NA	847000	840000	NA	NA
Hoverflies	*Neoascia tenur*	866000	843000	836000	776000	NA	NA
Hoverflies	*Orthonevra brevicornis*	466000	430000	444000	404000	NA	NA
Hoverflies	*Orthonevra geniculata*	756000	721000	585000	545000	NA	NA
Hoverflies	*Orthonevra nobilis*	693000	527000	568000	392000	334000	307000
Hoverflies	*Paragus haemorrhous*	734000	791000	543000	655000	NA	NA
Hoverflies	*Parasyrphus annulatus*	696000	336000	NA	NA	NA	NA
Hoverflies	*Parasyrphus punctulatus*	853000	844000	817000	807000	NA	NA
Hoverflies	*Parhelophilus frutetorum*	425000	345000	414000	344000	NA	NA
Hoverflies	*Parhelophilus versicolor*	585000	522000	524000	487000	NA	NA
Hoverflies	*Pipiza austriaca*	559000	499000	466000	436000	NA	NA
Hoverflies	*Pipiza bimaculata*	559000	504000	499000	440000	NA	NA
Hoverflies	*Pipiza fenestrata*	410000	270000	NA	NA	NA	NA
Hoverflies	*Pipiza lugubris*	237000	274000	190000	206000	NA	NA
Hoverflies	*Pipiza luteitarsis*	593000	496000	466000	442000	NA	NA
Hoverflies	*Pipiza noctiluca*	790000	759000	653000	530000	NA	NA
Hoverflies	*Pipizella viduata*	NA	NA	813000	735000	NA	NA
Hoverflies	*Pipizella virens*	340000	335000	315000	331000	285000	299000
Hoverflies	*Platycheirus ambiguus*	508000	401000	440000	361000	NA	NA
Hoverflies	*Platycheirus angustatus*	NA	NA	822000	838000	NA	NA
Hoverflies	*Platycheirus clypeatus*	NA	NA	847000	845000	NA	NA
Hoverflies	*Platycheirus europaeus*	693000	828000	NA	NA	NA	NA
Hoverflies	*Platycheirus fulviventris*	800000	679000	767000	561000	NA	NA
Hoverflies	*Platycheirus granditarsus*	NA	NA	846000	832000	NA	NA
Hoverflies	*Platycheirus occultus*	845000	821000	753000	652000	NA	NA
Hoverflies	*Platycheirus peltatus*	865000	859000	832000	827000	NA	NA
Hoverflies	*Platycheirus rosarum*	832000	816000	803000	760000	NA	NA
Hoverflies	*Platycheirus scambus*	877000	866000	NA	NA	NA	NA

Hoverflies	*Platycheirus scutatus*	877000	873000	NA	NA	NA	NA
Hoverflies	*Platycheirus tarsalis*	835000	562000	763000	481000	NA	NA
Hoverflies	*Portevinia maculata*	691000	687000	639000	660000	NA	NA
Hoverflies	*Rhingia campestris*	NA	NA	850000	849000	NA	NA
Hoverflies	*Rhingia rostrata*	200000	318000	NA	NA	NA	NA
Hoverflies	*Riponnensia splendens*	792000	665000	615000	444000	366000	341000
Hoverflies	*Scaeva pyrastri*	NA	NA	823000	817000	NA	NA
Hoverflies	*Scaeva selenitica*	729000	677000	543000	638000	320000	388000
Hoverflies	*Sphaerophoria batava*	645000	446000	559000	356000	NA	NA
Hoverflies	*Sphaerophoria interrupta*	859000	884000	819000	827000	NA	NA
Hoverflies	*Sphaerophoria philanthus*	841000	834000	817000	700000	NA	NA
Hoverflies	*Sphaerophoria rueppellii*	609000	356000	458000	285000	NA	NA
Hoverflies	*Sphaerophoria scripta*	744000	756000	549000	615000	NA	NA
Hoverflies	*Sphaerophoria taeniata*	239000	235000	204000	212000	186000	165000
Hoverflies	*Sphegina clunipes*	878000	854000	NA	NA	NA	NA
Hoverflies	*Sphegina elegans*	812000	657000	735000	446000	NA	NA
Hoverflies	*Sphegina verecunda*	661000	764000	473000	526000	NA	NA
Hoverflies	*Syritta pipiens*	874000	870000	NA	NA	NA	NA
Hoverflies	*Syrphus ribesii*	NA	NA	843000	851000	NA	NA
Hoverflies	*Syrphus torvus*	862000	887000	818000	848000	NA	NA
Hoverflies	*Syrphus vitripennis*	NA	NA	818000	846000	NA	NA
Hoverflies	*Trichopsomyia flavitarsis*	826000	709000	758000	546000	NA	NA
Hoverflies	*Tropidia scita*	594000	503000	486000	430000	NA	NA
Hoverflies	*Volucella bombylans*	NA	NA	804000	823000	NA	NA
Hoverflies	*Volucella inanis*	209000	370000	196000	362000	168000	343000
Hoverflies	*Volucella inflata*	237000	310000	220000	305000	217000	280000
Hoverflies	*Volucella pellucens*	866000	866000	840000	855000	NA	NA
Hoverflies	*Volucella zonaria*	191000	338000	184000	323000	NA	NA
Hoverflies	*Xanthandrus comtus*	467000	506000	401000	345000	305000	297000
Hoverflies	*Xanthogramma citrofasciatum*	409000	329000	378000	326000	297000	281000
Hoverflies	*Xanthogramma pedissequum*	495000	368000	375000	348000	316000	340000
Hoverflies	*Xylota abiens*	349000	227000	NA	NA	NA	NA
Hoverflies	*Xylota florum*	511000	379000	374000	305000	NA	NA
Hoverflies	*Xylota sylvarum*	827000	775000	769000	735000	NA	NA
Hoverflies	*Xylota xanthocnema*	331000	300000	NA	NA	NA	NA
Ladybirds	*Adalia bipunctata*	631000	684000	NA	NA	NA	NA
Ladybirds	*Anatis ocellata*	492000	559000	464000	513000	440000	401000
Ladybirds	*Anisosticta novemdecimpunctata*	467000	478000	446000	454000	421000	424000
Ladybirds	*Aphidecta obliterata*	NA	NA	NA	NA	413000	362000
Ladybirds	*Chilocorus bipustulatus*	440000	471000	426000	437000	348000	223000
Ladybirds	*Chilocorus renipustulatus*	501000	501000	NA	NA	NA	NA

Ladybirds	*Coccidula rufa*	567000	611000	NA	NA	438000	447000
Ladybirds	*Coccidula scutellata*	440000	393000	407000	365000	NA	NA
Ladybirds	*Coccinella undecimpunctata*	601000	580000	NA	NA	426000	414000
Ladybirds	*Exochomus quadripustulatus*	506000	491000	475000	478000	439000	429000
Ladybirds	*Halyzia sedecimguttata*	502000	690000	410000	682000	334000	427000
Ladybirds	*Hippodamia variegata*	409000	459000	403000	456000	402000	426000
Ladybirds	*Myrrha octodecimguttata*	540000	439000	480000	393000	353000	321000
Ladybirds	*Myzia oblongoguttata*	671000	598000	NA	NA	NA	NA
Ladybirds	*Nephus redtenbacheri*	525000	469000	426000	457000	NA	NA
Ladybirds	*Propylea quattuordecimpunctata*	505000	574000	NA	NA	NA	NA
Ladybirds	*Psyllobora vigintiduopunctata*	478000	526000	476000	468000	NA	NA
Ladybirds	*Rhyzobius litura*	557000	528000	NA	NA	411000	437000
Ladybirds	*Scymnus auritus*	365000	311000	NA	NA	NA	NA
Ladybirds	*Scymnus suturalis*	403000	479000	366000	460000	NA	NA
Ladybirds	*Subcoccinella vigintiquattuorpunctata*	490000	447000	461000	413000	357000	363000
Ladybirds	*Tytthaspis sedecimpunctata*	361000	424000	347000	413000	300000	398000
Macromoths	*Abraxas sylvata*	597000	637000	583000	581000	568000	558000
Macromoths	*Acasis viretata*	776000	865000	677000	851000	NA	NA
Macromoths	*Acherontia atropos*	581000	636000	464000	515000	406000	410000
Macromoths	*Achlya flavicornis*	877000	889000	NA	NA	NA	NA
Macromoths	*Acronicta aceris*	381000	397000	364000	391000	363000	376000
Macromoths	*Acronicta alni*	512000	663000	496000	601000	477000	573000
Macromoths	*Acronicta leporina*	776000	837000	747000	800000	NA	NA
Macromoths	*Acronicta megacephala*	720000	834000	708000	771000	NA	NA
Macromoths	*Acronicta psi*	841000	946000	821000	905000	764000	849000
Macromoths	*Acronicta rumicis*	868000	923000	NA	NA	NA	NA
Macromoths	*Acronicta tridens*	428000	508000	414000	463000	392000	458000
Macromoths	*Adscita geryon*	416000	472000	NA	NA	NA	NA
Macromoths	*Adscita statices*	588000	634000	464000	528000	362000	433000
Macromoths	*Aethalura punctulata*	742000	856000	667000	789000	NA	NA
Macromoths	*Agriopis leucophaearia*	647000	690000	607000	637000	598000	628000
Macromoths	*Agrius convolvuli*	NA	NA	784000	763000	582000	618000
Macromoths	*Agrochola helvola*	814000	845000	814000	826000	NA	NA
Macromoths	*Agrochola litura*	836000	872000	822000	845000	NA	NA
Macromoths	*Agrochola lota*	865000	912000	838000	892000	NA	NA
Macromoths	*Agrochola lychnidis*	563000	548000	550000	537000	539000	515000
Macromoths	*Agrotis cinerea*	287000	325000	276000	253000	221000	214000
Macromoths	*Agrotis clavis*	613000	770000	524000	563000	496000	501000
Macromoths	*Agrotis exclamationis*	860000	892000	NA	NA	NA	NA
Macromoths	*Agrotis ipsilon*	872000	929000	NA	NA	NA	NA
Macromoths	*Agrotis puta*	457000	655000	457000	643000	457000	571000
Macromoths	*Agrotis ripae*	523000	549000	408000	468000	295000	300000

Macromoths	*Agrotis segetum*	781000	869000	730000	826000	NA	NA
Macromoths	*Agrotis vestigialis*	839000	895000	749000	783000	500000	529000
Macromoths	*Alcis jubata*	833000	909000	797000	878000	NA	NA
Macromoths	*Aleucis distinctata*	221000	221000	NA	NA	NA	NA
Macromoths	*Allophyes oxyacanthae*	873000	883000	NA	NA	NA	NA
Macromoths	*Alsophila aescularia*	838000	863000	806000	839000	NA	NA
Macromoths	*Amphipoea fucosa*	724000	668000	665000	589000	540000	563000
Macromoths	*Amphipoea oculea*	862000	884000	828000	838000	NA	NA
Macromoths	*Amphipyra tragopoginis*	872000	878000	NA	NA	NA	NA
Macromoths	*Anaplectoides prasina*	866000	899000	NA	NA	NA	NA
Macromoths	*Anarta myrtilli*	817000	865000	734000	781000	472000	549000
Macromoths	*Angerona prunaria*	269000	295000	269000	284000	269000	274000
Macromoths	*Anticlea badiata*	854000	867000	819000	832000	NA	NA
Macromoths	*Anticlea derivata*	877000	897000	850000	885000	NA	NA
Macromoths	*Apamea anceps*	332000	375000	331000	364000	327000	359000
Macromoths	*Apamea epomidion*	583000	666000	561000	573000	503000	520000
Macromoths	*Apamea furva*	856000	871000	816000	772000	NA	NA
Macromoths	*Apamea oblonga*	398000	425000	372000	419000	351000	386000
Macromoths	*Apamea ophiogramma*	655000	834000	624000	775000	578000	695000
Macromoths	*Apamea scolopacina*	529000	738000	510000	677000	480000	659000
Macromoths	*Apamea sordens*	850000	861000	835000	840000	NA	NA
Macromoths	*Apamea sublustris*	320000	346000	320000	337000	312000	319000
Macromoths	*Apamea unanimis*	784000	851000	745000	737000	678000	666000
Macromoths	*Apeira syringaria*	601000	680000	584000	614000	573000	562000
Macromoths	*Aplocera efformata*	542000	624000	513000	576000	463000	525000
Macromoths	*Apocheima hispidaria*	393000	384000	362000	355000	350000	355000
Macromoths	*Apoda limacodes*	280000	299000	280000	299000	276000	299000
Macromoths	*Archanara dissoluta*	362000	456000	358000	432000	351000	393000
Macromoths	*Archanara geminipuncta*	344000	463000	344000	455000	341000	440000
Macromoths	*Archanara sparganii*	280000	379000	280000	379000	272000	343000
Macromoths	*Archiearis notha*	268000	268000	266000	256000	NA	NA
Macromoths	*Archiearis parthenias*	712000	835000	661000	786000	531000	606000
Macromoths	*Arctia villica*	258000	288000	258000	286000	258000	286000
Macromoths	*Arenostola phragmitidis*	450000	493000	448000	484000	448000	474000
Macromoths	*Asteroscopus sphinx*	507000	494000	502000	473000	480000	469000
Macromoths	*Asthena albulata*	619000	696000	522000	482000	482000	452000
Macromoths	*Atethmia centrago*	747000	864000	711000	841000	685000	816000
Macromoths	*Atolmis rubricollis*	436000	733000	414000	706000	392000	652000
Macromoths	*Autographa jota*	837000	873000	811000	841000	NA	NA
Macromoths	*Axylia putris*	715000	781000	687000	737000	NA	NA
Macromoths	*Bena bicolorana*	436000	522000	435000	513000	431000	492000
Macromoths	*Biston betularia*	864000	911000	840000	875000	NA	NA
Macromoths	*Biston strataria*	613000	757000	590000	687000	572000	660000
Macromoths	*Bupalus piniaria*	860000	923000	NA	NA	NA	NA

Macromoths	*Callimorpha dominula*	280000	308000	275000	293000	256000	281000
Macromoths	*Callistege mi*	788000	866000	745000	779000	582000	650000
Macromoths	*Calliteara pudibunda*	491000	557000	487000	544000	475000	503000
Macromoths	*Caradrina morpheus*	802000	853000	773000	739000	NA	NA
Macromoths	*Carsia sororiata*	782000	901000	NA	NA	NA	NA
Macromoths	*Catarhoe cuculata*	359000	372000	303000	365000	303000	316000
Macromoths	*Catarhoe rubidata*	248000	285000	246000	285000	246000	283000
Macromoths	*Catocala nupta*	506000	583000	480000	571000	479000	545000
Macromoths	*Cepphis advenaria*	208000	224000	208000	221000	197000	220000
Macromoths	*Cerastis leucographa*	376000	479000	362000	423000	362000	395000
Macromoths	*Cerura vinula*	838000	870000	813000	836000	NA	NA
Macromoths	*Charanyca trigrammica*	440000	487000	439000	474000	416000	467000
Macromoths	*Charissa obscurata*	649000	756000	570000	709000	417000	530000
Macromoths	*Chesias rufata*	757000	864000	703000	821000	538000	692000
Macromoths	*Chiasmia clathrata*	733000	813000	733000	789000	NA	NA
Macromoths	*Chilodes maritimus*	426000	523000	415000	474000	388000	458000
Macromoths	*Chloroclystis v-ata*	663000	796000	655000	776000	NA	NA
Macromoths	*Chortodes elymi*	574000	615000	NA	NA	NA	NA
Macromoths	*Chortodes fluxa*	330000	379000	330000	346000	317000	319000
Macromoths	*Cilix glaucata*	641000	632000	630000	604000	NA	NA
Macromoths	*Cleorodes lichenaria*	806000	865000	772000	822000	676000	724000
Macromoths	*Clostera curtula*	330000	411000	330000	404000	328000	358000
Macromoths	*Clostera pigra*	697000	409000	438000	320000	315000	195000
Macromoths	*Coenobia rufa*	390000	469000	390000	460000	384000	453000
Macromoths	*Colocasia coryli*	874000	902000	NA	NA	NA	NA
Macromoths	*Colotois pennaria*	871000	877000	850000	856000	NA	NA
Macromoths	*Comibaena bajularia*	422000	415000	409000	404000	405000	399000
Macromoths	*Conistra ligula*	566000	655000	547000	613000	537000	597000
Macromoths	*Conistra rubiginea*	204000	271000	201000	271000	193000	268000
Macromoths	*Conistra vaccinii*	874000	915000	NA	NA	NA	NA
Macromoths	*Cosmia affinis*	359000	378000	352000	377000	335000	371000
Macromoths	*Cosmia pyralina*	333000	350000	333000	322000	333000	314000
Macromoths	*Cosmia trapezina*	842000	859000	832000	830000	NA	NA
Macromoths	*Cossus cossus*	506000	690000	331000	325000	259000	295000
Macromoths	*Craniophora ligustri*	714000	863000	680000	844000	598000	788000
Macromoths	*Cryphia domestica*	766000	841000	731000	762000	661000	685000
Macromoths	*Cryphia muralis*	218000	331000	218000	311000	217000	297000
Macromoths	*Cucullia absinthii*	388000	374000	380000	336000	380000	331000
Macromoths	*Cucullia asteris*	338000	368000	313000	353000	277000	320000
Macromoths	*Cucullia chamomillae*	554000	845000	554000	766000	498000	605000
Macromoths	*Cucullia umbratica*	830000	876000	799000	858000	NA	NA
Macromoths	*Cybosia mesomella*	745000	802000	647000	687000	522000	611000
Macromoths	*Cyclophora albipunctata*	832000	873000	810000	849000	681000	817000
Macromoths	*Cyclophora annularia*	205000	244000	205000	244000	189000	228000
Macromoths	*Cyclophora linearia*	385000	509000	373000	494000	336000	475000

Macromoths	*Cyclophora porata*	274000	280000	NA	NA	NA	NA
Macromoths	*Cyclophora punctaria*	366000	420000	342000	401000	334000	396000
Macromoths	*Cymatophorima diluta*	390000	396000	354000	392000	321000	366000
Macromoths	*Deilephila elpenor*	833000	904000	775000	879000	689000	827000
Macromoths	*Deilephila porcellus*	715000	873000	688000	828000	549000	718000
Macromoths	*Deileptenia ribeata*	662000	887000	643000	846000	NA	NA
Macromoths	*Deltote uncula*	729000	789000	558000	773000	374000	569000
Macromoths	*Diacrisia sannio*	779000	857000	771000	821000	688000	782000
Macromoths	*Diaphora mendica*	640000	694000	604000	604000	564000	585000
Macromoths	*Dicallomera fascelina*	794000	866000	783000	817000	NA	NA
Macromoths	*Dichonia aprilina*	765000	878000	765000	857000	NA	NA
Macromoths	*Diloba caeruleocephala*	612000	582000	591000	554000	562000	528000
Macromoths	*Discestra trifolii*	591000	803000	537000	699000	509000	531000
Macromoths	*Discoloxia blomeri*	455000	490000	436000	459000	409000	405000
Macromoths	*Drepana falcataria*	834000	884000	800000	865000	NA	NA
Macromoths	*Drymonia dodonaea*	656000	720000	630000	618000	496000	555000
Macromoths	*Drymonia ruficornis*	637000	810000	626000	760000	588000	660000
Macromoths	*Dryobotodes eremita*	790000	824000	776000	742000	NA	NA
Macromoths	*Dypterygia scabriuscula*	395000	446000	395000	427000	374000	422000
Macromoths	*Dyscia fagaria*	850000	851000	802000	837000	NA	NA
Macromoths	*Earias clorana*	389000	465000	367000	454000	359000	442000
Macromoths	*Ectropis bistortata*	873000	909000	NA	NA	NA	NA
Macromoths	*Ectropis crepuscularia*	519000	561000	519000	501000	485000	466000
Macromoths	*Egira conspicillaris*	256000	262000	256000	261000	254000	257000
Macromoths	*Eilema complana*	412000	539000	373000	448000	361000	419000
Macromoths	*Eilema depressa*	348000	572000	333000	565000	330000	554000
Macromoths	*Eilema griseola*	375000	509000	375000	480000	358000	469000
Macromoths	*Eilema lurideola*	777000	864000	714000	774000	NA	NA
Macromoths	*Eilema sororcula*	288000	471000	288000	464000	278000	458000
Macromoths	*Elaphria venustula*	235000	279000	235000	278000	222000	277000
Macromoths	*Electrophaes corylata*	872000	904000	NA	NA	NA	NA
Macromoths	*Ematurga atomaria*	848000	941000	827000	896000	NA	NA
Macromoths	*Enargia paleacea*	831000	872000	804000	820000	NA	NA
Macromoths	*Ennomos alniaria*	850000	876000	813000	852000	NA	NA
Macromoths	*Ennomos autumnaria*	305000	350000	305000	340000	302000	324000
Macromoths	*Ennomos erosaria*	660000	785000	642000	629000	NA	NA
Macromoths	*Ennomos fuscantaria*	476000	535000	460000	534000	460000	499000
Macromoths	*Ennomos quercinaria*	472000	509000	437000	490000	417000	461000
Macromoths	*Epione repandaria*	877000	895000	NA	NA	NA	NA
Macromoths	*Epirrhoe galiata*	563000	669000	474000	529000	451000	444000
Macromoths	*Epirrhoe rivata*	383000	405000	381000	347000	333000	336000
Macromoths	*Epirrita christyi*	811000	814000	740000	780000	NA	NA
Macromoths	*Epirrita dilutata*	879000	907000	NA	NA	NA	NA
Macromoths	*Eremobia ochroleuca*	459000	521000	457000	513000	445000	473000
Macromoths	*Eriogaster lanestris*	320000	378000	285000	361000	279000	340000
Macromoths	*Euchoeca nebulata*	684000	802000	574000	733000	484000	617000

Macromoths	*Euclidia glyphica*	505000	578000	494000	497000	440000	439000
Macromoths	*Eulithis mellinata*	717000	734000	682000	633000	NA	NA
Macromoths	*Eulithis prunata*	844000	849000	820000	802000	766000	776000
Macromoths	*Euphyia biangulata*	278000	336000	263000	285000	257000	280000
Macromoths	*Euphyia unangulata*	319000	350000	319000	336000	319000	328000
Macromoths	*Eupithecia abbreviata*	830000	871000	804000	848000	NA	NA
Macromoths	*Eupithecia centaureata*	695000	852000	645000	725000	NA	NA
Macromoths	*Eupithecia dodoneata*	498000	611000	489000	573000	478000	549000
Macromoths	*Eupithecia exiguata*	713000	776000	652000	715000	NA	NA
Macromoths	*Eupithecia expallidata*	404000	501000	365000	325000	356000	301000
Macromoths	*Eupithecia haworthiata*	334000	415000	334000	415000	328000	383000
Macromoths	*Eupithecia icterata*	868000	877000	NA	NA	NA	NA
Macromoths	*Eupithecia indigata*	840000	870000	831000	843000	NA	NA
Macromoths	*Eupithecia innotata*	369000	581000	360000	483000	360000	338000
Macromoths	*Eupithecia insigniata*	307000	320000	305000	315000	279000	294000
Macromoths	*Eupithecia inturbata*	421000	437000	421000	416000	413000	402000
Macromoths	*Eupithecia irriguata*	280000	222000	270000	202000	240000	186000
Macromoths	*Eupithecia linariata*	592000	655000	582000	613000	551000	602000
Macromoths	*Eupithecia millefoliata*	234000	309000	234000	307000	207000	307000
Macromoths	*Eupithecia pimpinellata*	334000	332000	334000	330000	NA	NA
Macromoths	*Eupithecia plumbeolata*	360000	465000	317000	422000	312000	420000
Macromoths	*Eupithecia pygmaeata*	785000	844000	738000	824000	535000	562000
Macromoths	*Eupithecia simpliciata*	478000	506000	477000	502000	399000	427000
Macromoths	*Eupithecia subumbrata*	429000	572000	389000	432000	383000	391000
Macromoths	*Eupithecia succenturiata*	661000	677000	655000	656000	NA	NA
Macromoths	*Eupithecia tantillaria*	813000	842000	778000	818000	NA	NA
Macromoths	*Eupithecia tenuiata*	819000	835000	792000	811000	768000	760000
Macromoths	*Eupithecia tripunctaria*	832000	828000	773000	786000	NA	NA
Macromoths	*Eupithecia trisignaria*	624000	778000	614000	649000	497000	546000
Macromoths	*Eupithecia valerianata*	706000	775000	617000	684000	478000	552000
Macromoths	*Eupithecia venosata*	644000	621000	621000	549000	546000	434000
Macromoths	*Eupithecia virgaureata*	866000	894000	831000	864000	NA	NA
Macromoths	*Euplagia quadripunctaria*	133000	244000	132000	223000	132000	223000
Macromoths	*Euproctis chrysorrhoea*	479000	481000	470000	467000	395000	425000
Macromoths	*Euproctis similis*	544000	581000	544000	568000	528000	556000
Macromoths	*Eupsilia transversa*	845000	909000	819000	857000	NA	NA
Macromoths	*Eurois occulta*	823000	846000	813000	831000	NA	NA
Macromoths	*Euthrix potatoria*	NA	NA	832000	878000	764000	774000
Macromoths	*Euxoa cursoria*	750000	713000	NA	NA	NA	NA
Macromoths	*Euxoa nigricans*	837000	838000	804000	790000	NA	NA
Macromoths	*Euxoa obelisca*	446000	582000	NA	NA	NA	NA
Macromoths	*Euxoa tritici*	849000	906000	821000	838000	NA	NA
Macromoths	*Falcaria lacertinaria*	873000	880000	NA	NA	NA	NA
Macromoths	*Furcula bicuspis*	417000	456000	416000	438000	412000	424000
Macromoths	*Furcula bifida*	461000	543000	460000	535000	416000	468000

Macromoths	*Furcula furcula*	831000	866000	822000	838000	NA	NA
Macromoths	*Gastropacha quercifolia*	322000	280000	322000	274000	320000	247000
Macromoths	*Geometra papilionaria*	873000	896000	NA	NA	NA	NA
Macromoths	*Gortyna flavago*	827000	886000	768000	856000	NA	NA
Macromoths	*Gymnoscelis rufifasciata*	872000	939000	NA	NA	NA	NA
Macromoths	*Habrosyne pyritoides*	545000	577000	520000	564000	508000	539000
Macromoths	*Hadena bicruris*	851000	912000	NA	NA	NA	NA
Macromoths	*Hadena confusa*	806000	873000	776000	862000	NA	NA
Macromoths	*Hadena perplexa*	581000	568000	555000	534000	528000	492000
Macromoths	*Hadena rivularis*	875000	908000	NA	NA	NA	NA
Macromoths	*Hecatera bicolorata*	735000	853000	686000	743000	NA	NA
Macromoths	*Helicoverpa armigera*	429000	768000	378000	654000	374000	517000
Macromoths	*Heliothis peltigera*	554000	622000	442000	575000	396000	549000
Macromoths	*Heliothis viriplaca*	277000	334000	273000	332000	273000	325000
Macromoths	*Hemaris fuciformis*	336000	351000	317000	339000	305000	335000
Macromoths	*Hemaris tityus*	740000	845000	421000	821000	NA	NA
Macromoths	*Hemistola chrysoprasaria*	336000	509000	336000	395000	332000	389000
Macromoths	*Hemithea aestivaria*	466000	546000	466000	530000	462000	495000
Macromoths	*Hepialus hecta*	860000	877000	NA	NA	NA	NA
Macromoths	*Hepialus lupulinus*	725000	909000	694000	854000	674000	721000
Macromoths	*Hepialus sylvina*	849000	898000	811000	860000	NA	NA
Macromoths	*Herminia grisealis*	845000	868000	815000	830000	NA	NA
Macromoths	*Hoplodrina alsines*	665000	741000	661000	678000	NA	NA
Macromoths	*Hoplodrina ambigua*	340000	514000	340000	481000	340000	453000
Macromoths	*Hoplodrina blanda*	758000	895000	739000	839000	NA	NA
Macromoths	*Horisme tersata*	323000	333000	323000	329000	315000	317000
Macromoths	*Horisme vitalbata*	301000	331000	301000	331000	298000	322000
Macromoths	*Hydraecia petasitis*	563000	613000	536000	530000	437000	472000
Macromoths	*Hydrelia flammeolaria*	641000	703000	611000	639000	576000	615000
Macromoths	*Hydrelia sylvata*	263000	282000	252000	258000	242000	237000
Macromoths	*Hyles gallii*	525000	724000	417000	560000	328000	522000
Macromoths	*Hyles livornica*	256000	428000	NA	NA	NA	NA
Macromoths	*Hyloicus pinastri*	342000	460000	341000	456000	338000	446000
Macromoths	*Hypena crassalis*	337000	447000	333000	414000	320000	375000
Macromoths	*Hypena rostralis*	264000	328000	253000	328000	244000	328000
Macromoths	*Hypenodes humidalis*	599000	735000	599000	731000	464000	643000
Macromoths	*Hypomecis punctinalis*	326000	359000	326000	342000	326000	337000
Macromoths	*Hypomecis roboraria*	309000	298000	269000	239000	269000	239000
Macromoths	*Idaea aversata*	864000	882000	NA	NA	NA	NA
Macromoths	*Idaea dimidiata*	662000	714000	657000	659000	NA	NA
Macromoths	*Idaea emarginata*	368000	401000	367000	369000	359000	352000
Macromoths	*Idaea fuscovenosa*	403000	462000	402000	446000	393000	420000
Macromoths	*Idaea muricata*	384000	348000	364000	332000	326000	311000
Macromoths	*Idaea seriata*	835000	838000	787000	771000	NA	NA

Macromoths	*Idaea subsericeata*	412000	507000	379000	453000	351000	423000
Macromoths	*Idaea sylvestraria*	234000	190000	209000	177000	209000	161000
Macromoths	*Idaea trigeminata*	325000	338000	325000	336000	323000	333000
Macromoths	*Ipimorpha retusa*	339000	342000	322000	336000	322000	331000
Macromoths	*Ipimorpha subtusa*	560000	645000	538000	609000	517000	567000
Macromoths	*Jodis lactearia*	575000	673000	531000	574000	482000	533000
Macromoths	*Lacanobia contigua*	792000	831000	787000	800000	683000	652000
Macromoths	*Lacanobia suasa*	514000	558000	492000	528000	438000	486000
Macromoths	*Lacanobia w-latinum*	349000	373000	347000	361000	345000	354000
Macromoths	*Lampropteryx otregiata*	337000	416000	290000	386000	272000	361000
Macromoths	*Larentia clavaria*	431000	443000	402000	432000	398000	378000
Macromoths	*Lasiocampa quercus*	872000	916000	825000	894000	766000	825000
Macromoths	*Laspeyria flexula*	359000	430000	359000	422000	359000	412000
Macromoths	*Leucoma salicis*	456000	533000	448000	524000	447000	483000
Macromoths	*Ligdia adustata*	419000	464000	394000	455000	379000	443000
Macromoths	*Lithophane hepatica*	382000	663000	380000	608000	370000	560000
Macromoths	*Lithophane ornitopus*	366000	477000	362000	472000	362000	468000
Macromoths	*Lithophane semibrunnea*	390000	543000	385000	507000	377000	477000
Macromoths	*Lithosia quadra*	213000	455000	NA	NA	NA	NA
Macromoths	*Lobophora halterata*	810000	856000	798000	841000	NA	NA
Macromoths	*Lomaspilis marginata*	863000	885000	NA	NA	NA	NA
Macromoths	*Lomographa bimaculata*	407000	575000	402000	542000	389000	496000
Macromoths	*Lomographa temerata*	709000	821000	701000	785000	666000	719000
Macromoths	*Luperina testacea*	847000	902000	814000	844000	NA	NA
Macromoths	*Lycia hirtaria*	841000	871000	821000	823000	NA	NA
Macromoths	*Lygephila pastinum*	393000	480000	375000	453000	360000	444000
Macromoths	*Lymantria monacha*	326000	387000	326000	368000	321000	352000
Macromoths	*Macaria alternata*	348000	536000	336000	462000	312000	448000
Macromoths	*Macaria liturata*	848000	873000	809000	845000	NA	NA
Macromoths	*Macaria notata*	863000	897000	NA	NA	NA	NA
Macromoths	*Macaria wauaria*	709000	658000	705000	510000	688000	471000
Macromoths	*Macrochilo cribrumalis*	319000	332000	318000	327000	318000	324000
Macromoths	*Macroglossum stellatarum*	748000	886000	622000	865000	560000	770000
Macromoths	*Malacosoma neustria*	474000	458000	447000	444000	443000	421000
Macromoths	*Mamestra brassicae*	842000	871000	792000	835000	NA	NA
Macromoths	*Meganola albula*	265000	360000	264000	359000	264000	340000
Macromoths	*Melanchra persicariae*	551000	643000	550000	588000	487000	568000
Macromoths	*Melanthia procellata*	318000	387000	318000	374000	308000	343000
Macromoths	*Menophra abruptaria*	466000	506000	466000	489000	461000	477000
Macromoths	*Mesoleuca albicillata*	819000	872000	771000	852000	NA	NA
Macromoths	*Mesoligia furuncula*	694000	714000	691000	695000	660000	669000
Macromoths	*Mesoligia literosa*	877000	897000	NA	NA	765000	722000
Macromoths	*Miltochrista miniata*	331000	354000	331000	346000	327000	344000
Macromoths	*Mimas tiliae*	451000	534000	451000	525000	448000	496000

Macromoths	*Minoa murinata*	254000	243000	251000	238000	NA	NA
Macromoths	*Mormo maura*	655000	831000	596000	783000	546000	707000
Macromoths	*Mythimna albipuncta*	264000	386000	264000	367000	264000	340000
Macromoths	*Mythimna comma*	818000	853000	794000	818000	NA	NA
Macromoths	*Mythimna favicolor*	217000	240000	210000	237000	NA	NA
Macromoths	*Mythimna ferrago*	851000	869000	825000	838000	NA	NA
Macromoths	*Mythimna flammea*	314000	349000	314000	326000	314000	317000
Macromoths	*Mythimna l-album*	108000	273000	108000	267000	108000	265000
Macromoths	*Mythimna litoralis*	433000	489000	424000	438000	335000	306000
Macromoths	*Mythimna loreyi*	179000	340000	169000	320000	145000	261000
Macromoths	*Mythimna obsoleta*	425000	489000	413000	477000	394000	447000
Macromoths	*Mythimna pallens*	836000	940000	799000	900000	NA	NA
Macromoths	*Mythimna pudorina*	366000	438000	359000	398000	359000	370000
Macromoths	*Mythimna straminea*	434000	502000	434000	496000	432000	473000
Macromoths	*Mythimna turca*	235000	323000	235000	311000	NA	NA
Macromoths	*Mythimna unipuncta*	255000	522000	249000	480000	216000	448000
Macromoths	*Mythimna vitellina*	411000	568000	382000	514000	363000	479000
Macromoths	*Naenia typica*	812000	902000	788000	861000	NA	NA
Macromoths	*Noctua fimbriata*	837000	866000	801000	822000	NA	NA
Macromoths	*Noctua interjecta*	538000	657000	520000	627000	490000	587000
Macromoths	*Noctua orbona*	352000	365000	352000	330000	NA	NA
Macromoths	*Nola confusalis*	840000	886000	792000	854000	NA	NA
Macromoths	*Nola cucullatella*	532000	581000	528000	581000	515000	558000
Macromoths	*Nonagria typhae*	752000	834000	676000	752000	546000	666000
Macromoths	*Notodonta ziczac*	852000	941000	833000	911000	NA	NA
Macromoths	*Nudaria mundana*	799000	826000	789000	785000	NA	NA
Macromoths	*Nycteola revayana*	714000	800000	607000	767000	596000	691000
Macromoths	*Ochropacha duplaris*	869000	902000	NA	NA	NA	NA
Macromoths	*Odezia atrata*	828000	874000	798000	846000	675000	794000
Macromoths	*Odontosia carmelita*	833000	861000	821000	834000	NA	NA
Macromoths	*Oligia latruncula*	594000	793000	569000	701000	529000	629000
Macromoths	*Oligia strigilis*	833000	876000	821000	852000	NA	NA
Macromoths	*Oligia versicolor*	662000	765000	641000	700000	NA	NA
Macromoths	*Omphaloscelis lunosa*	789000	842000	772000	801000	686000	716000
Macromoths	*Operophtera fagata*	848000	854000	804000	819000	NA	NA
Macromoths	*Orgyia antiqua*	786000	899000	730000	843000	NA	NA
Macromoths	*Orthonama obstipata*	452000	659000	417000	584000	339000	542000
Macromoths	*Orthonama vittata*	860000	877000	813000	846000	NA	NA
Macromoths	*Orthosia cruda*	803000	862000	755000	820000	NA	NA
Macromoths	*Orthosia gracilis*	824000	898000	786000	891000	NA	NA
Macromoths	*Orthosia miniosa*	329000	383000	329000	381000	324000	352000
Macromoths	*Orthosia munda*	682000	793000	672000	782000	NA	NA
Macromoths	*Orthosia opima*	463000	490000	429000	406000	331000	390000
Macromoths	*Orthosia populeti*	639000	814000	603000	778000	568000	652000
Macromoths	*Ourapteryx sambucaria*	684000	810000	674000	789000	NA	NA

Macromoths	*Pachycnemia hippocastanaria*	146000	156000	146000	155000	146000	151000
Macromoths	*Panemeria tenebrata*	492000	520000	491000	507000	475000	481000
Macromoths	*Panolis flammea*	863000	908000	NA	NA	NA	NA
Macromoths	*Paradarisa consonaria*	289000	371000	283000	365000	281000	344000
Macromoths	*Paradrina clavipalpis*	868000	824000	NA	NA	764000	663000
Macromoths	*Parascotia fuliginaria*	298000	364000	282000	350000	277000	350000
Macromoths	*Parasemia plantaginis*	862000	887000	774000	824000	563000	619000
Macromoths	*Parastichtis suspecta*	817000	822000	770000	811000	NA	NA
Macromoths	*Parastichtis ypsillon*	600000	666000	595000	614000	516000	559000
Macromoths	*Parectropis similaria*	313000	328000	313000	325000	313000	325000
Macromoths	*Pasiphila chloerata*	447000	485000	422000	474000	415000	456000
Macromoths	*Pasiphila debiliata*	253000	372000	194000	339000	NA	NA
Macromoths	*Pasiphila rectangulata*	873000	879000	NA	NA	NA	NA
Macromoths	*Pelurga comitata*	740000	790000	710000	628000	NA	NA
Macromoths	*Perconia strigillaria*	534000	722000	483000	631000	378000	519000
Macromoths	*Peribatodes rhomboidaria*	812000	869000	790000	834000	NA	NA
Macromoths	*Peridea anceps*	495000	668000	495000	530000	430000	453000
Macromoths	*Peridroma saucia*	582000	793000	574000	749000	532000	631000
Macromoths	*Perizoma affinitata*	844000	865000	814000	839000	NA	NA
Macromoths	*Perizoma bifaciata*	580000	658000	521000	555000	496000	518000
Macromoths	*Perizoma flavofasciata*	855000	918000	836000	869000	NA	NA
Macromoths	*Phalera bucephala*	855000	891000	839000	868000	NA	NA
Macromoths	*Pheosia tremula*	833000	895000	815000	856000	NA	NA
Macromoths	*Phibalapteryx virgata*	284000	294000	283000	293000	NA	NA
Macromoths	*Phigalia pilosaria*	863000	883000	833000	858000	NA	NA
Macromoths	*Philereme transversata*	413000	452000	411000	444000	380000	412000
Macromoths	*Philereme vetulata*	356000	381000	348000	364000	331000	342000
Macromoths	*Phragmatobia fuliginosa*	846000	893000	811000	867000	NA	NA
Macromoths	*Phytometra viridaria*	797000	843000	683000	741000	457000	535000
Macromoths	*Plagodis dolabraria*	671000	836000	671000	787000	NA	NA
Macromoths	*Plagodis pulveraria*	785000	850000	742000	837000	662000	795000
Macromoths	*Plemyria rubiginata*	830000	862000	816000	832000	NA	NA
Macromoths	*Plusia putnami*	766000	907000	741000	871000	NA	NA
Macromoths	*Poecilocampa populi*	874000	882000	NA	NA	NA	NA
Macromoths	*Polia nebulosa*	797000	887000	760000	867000	685000	823000
Macromoths	*Polia trimaculosa*	644000	804000	NA	NA	NA	NA
Macromoths	*Polychrysia moneta*	536000	545000	536000	540000	504000	491000
Macromoths	*Polymixis flavicincta*	366000	428000	348000	372000	343000	354000
Macromoths	*Polymixis lichenea*	499000	544000	495000	485000	492000	461000
Macromoths	*Polyploca ridens*	336000	357000	326000	340000	326000	338000
Macromoths	*Protodeltote pygarga*	346000	490000	346000	472000	342000	446000
Macromoths	*Pseudoips prasinana*	715000	832000	688000	809000	505000	711000
Macromoths	*Pseudopanthera macularia*	791000	846000	669000	784000	475000	700000
Macromoths	*Pseudoterpna pruinata*	615000	636000	596000	595000	561000	549000

Macromoths	*Pterapherapteryx sexalata*	408000	359000	373000	331000	373000	330000
Macromoths	*Pterostoma palpina*	852000	899000	834000	865000	NA	NA
Macromoths	*Ptilodon cucullina*	323000	336000	323000	335000	323000	331000
Macromoths	*Pyrrhia umbra*	546000	615000	508000	579000	449000	521000
Macromoths	*Rheumaptera cervinalis*	413000	626000	345000	452000	345000	368000
Macromoths	*Rheumaptera hastata*	792000	919000	666000	858000	NA	NA
Macromoths	*Rheumaptera undulata*	517000	635000	492000	611000	477000	555000
Macromoths	*Rhizedra lutosa*	778000	859000	726000	819000	NA	NA
Macromoths	*Rhodometra sacraria*	586000	743000	586000	694000	544000	648000
Macromoths	*Rhyacia simulans*	750000	840000	666000	720000	562000	554000
Macromoths	*Rivula sericealis*	837000	902000	806000	871000	NA	NA
Macromoths	*Schrankia costaestrigalis*	799000	920000	754000	879000	661000	791000
Macromoths	*Schrankia taenialis*	201000	270000	201000	270000	201000	266000
Macromoths	*Scoliopteryx libatrix*	839000	907000	821000	877000	NA	NA
Macromoths	*Scopula emutaria*	324000	352000	306000	351000	292000	316000
Macromoths	*Scopula floslactata*	798000	850000	749000	828000	671000	712000
Macromoths	*Scopula imitaria*	445000	483000	445000	476000	445000	453000
Macromoths	*Scopula immutata*	427000	527000	419000	470000	416000	434000
Macromoths	*Scopula marginepunctata*	394000	483000	348000	452000	341000	431000
Macromoths	*Scotopteryx bipunctaria*	334000	423000	259000	325000	216000	237000
Macromoths	*Scotopteryx luridata*	777000	856000	751000	818000	520000	558000
Macromoths	*Scotopteryx mucronata*	792000	821000	739000	796000	549000	588000
Macromoths	*Selenia tetralunaria*	792000	866000	767000	833000	NA	NA
Macromoths	*Semiaspilates ochrearia*	341000	388000	340000	377000	326000	338000
Macromoths	*Sesia apiformis*	326000	328000	280000	326000	NA	NA
Macromoths	*Sesia bembeciformis*	744000	758000	658000	630000	567000	544000
Macromoths	*Shargacucullia verbasci*	453000	506000	449000	481000	447000	477000
Macromoths	*Sideridis albicolon*	458000	511000	391000	450000	335000	355000
Macromoths	*Simyra albovenosa*	323000	339000	322000	336000	320000	333000
Macromoths	*Smerinthus ocellata*	480000	505000	480000	472000	479000	461000
Macromoths	*Sphinx ligustri*	396000	413000	334000	374000	331000	363000
Macromoths	*Spilosoma luteum*	785000	867000	752000	856000	682000	760000
Macromoths	*Spodoptera exigua*	403000	604000	403000	575000	401000	484000
Macromoths	*Standfussiana lucernea*	814000	865000	678000	763000	NA	NA
Macromoths	*Stauropus fagi*	331000	339000	331000	337000	329000	332000
Macromoths	*Synanthedon culiciformis*	446000	718000	442000	417000	274000	398000
Macromoths	*Synanthedon formicaeformis*	315000	432000	301000	374000	NA	NA
Macromoths	*Synanthedon vespiformis*	322000	394000	283000	369000	283000	348000
Macromoths	*Tethea ocularis*	554000	588000	530000	568000	507000	507000
Macromoths	*Tethea or*	845000	878000	820000	861000	NA	NA
Macromoths	*Tetheella fluctuosa*	428000	760000	339000	425000	321000	299000
Macromoths	*Thalpophila matura*	777000	796000	737000	675000	NA	NA

Macromoths	*Thera firmata*	875000	915000	NA	NA	NA	NA
Macromoths	*Thera juniperata*	846000	821000	820000	707000	NA	NA
Macromoths	*Theria primaria*	637000	678000	617000	625000	NA	NA
Macromoths	*Tholera cespitis*	665000	795000	640000	736000	599000	573000
Macromoths	*Tholera decimalis*	641000	666000	632000	632000	597000	619000
Macromoths	*Thumatha senex*	511000	629000	483000	588000	443000	469000
Macromoths	*Thyatira batis*	828000	887000	823000	864000	NA	NA
Macromoths	*Timandra comae*	555000	611000	524000	567000	503000	527000
Macromoths	*Trichoplusia ni*	222000	368000	NA	NA	NA	NA
Macromoths	*Triphosa dubitata*	460000	528000	436000	500000	423000	414000
Macromoths	*Tyria jacobaeae*	689000	781000	652000	734000	593000	657000
Macromoths	*Watsonalla binaria*	470000	529000	468000	503000	458000	483000
Macromoths	*Watsonalla cultraria*	355000	467000	355000	459000	335000	446000
Macromoths	*Xanthia aurago*	441000	486000	420000	479000	419000	474000
Macromoths	*Xanthia citrago*	772000	847000	752000	830000	NA	NA
Macromoths	*Xanthia gilvago*	618000	666000	587000	578000	530000	538000
Macromoths	*Xanthorhoe ferrugata*	737000	839000	730000	801000	NA	NA
Macromoths	*Xanthorhoe quadrifasiata*	445000	499000	445000	490000	426000	480000
Macromoths	*Xanthorhoe spadicearia*	870000	880000	NA	NA	NA	NA
Macromoths	*Xestia castanea*	868000	895000	NA	NA	NA	NA
Macromoths	*Xestia ditrapezium*	774000	852000	701000	833000	584000	753000
Macromoths	*Xestia rhomboidea*	471000	663000	440000	573000	408000	462000
Macromoths	*Xestia triangulum*	877000	933000	NA	NA	NA	NA
Macromoths	*Xylena exsoleta*	828000	858000	818000	832000	NA	NA
Macromoths	*Xylocampa areola*	785000	883000	726000	861000	NA	NA
Macromoths	*Zanclognatha tarsipennalis*	667000	744000	660000	711000	NA	NA
Macromoths	*Zeuzera pyrina*	436000	474000	420000	463000	402000	458000
Macromoths	*Zygaena filipendulae*	877000	885000	826000	838000	NA	NA
Macromoths	*Zygaena lonicerae*	617000	682000	595000	650000	517000	554000
Macromoths	*Zygaena trifolii*	330000	329000	306000	317000	306000	315000
Shieldbugs*	*Acanthosoma haemorrhoidale*	547000	688000	NA	NA	NA	NA
Shieldbugs*	*Aelia acuminata*	352000	374000	NA	NA	NA	NA
Shieldbugs*	*Chorosoma schillingi*	360000	384000	NA	NA	NA	NA
Shieldbugs*	*Coreus marginatus*	228000	334000	194000	248000	NA	NA
Shieldbugs*	*Coriomeris denticulatus*	303000	396000	NA	NA	NA	NA
Shieldbugs*	*Corizus hyoscyami*	268000	361000	NA	NA	NA	NA
Shieldbugs*	*Dolycoris baccarum*	435000	486000	NA	NA	NA	NA
Shieldbugs*	*Elasmucha grisea*	NA	NA	435000	426000	NA	NA
Shieldbugs*	*Eurygaster testudinaria*	201000	228000	NA	NA	NA	NA
Shieldbugs*	*Legnotus limbosus*	275000	320000	NA	NA	NA	NA
Shieldbugs*	*Myrmus miriformis*	439000	396000	NA	NA	NA	NA
Shieldbugs*	*Palomena prasina*	394000	454000	317000	385000	NA	NA
Shieldbugs*	*Pentatoma rufipes*	NA	NA	436000	477000	NA	NA
Shieldbugs*	*Picromerus bidens*	550000	540000	NA	NA	NA	NA

Shieldbugs*	*Piezodorus lituratus*	538000	518000	NA	NA	NA	NA
Shieldbugs*	*Podops inuncta*	226000	241000	NA	NA	NA	NA
Shieldbugs*	*Rhacognathus punctatus*	456000	465000	NA	NA	NA	NA
Shieldbugs*	*Rhopalus subrufus*	232000	347000	211000	223000	NA	NA
Shieldbugs*	*Troilus luridus*	450000	509000	NA	NA	NA	NA
Shieldbugs*	*Zicrona caerulea*	463000	495000	NA	NA	NA	NA
Soldierflies*	*Asilus crabroniformis*	222000	162000	NA	NA	NA	NA
Soldierflies*	*Beris chalybata*	517000	593000	NA	NA	NA	NA
Soldierflies*	*Beris fuscipes*	376000	476000	NA	NA	NA	NA
Soldierflies*	*Beris morrisii*	372000	362000	267000	303000	NA	NA
Soldierflies*	*Bombylius major*	521000	449000	NA	NA	NA	NA
Soldierflies*	*Chloromyia formosa*	545000	579000	NA	NA	NA	NA
Soldierflies*	*Choerades marginatus*	266000	281000	NA	NA	NA	NA
Soldierflies*	*Chorisops nagatomii*	220000	240000	NA	NA	NA	NA
Soldierflies*	*Chorisops tibialis*	430000	399000	320000	355000	NA	NA
Soldierflies*	*Chrysopilus asiliformis*	402000	380000	318000	300000	NA	NA
Soldierflies*	*Chrysopilus cristatus*	594000	779000	NA	NA	NA	NA
Soldierflies*	*Chrysops caecutiens*	492000	423000	286000	308000	NA	NA
Soldierflies*	*Chrysops viduatus*	299000	294000	235000	273000	NA	NA
Soldierflies*	*Dioctria atricapilla*	383000	349000	NA	NA	NA	NA
Soldierflies*	*Dioctria baumhaueri*	350000	335000	311000	259000	NA	NA
Soldierflies*	*Dioctria linearis*	328000	316000	246000	239000	NA	NA
Soldierflies*	*Dioctria rufipes*	542000	518000	NA	NA	NA	NA
Soldierflies*	*Dysmachus trigonus*	377000	358000	276000	268000	NA	NA
Soldierflies*	*Haematopota crassicornis*	542000	565000	NA	NA	NA	NA
Soldierflies*	*Hybomitra bimaculata*	357000	354000	NA	NA	NA	NA
Soldierflies*	*Hybomitra distinguenda*	441000	373000	NA	NA	NA	NA
Soldierflies*	*Leptarthrus brevirostris*	482000	514000	NA	NA	NA	NA
Soldierflies*	*Leptogaster cylindrica*	403000	455000	315000	343000	NA	NA
Soldierflies*	*Machimus atricapillus*	459000	443000	NA	NA	NA	NA
Soldierflies*	*Machimus cingulatus*	324000	397000	222000	283000	NA	NA
Soldierflies*	*Microchrysa flavicornis*	550000	482000	NA	NA	NA	NA
Soldierflies*	*Microchrysa polita*	535000	445000	NA	NA	NA	NA
Soldierflies*	*Nemotelus nigrinus*	418000	405000	NA	NA	NA	NA
Soldierflies*	*Nemotelus notatus*	476000	343000	NA	NA	NA	NA
Soldierflies*	*Nemotelus pantherinus*	323000	274000	NA	NA	NA	NA
Soldierflies*	*Nemotelus uliginosus*	548000	434000	NA	NA	NA	NA
Soldierflies*	*Neoitamus cyanurus*	519000	364000	NA	NA	NA	NA
Soldierflies*	*Odontomyia tigrina*	244000	284000	NA	NA	NA	NA
Soldierflies*	*Oplodontha viridula*	469000	471000	NA	NA	NA	NA
Soldierflies*	*Oxycera morrisii*	443000	345000	NA	NA	NA	NA
Soldierflies*	*Oxycera nigricornis*	373000	321000	282000	250000	NA	NA
Soldierflies*	*Oxycera rara*	390000	353000	307000	294000	NA	NA
Soldierflies*	*Oxycera trilineata*	446000	340000	318000	266000	NA	NA

Soldierflies*	*Pachygaster atra*	338000	330000	296000	302000	NA	NA
Soldierflies*	*Pachygaster leachii*	311000	340000	247000	311000	NA	NA
Soldierflies*	*Philonicus albiceps*	423000	335000	NA	NA	NA	NA
Soldierflies*	*Rhagio tringarius*	516000	630000	NA	NA	NA	NA
Soldierflies*	*Sargus bipunctatus*	468000	401000	233000	222000	NA	NA
Soldierflies*	*Sargus flavipes*	489000	328000	NA	NA	NA	NA
Soldierflies*	*Sargus iridatus*	574000	506000	NA	NA	NA	NA
Soldierflies*	*Stratiomys potamida*	408000	396000	314000	301000	NA	NA
Soldierflies*	*Stratiomys singularior*	348000	308000	294000	254000	NA	NA
Soldierflies*	*Tabanus autumnalis*	285000	275000	NA	NA	NA	NA
Soldierflies*	*Tabanus bromius*	222000	264000	155000	197000	NA	NA
Soldierflies*	*Tabanus sudeticus*	488000	496000	NA	NA	NA	NA
Soldierflies*	*Thereva nobilitata*	544000	610000	NA	NA	NA	NA
Soldierflies*	*Vanoyia tenuicornis*	321000	254000	NA	NA	NA	NA
Wasps	*Agenioideus cinctellus*	232000	243000	183000	183000	NA	NA
Wasps	*Ammophila pubescens*	219000	208000	208000	208000	NA	NA
Wasps	*Ammophila sabulosa*	NA	NA	365000	361000	NA	NA
Wasps	*Ancistrocerus gazella*	427000	499000	363000	417000	NA	NA
Wasps	*Ancistrocerus oviventris*	469000	721000	NA	NA	NA	NA
Wasps	*Ancistrocerus parietinus*	449000	518000	NA	NA	NA	NA
Wasps	*Ancistrocerus parietum*	450000	494000	NA	NA	NA	NA
Wasps	*Ancistrocerus scoticus*	469000	382000	NA	NA	NA	NA
Wasps	*Ancistrocerus trifasciatus*	462000	464000	NA	NA	NA	NA
Wasps	*Anoplius infuscatus*	344000	355000	247000	288000	NA	NA
Wasps	*Anoplius viaticus*	358000	363000	313000	318000	NA	NA
Wasps	*Arachnospila minutula*	321000	233000	NA	NA	NA	NA
Wasps	*Arachnospila spissa*	NA	NA	374000	348000	NA	NA
Wasps	*Arachnospila trivialis*	289000	334000	NA	NA	NA	NA
Wasps	*Argogorytes mystaceus*	NA	NA	379000	273000	NA	NA
Wasps	*Astata boops*	191000	299000	187000	249000	NA	NA
Wasps	*Caliadurgus fasciatellus*	180000	247000	NA	NA	NA	NA
Wasps	*Cerceris arenaria*	311000	387000	258000	352000	NA	NA
Wasps	*Cerceris ruficornis*	165000	253000	141000	201000	NA	NA
Wasps	*Cerceris rybyensis*	282000	335000	240000	301000	NA	NA
Wasps	*Chrysis angustula*	463000	425000	NA	NA	NA	NA
Wasps	*Chrysis impressa*	472000	445000	NA	NA	NA	NA
Wasps	*Chrysis viridula*	303000	337000	NA	NA	NA	NA
Wasps	*Crabro cribrarius*	NA	NA	371000	368000	NA	NA
Wasps	*Crabro scutellatus*	161000	144000	NA	NA	NA	NA
Wasps	*Crossocerus annulipes*	440000	510000	NA	NA	NA	NA
Wasps	*Crossocerus capitosus*	382000	296000	NA	NA	NA	NA
Wasps	*Crossocerus cetratus*	427000	443000	269000	371000	NA	NA
Wasps	*Crossocerus distinguendus*	190000	331000	NA	NA	NA	NA
Wasps	*Crossocerus nigritus*	363000	317000	NA	NA	NA	NA

Wasps	*Crossocerus ovalis*	443000	476000	363000	384000	NA	NA
Wasps	*Crossocerus podagricus*	443000	454000	NA	NA	NA	NA
Wasps	*Crossocerus quadrimaculatus*	486000	502000	366000	407000	NA	NA
Wasps	*Crossocerus wesmaeli*	410000	403000	NA	NA	NA	NA
Wasps	*Diodontus luperus*	382000	276000	NA	NA	NA	NA
Wasps	*Diodontus minutus*	311000	360000	231000	259000	NA	NA
Wasps	*Dipogon subintermedius*	477000	362000	310000	294000	NA	NA
Wasps	*Dipogon variegatus*	418000	392000	NA	NA	NA	NA
Wasps	*Dolichovespula media*	438000	465000	279000	353000	NA	NA
Wasps	*Dolichovespula saxonica*	222000	414000	NA	NA	NA	NA
Wasps	*Dryudella pinguis*	499000	225000	NA	NA	NA	NA
Wasps	*Ectemnius cephalotes*	429000	384000	363000	285000	NA	NA
Wasps	*Ectemnius continuus*	478000	513000	NA	NA	NA	NA
Wasps	*Ectemnius dives*	274000	227000	NA	NA	NA	NA
Wasps	*Ectemnius lapidarius*	347000	367000	NA	NA	NA	NA
Wasps	*Ectemnius lituratus*	201000	289000	171000	226000	NA	NA
Wasps	*Ectemnius rubicola*	233000	270000	NA	NA	NA	NA
Wasps	*Ectemnius ruficornis*	364000	447000	NA	NA	NA	NA
Wasps	*Ectemnius sexcinctus*	419000	433000	NA	NA	NA	NA
Wasps	*Elampus panzeri*	310000	294000	271000	219000	NA	NA
Wasps	*Entomognathus brevis*	368000	350000	307000	318000	NA	NA
Wasps	*Episyron rufipes*	419000	420000	NA	NA	NA	NA
Wasps	*Eumenes coarctatus*	145000	144000	NA	NA	NA	NA
Wasps	*Evagetes crassicornis*	474000	499000	NA	NA	NA	NA
Wasps	*Gorytes quadrifasciatus*	372000	389000	NA	NA	NA	NA
Wasps	*Hedychridium ardens*	494000	399000	NA	NA	NA	NA
Wasps	*Hedychridium roseum*	151000	290000	148000	219000	NA	NA
Wasps	*Lestiphorus bicinctus*	215000	243000	NA	NA	NA	NA
Wasps	*Lindenius albilabris*	402000	477000	NA	NA	NA	NA
Wasps	*Lindenius panzeri*	195000	306000	NA	NA	NA	NA
Wasps	*Methocha articulata*	163000	268000	NA	NA	NA	NA
Wasps	*Mimesa lutaria*	358000	354000	274000	339000	NA	NA
Wasps	*Mimumesa dahlbomi*	434000	470000	NA	NA	NA	NA
Wasps	*Mutilla europaea*	149000	179000	NA	NA	NA	NA
Wasps	*Myrmosa atra*	431000	459000	NA	NA	NA	NA
Wasps	*Nysson spinosus*	487000	442000	NA	NA	NA	NA
Wasps	*Nysson trimaculatus*	309000	319000	NA	NA	NA	NA
Wasps	*Odynerus spinipes*	468000	407000	315000	253000	NA	NA
Wasps	*Oxybelus uniglumis*	478000	460000	NA	NA	NA	NA
Wasps	*Passaloecus corniger*	390000	404000	NA	NA	NA	NA
Wasps	*Passaloecus eremita*	174000	201000	NA	NA	NA	NA
Wasps	*Passaloecus gracilis*	371000	323000	232000	294000	NA	NA
Wasps	*Passaloecus insignis*	396000	269000	NA	NA	NA	NA
Wasps	*Passaloecus singularis*	436000	363000	NA	NA	NA	NA

Wasps	*Pemphredon inornata*	473000	480000	313000	334000	NA	NA
Wasps	*Pemphredon lethifer*	457000	397000	NA	NA	NA	NA
Wasps	*Philanthus triangulum*	264000	377000	230000	341000	NA	NA
Wasps	*Pompilus cinereus*	451000	468000	NA	NA	NA	NA
Wasps	*Priocnemis exaltata*	448000	388000	NA	NA	NA	NA
Wasps	*Priocnemis fennica*	362000	279000	NA	NA	NA	NA
Wasps	*Priocnemis parvula*	NA	NA	301000	320000	NA	NA
Wasps	*Priocnemis perturbator*	NA	NA	376000	327000	NA	NA
Wasps	*Priocnemis pusilla*	227000	211000	NA	NA	NA	NA
Wasps	*Psenulus concolor*	413000	212000	NA	NA	NA	NA
Wasps	*Psenulus pallipes*	425000	369000	278000	332000	NA	NA
Wasps	*Pseudomalus auratus*	417000	293000	259000	196000	NA	NA
Wasps	*Rhopalum clavipes*	427000	344000	NA	NA	NA	NA
Wasps	*Rhopalum coarctatum*	436000	366000	320000	297000	NA	NA
Wasps	*Sapyga quinquepunctata*	333000	274000	NA	NA	NA	NA
Wasps	*Smicromyrme rufipes*	165000	164000	NA	NA	NA	NA
Wasps	*Spilomena troglodytes*	248000	265000	NA	NA	NA	NA
Wasps	*Stigmus solskyi*	264000	347000	205000	270000	NA	NA
Wasps	*Symmorphus bifasciatus*	458000	435000	NA	NA	NA	NA
Wasps	*Symmorphus gracilis*	412000	285000	271000	245000	NA	NA
Wasps	*Tiphia femorata*	238000	309000	NA	NA	NA	NA
Wasps	*Tiphia minuta*	278000	374000	NA	NA	NA	NA
Wasps	*Trichrysis cyanea*	471000	424000	NA	NA	NA	NA
Wasps	*Trypoxylon attenuatum*	448000	401000	NA	NA	NA	NA
Wasps	*Trypoxylon clavicerum*	444000	386000	367000	340000	NA	NA
Wasps	*Trypoxylon medium*	232000	281000	218000	210000	NA	NA
Wasps	*Vespa crabro*	328000	431000	229000	345000	NA	NA
Wasps	*Vespula germanica*	462000	491000	NA	NA	NA	NA
Woodlice	*Androniscus dentiger*	777000	709000	762000	699000	NA	NA
Woodlice	*Armadillidium depressum*	257000	275000	228000	251000	NA	NA
Woodlice	*Armadillidium nasatum*	283000	316000	275000	308000	243000	245000
Woodlice	*Armadillidium pulchellum*	481000	499000	NA	NA	NA	NA
Woodlice	*Armadillidium vulgare*	551000	612000	NA	NA	NA	NA
Woodlice	*Asellus aquaticus*	594000	644000	576000	586000	NA	NA
Woodlice	*Haplophthalmus danicus*	396000	501000	374000	466000	302000	289000
Woodlice	*Haplophthalmus mengii*	527000	528000	480000	494000	NA	NA
Woodlice	*Ligia oceanica*	862000	817000	NA	NA	NA	NA
Woodlice	*Ligidium hypnorum*	297000	221000	269000	215000	NA	NA
Woodlice	*Platyarthrus hoffmannseggii*	504000	487000	449000	485000	335000	328000
Woodlice	*Porcellio spinicornis*	793000	773000	765000	685000	NA	NA
Woodlice	*Porcellionides cingendus*	272000	212000	265000	209000	NA	NA

Woodlice	*Porcellionides pruinosus*	563000	381000	NA	NA	NA	NA
Woodlice	*Proasellus meridianus*	510000	553000	443000	514000	322000	386000
Woodlice	*Trachelipus rathkii*	294000	261000	277000	256000	NA	NA
Woodlice	*Trichoniscus pygmaeus*	744000	674000	NA	NA	NA	NA

Table A2.6. Seasonal and annual temperature trends across the study period (1966-2010). P values in bold denote a significant change in the temperature measurement over each interval period. Seasons are defined by three month bins: Winter (December, January, February; assigned to the year represented by January and February); Spring (March, April, May); Summer (June, July, August); Autumn (September, October, November). The annual temperature of year T is, thus, the average temperature taken across December of year T-1 and January through November of year T.

Response variable	Fixed effects	Slope (°C/decade)	SE	Multiple R^2	F-statistic	df	p value
Mean annual temperature	Year (Interval 1 - 1966-1995)	0.21	0.11	0.1	3.4	1,28	0.078
Mean winter temperature	Year (Interval 1 - 1966-1995)	0.18	0.25	0.0	0.5	1,28	0.486
Mean spring temperature	Year (Interval 1 - 1966-1995)	0.39	0.11	0.3	11.9	1,28	**0.002**
Mean summer temperature	Year (Interval 1 - 1966-1995)	0.23	0.20	0.0	1.3	1,28	0.259
Mean autumn temperature	Year (Interval 1 - 1966-1995)	0.03	0.15	0.0	0.0	1,28	0.850
Mean annual temperature	Year (Interval 2 - 1986-2010)	0.28	0.16	0.1	3.0	1,22	0.095
Mean winter temperature	Year (Interval 2 - 1986-2010)	0.02	0.33	0.0	0.0	1,23	0.954
Mean spring temperature	Year (Interval 2 - 1986-2010)	0.33	0.19	0.1	3.0	1,23	0.096
Mean summer temperature	Year (Interval 2 - 1986-2010)	0.31	0.20	0.1	2.4	1,23	0.139
Mean autumn temperature	Year (Interval 2 - 1986-2010)	0.46	0.21	0.2	4.6	1,23	**0.043**

Table A2.7. Summary table and statistics for Figure 4 (taxonomic groups studied over both intervals). Mean rates of range margin change were compared between the two intervals using paired t-tests (species as pairs; shifts that are significantly different from zero are given in bold).

				Interval 1		Interval 2		paired t test		
Taxonomic group	Level of recording effort control	Number of hectads	No. spp	Mean range shift (km decade^{-1})	95% CI	Mean range shift (km decade^{-1})	95% CI	df	t	p value
Birds	Well recorded	2561	31	7.7	15.8	6.3	21.6	30	0.12	0.908
Birds	Heavily recorded	2500	31	6.7	16.3	6.5	20.8	30	0.02	0.983
Butterflies	Well recorded	1729	35	**18.3**	8.0	**30.3**	10.7	34	-2.26	**0.030**
Butterflies	Heavily recorded	1218	35	**16.9**	8.2	**28.0**	9.5	34	-2.26	**0.031**
Dragonflies*	Well recorded	414	7	**32.0**	13.3	**43.3**	23.8	6	-1.32	0.236
Dragonflies*	Heavily recorded	119	7	**25.1**	7.5	**37.4**	23.8	6	-1.00	0.356
Macromoths	Well recorded	477	132	**11.4**	4.4	**31.2**	6.5	131	-5.77	**<0.001**
Macromoths	Heavily recorded	205	132	**9.4**	3.3	**26.1**	5.6	131	-5.41	**<0.002**

Table A2.8. Northings (in metres, on the GB Ordnance Survey Grid) of all 205 species included in Figure 4, with their northern range margin locations for each time period, for well-recorded and heavily-recorded cells that were common to all three time periods (T1: 1966-75, T2: 1986-95, T3: 2001-2010). Note that for bird species, the time period years are 1968-72, 1988-1991, and 2007-2011.

Taxonomic group	Species	Well recorded T1	Well recorded T2	Well recorded T3	Heavily recorded T1	Heavily recorded T2	Heavily recorded T3
Birds	*Acrocephalus scirpaceus*	533000	648000	712000	533000	648000	710000
Birds	*Alcedo atthis*	774000	822000	844000	774000	822000	844000
Birds	*Anas querquedula*	569000	757000	727000	569000	757000	727000
Birds	*Burhinus oedicnemus*	327000	303000	306000	327000	303000	306000
Birds	*Caprimulgus europaeus*	829000	654000	629000	829000	654000	629000
Birds	*Charadrius dubius*	566000	601000	797000	566000	601000	797000
Birds	*Circus aeruginosus*	466000	683000	841000	466000	683000	841000
Birds	*Circus pygargus*	C	C	C	C	C	C
Birds	*Coccothraustes coccothraustes*	733000	747000	681000	733000	747000	681000
Birds	*Dendrocopos minor*	511000	542000	515000	511000	542000	515000
Birds	*Emberiza cirlus*	253000	133000	78000	253000	133000	78000
Birds	*Falco subbuteo*	528000	599000	768000	528000	599000	768000
Birds	*Garrulus glandarius*	798000	839000	861000	798000	839000	861000
Birds	*Limosa limosa*	621000	762000	452000	621000	762000	452000
Birds	*Lullula arborea*	335000	310000	423000	335000	310000	423000
Birds	*Luscinia megarhynchos*	413000	391000	417000	413000	391000	417000
Birds	*Motacilla flava*	692000	673000	658000	692000	673000	657000
Birds	*Panurus biarmicus*	384000	388000	590000	384000	388000	590000
Birds	*Phoenicurus ochruros*	347000	448000	587000	347000	448000	538000
Birds	*Picus viridis*	782000	851000	824000	782000	851000	824000
Birds	*Podiceps cristatus*	798000	813000	788000	798000	813000	788000
Birds	*Poecile montana*	733000	655000	623000	733000	655000	623000
Birds	*Poecile palustris*	645000	659000	647000	645000	658000	647000
Birds	*Porzana porzana*	784000	823000	755000	784000	823000	755000
Birds	*Pyrrhocorax pyrrhocorax*	679000	682000	668000	679000	674000	668000
Birds	*Sitta europaea*	614000	626000	717000	614000	626000	717000
Birds	*Sterna dougallii*	774000	676000	416000	774000	658000	416000
Birds	*Streptopelia turtur*	777000	679000	525000	777000	645000	525000
Birds	*Sylvia curruca*	775000	834000	790000	775000	834000	790000
Birds	*Sylvia undata*	115000	147000	342000	115000	147000	342000
Birds	*Tyto alba*	864000	871000	959000	864000	871000	959000

Butterflies	*Aglais polychloros*	337000	366000	347000	337000	286000	327000
Butterflies	*Anthocharis cardamines*	831000	860000	914000	732000	833000	875000
Butterflies	*Apatura iris*	208000	235000	268000	208000	216000	268000
Butterflies	*Aphantopus hyperantus*	734000	849000	866000	718000	823000	859000
Butterflies	*Argynnis adippe*	405000	407000	462000	395000	407000	441000
Butterflies	*Argynnis paphia*	323000	411000	466000	313000	411000	466000
Butterflies	*Aricia agestis*	380000	421000	507000	378000	420000	487000
Butterflies	*Boloria euphrosyne*	822000	816000	869000	746000	785000	791000
Butterflies	*Callophrys rubi*	805000	843000	876000	798000	816000	840000
Butterflies	*Celastrina argiolus*	563000	580000	664000	542000	575000	646000
Butterflies	*Erynnis tages*	676000	793000	851000	647000	734000	746000
Butterflies	*Euphydryas aurinia*	750000	723000	740000	694000	645000	719000
Butterflies	*Gonepteryx rhamni*	487000	508000	561000	487000	505000	551000
Butterflies	*Hamearis lucina*	390000	464000	414000	390000	430000	387000
Butterflies	*Hesperia comma*	175000	168000	184000	175000	168000	184000
Butterflies	*Inachis io*	782000	784000	944000	768000	780000	908000
Butterflies	*Lasiommata megera*	620000	625000	646000	560000	606000	629000
Butterflies	*Leptidea sinapis*	278000	318000	355000	278000	283000	344000
Butterflies	*Limenitis camilla*	308000	371000	406000	308000	369000	401000
Butterflies	*Lycaena phlaeas*	862000	872000	899000	855000	856000	872000
Butterflies	*Lysandra bellargus*	176000	179000	208000	176000	172000	208000
Butterflies	*Lysandra coridon*	275000	274000	292000	274000	272000	286000
Butterflies	*Melanargia galathea*	361000	484000	530000	361000	482000	523000
Butterflies	*Neozephyrus quercus*	551000	610000	730000	494000	555000	655000
Butterflies	*Ochlodes faunus*	562000	607000	632000	562000	601000	618000
Butterflies	*Plebejus argus*	366000	374000	377000	366000	367000	368000
Butterflies	*Polygonia c-album*	396000	573000	785000	396000	561000	768000
Butterflies	*Pyrgus malvae*	428000	377000	366000	428000	371000	359000
Butterflies	*Pyronia tithonus*	469000	497000	539000	469000	491000	520000
Butterflies	*Satyrium pruni*	286000	274000	297000	286000	274000	297000
Butterflies	*Satyrium w-album*	413000	512000	578000	411000	494000	558000
Butterflies	*Thecla betulae*	306000	296000	300000	306000	296000	300000
Butterflies	*Thymelicus lineola*	330000	382000	408000	329000	382000	405000
Butterflies	*Thymelicus sylvestris*	485000	554000	633000	480000	542000	617000
Butterflies	*Vanessa cardui*	848000	859000	944000	806000	851000	908000
Dragonflies	*Aeshna mixta*	340000	396000	509000	286000	321000	438000
Dragonflies	*Anax imperator*	281000	409000	529000	255000	335000	426000
Dragonflies	*Brachytron pratense*	343000	410000	436000	305000	337000	361000
Dragonflies	*Ceriagrion tenellum*	225000	259000	259000	190000	217000	230000
Dragonflies	*Erythromma najas*	371000	386000	408000	274000	345000	334000
Dragonflies	*Libellula depressa*	332000	400000	488000	267000	325000	421000
Dragonflies	*Orthetrum cancellatum*	283000	363000	449000	272000	320000	383000
Macromoths	*Acherontia atropos*	461000	426000	433000	349000	388000	343000
Macromoths	*Acronicta aceris*	304000	341000	370000	268000	335000	352000
Macromoths	*Acronicta alni*	405000	459000	580000	385000	409000	517000

Macromoths	*Acronicta tridens*	400000	372000	430000	390000	351000	403000
Macromoths	*Anarta myrtilli*	715000	620000	636000	342000	348000	359000
Macromoths	*Angerona prunaria*	248000	250000	279000	238000	240000	250000
Macromoths	*Apamea anceps*	328000	328000	358000	319000	322000	341000
Macromoths	*Apamea scolopacina*	410000	467000	667000	377000	424000	583000
Macromoths	*Apamea sublustris*	254000	291000	306000	248000	249000	286000
Macromoths	*Aplocera efformata*	317000	457000	559000	305000	326000	500000
Macromoths	*Apocheima hispidaria*	330000	318000	324000	284000	284000	315000
Macromoths	*Archanara dissoluta*	344000	338000	382000	339000	322000	348000
Macromoths	*Archanara geminipuncta*	307000	339000	430000	291000	323000	372000
Macromoths	*Arctia villica*	237000	246000	266000	229000	230000	249000
Macromoths	*Arenostola phragmitidis*	417000	438000	465000	374000	402000	392000
Macromoths	*Asteroscopus sphinx*	386000	462000	419000	352000	336000	371000
Macromoths	*Asthena albulata*	374000	501000	453000	359000	414000	384000
Macromoths	*Bena bicolorana*	334000	424000	479000	320000	384000	437000
Macromoths	*Catarhoe rubidata*	296000	233000	268000	260000	207000	265000
Macromoths	*Cepphis advenaria*	197000	202000	221000	175000	189000	209000
Macromoths	*Cerastis leucographa*	295000	309000	362000	284000	303000	295000
Macromoths	*Charanyca trigrammica*	422000	402000	454000	385000	373000	424000
Macromoths	*Charissa obscurata*	314000	409000	416000	260000	285000	353000
Macromoths	*Chilodes maritimus*	314000	395000	443000	312000	346000	408000
Macromoths	*Cleorodes lichenaria*	549000	561000	665000	358000	340000	387000
Macromoths	*Clostera curtula*	312000	324000	403000	302000	323000	348000
Macromoths	*Coenobia rufa*	394000	383000	430000	384000	358000	421000
Macromoths	*Comibaena bajularia*	348000	398000	373000	348000	355000	357000
Macromoths	*Cosmia affinis*	349000	303000	349000	296000	290000	349000
Macromoths	*Cosmia pyralina*	312000	326000	319000	294000	320000	302000
Macromoths	*Cryphia muralis*	195000	209000	287000	164000	189000	280000
Macromoths	*Cybosia mesomella*	549000	573000	609000	418000	405000	446000
Macromoths	*Cyclophora albipunctata*	452000	570000	810000	298000	359000	529000
Macromoths	*Cyclophora annularia*	224000	205000	244000	208000	185000	215000
Macromoths	*Cyclophora linearia*	272000	347000	476000	255000	299000	442000
Macromoths	*Cyclophora punctaria*	310000	315000	362000	287000	287000	354000
Macromoths	*Cymatophorima diluta*	331000	306000	345000	298000	276000	314000
Macromoths	*Deltote uncula*	397000	436000	597000	340000	360000	373000
Macromoths	*Drymonia dodonaea*	478000	517000	534000	366000	384000	409000
Macromoths	*Dypterygia scabriuscula*	343000	380000	408000	340000	359000	382000
Macromoths	*Ectropis crepuscularia*	561000	476000	423000	429000	399000	380000
Macromoths	*Eilema complana*	340000	364000	446000	323000	352000	367000
Macromoths	*Eilema depressa*	290000	327000	565000	269000	322000	521000
Macromoths	*Eilema griseola*	332000	359000	463000	298000	347000	449000
Macromoths	*Ennomos quercinaria*	453000	411000	453000	375000	353000	382000
Macromoths	*Epirrhoe galiata*	462000	426000	411000	352000	415000	358000

Macromoths	*Epirrhoe rivata*	363000	381000	327000	340000	312000	315000
Macromoths	*Eremobia ochroleuca*	382000	428000	490000	361000	383000	429000
Macromoths	*Euclidia glyphica*	397000	461000	413000	376000	376000	370000
Macromoths	*Euphyia unangulata*	335000	314000	333000	316000	282000	300000
Macromoths	*Eupithecia dodoneata*	294000	461000	571000	275000	429000	498000
Macromoths	*Eupithecia haworthiata*	283000	288000	349000	263000	278000	337000
Macromoths	*Eupithecia inturbata*	321000	364000	342000	286000	348000	320000
Macromoths	*Eupithecia simpliciata*	368000	412000	443000	284000	309000	394000
Macromoths	*Eupithecia subumbrata*	420000	342000	419000	330000	314000	329000
Macromoths	*Euproctis chrysorrhoea*	296000	427000	432000	236000	344000	351000
Macromoths	*Furcula bifida*	439000	424000	506000	375000	385000	397000
Macromoths	*Gastropacha quercifolia*	327000	312000	245000	309000	308000	186000
Macromoths	*Hemistola chrysoprasaria*	336000	333000	329000	318000	328000	317000
Macromoths	*Hoplodrina ambigua*	238000	339000	461000	238000	327000	387000
Macromoths	*Horisme tersata*	299000	315000	323000	287000	280000	303000
Macromoths	*Horisme vitalbata*	265000	282000	326000	259000	280000	312000
Macromoths	*Hyloicus pinastri*	235000	334000	439000	211000	328000	392000
Macromoths	*Hypena crassalis*	311000	321000	400000	242000	271000	336000
Macromoths	*Hypomecis punctinalis*	282000	325000	339000	263000	309000	331000
Macromoths	*Hypomecis roboraria*	237000	260000	229000	233000	247000	228000
Macromoths	*Idaea emarginata*	342000	363000	355000	329000	350000	343000
Macromoths	*Idaea fuscovenosa*	328000	386000	414000	314000	356000	382000
Macromoths	*Idaea subsericeata*	417000	343000	431000	333000	342000	362000
Macromoths	*Idaea sylvestraria*	280000	177000	177000	264000	177000	158000
Macromoths	*Idaea trigeminata*	286000	324000	332000	279000	303000	327000
Macromoths	*Ipimorpha subtusa*	475000	491000	607000	423000	422000	503000
Macromoths	*Lacanobia contigua*	678000	729000	781000	307000	428000	488000
Macromoths	*Lacanobia suasa*	407000	454000	505000	350000	362000	408000
Macromoths	*Lacanobia w-latinum*	308000	338000	356000	276000	320000	335000
Macromoths	*Larentia clavaria*	429000	393000	395000	383000	357000	334000
Macromoths	*Laspeyria flexula*	324000	356000	392000	307000	343000	366000
Macromoths	*Leucoma salicis*	416000	426000	502000	370000	405000	470000
Macromoths	*Ligdia adustata*	329000	341000	373000	329000	325000	371000
Macromoths	*Lithophane hepatica*	257000	350000	590000	194000	329000	492000
Macromoths	*Lithophane ornitopus*	324000	361000	451000	304000	343000	430000
Macromoths	*Lithophane semibrunnea*	318000	369000	498000	289000	343000	449000
Macromoths	*Lomographa bimaculata*	350000	367000	506000	322000	356000	454000
Macromoths	*Lygephila pastinum*	361000	375000	438000	336000	332000	420000
Macromoths	*Lymantria monacha*	321000	323000	359000	299000	309000	338000
Macromoths	*Macaria alternata*	282000	302000	356000	282000	273000	294000
Macromoths	*Macaria notata*	607000	739000	804000	315000	414000	561000
Macromoths	*Malacosoma neustria*	371000	437000	416000	334000	405000	349000
Macromoths	*Melanthia procellata*	308000	305000	347000	283000	297000	329000

Macromoths	*Menophra abruptaria*	404000	430000	470000	384000	400000	455000
Macromoths	*Miltochrista miniata*	327000	329000	337000	313000	307000	328000
Macromoths	*Mimas tiliae*	390000	432000	501000	373000	406000	461000
Macromoths	*Mythimna pudorina*	386000	357000	352000	324000	356000	342000
Macromoths	*Mythimna straminea*	375000	411000	475000	359000	384000	416000
Macromoths	*Orthosia miniosa*	283000	318000	353000	262000	300000	319000
Macromoths	*Pachycnemia hippocastanaria*	227000	146000	155000	225000	144000	149000
Macromoths	*Paradarisa consonaria*	309000	274000	335000	286000	245000	315000
Macromoths	*Parascotia fuliginaria*	229000	276000	329000	214000	253000	326000
Macromoths	*Parectropis similaria*	268000	304000	320000	263000	278000	309000
Macromoths	*Perconia strigillaria*	486000	373000	576000	259000	263000	337000
Macromoths	*Peridea anceps*	368000	407000	454000	351000	359000	423000
Macromoths	*Philereme transversata*	356000	344000	361000	350000	341000	354000
Macromoths	*Philereme vetulata*	313000	334000	342000	312000	313000	339000
Macromoths	*Phytometra viridaria*	613000	533000	590000	297000	303000	264000
Macromoths	*Polymixis flavicincta*	356000	348000	372000	342000	336000	341000
Macromoths	*Polyploca ridens*	307000	321000	337000	291000	299000	328000
Macromoths	*Protodeltote pygarga*	318000	342000	432000	302000	337000	400000
Macromoths	*Pseudopanthera macularia*	431000	581000	657000	326000	404000	396000
Macromoths	*Pterapherapteryx sexalata*	312000	359000	329000	295000	302000	321000
Macromoths	*Ptilodon cucullina*	300000	322000	330000	296000	316000	323000
Macromoths	*Pyrrhia umbra*	448000	487000	515000	403000	353000	432000
Macromoths	*Rheumaptera cervinalis*	272000	301000	346000	248000	280000	274000
Macromoths	*Rheumaptera undulata*	359000	454000	588000	351000	386000	550000
Macromoths	*Rhodometra sacraria*	382000	557000	539000	320000	364000	429000
Macromoths	*Scopula imitaria*	411000	424000	473000	366000	392000	426000
Macromoths	*Scopula immutata*	352000	392000	401000	341000	356000	365000
Macromoths	*Scopula marginepunctata*	303000	322000	431000	272000	283000	371000
Macromoths	*Semiaspilates ochrearia*	282000	290000	367000	223000	271000	305000
Macromoths	*Shargacucullia verbasci*	421000	417000	476000	400000	371000	452000
Macromoths	*Smerinthus ocellata*	444000	463000	457000	425000	421000	440000
Macromoths	*Sphinx ligustri*	368000	328000	355000	346000	323000	342000
Macromoths	*Spodoptera exigua*	278000	361000	487000	209000	318000	427000
Macromoths	*Stauropus fagi*	310000	326000	334000	290000	306000	318000
Macromoths	*Tetheella fluctuosa*	280000	322000	302000	233000	234000	249000
Macromoths	*Thumatha senex*	365000	446000	472000	357000	351000	347000
Macromoths	*Triphosa dubitata*	429000	395000	407000	374000	345000	372000
Macromoths	*Watsonalla binaria*	420000	456000	487000	400000	420000	463000
Macromoths	*Watsonalla cultraria*	305000	318000	417000	258000	297000	389000
Macromoths	*Xanthia aurago*	370000	400000	463000	333000	384000	420000
Macromoths	*Xanthorhoe quadrifasiata*	347000	402000	474000	324000	359000	443000
Macromoths	*Zeuzera pyrina*	358000	412000	445000	330000	384000	412000
Macromoths	*Zygaena trifolii*	338000	300000	294000	320000	265000	288000

Table A2.9. Results of linear mixed effects models for the rate of range margin change between two intervals spanning 1966-2010 (response variable is change in northern range margin in km per decade), for well-recorded and heavily-recorded hectads. Numbers in cells show differences in Akaike information criterion (ΔAIC) values between the best model (shown as 0.0) in each column and the other models. Comparisons with all four taxonomic groups included ('All groups'), models excluding each taxon in turn (columns 6-9), and models excluding both butterflies and macromoths ('Without Lepidoptera'), all found that the best model was always the one that included an interval*group interaction term (these models also included group and interval as fixed effects). The numbers of species given in each column (in parentheses) are the numbers of species remaining in the analysis after the specified taxonomic group(s) had been excluded.

Model	Recording effort	Fixed effects	Null model	All groups (205)	Without birds (174)	Without butterflies (170)	Without dragonflies* (198)	Without macromoths (73)	Without Lepidoptera (38)
1	WR	1	64.6	NA	NA	NA	NA	NA	NA
2	WR	Group	NA	43.0	45.0	34.7	36.5	16.5	11.1
3	WR	Interval	NA	41.2	20.8	32.2	28.1	28.1	15.5
4	WR	Interval + Group	NA	19.6	10.4	15.0	14.0	12.0	6.6
5	WR	Interval + Group + Interval:Group	NA	0.0	0.0	0.0	0.0	0.0	0.0
6	HR	1	60.2	NA	NA	NA	NA	NA	NA
7	HR	Group	NA	40.6	46.6	32.6	34.4	16.2	11.1
8	HR	Interval	NA	37.3	19.6	28.3	25.4	26.2	14.3
9	HR	Interval + Group	NA	17.8	9.3	13.6	12.5	11.6	6.6
10	HR	Interval + Group + Interval:Group	NA	0.0	0.0	0.0	0.0	0.0	0.0

Table A2.10. Results of ANCOVAs of seasonal and annual temperatures in each interval. Seasons are defined by three month bins: Winter (December, January, February); Spring (March, April, May); Summer (June, July, August); Autumn (September, October, November); annual as December year t-1 through to November year t. Intervals are as follows: Interval 1: 1966-1995, Interval 2: 1986-2010, all years inclusive. There was no significant change in the rate of seasonal or annual temperature change between the two intervals, except for mean autumn temperature, which significantly increased between intervals.

Response variable	Multiple R^2	F-statistic	df	Fixed effects	Coefficient	SE	p value
Mean annual temperature	0.23	5.29	3,52	Year	0.02	0.03	0.562
				Interval	-9.21	36.82	0.803
				Year:Interval	0.00	0.02	0.802
Mean winter temperature	0.03	0.56	3,52	Year	0.05	0.06	0.427
				Interval	60.12	80.76	0.460
				Year:Interval	-0.03	0.04	0.462
Mean spring temperature	0.41	12.05	3,52	Year	0.04	0.03	0.202
				Interval	0.02	40.82	1.000
				Year:Interval	0.00	0.02	0.999
Mean summer temperature	0.07	1.37	3,52	Year	0.03	0.04	0.527
				Interval	8.85	57.25	0.878
				Year:Interval	0.00	0.03	0.877
Mean autumn temperature	0.20	4.33	3,52	Year	-0.05	0.04	0.181
				Interval	-105.84	49.98	**0.039**
				Year:Interval	0.05	0.03	**0.039**

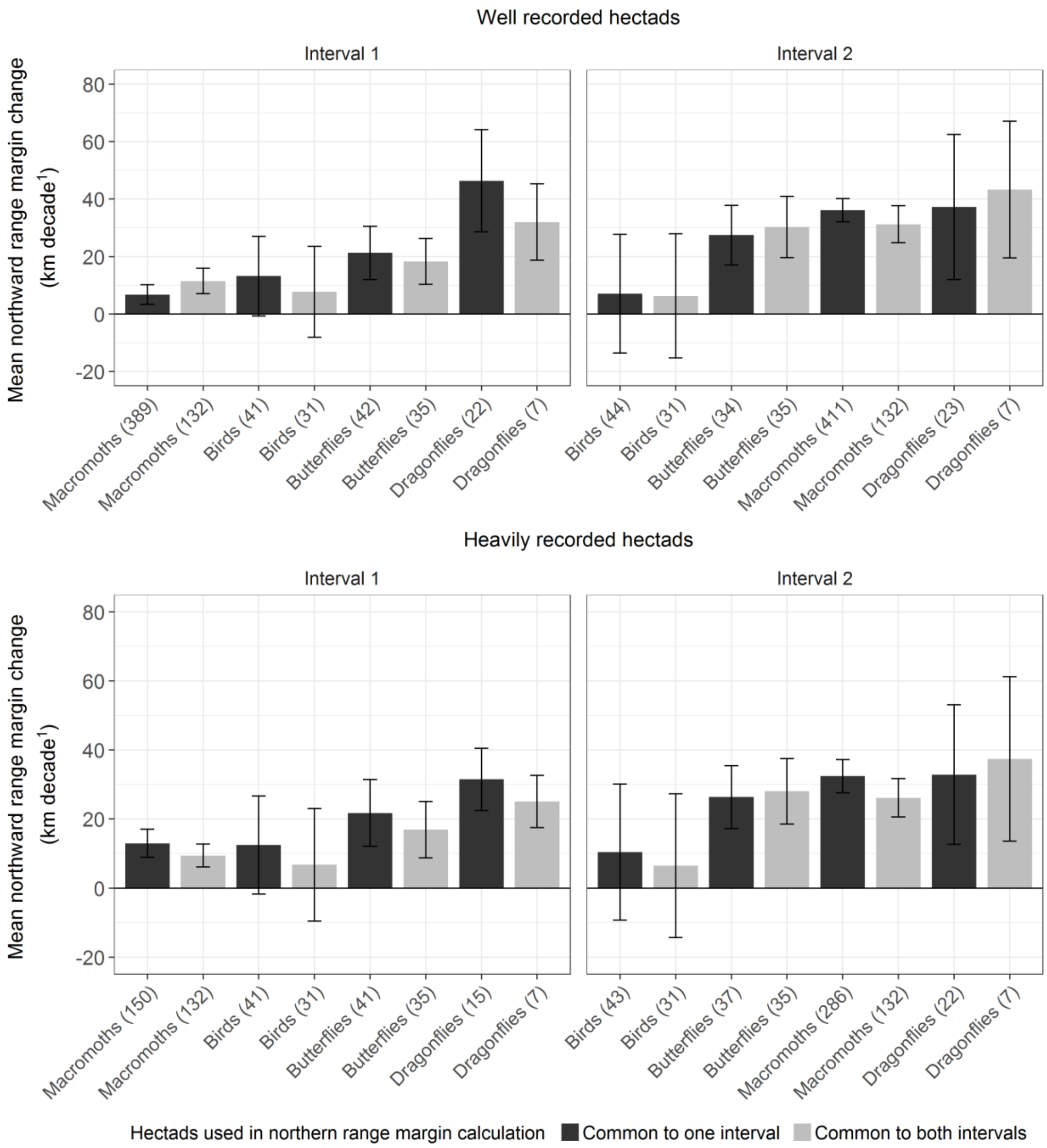

Figure A2.1. Comparison of mean rates of range margin change calculated for four taxonomic groups when the hectads selected for analysis are common to two time periods in a single interval or the subset of hectads common to intervals 1 and 2.

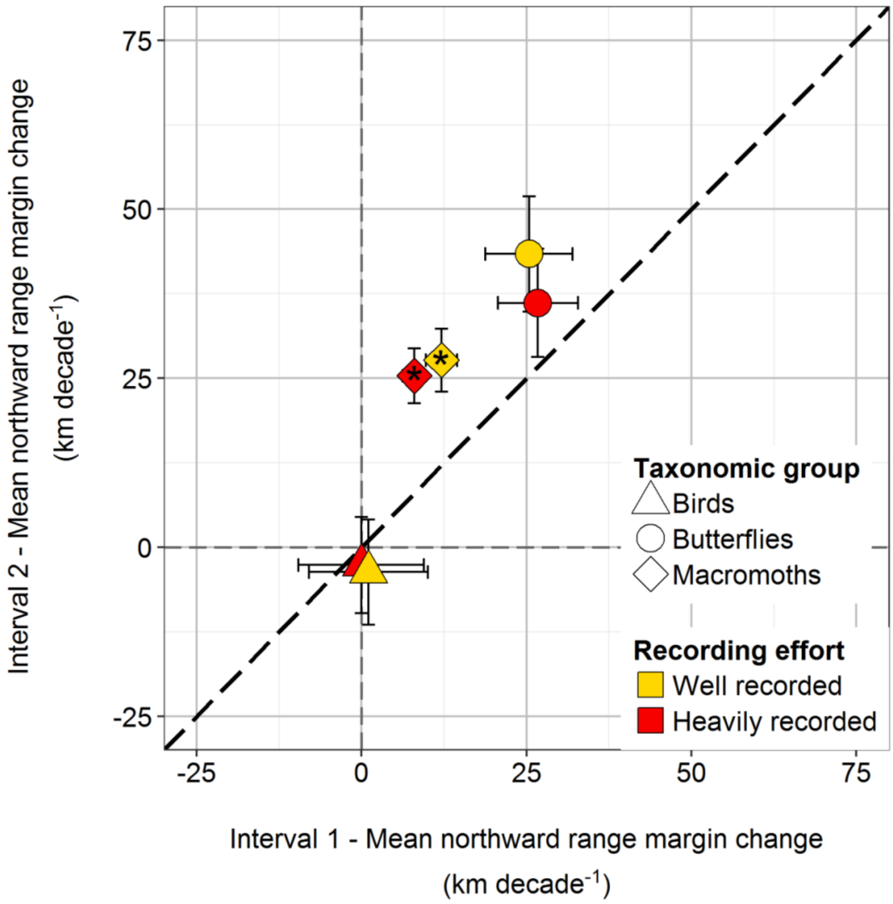

Figure A2.2. Comparison of mean rates of range margin change for common species in three taxonomic groups across two intervals (as in Figure 2.4).

Appendix Chapter 3

Table A3.1. (see next page) Details of citizen-science recording schemes. Data were obtained on 02 June 2017 from the UK Biological Records Centre (https://www.brc.ac.uk/theme/datasets), and represent *ad hoc* point observations at or near breeding sites (but see Remarks). Recording level is the number of 10-km grid squares (out of a possible 2566 in the study area) where at least 10% or 25% of the regional species pool was sampled in both recording periods (1976-1990 and 2001-2015).

Taxonomic group	Recording scheme name and affiliation	National organiser(s)	Remarks	Number of species	Recording level (10%)	Recording level (25%)
Aquatic bugs	Aquatic Heteroptera Recording Scheme (Aquatic Coleoptera Conservation Trust)	Dr Garth Foster	The Trust is a Registered Charity No. SCO37556	9	166	35
Bees	Bees, Wasps and Ants Recording Scheme / Society	Mr Mike Edwards	Thanks to the committee and members of BWARS for permission to use their data	48	164	39
Butterflies	Butterflies for the New Millennium (Butterfly Conservation, BC)	Mr Richard Fox	Includes long-term monitoring transects. BC is a Registered Charity No. 254937 and No. SCO39268	16	2157	1710
Dragonflies and damselflies	Dragonfly Recording Network (British Dragonfly Society)	Mr David Hepper	Registered charity (1168300)	9	1350	813
Grasshoppers and allies	Grasshoppers and Related Insects Recording Scheme of Britain and Ireland	Prof Peter Sutton Dr Björn Beckmann	Both visual and acoustic identification	14	831	234
Ground beetles	Ground Beetle Recording Scheme	Dr Mark Telfer	–	11	182	23
Hoverflies	Hoverfly Recording Scheme (Dipterists Forum)	Dr Roger Morris Dr Stuart Ball	–	19	540	116
Macromoths	National Moth Recording Scheme (Butterfly Conservation, BC)	Mr Richard Fox	Includes use of light traps at night	132	1034	600
Non-marine molluscs	Non-marine Mollusc Recording Scheme (Conchological Society of Great Britain and Ireland)	Mr Adrian Norris	The Society is a Registered Charity No. 208205	7	243	54
Shieldbugs and allies	Terrestrial Heteroptera Recording Scheme	Dr Tristan Bantock	–	6	134	17
Soldierflies and allies	Soldierflies and Allies Recording Scheme (Dipterists Forum)	Mr Martin Harvey	Additional records obtained direct from recording scheme (28.06.2017)	21	182	15
Spiders	Spider Recording Scheme (British Arachnological Society)	Mr Peter Harvey	The Society is a Registered Charity No. 260346 and No. SC044090	38	242	38
Wasps	Bees, Wasps and Ants Recording Scheme / Society	Mr Mike Edwards	–	12	94	18
Woodlice	Non-marine Isopoda Recording Scheme (British Myriapod and Isopod Group)	Mr Steve Gregory	Includes ex situ identification using microscopes	5	617	112

Table A3.2. Descriptive statistics for species' range shifts (km y^{-1}), detailed by taxonomic group. Positive values indicate northward (poleward) expansion, negative values indicate southward retreat, measured over a 25-year period (1976-1990 to 2001-2015). Range shifts varied significantly between taxonomic groups ($F_{13, 333}$ = 2.503, P = 0.003), with group explaining 9% of the variation in linear regression.

Taxonomic group	Median	Mean	SD	Min	Max
Aquatic bugs	1.64	2.03	2.58	-2.16	5.96
Bees	1.10	1.67	2.47	-2.04	9.96
Butterflies	1.84	1.80	1.90	-1.60	5.40
Dragonflies and damselflies	1.04	3.71	4.01	0.04	10.36
Grasshoppers and allies	2.04	2.31	2.62	-1.72	9.12
Ground beetles	0.44	1.49	4.47	-2.76	14.12
Hoverflies	0.20	-0.24	3.48	-7.88	6.68
Macromoths	1.64	2.20	2.71	-4.32	13.08
Non-marine molluscs	4.56	4.87	2.94	0.88	9.32
Shieldbugs and allies	1.68	1.12	3.16	-4.68	4.08
Soldierflies and allies	1.28	0.85	2.13	-4.48	4.00
Spiders	1.82	1.57	1.97	-2.44	7.40
Wasps	1.04	1.06	1.19	-1.04	2.68
Woodlice	1.04	2.49	4.63	-1.56	10.48
All groups	1.32	1.84	2.78	-7.88	14.12

Table A3.3. Descriptive statistics for species' specialisation indices (SSIs), detailed by taxonomic group. Low values indicate a generalist, and high values indicate a high level of habitat specialisation. Specialisation varied significantly between taxonomic groups ($F_{13, 333}$ = 1.919, P = 0.027), with group explaining 7% of the variation in linear regression.

Taxonomic group	Median	Mean	SD	Min	Max
Aquatic bugs	1.44	1.35	0.42	0.76	2.02
Bees	1.40	1.34	0.43	0.55	2.56
Butterflies	1.44	1.25	0.56	0.36	2.23
Dragonflies and damselflies	1.10	1.16	0.44	0.71	2.17
Grasshoppers and allies	1.27	1.37	0.48	0.75	2.38
Ground beetles	1.31	1.30	0.17	0.98	1.59
Hoverflies	1.31	1.32	0.38	0.67	2.14
Macromoths	1.18	1.28	0.52	0.44	2.89
Non-marine molluscs	1.49	1.59	0.25	1.32	1.96
Shieldbugs and allies	1.11	1.12	0.33	0.75	1.58
Soldierflies and allies	1.39	1.42	0.24	1.04	1.95
Spiders	1.40	1.45	0.36	0.85	2.43
Wasps	1.39	1.49	0.50	0.91	2.72
Woodlice	1.91	2.07	0.69	1.41	3.22
All groups	1.31	1.34	0.46	0.36	3.22

Table A3.4. Descriptive statistics for habitat availability at the range margin (%), detailed by taxonomic group. Values in parentheses are on the log_{10} scale used in models of range shift. Log_{10}-habitat availability varied significantly between taxonomic groups ($F_{13, 333} = 4.443$, $P < 10^{-6}$), with group explaining 15% of the variation.

Taxonomic group	Median		Mean		SD		Min		Max	
Aquatic bugs	7.1	(0.85)	11.9	(0.99)	8.3	(0.28)	4.6	(0.66)	26.8	(1.43)
Bees	7.5	(0.88)	9.2	(0.90)	5.5	(0.23)	3.6	(0.56)	23.5	(1.37)
Butterflies	7.5	(0.87)	12.8	(0.91)	13.7	(0.43)	1.3	(0.11)	55.7	(1.75)
Dragonflies and damselflies	13.4	(1.13)	16.3	(1.12)	10.9	(0.33)	3.6	(0.56)	36.4	(1.56)
Grasshoppers and allies	5.3	(0.71)	10.4	(0.81)	9.4	(0.47)	1.5	(0.17)	28.7	(1.46)
Ground beetles	5.5	(0.74)	5.8	(0.74)	2.1	(0.14)	3.4	(0.53)	10.7	(1.03)
Hoverflies	3.5	(0.54)	4.5	(0.58)	3.4	(0.26)	1.4	(0.14)	15.5	(1.19)
Macromoths	7.8	(0.89)	9.5	(0.84)	7.1	(0.38)	0.4	(-0.41)	35.4	(1.55)
Non-marine molluscs	8.1	(0.91)	11.2	(0.98)	6.8	(0.28)	4.6	(0.66)	21.6	(1.33)
Shieldbugs and allies	12.6	(1.02)	14.0	(1.03)	10.2	(0.37)	4.3	(0.64)	26.4	(1.42)
Soldierflies and allies	4.6	(0.67)	6.0	(0.72)	3.3	(0.22)	2.3	(0.35)	15.5	(1.19)
Spiders	3.6	(0.55)	4.6	(0.56)	3.5	(0.30)	1.1	(0.04)	15.4	(1.19)
Wasps	7.2	(0.86)	8.7	(0.85)	6.1	(0.29)	2.5	(0.40)	22.3	(1.35)
Woodlice	3.4	(0.53)	3.6	(0.52)	1.6	(0.19)	1.9	(0.28)	5.9	(0.77)
All groups	6.2	(0.79)	8.7	(0.81)	7.3	(0.35)	0.4	(-0.41)	55.7	(1.75)

Table A3.5. Descriptive statistics for habitat availability at the range margin, as a percentage of the range-wide average, detailed by taxonomic group. Low values indicate habitat-poor margins relative to the average across a species' range; high values indicate habitat-rich margins. This variable did not vary significantly between taxonomic groups ($F_{13, 333}$ = 0.859, P = 0.598), with group explaining 3% of the variation.

Taxonomic group	Median	Mean	SD	Min	Max
Aquatic bugs	100.7	100.9	3.7	95.1	107.1
Bees	100.4	99.9	6.2	79.8	121.4
Butterflies	95.4	97.1	21.5	76.1	171.4
Dragonflies and damselflies	102.4	99.5	6.2	86.5	106.1
Grasshoppers and allies	96.9	99.1	11.2	76.3	122.0
Ground beetles	102	102.5	4.7	96.6	109.6
Hoverflies	98.1	100.3	12.5	85.8	146.2
Macromoths	97.6	97.7	8.6	75.6	141.9
Non-marine molluscs	96.2	98.0	4.6	94.1	106.1
Shieldbugs and allies	101.6	101.7	2.2	98.7	104.4
Soldierflies and allies	99.9	102.1	8.5	90.8	125.9
Spiders	98.6	97.7	6.6	84.8	110.3
Wasps	100.0	99.4	5.0	89.6	107.6
Woodlice	93.8	94.9	6.4	88.0	102.6
All groups	98.8	98.8	9	75.6	171.4

Random effects (var.) Fixed effects (coefficients, mean over groups)

Interc.	Slope	Resid.	Interc.	SSI	HA	HR	HA:HR	R^2 [m, c]	AIC	cAIC
Specialisation model (*N* = 352 species)										
0.65	–	6.95	1.85***	-0.60***	–	–	–	0.04, 0.13	1679	1663
0.65 ||	0.00 ||	6.95	1.85***	-0.60***	–	–	–	0.04, 0.13	1681	1665
0.78 |	0.10 |	6.88	1.88***	-0.58*	–	–	–	0.04, 0.15	1682	1665
Habitat availability model (*N* = 352 species)										
0.21	–	6.28	1.78***	–	1.07***	–	–	0.15, 0.17	1643	1632
0.09 ||	0.27 ||	6.29	1.77***	–	1.15**	–	–	0.17, 0.21	1644	1628
0.12 |	0.20 |	6.31	1.78***	–	1.20**	–	–	0.18, 0.22	1645	1633
Habitat interaction model (*N* = 352 species)										
0.33	–	6.14	1.71***	–	1.10***	0.26	0.44**	0.17, 0.21	1636	1624
0.33 ||	0.00 ||	6.14	1.71***	–	1.10***	0.26	0.44***	0.17, 0.21	1638	1626
0.24 |	0.05 |	6.14	1.72***	–	1.18***	0.24	0.42**	0.19, 0.23	1639	1628
Fig. 3, A-C: Four groups with high levels of recording (*N* = 58 species)										
1.20	–	8.74	1.76	-0.61	–	–	–	0.04, 0.15	303	296
0.00 ||	1.29 ||	6.16	1.67***	–	1.95*	–	–	0.34, 0.45	285	277
0.07	–	6.52	1.35*	–	1.91***	0.16	1.33*	0.36, 0.37	286	282
Fig. 3, E-G: Macromoths only (*N* = 132 species, no group effects)										
–	–	–	2.20***	-0.62**	–	–	–	0.05, –	636	–
–	–	–	2.20***	–	1.07***	–	–	0.16, –	620	–
–	–	–	2.22***	–	1.08***	0.41	0.41*	0.19, –	619	–
Fig. 3, I-K: Nine groups with low levels of recording (*N* = 157 species)										
0.52	–	6.27	1.79*	-0.57**	–	–	–	0.05, 0.12	749	737
0.19 ||	0.00 ||	6.19	1.68*	–	0.77***	–	–	0.08, 0.11	745	737
0.27	–	6.10	1.65*	–	0.80***	0.19	0.28	0.09, 0.13	746	737

***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$ (t-tests using Satterthwaite approximation)

Table A3.6. Linear mixed-effects models of range shift (km y^{-1}) *vs*. habitat specialisation (SSI), $\log_{10}$-habitat availability at the range margin (HA), and margin habitat relative to the range-wide average for a species (HR). We fitted models using the R function 'lmer' via maximum likelihood, with all predictors centred and scaled. The grouping variable for random effects was taxonomic group. For each set of fixed effects, we tested models with a random intercept only, and models with both random slope and intercept terms (with either uncorrelated (||) or correlated (|) random effects). In each case, coloured text identifies the top model (lowest conditional AIC), as reported in the main text and applied to the subsets of groups in Figure 3.3.

Table A3.7. R packages used in the analysis (in addition to base R).

R package	Application	Author(s)
raster	Manipulation of species, climate and land cover data	Robert J. Hijmans
rgeos	Spatial buffers around species data	Roger Bivand and Colin Rundel
mgcv	Fitting phenology curves using penalized regression splines	Simon N. Wood
lme4	Fitting linear mixed-effects models	Douglas Bates, Martin Maechler, Ben Bolker and Steve Walker
lmerTest	t-tests in linear mixed-effects models	Alexandra Kuznetsova, Per Bruun Brockhoff and Rune Haubo Bojesen Christensen
MuMIn	Marginal and conditional R^2	Kamil Barton
cAIC4	Corrected conditional AIC (using conditional bootstrap)	Benjamin Saefken and David Ruegamer, with contributions from Sonja Greven and Thomas Kneib
doParallel	Parallel processing	Revolution Analytics and Steve Weston

Table A3.8 Study results summarised for 347 species: range shifts, specialisation index scores, habitat availability at the margin and at the margin vs across the whole range. Range shifts in the polewards range margin are given in km per year. The specialisation index is the coefficient of variation across 18 habitat classes. Habitat availability at the margin is the mean species' probability of occurrence in a 50km buffer around the margin. Margin vs range-wide habitat availability is the division of margin habitat availability by the range-wide habitat availability.

Group	Species	Range shift (km per y)	Specialisation index	Habitat availability at margin (%)	Margin vs range-wide habitat (%)
Aquatic bugs	*Corixa panzeri*	1.64	1.62	6.29	99.81
Aquatic bugs	*Cymatia coleoptrata*	-0.16	1.45	7.10	107.06
Aquatic bugs	*Ilyocoris cimicoides*	3.36	0.76	26.78	95.12
Aquatic bugs	*Microvelia reticulata*	2	0.95	20.30	100.82
Aquatic bugs	*Notonecta maculata*	0.72	1.44	5.68	100.66
Aquatic bugs	*Notonecta viridis*	5.96	1.73	8.87	106.07
Aquatic bugs	*Plea minutissima*	1.44	0.85	20.29	98.58
Aquatic bugs	*Ranatra linearis*	5.44	1.33	6.76	100.69
Aquatic bugs	*Sigara stagnalis*	-2.16	2.02	4.58	99.19
Bees	*Andrena bicolor*	5.92	0.80	18.18	95.53
Bees	*Andrena denticulata*	6	1.89	5.32	83.14
Bees	*Andrena dorsata*	1.36	0.80	21.42	100.59
Bees	*Andrena flavipes*	2.44	0.72	22.78	99.56
Bees	*Andrena helvola*	-1.48	1.56	5.24	103.40
Bees	*Andrena labialis*	0.04	2.14	7.56	91.57
Bees	*Andrena minutula*	3.12	0.69	16.11	103.73
Bees	*Andrena nigroaenea*	0.28	0.81	19.93	97.94
Bees	*Andrena ovatula*	3.24	1.67	3.91	79.85
Bees	*Andrena praecox*	2.76	1.25	10.35	100.07
Bees	*Andrena thoracica*	-0.24	1.83	4.48	110.67
Bees	*Andrena trimmerana*	0	1.80	4.22	101.91
Bees	*Anthidium manicatum*	7.6	1.42	6.55	121.36
Bees	*Anthophora bimaculata*	1.32	1.34	8.45	99.51

Bees	*Anthophora furcata*	-0.2	1.14	4.08	95.59
Bees	*Chelostoma campanularum*	0.32	1.69	8.09	104.68
Bees	*Colletes daviesanus*	-1.36	1.61	6.54	91.29
Bees	*Colletes fodiens*	-2.04	1.46	5.52	102.83
Bees	*Colletes similis*	-0.52	1.74	3.59	102.45
Bees	*Epeolus cruciger*	1.08	1.46	6.05	102.68
Bees	*Epeolus variegatus*	1.12	1.15	5.72	100.30
Bees	*Halictus tumulorum*	2.96	0.76	17.08	98.43
Bees	*Hoplitis claviventris*	0.28	1.45	4.63	102.04
Bees	*Hylaeus brevicornis*	-2.04	1.16	6.61	100.54
Bees	*Hylaeus communis*	0.64	0.91	16.01	94.56
Bees	*Hylaeus confusus*	0.6	1.42	4.25	94.27
Bees	*Hylaeus hyalinatus*	1.96	0.95	8.36	103.61
Bees	*Hylaeus signatus*	0.64	1.88	4.63	107.79
Bees	*Lasioglossum laevigatum*	0.32	1.47	4.73	98.21
Bees	*Lasioglossum leucozonium*	2.6	0.55	14.50	98.62
Bees	*Lasioglossum minutissimum*	2.08	1.28	8.70	99.48
Bees	*Lasioglossum morio*	2.32	0.82	17.53	99.71
Bees	*Lasioglossum parvulum*	3	1.54	8.74	98.71
Bees	*Lasioglossum punctatissimum*	0.2	1.48	5.93	97.29
Bees	*Lasioglossum smeathmanellum*	1.32	1.17	7.54	100.60
Bees	*Megachile centuncularis*	-0.28	1.71	5.82	100.55
Bees	*Megachile ligniseca*	4.2	1.69	6.28	105.46
Bees	*Melitta tricincta*	-0.04	2.56	7.82	93.86
Bees	*Nomada flava*	9.96	0.94	23.49	102.27
Bees	*Nomada fucata*	1.12	1.00	10.00	97.62
Bees	*Osmia aurulenta*	0.04	1.96	4.62	102.10
Bees	*Osmia leaiana*	0.64	1.26	5.30	101.39
Bees	*Panurgus calcaratus*	-0.4	1.39	7.80	102.55
Bees	*Sphecodes crassus*	4.8	1.43	7.99	99.91
Bees	*Sphecodes ephippius*	5.2	0.78	14.23	103.32
Bees	*Sphecodes monilicornis*	4.36	1.19	9.74	101.67
Bees	*Sphecodes pellucidus*	-0.08	1.40	4.66	98.79
Bees	*Sphecodes puncticeps*	3	1.10	8.55	101.13

Butterflies	*Apatura iris*	1.84	1.52	2.70	88.79
Butterflies	*Aricia agestis*	3.76	0.84	12.50	97.16
Butterflies	*Celastrina argiolus*	5.4	0.56	17.97	82.54
Butterflies	*Gonepteryx rhamni*	2.68	0.62	24.18	90.40
Butterflies	*Hamearis lucina*	-1.6	1.71	3.27	85.56
Butterflies	*Hesperia comma*	-0.08	1.59	6.08	101.87
Butterflies	*Leptidea sinapis*	3.08	2.23	1.28	76.11
Butterflies	*Limenitis camilla*	1.84	1.50	5.05	81.66
Butterflies	*Melanargia galathea*	3.4	0.69	24.67	99.24
Butterflies	*Plebejus argus*	-0.04	1.59	6.38	171.40
Butterflies	*Polyommatus bellargus*	0.84	1.82	7.06	102.76
Butterflies	*Polyommatus coridon*	3.2	1.37	7.88	96.84
Butterflies	*Pyrgus malvae*	-0.36	1.05	9.58	95.14
Butterflies	*Pyronia tithonus*	0.8	0.36	55.70	95.63
Butterflies	*Satyrium pruni*	0.48	1.91	2.41	85.24
Butterflies	*Thymelicus lineola*	3.64	0.72	17.77	104.01
Dragonflies*	*Aeshna mixta*	6.32	0.76	36.43	102.44
Dragonflies*	*Anax imperator*	10.4	0.71	28.69	102.65
Dragonflies*	*Brachytron pratense*	0.6	1.28	8.66	86.50
Dragonflies*	*Erythromma najas*	1.04	1.20	10.44	100.72
Dragonflies*	*Gomphus vulgatissimus*	0.16	1.37	5.97	94.73
Dragonflies*	*Libellula fulva*	0.04	2.17	3.60	95.53
Dragonflies*	*Orthetrum cancellatum*	8.12	0.93	19.64	106.14
Dragonflies*	*Platycnemis pennipes*	0.64	1.10	13.37	103.51
Dragonflies*	*Sympetrum sanguineum*	6.08	0.89	20.36	103.68
Grasshoppers*	*Chorthippus albomarginatus*	1.24	1.15	16.25	114.94
Grasshoppers*	*Conocephalus discolor*	9.12	0.98	21.44	102.50
Grasshoppers*	*Conocephalus dorsalis*	4.52	1.53	4.03	95.89
Grasshoppers*	*Labia minor*	-1.72	1.44	1.72	109.75
Grasshoppers*	*Leptophyes punctatissima*	2.96	0.82	22.43	99.45
Grasshoppers*	*Meconema thalassinum*	1.4	1.27	13.85	92.02
Grasshoppers*	*Metrioptera brachyptera*	1.88	2.06	2.84	121.98
Grasshoppers*	*Metrioptera roeselii*	3.48	0.87	28.68	97.62
Grasshoppers*	*Omocestus rufipes*	0.2	1.55	1.68	102.45

Grasshoppers*	*Pholidoptera griseoaptera*	-0.88	0.75	18.25	91.14
Grasshoppers*	*Platycleis albopunctata*	2.2	2.38	3.90	92.78
Grasshoppers*	*Stenobothrus lineatus*	2.68	1.84	1.47	76.31
Grasshoppers*	*Tetrix subulata*	3.8	1.27	6.56	96.10
Grasshoppers*	*Tettigonia viridissima*	1.4	1.27	2.98	94.31
Ground beetles	*Bembidion articulatum*	2.64	1.31	5.02	105.45
Ground beetles	*Bembidion assimile*	1.04	1.36	5.51	109.63
Ground beetles	*Bembidion illigeri*	-1.84	1.23	3.40	96.56
Ground beetles	*Bembidion varium*	0	1.59	3.64	106.54
Ground beetles	*Demetrias atricapillus*	0.12	1.21	10.67	109.17
Ground beetles	*Leistus spinibarbis*	0.88	1.17	5.98	103.34
Ground beetles	*Ophonus rufibarbis*	-0.36	1.44	5.83	100.06
Ground beetles	*Poecilus cupreus*	2.08	1.26	8.36	98.12
Ground beetles	*Pterostichus nigrita*	14.1	0.98	5.51	101.97
Ground beetles	*Stenolophus mixtus*	0.44	1.31	4.90	100.04
Ground beetles	*Syntomus foveatus*	-2.76	1.48	4.81	96.75
Hoverflies	*Cheilosia soror*	1.04	1.53	3.50	99.03
Hoverflies	*Cheilosia vulpina*	-2.04	1.21	2.28	97.64
Hoverflies	*Chrysotoxum cautum*	-0.28	1.32	5.45	99.01
Hoverflies	*Chrysotoxum festivum*	1.32	0.76	5.85	100.36
Hoverflies	*Chrysotoxum verralli*	0.16	1.60	3.85	93.96
Hoverflies	*Epistrophe nitidicollis*	0.32	1.25	1.40	96.01
Hoverflies	*Eumerus ornatus*	0.2	1.97	1.63	98.10
Hoverflies	*Eumerus strigatus*	-3.32	1.01	2.77	99.53
Hoverflies	*Paragus haemorrhous*	0	0.81	5.12	107.44
Hoverflies	*Parhelophilus frutetorum*	-1.24	1.12	2.81	102.82
Hoverflies	*Parhelophilus versicolor*	-3.36	1.39	3.12	96.79
Hoverflies	*Pipizella virens*	0.64	1.25	2.64	104.12
Hoverflies	*Platycheirus ambiguus*	-7.88	1.31	2.62	86.71
Hoverflies	*Sphaerophoria taeniata*	-6.76	1.47	3.58	93.90
Hoverflies	*Tropidia scita*	2.16	1.23	4.42	93.72
Hoverflies	*Volucella inanis*	6.68	1.39	15.51	107.85
Hoverflies	*Volucella inflata*	2.44	1.66	2.71	85.78
Hoverflies	*Volucella zonaria*	5	2.14	9.95	146.24

Hoverflies	*Xanthogramma pedissequum*	0.36	0.67	7.10	97.58
Macromoths	*Acronicta aceris*	2.44	0.80	14.25	99.47
Macromoths	*Acronicta tridens*	1.44	1.52	3.22	91.67
Macromoths	*Agrotis cinerea*	-0.08	2.12	1.43	98.74
Macromoths	*Agrotis puta*	6.2	0.66	16.85	84.19
Macromoths	*Agrotis ripae*	0.68	2.27	2.20	110.76
Macromoths	*Agrotis trux*	1.12	1.78	2.94	94.51
Macromoths	*Amphipyra pyramidea*	9.76	0.64	24.61	98.87
Macromoths	*Angerona prunaria*	0.16	1.82	2.15	95.87
Macromoths	*Apamea anceps*	0.8	0.89	13.13	102.64
Macromoths	*Apamea oblonga*	1	2.07	2.33	101.19
Macromoths	*Apamea sublustris*	2.08	1.70	5.31	99.77
Macromoths	*Apoda limacodes*	1.68	1.11	5.06	95.42
Macromoths	*Aporophyla australis*	3.4	1.50	7.84	102.40
Macromoths	*Archanara dissoluta*	1.32	1.33	4.58	105.80
Macromoths	*Arctia villica*	1.8	1.11	8.97	107.73
Macromoths	*Arenostola phragmitidis*	1.68	1.54	7.93	93.70
Macromoths	*Aspitates ochrearia*	2.64	1.17	7.22	101.66
Macromoths	*Bena bicolorana*	5.04	0.92	10.28	100.91
Macromoths	*Boudinotiana notha*	0.08	2.47	0.92	83.24
Macromoths	*Catarhoe cuculata*	-1.32	1.34	3.26	91.76
Macromoths	*Catarhoe rubidata*	1.24	1.32	4.00	101.20
Macromoths	*Catocala nupta*	4.16	0.83	22.20	92.09
Macromoths	*Cepphis advenaria*	1.16	1.91	2.05	91.81
Macromoths	*Chilodes maritima*	2.92	1.71	3.11	104.44
Macromoths	*Chlorissa viridata*	-2.08	2.41	0.39	97.77
Macromoths	*Clostera curtula*	0.24	0.78	16.17	91.79
Macromoths	*Coenobia rufa*	2.96	0.89	9.70	104.57
Macromoths	*Comibaena bajularia*	-0.44	1.10	6.93	92.06
Macromoths	*Conistra rubiginea*	3.8	1.10	21.92	97.90
Macromoths	*Cosmia affinis*	-0.8	1.27	4.09	91.56
Macromoths	*Cosmia diffinis*	-0.28	2.50	5.03	116.73
Macromoths	*Cosmia pyralina*	-0.2	1.26	10.43	96.07

Macromoths	*Cucullia absinthii*	-0.4	2.49	2.06	93.68
Macromoths	*Cucullia asteris*	1.08	1.46	3.33	107.96
Macromoths	*Cyclophora annularia*	0.76	1.65	3.87	95.15
Macromoths	*Cyclophora linearia*	3	1.37	4.10	93.41
Macromoths	*Cyclophora punctaria*	3.24	0.85	12.45	99.60
Macromoths	*Deltote pygarga*	5.8	0.75	12.14	95.93
Macromoths	*Dypterygia scabriuscula*	1.92	0.80	9.59	102.57
Macromoths	*Earias clorana*	4.56	1.23	7.98	109.28
Macromoths	*Eilema caniola*	3.32	1.58	5.62	90.72
Macromoths	*Eilema complana*	2.24	0.44	22.35	97.61
Macromoths	*Eilema depressa*	13.1	0.87	14.98	92.39
Macromoths	*Eilema griseola*	6.12	0.58	32.10	102.86
Macromoths	*Eilema sororcula*	8.24	0.91	14.95	102.20
Macromoths	*Elaphria venustula*	2.36	1.34	3.09	100.77
Macromoths	*Ennomos autumnaria*	1.04	1.72	11.84	106.63
Macromoths	*Ennomos quercinaria*	0.96	0.97	7.78	75.59
Macromoths	*Eremobia ochroleuca*	2.08	0.81	23.65	93.34
Macromoths	*Eriogaster lanestris*	3.36	1.62	11.44	102.36
Macromoths	*Euphyia biangulata*	1.96	1.37	4.59	103.41
Macromoths	*Euphyia unangulata*	0.56	0.83	4.68	96.85
Macromoths	*Eupithecia haworthiata*	2.44	0.82	5.30	91.43
Macromoths	*Eupithecia inturbata*	0.68	1.19	6.25	88.03
Macromoths	*Eupithecia millefoliata*	4.68	1.93	4.36	110.35
Macromoths	*Eupithecia simpliciata*	2.76	1.21	7.81	98.96
Macromoths	*Eupithecia subumbrata*	3.44	0.98	2.86	78.66
Macromoths	*Euplagia quadripunctaria*	6.24	1.33	32.22	99.88
Macromoths	*Euproctis chrysorrhoea*	2.88	0.85	17.97	101.16
Macromoths	*Gastropacha quercifolia*	-4.32	1.11	4.30	107.72
Macromoths	*Globia sparganii*	4.6	1.45	6.33	103.78
Macromoths	*Hemaris fuciformis*	1.6	1.58	1.16	99.28
Macromoths	*Hemistola chrysoprasaria*	1.64	0.83	14.77	98.78
Macromoths	*Hemithea aestivaria*	0.24	0.73	20.38	86.95
Macromoths	*Horisme tersata*	0.52	0.99	7.82	104.89
Macromoths	*Horisme vitalbata*	1.44	0.91	12.44	104.19

Macromoths	*Hypena rostralis*	3.96	2.04	9.29	111.51
Macromoths	*Hypomecis punctinalis*	-1.32	0.84	9.20	88.30
Macromoths	*Hypomecis roboraria*	-0.64	1.63	3.13	91.53
Macromoths	*Idaea emarginata*	-0.32	0.73	10.46	100.68
Macromoths	*Idaea fuscovenosa*	0.16	0.78	13.85	102.28
Macromoths	*Idaea muricata*	-0.48	1.41	0.87	141.95
Macromoths	*Idaea rusticata*	6.96	1.07	14.41	112.38
Macromoths	*Idaea subsericeata*	1.12	1.05	5.60	98.70
Macromoths	*Idaea sylvestraria*	-2.52	2.07	1.37	99.48
Macromoths	*Idaea trigeminata*	0.8	1.17	14.39	103.94
Macromoths	*Lacanobia suasa*	2.88	1.77	4.00	90.54
Macromoths	*Lacanobia w-latinum*	0.32	0.72	11.71	96.20
Macromoths	*Larentia clavaria*	-1.8	1.12	18.45	91.34
Macromoths	*Laspeyria flexula*	5.16	0.90	17.21	104.96
Macromoths	*Lenisa geminipuncta*	7.52	0.86	8.29	125.14
Macromoths	*Leucania obsoleta*	2.88	1.33	3.68	111.15
Macromoths	*Leucoma salicis*	1.04	1.07	9.23	80.70
Macromoths	*Ligdia adustata*	1.08	1.06	9.07	86.71
Macromoths	*Lithophane ornitopus*	5.76	0.91	35.39	100.21
Macromoths	*Lithophane semibrunnea*	6.04	1.34	13.34	93.57
Macromoths	*Lomographa bimaculata*	5.04	1.05	10.72	91.02
Macromoths	*Lygephila pastinum*	3.04	0.86	12.58	106.15
Macromoths	*Lymantria monacha*	2.92	0.73	18.78	96.83
Macromoths	*Macaria alternata*	7.24	0.66	10.07	97.97
Macromoths	*Macrochilo cribrumalis*	0.88	1.61	6.53	98.13
Macromoths	*Malacosoma neustria*	-0.56	0.66	15.10	97.44
Macromoths	*Meganola albula*	6.36	1.24	10.63	101.43
Macromoths	*Meganola strigula*	-1.32	2.89	0.54	96.59
Macromoths	*Melanthia procellata*	2.88	1.10	4.55	94.02
Macromoths	*Miltochrista miniata*	1.16	0.67	17.81	97.30
Macromoths	*Mimas tiliae*	3.96	0.83	17.61	96.84
Macromoths	*Minoa murinata*	-0.6	2.46	1.79	89.29
Macromoths	*Mythimna favicolor*	0.72	1.99	2.78	102.83
Macromoths	*Mythimna l-album*	6.76	1.19	13.97	94.35

Macromoths	*Mythimna pudorina*	4.32	1.47	5.94	97.56
Macromoths	*Mythimna straminea*	3.96	1.45	6.86	103.05
Macromoths	*Nyctobrya muralis*	2.52	1.28	11.39	98.03
Macromoths	*Pachycnemia hippocastanaria*	-2.96	1.32	3.83	110.34
Macromoths	*Paradarisa consonaria*	7.52	1.63	3.50	94.25
Macromoths	*Parascotia fuliginaria*	4.24	1.26	6.81	97.09
Macromoths	*Parectropis similaria*	1.2	1.45	3.26	84.68
Macromoths	*Pechipogo strigilata*	0	2.77	1.06	85.43
Macromoths	*Philereme transversata*	1.32	1.19	7.89	86.68
Macromoths	*Philereme vetulata*	0.4	1.30	5.42	88.99
Macromoths	*Photedes fluxa*	0.44	1.90	4.58	96.75
Macromoths	*Polymixis flavicincta*	1.08	1.07	18.58	93.23
Macromoths	*Polyploca ridens*	2.48	1.17	18.55	97.58
Macromoths	*Ptilodon cucullina*	0.52	0.90	8.79	96.37
Macromoths	*Schrankia taenialis*	1.16	1.72	1.53	97.55
Macromoths	*Scopula emutaria*	0.6	1.78	2.79	97.74
Macromoths	*Scopula imitaria*	0.92	0.67	15.62	94.66
Macromoths	*Scopula marginepunctata*	0.56	1.15	5.47	90.02
Macromoths	*Simyra albovenosa*	0.56	1.88	5.32	104.99
Macromoths	*Sphinx ligustri*	2.68	0.71	18.35	104.25
Macromoths	*Sphinx pinastri*	4.8	0.88	11.24	98.26
Macromoths	*Spilosoma urticae*	2	1.92	2.88	102.08
Macromoths	*Stauropus fagi*	0.36	0.88	10.52	90.35
Macromoths	*Thumatha senex*	1.4	1.21	6.65	95.26
Macromoths	*Tiliacea aurago*	0.8	1.00	29.74	87.79
Macromoths	*Timandra comae*	1.64	0.66	17.62	86.33
Macromoths	*Trichopteryx polycommata*	10.7	2.78	2.57	80.30
Macromoths	*Watsonalla binaria*	1.8	0.70	16.65	89.03
Macromoths	*Watsonalla cultraria*	3.44	1.06	5.04	95.86
Macromoths	*Xanthorhoe quadrifasiata*	4.76	0.66	12.33	99.65

Soldierflies*	*Tabanus autumnalis*	2.64	1.48	4.10	100.49
Soldierflies*	*Tabanus bromius*	1.16	1.30	4.65	100.93
Spiders	*Achaearanea lunata*	1.8	1.96	1.79	87.90
Spiders	*Agalenatea redii*	3.56	1.10	5.30	99.31
Spiders	*Agelena labyrinthica*	2.4	0.90	9.56	105.07
Spiders	*Agroeca brunnea*	-2.44	1.92	1.52	91.13
Spiders	*Anelosimus vittatus*	7.4	1.15	9.09	104.46
Spiders	*Clubiona corticalis*	-1.12	1.56	1.94	89.89
Spiders	*Clubiona pallidula*	2.44	1.43	2.87	99.41
Spiders	*Clubiona subtilis*	-1.4	1.25	2.39	110.25
Spiders	*Crustulina guttata*	-0.24	1.59	1.09	102.91
Spiders	*Diaea dorsata*	2.16	1.78	1.72	87.00
Spiders	*Dictyna latens*	0.8	1.36	4.52	99.72
Spiders	*Dictyna uncinata*	-0.28	1.02	13.41	98.49
Spiders	*Enoplognatha latimana*	4.48	1.31	11.90	103.85
Spiders	*Enoplognatha thoracica*	2.2	1.24	2.96	84.85
Spiders	*Gibbaranea gibbosa*	0.76	1.45	2.11	95.75
Spiders	*Hylyphantes graminicola*	2.52	0.99	2.89	101.66
Spiders	*Larinioides sclopetarius*	2.8	2.43	1.66	108.90
Spiders	*Lathys humilis*	-0.48	1.51	3.07	89.39
Spiders	*Mangora acalypha*	0.44	1.84	2.23	96.30
Spiders	*Microlinyphia impigra*	1.84	2.15	1.87	104.35
Spiders	*Misumena vatia*	0.32	1.27	4.56	100.57
Spiders	*Neoscona adianta*	0.56	1.04	8.21	102.77
Spiders	*Ozyptila praticola*	3.72	1.53	4.27	103.92
Spiders	*Ozyptila simplex*	0	1.42	4.23	101.55
Spiders	*Pardosa prativaga*	-0.52	0.91	15.38	94.81
Spiders	*Philodromus albidus*	2.2	1.65	6.76	98.49
Spiders	*Philodromus dispar*	2.76	1.24	5.85	94.35
Spiders	*Philodromus praedatus*	1.96	1.73	3.41	85.18
Spiders	*Phrurolithus festivus*	3.24	1.28	3.78	98.67
Spiders	*Pocadicnemis juncea*	3.72	0.85	8.20	107.42
Spiders	*Porrhomma microphthalmum*	1.68	1.26	4.55	100.38
Spiders	*Simitidion simile*	1.2	1.57	1.87	89.52

Macromoths	*Zeuzera pyrina*	1.64	0.68	13.50	95.96
Macromoths	*Zygaena trifolii*	-2.04	1.42	3.51	93.79
Non-marine molluscs	*Acroloxus lacustris*	9.32	1.49	6.90	106.11
Non-marine molluscs	*Anisus leucostoma*	4.56	1.96	4.64	102.77
Non-marine molluscs	*Anisus vortex*	4.56	1.35	16.20	94.10
Non-marine molluscs	*Bithynia tentaculata*	7.76	1.48	16.28	96.23
Non-marine molluscs	*Planorbis planorbis*	2.12	1.32	21.62	97.08
Non-marine molluscs	*Pomatias elegans*	0.88	1.64	4.59	95.23
Non-marine molluscs	*Valvata cristata*	4.88	1.85	8.07	94.83
Shieldbugs*	*Coreus marginatus*	3.48	0.75	23.04	99.95
Shieldbugs*	*Coriomeris denticulatus*	4.08	1.58	5.43	104.44
Shieldbugs*	*Dolycoris baccarum*	1	0.79	19.82	101.80
Shieldbugs*	*Myrmus miriformis*	-4.68	1.25	5.04	103.78
Shieldbugs*	*Palomena prasina*	2.36	0.97	26.36	98.66
Shieldbugs*	*Troilus luridus*	0.48	1.36	4.34	101.46
Soldierflies*	*Asilus crabroniformis*	0.12	1.43	11.32	98.17
Soldierflies*	*Choerades marginatus*	1.72	1.95	2.26	107.31
Soldierflies*	*Chorisops tibialis*	1.28	1.22	4.28	90.83
Soldierflies*	*Chrysopilus asiliformis*	1.4	1.15	8.25	95.85
Soldierflies*	*Chrysops viduatus*	-4.48	1.58	4.23	125.90
Soldierflies*	*Dioctria atricapilla*	-1.4	1.07	6.57	98.92
Soldierflies*	*Dioctria baumhaueri*	2.64	1.72	7.75	99.77
Soldierflies*	*Dioctria linearis*	-0.16	1.66	3.14	92.76
Soldierflies*	*Dysmachus trigonus*	1.44	1.33	3.01	121.54
Soldierflies*	*Leptogaster cylindrica*	3.28	1.20	15.50	104.86
Soldierflies*	*Machimus cingulatus*	3.36	1.28	4.88	95.97
Soldierflies*	*Nemotelus notatus*	-2.68	1.74	3.87	108.89
Soldierflies*	*Odontomyia tigrina*	-0.08	1.72	7.20	96.36
Soldierflies*	*Oxycera nigricornis*	-0.88	1.61	3.10	97.93
Soldierflies*	*Oxycera rara*	1.28	1.04	3.39	99.94
Soldierflies*	*Oxycera trilineata*	0.04	1.39	3.48	97.65
Soldierflies*	*Pachygaster atra*	4	1.28	9.93	102.14
Soldierflies*	*Pachygaster leachii*	3.48	1.34	8.88	107.53
Soldierflies*	*Stratiomys singularior*	-0.4	1.43	6.22	100.80

Spiders	*Tegenaria silvestris*	5.08	1.63	1.39	96.94
Spiders	*Thanatus striatus*	-0.88	1.81	2.07	91.44
Spiders	*Theridion pictum*	-0.2	1.92	1.37	101.75
Spiders	*Theridion tinctum*	2.44	1.30	5.12	95.93
Spiders	*Xysticus kochi*	1.88	1.36	4.84	95.11
Spiders	*Zilla diodia*	0.88	1.38	4.08	91.92
Wasps	*Ammophila pubescens*	0.96	1.63	3.55	94.40
Wasps	*Caliadurgus fasciatellus*	0.36	1.31	4.19	101.06
Wasps	*Cerceris arenaria*	2.68	0.95	13.27	100.41
Wasps	*Cerceris ruficornis*	1.2	1.96	2.50	95.25
Wasps	*Cerceris rybyensis*	1.88	0.91	22.27	99.69
Wasps	*Crossocerus cetratus*	1	1.82	6.60	98.25
Wasps	*Episyron rufipes*	2.12	1.31	7.81	103.92
Wasps	*Evagetes crassicornis*	-1.04	1.38	10.00	107.63
Wasps	*Hedychridium ardens*	-0.8	1.40	8.57	100.55
Wasps	*Oxybelus uniglumis*	0.6	1.07	17.38	104.94
Wasps	*Passaloecus gracilis*	2.64	1.40	3.83	96.77
Wasps	*Priocnemis pusilla*	1.08	2.72	4.83	89.60
Woodlice	*Armadillidium depressum*	1.72	2.10	3.36	93.77
Woodlice	*Armadillidium nasatum*	1.04	1.91	1.89	89.71
Woodlice	*Haplophthalmus danicus*	10.5	1.73	4.19	102.62
Woodlice	*Ligidium hypnorum*	-1.56	3.22	2.56	88.04
Woodlice	*Platyarthrus hoffmannseggii*	0.76	1.41	5.90	100.21

Table A3.9 Summaries of habitat associations for 352 species. The columns below show species' probability of occurrence values for 18 habitat classes derived from the Land Cover Map 2007. Four categories are the result of combining narrower categories: Heather and Heather Grassland became Dwarf Shrub Heath [1]; Supra-littoral Rock and Littoral Rock became Coastal Rock [2]; Supra-littoral Sediment and Littoral Sediment became Coastal Sediment [3]; Suburban and Urban became Built-up and Gardens [4].

Group	Species	Broadleaved woodland	Coniferous woodland	Arable and horticulture	Improved grassland	Rough grassland	Neutral grassland	Calcareous grassland	Acid grassland	Fen, marsh and swamp	Dwarf shrub heath [1]	Bog	Montane habitats	Inland rock	Freshwater	Coastal rock [2]	Coastal sediment [3]	Saltmarsh	Built-up and gardens [4]
Aquatic bugs	*Corixa panzeri*	2.79	0.00	7.19	5.66	0.00	0.00	0.00	0.00	4.40	2.01	1.92	0.00	28.74	14.19	0.00	30.47	0.00	8.04
	Cymatia coleoptrata	2.75	0.00	8.91	5.78	1.21	7.27	0.00	0.00	7.50	0.00	0.00	0.00	0.00	20.41	0.00	13.53	0.00	4.23
	Ilyocoris cimicoides	13.09	22.43	23.50	44.44	52.30	31.37	0.00	0.00	34.51	18.22	7.39	0.00	13.75	45.69	51.71	44.64	10.04	17.34
	Microvelia reticulata	12.49	23.54	19.80	26.24	50.33	0.00	0.00	2.24	51.77	13.02	26.41	0.00	21.23	28.95	0.00	6.68	13.35	6.79
	Notonecta maculata	6.55	0.00	4.79	5.90	6.33	0.00	0.00	0.00	0.00	6.13	0.00	0.00	0.00	13.97	0.00	0.00	0.00	9.83
	Notonecta viridis	4.91	0.00	8.94	9.21	4.54	0.00	0.00	0.00	8.50	0.00	0.00	0.00	0.00	28.22	0.00	40.16	0.00	9.77
	Plea minutissima	6.76	14.33	20.45	27.83	39.14	35.69	0.00	0.00	14.54	8.40	3.05	0.00	40.29	26.95	0.00	32.32	17.11	12.42
	Ranatra linearis	2.52	0.00	7.35	8.52	16.69	0.00	0.00	0.00	7.61	6.37	0.00	0.00	0.00	15.84	0.00	7.53	0.00	2.02
	Sigara stagnalis	1.00	0.00	4.47	5.61	9.22	0.00	0.00	0.00	1.72	0.00	0.00	0.00	0.00	4.21	0.00	37.44	24.65	1.56

Bees	*Andrena bicolor*	20.72	16.78	22.92	17.40	12.24	15.67	17.70	0.00	14.86	8.85	15.67	0.00	54.57	11.99	18.85	5.38	0.00	27.70
	Andrena denticulata	5.59	21.03	2.85	8.08	14.49	0.00	0.00	0.00	17.19	5.80	62.99	0.00	0.00	0.00	0.00	3.39	0.00	3.07
	Andrena dorsata	22.09	21.74	20.19	24.79	25.12	49.50	7.85	0.00	33.11	22.11	0.00	0.00	19.59	24.81	0.00	15.40	0.00	17.62
	Andrena flavipes	19.26	11.28	22.66	26.87	20.18	49.69	10.25	41.86	0.00	12.00	0.00	0.00	44.01	24.45	33.31	19.09	16.27	16.68
	Andrena helvola	12.43	5.83	4.51	6.29	9.74	0.00	0.00	0.00	0.00	1.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.93
	Andrena labialis	4.88	2.90	12.90	7.28	8.22	19.16	0.00	59.66	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.62	0.00	1.28
	Andrena minutula	22.44	11.02	16.74	15.13	14.75	13.82	6.88	0.00	13.15	10.23	20.39	0.00	19.51	5.60	33.37	7.41	0.00	14.90
	Andrena nigroaenea	10.80	17.45	24.22	17.92	22.76	29.85	32.83	40.75	22.06	4.65	0.00	0.00	22.38	0.00	59.83	24.22	0.00	20.02
	Andrena ovatula	4.77	8.52	3.31	4.75	5.66	0.00	0.00	46.54	0.00	15.66	22.39	0.00	0.00	0.00	0.00	12.57	0.00	2.68
	Andrena praecox	10.39	14.52	11.83	10.52	14.02	0.00	0.00	0.00	0.00	17.25	0.00	0.00	0.00	15.52	0.00	0.00	0.00	4.23
	Andrena thoracica	1.54	0.00	3.61	2.71	9.53	0.00	0.00	50.20	0.00	2.62	12.76	0.00	0.00	0.00	13.50	7.47	12.57	1.21
	Andrena trimmerana	3.38	5.52	4.45	4.86	2.55	0.00	0.00	0.00	39.11	3.85	0.00	0.00	0.00	7.81	0.00	4.64	10.68	3.57
	Anthidium manicatum	4.43	5.57	4.23	4.42	4.44	0.00	2.51	0.00	0.00	0.83	0.00	0.00	0.00	10.78	0.00	7.91	0.00	19.48
	Anthophora bimaculata	6.80	28.29	8.52	5.19	17.78	0.00	0.00	0.00	0.00	30.27	0.00	0.00	0.00	20.38	0.00	33.26	0.00	7.98
	Anthophora furcata	6.94	5.13	3.52	4.41	3.00	0.00	2.58	0.00	0.00	5.34	0.00	0.00	0.00	0.00	0.00	3.52	0.00	7.12
	Chelostoma campanularum	5.65	0.00	6.72	7.15	7.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.26	0.00	0.00	0.00	18.74
	Colletes daviesanus	3.46	6.72	6.79	9.90	3.03	0.00	15.28	0.00	0.00	3.36	0.00	0.00	44.16	15.28	0.00	2.13	0.00	9.47
	Colletes fodiens	2.45	13.61	5.58	3.61	11.03	0.00	0.00	0.00	0.00	8.43	0.00	0.00	0.00	11.07	0.00	34.05	23.18	2.98
	Colletes similis	2.36	5.34	4.25	3.50	1.47	0.00	0.00	0.00	0.00	4.12	0.00	0.00	22.42	0.00	0.00	12.34	0.00	3.43
	Epeolus cruciger	8.55	27.99	3.99	4.07	13.86	0.00	0.00	0.00	0.00	35.18	0.00	0.00	0.00	15.94	0.00	17.48	0.00	4.49

Bees	*Epeolus variegatus*	4.35	20.07	6.08	3.64	5.06	0.00	0.00	0.00	0.00	7.76	0.00	0.00	0.00	21.20	20.11	20.89	12.95	6.08
	Halictus tumulorum	19.68	8.03	20.70	19.12	15.00	10.48	28.28	15.12	0.00	10.22	0.00	0.00	17.01	0.00	0.00	11.24	25.76	18.43
	Hoplitis claviventris	6.35	10.32	5.30	4.64	0.00	0.00	0.00	0.00	0.00	8.19	0.00	0.00	0.00	0.00	0.00	8.09	0.00	1.79
	Hylaeus brevicornis	7.32	14.07	7.05	6.03	6.01	0.00	2.47	0.00	0.00	13.89	0.00	0.00	25.12	0.00	20.47	10.60	0.00	5.12
	Hylaeus communis	24.59	25.55	15.05	19.21	15.84	15.28	6.34	0.00	43.57	12.78	0.00	0.00	38.42	31.37	0.00	4.63	0.00	18.50
	Hylaeus confusus	10.70	14.29	3.09	4.27	6.92	0.00	0.00	0.00	0.00	12.75	19.58	0.00	0.00	0.00	0.00	1.40	0.00	3.93
	Hylaeus hyalinatus	3.10	7.40	7.37	6.49	10.27	15.79	0.00	0.00	0.00	2.31	29.33	0.00	22.82	17.01	0.00	19.39	13.56	18.73
	Hylaeus signatus	1.87	0.00	4.71	4.49	0.00	0.00	4.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.64
	Lasioglossum laevigatum	5.45	4.21	5.23	6.64	3.39	0.00	10.38	0.00	0.00	1.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.79
	Lasioglossum leucozonium	15.41	29.02	13.89	13.27	20.61	24.26	12.25	30.64	7.09	17.26	14.23	0.00	16.19	7.26	0.00	19.10	18.06	14.90
	Lasioglossum minutissimum	6.04	4.85	10.86	8.68	8.76	0.00	0.00	0.00	0.00	8.02	0.00	0.00	0.00	0.00	0.00	14.08	0.00	4.57
	Lasioglossum morio	19.82	10.96	19.31	14.11	21.73	40.90	3.99	12.32	6.54	7.12	0.00	0.00	41.58	27.97	41.88	14.49	0.00	21.31
	Lasioglossum parvulum	12.97	15.16	8.96	8.72	10.88	0.00	0.00	39.76	0.00	13.09	0.00	0.00	0.00	0.00	0.00	2.01	0.00	4.95
	Lasioglossum punctatissimum	7.72	26.78	5.60	5.13	14.81	0.00	2.54	34.69	0.00	14.81	0.00	0.00	0.00	0.00	0.00	7.71	0.00	2.28
	Lasioglossum smeathmanellum	3.73	0.00	8.46	5.35	9.19	0.00	0.00	0.00	0.00	0.56	19.93	0.00	15.93	5.76	32.43	10.90	8.40	17.79
	Megachile centuncularis	4.36	4.88	4.62	6.47	1.60	0.00	2.35	0.00	0.00	3.31	0.00	0.00	0.00	0.00	0.00	1.78	0.00	18.98
	Megachile ligniseca	6.69	7.15	3.56	7.18	3.99	16.36	4.97	0.00	59.55	5.66	0.00	0.00	0.00	16.96	0.00	2.67	0.00	13.26

Bees	*Melitta tricincta*	8.47	2.78	5.79	15.39	2.30	0.00	28.78	0.00	0.00	0.74	0.00	0.00	0.00	0.00	100.00	0.00	0.00	3.42
	Nomada flava	39.07	29.10	21.37	26.22	28.35	29.04	14.79	0.00	0.00	18.24	0.00	0.00	56.94	17.92	0.00	12.47	0.00	14.65
	Nomada fucata	7.58	3.86	10.13	13.01	12.89	0.00	23.15	0.00	0.00	6.65	0.00	0.00	36.00	8.41	29.67	12.66	15.79	7.37
	Osmia aurulenta	0.86	3.44	3.86	7.84	3.45	0.00	15.40	0.00	0.00	1.03	0.00	0.00	0.00	0.00	0.00	24.45	0.00	0.00
	Osmia leaiana	4.94	3.11	3.51	7.47	6.86	0.00	2.40	0.00	0.00	1.78	0.00	0.00	0.00	8.75	0.00	0.00	0.00	9.63
	Panurgus calcaratus	6.34	17.36	8.42	6.45	3.84	0.00	0.00	0.00	0.00	18.04	0.00	0.00	0.00	0.00	0.00	6.76	0.00	12.42
	Sphecodes crassus	4.85	0.00	9.47	7.95	17.14	20.71	6.87	0.00	0.00	7.71	0.00	0.00	32.00	0.00	0.00	0.00	0.00	6.15
	Sphecodes ephippius	16.16	16.37	16.91	12.03	13.43	23.60	12.89	0.00	0.00	19.34	19.48	0.00	21.24	6.69	0.00	5.94	0.00	6.65
	Sphecodes monilicornis	9.69	10.01	9.81	11.35	5.66	15.52	11.91	0.00	0.00	8.69	14.01	0.00	50.66	7.76	0.00	10.03	0.00	8.09
	Sphecodes pellucidus	6.03	11.48	3.94	4.91	6.98	13.85	0.00	0.00	0.00	21.29	0.00	0.00	0.00	0.00	0.00	8.04	0.00	1.56
	Sphecodes puncticeps	6.89	10.91	10.33	5.90	11.55	0.00	5.43	0.00	0.00	12.25	0.00	0.00	0.00	0.00	0.00	7.53	0.00	9.57
Butterflies	*Apatura iris*	16.79	10.84	1.58	2.00	0.00	7.70	0.75	0.00	15.07	1.07	0.00	0.00	6.07	2.28	0.00	0.00	0.00	0.44
	Aricia agestis	16.29	7.19	12.84	16.66	19.04	12.01	44.92	5.10	7.80	2.97	1.87	0.00	17.36	14.68	7.90	19.91	12.21	2.36
	Celastrina argiolus	32.62	13.40	21.78	23.82	15.99	21.61	11.83	5.68	36.62	14.44	5.69	0.00	15.59	25.67	20.53	11.31	20.59	37.79
	Gonepteryx rhamni	47.00	31.80	28.47	26.70	22.60	28.87	35.17	3.65	58.64	24.14	13.60	0.00	20.26	34.65	5.56	8.35	19.93	26.76
	Hamearis lucina	8.59	2.89	3.97	2.97	10.21	15.20	29.55	0.00	0.00	1.48	0.00	0.00	5.40	0.00	0.00	0.00	0.00	0.14
	Hesperia comma	4.85	0.81	3.25	12.24	16.31	9.16	13.63	0.00	0.00	0.28	0.00	0.00	0.00	1.25	0.00	0.00	0.00	0.12
	Leptidea sinapis	6.06	15.72	0.63	0.58	0.55	0.85	0.00	5.40	0.00	0.61	0.00	0.00	0.00	0.00	0.00	1.10	0.00	0.08
	Limenitis camilla	39.31	34.17	2.94	3.17	2.69	3.98	0.00	0.00	21.35	3.39	24.89	0.00	5.44	3.23	0.00	1.34	2.11	1.34
	Melanargia galathea	30.40	16.98	25.62	31.54	35.48	27.39	67.63	12.49	8.25	9.14	4.20	0.00	35.49	20.85	37.36	21.57	32.44	7.01
	Plebejus argus	2.87	10.07	1.11	1.09	15.06	3.28	0.00	7.60	1.04	63.13	0.00	0.00	18.86	0.58	25.29	24.37	3.34	0.42

Butterflies	*Polyommatus bellargus*	2.30	0.33	3.60	12.96	23.68	8.02	41.85	1.18	0.00	0.19	0.00	0.00	7.12	0.74	0.00	5.12	0.00	0.29
	Polyommatus coridon	6.06	1.22	5.51	13.66	25.15	11.17	42.74	1.40	0.00	0.92	0.00	0.00	13.11	1.09	10.29	4.10	7.13	0.54
	Pyrgus malvae	18.30	16.31	9.21	12.22	14.25	19.13	44.64	1.18	0.00	5.21	3.11	0.00	28.73	6.76	4.80	11.61	2.02	1.00
	Pyronia tithonus	66.17	54.43	63.69	63.74	56.28	64.04	43.04	21.52	72.87	52.90	24.80	0.00	53.05	64.94	56.77	63.97	59.01	45.42
	Satyrium pruni	11.87	8.28	2.13	3.07	0.81	8.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Thymelicus lineola	19.18	13.04	20.15	19.18	17.70	24.90	32.19	3.55	12.14	7.36	5.99	0.00	16.75	21.67	0.00	26.05	42.69	3.66
Dragonflies and damselflies	*Aeshna mixta*	49.12	35.94	44.83	33.59	13.92	31.51	0.00	0.00	74.04	12.59	9.15	0.00	35.07	53.39	0.00	46.98	47.35	41.36
	Anax imperator	34.12	33.34	31.91	28.14	12.49	25.31	100.00	6.44	18.49	36.82	3.63	0.00	54.65	36.43	39.34	49.83	33.94	25.19
	Brachytron pratense	11.23	12.16	12.45	10.59	7.18	9.80	0.00	0.00	72.87	2.64	7.40	0.00	14.87	19.60	0.00	23.01	31.31	5.34
	Erythromma najas	12.78	11.93	11.51	9.85	8.76	17.10	0.00	0.00	47.45	1.58	0.00	0.00	29.79	36.09	0.00	0.86	9.76	7.70
	Gomphus vulgatissimus	8.42	5.80	10.67	5.45	0.26	3.18	0.00	0.00	0.00	1.47	0.00	0.00	0.00	4.64	0.00	0.00	0.00	4.22
	Libellula fulva	2.65	1.10	2.88	6.55	0.00	24.25	0.00	0.00	1.43	0.00	0.00	0.00	0.00	7.89	0.00	0.00	0.00	1.77
	Orthetrum cancellatum	18.14	17.87	23.92	16.73	13.58	18.94	58.03	0.00	66.38	13.90	5.02	0.00	54.00	49.32	0.00	27.29	8.59	11.52
	Platycnemis pennipes	9.40	7.20	15.85	16.68	5.88	20.23	0.00	0.00	7.13	2.58	0.00	0.00	7.03	7.88	0.00	0.00	0.00	4.63
	Sympetrum sanguineum	24.99	25.78	26.48	18.90	5.44	29.89	0.00	0.00	56.88	6.94	5.65	0.00	24.91	27.25	0.00	33.00	14.00	10.45
Grasshoppers and allies	*Chorthippus albomarginatus*	6.36	4.25	17.87	13.24	11.90	16.17	0.00	0.00	24.10	0.72	0.00	0.00	12.14	20.97	26.38	32.76	68.97	8.60
	Conocephalus discolor	22.90	19.79	20.67	26.07	21.94	15.94	54.76	0.00	35.66	14.04	0.00	0.00	0.00	17.14	0.00	9.48	0.00	13.01
	Conocephalus dorsalis	4.50	2.76	2.28	5.81	9.62	9.01	0.00	0.00	65.67	4.96	14.09	0.00	0.00	7.89	12.55	14.16	35.08	1.84
	Labia minor	0.26	0.00	1.81	1.63	1.18	0.00	0.00	0.00	0.00	1.42	0.00	0.00	0.00	0.00	0.00	1.05	0.00	1.73
	Leptophyes punctatissima	31.95	24.60	25.69	21.90	20.00	19.63	0.00	0.00	8.70	5.48	0.00	0.00	12.43	20.79	22.11	5.75	0.00	24.60

Grasshoppers and allies	*Meconema thalassinum*	22.09	14.69	17.25	15.23	11.01	9.88	0.00	0.00	0.00	0.52	0.00	0.00	0.00	4.90	0.00	0.46	0.00	21.22
	Metrioptera brachyptera	3.23	9.76	0.53	0.07	5.71	4.31	0.00	0.00	0.00	25.33	33.58	0.00	0.00	0.00	0.00	0.00	0.00	0.72
	Metrioptera roeselii	26.38	21.10	32.75	37.53	20.20	0.00	35.87	0.00	0.00	12.91	0.00	0.00	13.69	21.75	0.00	12.20	15.29	19.80
	Omocestus rufipes	9.31	8.95	0.35	0.99	2.09	9.58	3.79	0.00	0.00	7.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.47
	Pholidoptera griseoaptera	29.66	19.92	28.39	16.09	17.83	18.71	12.89	0.00	9.98	4.68	0.00	0.00	0.00	12.81	13.71	9.36	10.23	13.58
	Platycleis albopunctata	2.80	0.00	4.90	2.39	9.86	0.00	0.00	0.00	0.00	1.41	0.00	0.00	100.00	0.00	56.50	15.78	0.00	2.46
	Stenobothrus lineatus	1.62	10.21	0.92	2.40	5.00	7.93	25.63	28.79	0.00	1.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.12
	Tetrix subulata	16.85	8.74	6.07	7.68	4.26	12.82	0.00	0.00	29.08	2.84	0.00	0.00	0.00	29.47	0.00	3.25	7.83	3.18
	Tettigonia viridissima	1.74	0.90	1.64	2.98	7.31	3.84	3.20	5.02	28.03	4.25	0.00	0.00	0.00	4.45	15.11	27.95	9.87	5.16
Ground beetles	*Bembidion articulatum*	2.47	0.00	5.44	6.19	10.68	8.14	0.00	0.00	17.37	0.00	0.00	0.00	15.44	20.44	0.00	5.23	0.00	0.78
	Bembidion assimile	2.02	0.00	7.70	3.28	8.60	14.66	0.00	0.00	20.90	1.14	2.55	0.00	0.00	27.30	0.00	6.09	11.99	0.41
	Bembidion illigeri	0.95	1.87	4.93	3.05	1.83	7.34	0.00	0.00	1.71	0.84	2.33	0.00	13.18	6.74	0.00	9.21	0.00	1.12
	Bembidion varium	0.84	0.00	4.40	2.37	10.95	20.00	0.00	0.00	3.27	0.00	0.00	0.00	0.00	22.08	0.00	15.89	33.33	0.00
	Demetrias atricapillus	3.63	1.48	17.75	5.89	4.67	12.28	0.00	0.00	3.28	0.00	3.63	0.00	11.30	11.62	30.00	7.15	0.00	3.59
	Leistus spinibarbis	5.76	15.22	7.97	2.70	0.00	0.00	0.00	6.00	0.00	3.83	9.43	0.00	0.00	5.18	0.00	3.18	0.00	7.56
	Ophonus rufibarbis	1.38	0.00	8.92	2.70	3.31	11.56	10.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.96	0.00	6.72
	Poecilus cupreus	5.85	2.19	9.75	10.61	9.45	21.32	21.78	0.00	0.00	1.27	3.14	0.00	0.00	4.48	0.00	2.70	0.00	5.67
	Pterostichus nigrita	3.95	1.96	5.30	7.19	6.58	22.96	0.00	2.92	10.64	6.12	7.58	0.00	15.91	12.72	0.00	5.76	0.00	3.21

Hoverflies	*Stenolophus mixtus*	2.42	1.80	5.16	6.67	7.49	19.62	0.00	0.00	5.00	1.69	0.00	0.00	0.00	17.71	0.00	5.69	4.74	1.45
	Syntomus foveatus	1.43	3.52	4.25	5.74	3.53	0.00	28.52	1.91	0.00	9.81	0.00	0.00	0.00	0.00	38.14	17.25	6.75	8.79
	Cheilosia soror	8.73	2.16	4.22	3.10	2.86	0.00	7.05	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.75
	Cheilosia vulpina	4.05	2.93	1.60	3.07	4.30	0.00	0.00	0.00	0.00	2.19	0.00	0.00	0.00	6.82	0.00	1.62	6.29	0.78
	Chrysotoxum cautum	4.33	11.08	5.24	6.25	1.87	18.94	0.00	0.00	0.00	5.52	0.00	0.00	0.00	3.66	0.00	3.34	0.00	9.12
	Chrysotoxum festivum	6.04	10.24	4.96	6.20	3.87	0.00	9.98	0.00	2.68	4.62	4.46	0.00	0.00	5.16	10.02	10.16	3.54	12.03
	Chrysotoxum verralli	3.28	1.98	3.91	4.65	6.06	0.00	19.53	0.00	1.67	0.00	0.00	0.00	0.00	3.56	0.00	2.27	0.00	5.49
	Epistrophe nitidicollis	4.78	6.16	1.41	0.39	1.41	0.00	0.00	0.00	6.25	1.46	0.00	0.00	0.00	5.88	0.00	4.52	0.00	2.58
	Eumerus ornatus	6.31	7.32	0.69	1.37	3.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.60
	Eumerus strigatus	2.35	1.42	3.75	2.30	1.45	4.44	0.00	0.00	7.05	2.10	0.00	0.00	0.00	4.94	0.00	8.48	5.19	2.88
	Paragus haemorrhous	3.36	6.13	4.47	3.20	10.04	0.00	9.45	6.84	5.97	13.48	0.00	0.00	9.93	4.70	10.84	16.66	0.00	3.70
	Parhelophilus frutetorum	3.28	2.47	1.57	3.10	3.64	6.80	0.00	6.77	5.33	0.00	0.00	0.00	0.00	10.35	0.00	1.07	0.00	4.46
	Parhelophilus versicolor	2.08	2.96	4.00	3.14	3.53	0.00	0.00	0.00	9.61	0.00	7.21	0.00	0.00	15.96	0.00	2.72	0.00	3.60
	Pipizella virens	2.64	3.42	2.52	1.43	2.85	0.00	0.00	0.00	6.19	1.77	0.00	0.00	0.00	9.20	0.00	2.40	0.00	4.70
	Platycheirus ambiguus	2.41	5.35	2.86	2.74	4.47	16.50	0.00	0.00	9.80	0.00	0.00	0.00	0.00	9.85	0.00	3.81	0.00	4.96
	Sphaerophoria taeniata	3.22	2.72	3.96	6.16	1.24	5.65	0.00	0.00	15.91	2.34	0.00	0.00	0.00	4.01	0.00	0.00	0.00	2.78
	Tropidia scita	3.31	2.60	5.64	4.61	4.37	5.83	0.00	0.00	32.81	1.71	10.92	0.00	0.00	9.22	9.07	10.01	7.32	3.53
	Volucella inanis	13.38	5.44	15.55	12.36	0.00	23.33	0.00	0.00	0.00	3.46	0.00	0.00	0.00	17.26	0.00	0.00	0.00	26.61
	Volucella inflata	11.66	8.51	1.80	2.88	2.67	0.00	0.00	11.14	0.00	2.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.01
	Volucella zonaria	3.29	1.15	2.78	5.96	0.00	0.00	0.00	14.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.86	5.75	36.37

	Xanthogramma pedissequum	9.34	10.48	5.12	7.94	3.78	4.85	6.10	5.14	1.20	5.95	2.70	0.00	12.25	9.35	0.00	7.98	5.77	16.11
Macromoths	*Acronicta aceris*	13.83	7.26	13.33	13.39	15.68	19.56	6.75	0.00	26.50	7.52	0.00	0.00	11.19	12.86	0.00	14.33	13.83	35.33
	Acronicta tridens	2.81	1.68	4.58	3.30	0.96	0.00	0.00	2.38	14.67	0.44	1.42	0.00	0.00	0.00	0.00	5.45	0.00	5.11
	Agrotis cinerea	1.10	0.00	1.24	2.25	0.00	0.00	8.60	0.00	0.00	1.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.18
	Agrotis puta	19.66	10.40	25.05	19.26	10.87	10.58	8.90	1.87	19.71	9.35	5.25	0.00	9.19	15.01	31.15	22.43	22.18	39.43
	Agrotis ripae	0.00	0.88	2.68	0.89	2.30	0.00	0.00	0.00	0.00	0.72	0.00	0.00	0.00	0.00	0.00	18.20	16.62	1.52
	Agrotis trux	1.79	0.00	5.48	1.96	7.21	0.00	0.00	1.11	0.00	1.01	3.24	0.00	0.00	0.00	21.42	4.00	0.00	4.64
	Amphipyra pyramidea	45.83	24.77	26.66	27.08	15.38	30.11	25.75	5.87	24.60	12.43	8.68	0.00	4.66	19.06	17.63	11.22	4.14	33.51
	Angerona prunaria	9.90	7.99	1.55	1.48	1.20	4.97	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.61	0.00	1.41
	Apamea anceps	10.24	4.79	20.81	7.58	3.98	11.10	10.22	0.00	0.00	0.51	0.00	0.00	12.44	11.17	0.00	10.80	6.45	15.33
	Apamea oblonga	0.00	2.90	3.06	1.36	3.40	0.00	0.00	0.00	42.33	1.74	0.00	0.00	0.00	0.00	0.00	17.90	26.52	1.51
	Apamea sublustris	4.31	3.23	6.64	5.14	4.27	0.00	25.14	0.00	0.00	1.55	0.00	0.00	0.00	0.00	0.00	0.00	6.68	6.87
	Apoda limacodes	13.51	10.28	3.27	4.88	6.05	20.80	0.00	0.00	0.00	12.20	0.00	0.00	13.46	4.32	0.00	3.98	0.00	8.35
	Aporophyla australis	3.87	0.00	8.47	8.24	9.37	0.00	0.00	0.00	0.00	2.96	0.00	0.00	0.00	0.00	15.33	33.27	21.65	7.53
	Archanara dissoluta	3.40	0.71	4.51	3.85	4.69	10.75	0.00	0.00	32.20	2.39	9.70	0.00	0.00	9.76	0.00	10.52	26.25	4.18
	Arctia villica	4.32	8.03	8.53	7.25	15.08	0.00	0.00	4.61	15.92	6.64	0.00	0.00	16.15	0.00	36.63	36.99	30.76	7.39
	Arenostola phragmitidis	7.56	3.88	9.51	7.67	9.60	13.33	0.00	0.00	71.06	2.26	3.38	0.00	0.00	12.33	0.00	19.57	31.18	7.76
	Aspitates ochrearia	2.10	3.61	6.75	6.31	16.39	0.00	3.76	0.00	0.00	4.84	16.36	0.00	13.79	17.56	17.61	48.23	14.26	6.49
	Bena bicolorana	17.12	11.50	8.66	10.79	6.31	11.21	7.11	1.67	9.59	8.09	2.16	0.00	0.00	0.00	0.00	0.79	6.78	22.40
	Boudinotiana notha	8.17	1.13	0.50	0.59	2.62	0.00	0.00	0.00	0.00	1.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Macromoths	*Catarhoe cuculata*	3.87	6.44	4.39	3.90	3.53	0.00	10.95	0.00	0.00	0.00	11.90	0.00	0.00	0.00	0.00	2.22	0.00	3.02
	Catarhoe rubidata	3.74	1.90	4.82	2.95	1.48	0.00	7.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.55	9.26	0.00	5.56
	Catocala nupta	18.44	10.86	29.39	26.00	20.65	30.97	0.00	0.00	45.07	5.62	13.20	0.00	0.00	28.10	0.00	21.33	23.56	40.30
	Cepphis advenaria	10.48	12.74	1.00	1.42	1.97	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.32	1.77
	Chilodes maritima	1.89	0.81	3.02	2.49	2.68	0.00	0.00	0.00	53.34	2.55	15.23	0.00	3.58	8.47	5.84	9.94	18.57	4.83
	Chlorissa viridata	0.18	1.87	0.37	0.14	1.27	0.00	0.00	0.00	0.00	13.02	0.00	0.00	0.00	10.47	0.00	0.00	0.00	0.80
	Clostera curtula	20.93	15.41	18.68	18.12	12.05	8.44	0.00	9.84	20.37	4.51	8.09	0.00	0.00	3.95	0.00	11.55	10.15	26.32
	Coenobia rufa	11.33	7.83	6.74	10.84	8.73	11.43	0.00	8.04	41.31	10.68	41.54	0.00	15.53	7.78	11.10	12.45	14.42	7.58
	Comibaena bajularia	26.69	15.98	5.93	5.55	3.16	3.84	10.54	0.00	10.49	5.60	0.00	0.00	0.00	5.17	0.00	2.12	7.74	8.92
	Conistra rubiginea	27.08	24.76	26.94	19.11	7.05	41.82	0.00	0.00	0.00	12.72	0.00	0.00	45.67	0.00	0.00	28.56	0.00	22.70
	Cosmia affinis	7.39	1.96	4.52	4.89	2.75	0.00	0.00	0.00	4.52	0.82	0.00	0.00	0.00	0.00	0.00	2.11	0.00	5.28
	Cosmia diffinis	3.46	0.00	8.40	1.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.42
	Cosmia pyralina	16.26	3.54	12.77	11.35	3.46	27.27	0.00	0.00	5.15	0.62	0.00	0.00	0.00	8.20	0.00	7.86	0.00	10.18
	Cucullia absinthii	0.29	0.00	2.77	1.62	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.37	0.00	3.33
	Cucullia asteris	0.88	0.00	3.47	2.27	3.96	0.00	0.00	9.92	11.88	0.83	0.00	0.00	0.00	0.00	0.00	18.35	13.22	4.47
	Cyclophora annularia	13.85	8.62	2.68	3.70	1.65	0.00	0.00	0.00	0.00	0.43	0.00	0.00	8.77	0.00	0.00	0.00	0.00	4.29
	Cyclophora linearia	18.55	10.63	3.34	3.18	2.75	0.00	5.86	0.00	0.00	2.05	0.00	0.00	2.80	0.00	8.92	0.59	0.00	6.98
	Cyclophora punctaria	32.45	20.75	10.30	11.56	9.16	8.22	2.85	1.32	9.79	8.40	0.00	0.00	10.57	11.20	0.00	5.20	17.55	19.05
	Deltote pygarga	37.41	32.44	8.59	9.85	14.54	14.67	10.38	5.27	25.97	21.80	28.84	0.00	4.54	6.77	4.12	7.34	13.14	11.80
	Dypterygia scabriuscula	9.22	13.78	7.88	7.95	12.35	5.21	0.00	0.00	5.05	13.05	3.53	0.00	11.17	3.34	0.00	9.23	18.34	20.02
	Earias clorana	3.94	3.69	8.27	5.98	4.57	13.29	0.00	0.00	47.81	7.78	27.90	0.00	0.00	6.89	0.00	20.77	21.95	9.83
	Eilema caniola	3.13	0.00	11.13	2.99	3.80	0.00	0.00	10.97	0.00	1.12	0.00	0.00	0.00	29.17	31.46	15.69	0.00	3.34

Macromoths	*Eilema complana*	36.23	29.70	23.37	20.57	17.70	23.79	35.78	5.53	37.31	25.43	29.69	0.00	18.79	22.15	19.85	35.55	42.80	24.57
	Eilema depressa	43.25	48.54	12.86	13.67	12.19	5.78	15.44	8.88	18.59	12.36	5.76	0.00	16.24	7.67	12.98	5.82	3.87	14.10
	Eilema griseola	47.66	37.72	35.18	30.91	21.94	40.30	5.40	8.49	69.07	14.41	35.62	0.00	22.75	25.48	23.32	25.07	28.26	27.54
	Eilema sororcula	34.45	25.54	13.39	11.86	6.38	10.80	3.71	8.44	5.96	3.23	28.55	0.00	0.00	18.94	6.85	5.70	0.00	24.14
	Elaphria venustula	8.63	7.26	1.82	3.02	4.41	0.00	4.08	0.00	0.00	4.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.57
	Ennomos autumnaria	4.82	0.00	12.91	12.76	6.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	22.63	0.00	8.30
	Ennomos quercinaria	18.70	4.57	10.10	14.37	5.12	0.00	7.47	4.81	0.00	6.50	6.08	0.00	0.00	0.00	11.63	3.55	0.00	13.23
	Eremobia ochroleuca	18.34	10.79	34.47	22.51	16.66	43.96	17.67	0.00	19.45	4.21	0.00	0.00	15.49	12.74	0.00	45.15	29.31	22.63
	Eriogaster lanestris	1.07	0.00	15.70	14.57	0.00	0.00	0.00	0.00	0.00	3.97	0.00	0.00	0.00	11.78	33.84	0.00	21.76	5.31
	Euphyia biangulata	6.99	6.23	2.85	6.55	2.41	0.00	0.00	3.91	0.00	0.58	0.00	0.00	0.00	0.00	12.36	0.92	0.00	2.82
	Euphyia unangulata	7.55	8.08	4.36	5.52	6.03	5.30	0.00	1.82	10.88	3.31	0.00	0.00	0.00	8.14	9.31	3.00	0.00	3.47
	Eupithecia haworthiata	9.56	5.61	6.90	4.38	6.19	4.06	4.92	0.00	0.00	0.00	0.00	0.00	4.65	4.03	7.82	6.52	0.00	8.87
	Eupithecia inturbata	14.33	4.90	9.17	6.30	3.38	16.57	0.00	0.00	0.00	2.53	0.00	0.00	0.00	8.31	0.00	5.40	0.00	7.20
	Eupithecia millefoliata	1.55	0.00	4.13	4.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.04	0.00	8.56
	Eupithecia simpliciata	4.70	0.00	10.15	7.30	3.05	8.08	0.00	0.00	13.74	3.66	0.00	0.00	15.94	0.00	0.00	15.60	31.97	12.53
	Eupithecia subumbrata	2.88	2.93	4.13	3.57	5.67	13.60	12.05	0.00	7.03	0.53	1.78	0.00	0.00	2.91	0.00	11.75	11.50	4.46
	Euplagia quadripunctaria	12.71	22.38	43.98	23.21	10.75	0.00	0.00	0.00	0.00	13.72	0.00	0.00	0.00	0.00	28.42	0.00	42.99	63.46
	Euproctis chrysorrhoea	14.98	16.94	17.56	13.99	20.04	27.69	9.81	0.00	32.85	6.85	0.00	0.00	29.19	9.53	0.00	52.46	41.94	31.59

Macromoths

Gastropacha quercifolia	3.09	2.67	4.86	3.59	3.38	9.01	8.91	0.00	0.00	1.66	0.00	0.00	0.00	0.00	0.00	2.18	7.85	2.86
Globia sparganii	3.70	2.72	6.49	7.04	6.29	0.00	0.00	0.00	40.58	1.52	33.17	0.00	0.00	8.23	0.00	17.84	10.59	6.10
Hemaris fuciformis	2.85	3.83	1.15	1.02	0.00	0.00	0.00	0.00	0.00	2.61	0.00	0.00	0.00	0.00	0.00	0.94	6.20	1.08
Hemistola chrysoprasaria	18.26	14.83	13.89	16.20	8.20	24.13	12.17	1.96	10.33	2.27	0.00	0.00	13.59	13.02	0.00	14.89	0.00	31.57
Hemithea aestivaria	46.36	23.48	23.29	23.83	12.37	15.93	0.00	1.39	30.10	10.48	11.65	0.00	11.01	21.83	15.42	15.16	9.28	39.61
Horisme tersata	11.42	6.48	8.00	6.32	6.62	10.04	14.61	0.00	0.00	0.50	0.00	0.00	7.11	0.00	0.00	7.16	0.00	9.90
Horisme vitalbata	12.26	4.19	14.70	10.11	9.17	6.30	11.74	0.00	0.00	2.04	10.02	0.00	0.00	0.00	0.00	10.76	5.73	16.21
Hypena rostralis	4.67	0.00	10.25	7.48	2.18	0.00	0.00	0.00	0.00	1.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	19.11
Hypomecis punctinalis	30.22	17.10	8.21	8.81	12.81	9.92	3.35	0.00	11.48	7.75	0.00	0.00	14.27	9.97	0.00	5.51	7.36	15.34
Hypomecis roboraria	14.49	9.76	1.88	2.54	3.06	7.32	0.00	0.00	0.00	3.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.10
Idaea emarginata	11.96	9.46	12.43	10.37	6.46	11.29	0.00	0.00	19.10	8.30	15.80	0.00	0.00	12.01	0.00	10.57	7.07	9.10
Idaea fuscovenosa	14.75	7.85	16.81	9.40	7.53	4.53	0.00	5.54	15.74	9.75	0.00	0.00	0.00	13.94	13.98	24.07	22.39	25.67
Idaea muricata	0.77	2.38	0.34	0.25	0.53	6.23	0.00	0.00	6.68	9.90	9.94	0.00	4.09	0.00	0.00	3.05	0.00	0.09
Idaea rusticata	13.45	4.01	13.50	9.46	10.09	12.08	12.64	0.00	0.00	3.91	0.00	0.00	18.75	17.71	0.00	5.50	0.00	35.40
Idaea subsericeata	9.67	9.13	5.04	4.81	4.44	0.00	19.45	2.03	4.93	7.27	1.37	0.00	0.00	2.16	21.71	18.25	0.00	7.53
Idaea sylvestraria	1.58	4.03	1.16	0.61	1.29	0.00	0.00	0.00	39.72	22.91	0.00	0.00	0.00	0.00	0.00	2.57	19.15	1.48
Idaea trigeminata	27.32	17.83	12.64	9.54	7.58	6.27	0.00	0.00	4.87	3.70	0.00	0.00	0.00	8.56	0.00	7.65	7.05	32.40
Lacanobia suasa	1.70	1.12	5.47	4.75	4.06	0.00	0.00	0.00	24.80	1.57	3.43	0.00	0.00	1.81	9.23	13.13	52.70	7.82
Lacanobia w-latinum	8.66	8.09	12.41	12.22	10.16	11.88	18.02	2.07	14.67	7.71	0.00	0.00	10.89	3.61	0.00	16.92	21.64	25.43
Larentia clavaria	9.20	8.57	25.91	22.23	8.43	40.96	58.11	8.31	18.41	11.38	0.00	0.00	0.00	0.00	0.00	35.28	0.00	19.25
Laspeyria flexula	31.26	30.32	17.39	15.19	9.24	13.95	11.21	1.22	9.38	6.91	0.00	0.00	7.07	11.80	0.00	6.70	0.00	21.79

Macromoths	*Lenisa geminipuncta*	4.50	4.36	8.84	3.89	6.54	11.04	0.00	0.00	10.46	6.54	19.97	0.00	12.25	14.14	13.69	20.00	33.19	6.30
	Leucania obsoleta	1.72	0.68	3.39	3.01	3.69	0.00	0.00	0.00	18.09	2.62	29.87	0.00	0.00	5.75	13.54	9.33	19.81	3.88
	Leucoma salicis	10.63	4.06	15.35	9.86	8.34	4.89	0.00	0.00	42.16	2.45	5.02	0.00	7.23	15.14	0.00	18.66	9.85	18.02
	Ligdia adustata	22.35	9.93	11.51	10.35	3.34	12.65	5.41	0.66	2.69	1.00	0.00	0.00	2.92	3.08	0.00	2.79	3.12	13.16
	Lithophane ornitopus	40.00	27.28	37.72	37.83	34.95	68.58	0.00	32.95	15.19	23.37	10.86	0.00	0.00	0.00	0.00	22.95	0.00	34.22
	Lithophane semibrunnea	8.21	6.62	15.73	18.57	8.84	0.00	0.00	0.00	0.00	5.42	0.00	0.00	0.00	0.00	0.00	12.42	0.00	20.91
	Lomographa bimaculata	33.50	19.06	10.61	11.17	6.67	11.04	0.00	3.25	4.50	4.59	1.47	0.00	0.00	10.51	13.76	2.39	0.00	14.97
	Lygephila pastinum	12.14	11.45	14.10	11.72	5.30	27.82	25.44	0.00	22.48	3.35	2.05	0.00	10.84	10.50	0.00	10.21	0.00	15.93
	Lymantria monacha	54.26	38.34	15.60	19.06	14.12	21.55	9.67	4.45	31.13	15.23	9.36	0.00	16.33	9.35	23.63	9.89	9.75	17.91
	Macaria alternata	17.48	15.10	9.34	11.71	8.58	10.41	0.00	3.93	31.02	9.45	6.02	0.00	14.50	6.59	8.64	15.53	17.04	11.27
	Macrochilo cribrumalis	5.76	3.71	5.61	8.85	11.46	0.00	0.00	0.00	40.01	7.83	0.00	0.00	0.00	7.17	0.00	8.72	0.00	5.65
	Malacosoma neustria	17.07	12.25	16.73	14.29	12.93	20.43	0.00	1.00	14.61	7.60	24.01	0.00	6.79	13.34	35.30	29.18	29.11	20.06
	Meganola albula	9.74	7.07	9.14	11.91	11.38	32.14	12.99	0.00	69.84	12.24	0.00	0.00	17.96	0.00	0.00	30.73	8.87	11.19
	Meganola strigula	4.51	0.94	0.20	0.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.59
	Melanthia procellata	14.33	8.70	4.65	3.66	4.57	3.55	8.11	0.00	0.00	0.00	0.00	0.00	4.51	0.00	4.10	3.64	0.00	3.59
	Miltochrista miniata	39.44	33.36	16.47	18.28	15.36	19.85	0.00	2.17	30.78	21.64	6.33	0.00	22.67	8.74	10.22	12.35	21.16	17.17
	Mimas tiliae	22.68	11.35	18.75	15.70	12.79	4.34	0.00	2.65	17.94	5.31	3.35	0.00	7.30	15.68	13.02	13.01	20.49	43.73
	Minoa murinata	12.01	17.52	0.71	0.34	4.93	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17
	Mythimna favicolor	0.72	0.00	2.47	4.00	2.63	0.00	0.00	0.00	13.00	2.38	0.00	0.00	0.00	0.00	0.00	9.24	30.43	3.35

Macromoths	*Mythimna l-album*	5.37	0.00	19.86	10.97	8.83	0.00	0.00	17.00	0.00	1.17	0.00	0.00	0.00	0.00	29.78	20.75	22.95	24.62
	Mythimna pudorina	5.67	7.42	4.75	6.18	7.35	0.00	0.00	4.21	62.68	18.71	38.54	0.00	10.48	0.00	0.00	9.66	17.00	3.09
	Mythimna straminea	5.29	2.28	8.01	6.08	7.63	9.77	0.00	0.00	73.50	4.86	15.26	0.00	4.87	17.55	5.33	18.14	32.19	4.92
	Nyctobrya muralis	4.03	0.00	11.41	10.58	7.64	0.00	9.85	0.00	0.00	2.17	0.00	0.00	16.76	7.87	52.27	24.38	15.31	32.47
	Pachycnemia hippocastanaria	4.16	10.31	1.09	1.42	6.53	7.35	0.00	5.09	28.78	36.28	0.00	0.00	12.78	0.00	0.00	16.94	6.19	3.31
	Paradarisa consonaria	13.36	18.54	2.09	2.69	3.23	0.00	0.00	0.00	0.00	3.92	1.53	0.00	0.00	0.00	12.12	1.19	0.00	1.98
	Parascotia fuliginaria	16.59	6.47	6.02	6.54	0.00	13.12	14.19	0.00	0.00	6.71	0.00	0.00	0.00	0.00	0.00	1.50	0.00	11.89
	Parectropis similaria	20.57	14.78	1.92	2.07	3.52	0.00	0.00	0.00	0.00	2.56	13.22	0.00	8.11	0.00	0.00	0.63	5.60	2.76
	Pechipogo strigilata	9.63	8.40	0.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23
	Philereme transversata	14.19	5.45	11.05	9.17	5.83	26.75	22.83	0.00	10.98	0.00	0.00	0.00	0.00	7.70	0.00	0.00	0.00	9.49
	Philereme vetulata	10.44	5.08	6.64	5.97	8.20	12.34	19.28	0.00	0.00	0.00	0.00	0.00	0.00	3.65	0.00	0.00	0.00	5.15
	Photedes fluxa	15.95	7.97	4.85	3.17	0.00	0.00	0.00	0.00	29.83	0.00	0.00	0.00	0.00	8.77	0.00	0.00	0.00	2.95
	Polymixis flavicincta	10.00	0.00	21.25	17.67	17.01	29.71	0.00	0.00	0.00	3.77	45.15	0.00	0.00	31.07	42.31	20.82	0.00	45.94
	Polyploca ridens	41.41	34.59	18.27	19.02	17.81	38.76	0.00	8.03	0.00	9.80	0.00	0.00	0.00	11.66	0.00	2.69	0.00	14.07
	Ptilodon cucullina	20.43	12.79	8.49	6.22	12.27	7.68	5.80	0.00	18.67	2.35	0.00	0.00	0.00	3.45	0.00	10.19	8.08	13.05
	Schrankia taenialis	7.49	2.74	0.94	0.68	0.59	8.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.23	1.25	0.00	0.84
	Scopula emutaria	1.38	3.39	2.23	3.36	2.62	0.00	0.00	0.00	9.86	5.84	0.00	0.00	0.00	0.00	0.00	20.18	29.71	2.89
	Scopula imitaria	17.03	9.93	19.59	13.72	7.22	10.89	18.16	2.26	12.48	4.31	1.10	0.00	13.08	12.28	19.84	13.40	7.50	32.78
	Scopula marginepunctata	4.00	1.13	5.95	5.59	6.31	0.00	0.00	1.91	13.20	3.14	0.00	0.00	4.23	10.06	31.85	25.20	15.92	12.30

Macromoths	*Simyra albovenosa*	3.35	0.00	5.41	6.27	8.90	0.00	0.00	0.00	49.06	0.71	0.00	0.00	0.00	7.24	0.00	10.78	18.69	3.03
	Sphinx ligustri	17.90	9.17	20.75	16.52	9.62	5.61	10.35	1.58	31.94	5.43	3.04	0.00	7.65	11.93	11.06	18.22	9.35	27.08
	Sphinx pinastri	19.54	37.86	8.98	9.89	14.90	7.59	8.99	0.00	27.43	24.88	0.00	0.00	26.31	2.60	0.00	8.93	13.80	14.94
	Spilosoma urticae	1.82	0.00	3.37	2.45	8.68	0.00	0.00	0.00	22.37	2.14	0.00	0.00	0.00	0.00	0.00	14.35	0.00	1.90
	Stauropus fagi	32.43	24.45	8.84	11.57	8.02	8.24	10.59	3.26	8.81	7.43	0.00	0.00	5.89	4.32	4.68	5.03	8.29	10.78
	Thumatha senex	7.78	4.26	7.87	7.37	6.59	6.03	0.00	0.00	47.61	8.60	21.55	0.00	3.88	12.42	0.00	10.46	23.05	4.06
	Tiliacea aurago	50.04	33.02	41.47	34.86	22.97	33.09	0.00	0.00	12.22	13.63	0.00	0.00	0.00	15.56	0.00	16.42	0.00	34.33
	Timandra comae	31.15	16.39	25.20	21.55	12.68	9.84	2.61	1.16	31.03	4.48	8.06	0.00	24.81	18.02	10.30	11.72	25.39	24.57
	Trichopteryx polycommata	8.58	3.17	0.79	8.77	0.00	39.61	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27
	Watsonalla binaria	33.82	19.15	19.08	19.66	13.72	17.96	7.42	2.55	24.66	9.16	6.37	0.00	3.80	14.78	0.00	8.98	14.24	23.19
	Watsonalla cultraria	12.49	8.97	5.03	4.99	5.66	0.00	7.17	3.00	0.00	2.24	1.80	0.00	0.00	3.87	0.00	0.90	0.00	4.85
	Xanthorhoe quadrifasiata	27.32	22.36	12.08	9.69	13.12	15.83	19.77	12.38	24.04	3.33	18.12	0.00	18.73	14.64	0.00	5.40	0.00	11.18
	Zeuzera pyrina	19.73	11.38	12.67	14.17	13.16	9.45	27.01	3.64	26.34	4.95	3.65	0.00	11.18	12.73	0.00	10.05	14.52	24.91
	Zygaena trifolii	2.12	1.59	1.91	6.36	10.36	0.00	31.32	5.28	4.15	4.00	13.99	0.00	0.00	2.22	0.00	6.00	6.07	0.42
Non-marine molluscs	*Acroloxus lacustris*	2.45	0.00	8.92	8.02	6.10	9.96	0.00	0.00	24.74	5.24	0.00	0.00	0.00	6.70	0.00	0.00	0.00	3.36
	Anisus leucostoma	1.68	0.00	6.43	4.59	1.26	28.43	0.00	0.00	39.76	9.57	0.00	0.00	0.00	0.00	0.00	8.10	0.00	0.85
	Anisus vortex	1.90	8.56	18.42	22.79	61.28	50.79	0.00	0.00	60.76	3.03	17.11	0.00	14.68	9.36	0.00	5.15	0.00	3.84
	Bithynia tentaculata	3.04	0.00	16.37	22.95	70.38	29.47	0.00	0.00	72.27	8.00	0.00	0.00	12.99	19.59	0.00	4.53	0.00	12.36
	Planorbis planorbis	2.12	6.56	19.33	35.94	71.54	47.08	0.00	0.00	68.38	25.67	50.93	0.00	0.00	4.71	0.00	5.45	0.00	1.99
	Pomatias elegans	12.15	4.74	5.22	4.36	3.41	0.00	35.12	0.00	0.00	5.08	0.00	0.00	0.00	0.00	21.30	9.26	0.00	0.77
	Valvata cristata	1.64	0.00	5.06	12.65	59.99	20.54	0.00	0.00	53.83	2.87	0.00	0.00	0.00	19.92	0.00	0.00	0.00	2.06

Shieldbugs and allies	*Coreus marginatus*	28.50	13.78	21.41	27.92	26.51	38.10	19.21	0.00	0.00	15.41	0.00	0.00	38.10	21.22	32.99	15.53	0.00	18.59
	Coriomeris denticulatus	3.96	0.00	5.11	6.44	12.41	0.00	0.00	0.00	0.00	2.38	0.00	0.00	0.00	12.78	0.00	0.00	0.00	4.86
	Dolycoris baccarum	20.79	26.71	18.51	19.22	35.62	29.78	33.28	13.57	0.00	16.75	0.00	0.00	0.00	29.51	45.89	40.27	0.00	12.87
	Myrmus miriformis	6.92	10.57	3.39	4.29	9.19	32.77	28.89	0.00	0.00	19.40	0.00	0.00	37.86	7.01	53.85	10.83	0.00	2.00
	Palomena prasina	28.84	26.23	27.44	25.36	19.35	28.66	0.00	37.60	0.00	6.70	19.31	0.00	0.00	6.53	0.00	3.71	0.00	42.58
	Troilus luridus	7.52	11.54	3.82	3.73	0.00	0.00	0.00	8.66	23.67	6.77	21.26	0.00	0.00	5.48	0.00	1.56	0.00	1.05
Soldierflies and allies	*Asilus crabroniformis*	5.82	14.14	17.04	11.02	24.31	0.00	5.95	0.00	22.80	20.71	0.00	0.00	54.89	0.00	0.00	0.00	0.00	2.71
	Choerades marginatus	12.80	2.06	0.55	1.90	2.83	10.71	0.00	0.00	0.00	2.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.04
	Chorisops tibialis	3.99	4.33	5.13	4.42	5.53	12.57	0.00	0.00	0.00	0.99	0.00	0.00	0.00	3.34	0.00	3.39	0.00	8.64
	Chrysopilus asiliformis	8.79	0.00	8.49	9.66	9.45	17.20	10.22	0.00	4.46	1.09	0.00	0.00	0.00	0.00	0.00	5.08	0.00	14.94
	Chrysops viduatus	8.28	6.51	1.05	1.00	10.40	0.00	0.00	0.00	1.98	20.75	23.48	0.00	0.00	8.13	0.00	0.00	0.00	1.21
	Dioctria atricapilla	7.22	8.02	7.80	6.33	7.13	7.50	15.41	0.00	0.00	4.55	17.93	0.00	0.00	16.18	0.00	0.00	0.00	2.47
	Dioctria baumhaueri	8.51	4.63	8.25	4.79	5.66	0.00	0.00	25.38	0.00	12.66	0.00	0.00	0.00	0.00	57.64	6.53	0.00	13.46
	Dioctria linearis	14.65	8.84	2.69	1.99	1.62	13.67	0.00	0.00	0.00	2.55	0.00	0.00	0.00	0.00	0.00	2.57	0.00	1.86
	Dysmachus trigonus	1.29	1.74	1.86	1.97	2.81	0.00	0.00	13.49	3.13	5.68	0.00	0.00	24.19	11.63	13.76	28.92	6.85	0.00

Soldierflies and allies	*Leptogaster cylindrica*	7.92	8.00	17.01	20.04	11.33	13.21	45.00	0.00	0.00	2.40	0.00	0.00	53.39	10.17	0.00	5.44	33.75	8.68
	Machimus cingulatus	1.72	10.29	4.41	6.04	8.23	0.00	0.00	0.00	0.00	19.92	0.00	0.00	0.00	5.51	15.56	1.74	5.55	2.83
	Nemotelus notatus	0.69	1.26	2.71	4.28	5.02	9.90	0.00	0.00	5.24	0.97	7.77	0.00	0.00	4.19	0.00	21.73	41.02	1.44
	Odontomyia tigrina	1.11	1.90	6.33	13.52	21.42	0.00	0.00	0.00	2.07	0.00	36.23	0.00	0.00	29.01	0.00	3.19	0.00	1.82
	Oxycera nigricornis	3.16	1.17	2.72	4.91	7.60	13.71	0.00	0.00	13.92	0.00	0.00	0.00	0.00	0.00	0.00	3.04	0.00	0.38
	Oxycera rara	2.14	1.16	3.50	3.76	5.19	6.74	0.00	0.00	6.18	1.62	0.00	0.00	0.00	5.19	0.00	7.97	0.00	3.50
	Oxycera trilineata	1.84	0.00	3.30	5.96	4.03	0.00	0.00	0.00	4.92	0.96	0.00	0.00	0.00	8.97	0.00	8.45	0.00	1.00
	Pachygaster atra	6.03	0.00	9.11	11.68	6.11	18.76	0.00	0.00	1.78	0.00	0.00	0.00	0.00	10.82	0.00	8.11	0.00	18.03
	Pachygaster leachii	4.58	0.00	10.57	6.74	0.00	8.31	0.00	0.00	5.88	0.00	0.00	0.00	0.00	4.14	0.00	1.73	3.40	15.45
	Stratiomys singularior	0.59	2.83	6.59	9.96	5.45	0.00	0.00	0.00	23.35	0.00	7.08	0.00	0.00	10.48	0.00	8.96	0.00	1.98
	Tabanus autumnalis	2.61	3.46	4.13	3.59	8.91	22.89	0.00	0.00	3.83	2.22	20.16	0.00	0.00	0.00	0.00	0.00	4.05	5.48
	Tabanus bromius	12.05	15.86	2.93	3.71	4.88	0.00	0.00	0.00	0.00	10.59	0.00	0.00	0.00	8.11	0.00	4.89	0.00	5.52
Spiders	*Achaearanea lunata*	10.38	3.24	1.48	2.44	0.00	0.00	0.00	0.00	0.00	3.14	0.00	0.00	0.00	1.76	0.00	0.00	0.00	0.91
	Agalenatea redii	4.82	5.52	4.96	6.12	11.84	13.09	19.54	0.00	0.00	14.05	0.00	0.00	16.30	2.22	0.00	3.49	0.00	2.49
	Agelena labyrinthica	9.17	16.51	10.81	7.57	15.26	0.00	0.00	1.72	1.05	18.44	1.30	0.00	0.00	15.53	12.80	9.32	11.68	2.27
	Agroeca brunnea	5.66	2.77	2.03	1.24	0.00	0.00	0.00	0.00	0.00	2.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17
	Anelosimus vittatus	16.90	5.94	9.69	9.79	7.33	4.54	0.00	0.00	0.00	8.12	0.00	0.00	5.88	9.49	31.36	3.57	2.47	4.90
	Clubiona corticalis	4.13	3.75	1.41	2.87	2.15	0.00	0.00	0.00	10.99	0.81	0.00	0.00	0.00	0.00	0.00	1.91	0.00	3.87
	Clubiona pallidula	3.85	1.49	3.55	2.52	1.66	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.58	0.00	0.00	0.00	1.96
	Clubiona subtilis	1.43	0.99	1.96	1.72	8.11	0.00	0.00	0.00	11.03	6.10	2.26	0.00	0.00	3.51	0.00	10.27	5.22	0.41

Spiders	*Crustulina guttata*	1.42	3.54	1.31	0.50	0.00	7.82	0.00	19.74	0.00	7.89	4.55	0.00	0.00	2.27	0.00	8.90	0.00	0.22
	Diaea dorsata	8.86	11.56	0.90	1.65	2.55	4.17	0.00	0.00	1.05	1.23	0.00	0.00	0.00	0.00	0.00	0.75	0.00	0.32
	Dictyna latens	5.75	1.99	5.09	4.38	8.99	0.00	0.00	0.00	0.00	10.65	0.00	0.00	12.48	0.00	0.00	1.78	0.00	2.70
	Dictyna uncinata	9.19	1.43	19.25	12.53	6.57	17.97	0.00	2.96	2.37	2.20	0.00	0.00	20.49	26.73	0.00	4.29	12.66	8.18
	Enoplognatha latimana	6.80	22.42	12.52	12.60	13.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.79	7.37	11.49
	Enoplognatha thoracica	4.04	1.47	2.29	5.22	9.75	0.00	0.00	3.38	0.00	3.37	0.00	0.00	6.25	0.00	0.00	13.95	3.55	2.27
	Gibbaranea gibbosa	4.45	4.05	2.25	2.78	0.00	0.00	0.00	0.00	0.00	4.23	0.00	0.00	0.00	0.00	0.00	0.00	3.02	0.71
	Hylyphantes graminicola	4.56	3.32	2.94	3.09	3.97	5.53	0.00	0.00	2.20	4.09	0.00	0.00	0.00	6.81	0.00	0.88	2.96	0.00
	Larinioides sclopetarius	0.34	0.00	1.97	1.04	0.80	4.78	0.00	0.00	0.00	0.00	0.00	0.00	3.07	23.42	0.00	0.67	2.09	2.26
	Lathys humilis	8.65	4.26	1.71	4.60	1.74	0.00	0.00	0.00	2.12	6.81	0.00	0.00	5.01	4.35	24.71	1.69	0.00	3.78
	Mangora acalypha	4.64	9.28	1.26	2.09	10.73	0.00	0.00	0.00	0.00	28.19	0.00	0.00	0.00	0.00	13.19	1.69	0.00	0.74
	Microlinyphia impigra	0.94	0.00	1.68	3.19	0.83	0.00	0.00	0.00	13.86	0.00	0.00	0.00	0.00	9.94	0.00	1.67	0.00	0.11
	Misumena vatia	8.00	10.87	3.59	4.44	1.44	0.00	0.00	0.00	1.15	2.67	0.00	0.00	0.00	0.00	10.26	0.00	3.18	7.53
	Neoscona adianta	3.14	7.21	8.43	10.21	15.69	0.00	15.66	0.00	0.00	14.38	30.56	0.00	9.31	0.00	0.00	9.89	19.95	4.08
	Ozyptila praticola	2.49	2.37	4.55	4.16	0.00	0.00	0.00	0.00	17.70	1.07	0.00	0.00	9.07	4.34	0.00	1.92	0.00	4.78
	Ozyptila simplex	1.99	0.00	4.59	4.66	10.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.81	0.00	6.68	4.98	1.31
	Pardosa prativaga	17.32	6.23	23.17	16.12	5.69	27.73	0.00	1.71	34.07	1.25	4.65	0.00	33.25	19.30	0.00	11.99	20.73	6.65
	Philodromus albidus	14.39	1.92	5.57	9.76	1.80	0.00	0.00	0.00	0.00	2.30	0.00	0.00	25.56	10.94	0.00	0.00	0.00	3.17
	Philodromus dispar	11.56	8.00	6.44	5.94	1.30	0.00	6.61	0.00	0.00	1.59	0.00	0.00	9.90	4.57	25.75	2.87	0.00	8.99
	Philodromus praedatus	8.21	7.91	2.54	7.67	2.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.14

Spiders	*Phrurolithus festivus*	2.98	1.70	3.57	3.34	5.11	0.00	0.00	0.00	0.00	1.26	0.00	0.00	5.60	7.06	0.00	17.32	8.03	6.78
	Pocadicnemis juncea	8.00	1.95	9.50	8.46	5.94	13.94	0.00	1.31	18.35	0.85	4.79	0.00	0.00	11.27	11.28	19.21	12.93	3.82
	Porrhomma microphthalmum	7.18	2.12	5.11	5.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.36	3.93	0.00	7.69	9.05	1.85
	Simitidion simile	2.72	4.72	2.19	1.37	3.82	0.00	7.71	0.00	0.00	16.42	0.00	0.00	5.64	0.00	0.00	2.56	0.00	0.35
	Tegenaria silvestris	5.00	4.34	1.32	0.64	2.08	0.00	0.00	3.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.25
	Thanatus striatus	0.29	0.00	1.35	3.77	8.98	0.00	0.00	0.00	2.41	3.84	0.00	0.00	0.00	3.02	0.00	21.66	16.40	0.00
	Theridion pictum	0.81	0.75	1.18	2.11	0.00	15.42	0.00	0.00	4.29	1.69	2.14	0.00	0.00	11.50	0.00	0.00	0.00	0.42
	Theridion tinctum	10.72	8.42	3.62	5.39	2.46	4.21	0.00	0.00	0.00	12.63	0.00	0.00	28.15	10.27	0.00	0.71	2.84	9.48
	Xysticus kochi	1.98	2.77	2.76	9.28	7.78	0.00	0.00	0.00	0.00	2.10	0.00	0.00	21.09	0.00	20.53	19.70	5.07	5.26
	Zilla diodia	9.75	13.00	4.35	4.15	8.66	0.00	0.00	0.00	0.00	5.13	0.00	0.00	0.00	0.00	0.00	1.52	4.06	1.39
Wasps	*Ammophila pubescens*	5.70	20.27	3.87	0.75	12.78	0.00	0.00	0.00	0.00	32.70	0.00	0.00	20.91	0.00	0.00	8.45	0.00	0.95
	Caliadurgus fasciatellus	8.10	4.69	3.70	3.25	10.05	0.00	0.00	0.00	0.00	6.36	0.00	0.00	0.00	0.00	0.00	5.08	0.00	3.40
	Cerceris arenaria	15.98	47.59	11.24	11.24	31.63	0.00	0.00	0.00	0.00	23.09	0.00	0.00	19.24	31.18	41.05	24.26	17.08	11.71
	Cerceris ruficornis	2.29	15.61	1.51	2.78	6.36	0.00	0.00	0.00	0.00	21.66	0.00	0.00	0.00	0.00	0.00	4.33	0.00	0.90
	Cerceris rybyensis	21.19	26.90	19.29	26.82	35.63	71.87	22.96	0.00	8.62	29.57	0.00	0.00	0.00	23.65	0.00	32.47	16.59	19.63
	Crossocerus cetratus	13.82	1.89	6.10	9.72	0.00	26.64	0.00	0.00	0.00	5.33	0.00	0.00	0.00	0.00	0.00	4.49	0.00	0.85
	Episyron rufipes	3.08	21.02	9.55	3.73	12.72	0.00	0.00	0.00	0.00	12.52	0.00	0.00	17.31	0.00	0.00	32.99	24.49	2.88
	Evagetes crassicornis	8.13	25.18	10.60	7.80	25.21	0.00	0.00	0.00	0.00	9.04	0.00	0.00	0.00	0.00	0.00	8.75	23.76	1.27
	Hedychridium ardens	3.33	26.90	12.06	4.06	13.05	0.00	0.00	0.00	0.00	9.47	0.00	0.00	0.00	12.48	0.00	18.73	0.00	2.53
	Oxybelus uniglumis	13.57	18.98	19.80	12.30	22.87	0.00	0.00	61.84	0.00	21.82	0.00	0.00	0.00	8.29	35.08	35.90	23.11	7.33
	Passaloecus gracilis	6.66	7.36	0.00	5.87	5.07	0.00	0.00	0.00	0.00	8.98	0.00	0.00	0.00	0.00	0.00	7.01	0.00	13.59

	Priocnemis pusilla	6.22	8.86	4.15	6.68	16.33	0.00	0.00	100.00	0.00	4.04	0.00	0.00	0.00	0.00	0.00	6.88	0.00	0.68
Woodlice	*Armadillidium depressum*	1.51	0.00	0.95	3.15	5.74	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.80	1.40	0.00	18.67
	Armadillidium nasatum	1.75	3.08	1.16	1.31	10.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.89	12.53	35.06	5.51
	Haplophthalmus danicus	13.35	3.76	4.68	1.96	8.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.10	0.00	3.71
	Ligidium hypnorum	19.15	0.00	1.68	1.10	2.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42
	Platyarthrus hoffmannseggii	4.62	6.08	3.68	5.55	14.34	0.00	9.58	8.32	0.00	0.00	0.00	0.00	61.39	2.50	32.51	17.24	20.95	9.16

Appendix Chapter 4

Table A4.1. Results of the best model explaining the inter-annual distribution-abundance relationship. Two outlying species, *Celastrina argiolus* and *Vanessa cardui* were excluded from this analysis. One biogeographical attribute was included as an explanatory variable: mean absolute year-to- year change in distribution records. PGLS model results: $\lambda = 0.049$, $R^2 = 0.43$, $F_{1,28} = 20.86$, AIC = -31.11, P =<0.001.

Coefficients	Estimate	Std. Error	t value	P
Intercept	-0.206	0.119	-1.739	0.093
Mean absolute year-to-year change in distribution records	4.702	1.029	4.567	<0.001

Table A4.2. Results of two models examining the relationship between dispersal ability and the inter-annual distribution-abundance relationship. The explanatory variable in Model 1 is a dispersal ranking from Cowley et al. (2001), PGLS model results: $\lambda = 0.904$, $R^2 = 0.13$, $F_{1,26} = 3.776$, AIC= -17.52, P = 0.063; and the explanatory variable in Model 2 is a dispersal score from (Dennis *et al.* 2004) PGLS model results: $\lambda = 0.874$, $R^2 = 0.08$, $F_{1,26} = 2.119$, AIC = -15.78, P =<0.157.

Model	Coefficients	Estimate	Std. Error	t value	P
1	*Intercept*	0.13	0.12	1.04	0.31
	Mobility ranking (Cowley et al.)	0.01	0.004	1.94	0.06
2	*Intercept*	0.20	0.11	1.75	0.09
	Mobility score (Dennis et al.)	0.03	0.02	1.46	0.16

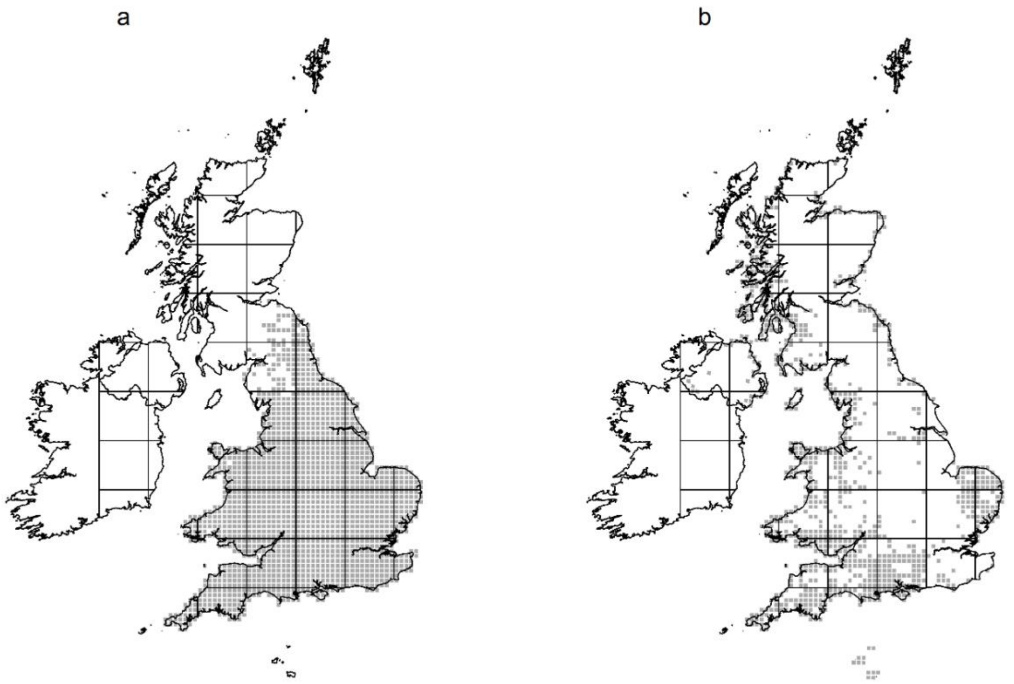

Figure A4.1. The ranges of a) the small skipper butterfly, *Thymelicus sylvestris*, a species with a well-filled range (fractal dimension: 0.257), and b) the Grayling butterfly, *Hipparchia semele*, a species with the most minimally filled range of the 33 species studied (fractal dimension: 0.716).

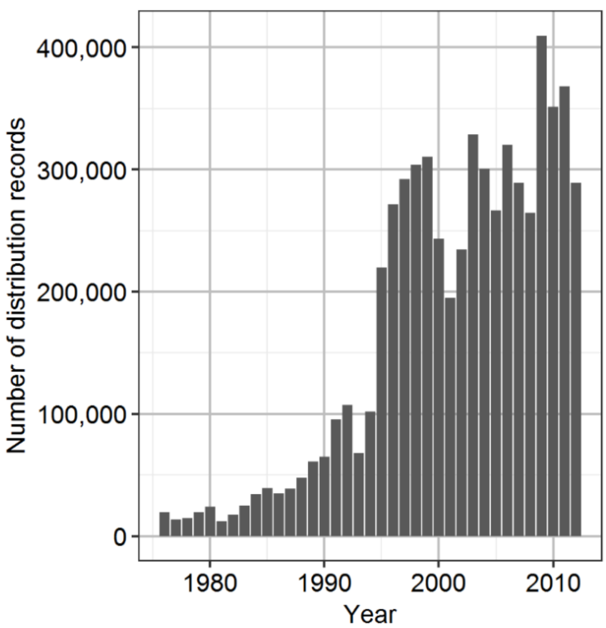

Figure A4.2. The annual total number of distribution records for all 33 study butterfly species across the study period 1972–2012.

References

Altermatt, F. (2010). Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1281–1287.

Amano, T., Lamming, J.D.L. & Sutherland, W.J. (2016). Spatial gaps in global biodiversity information and the role of citizen science. *BioScience*, **66**, 393–400.

Andrew, N.R., Hart, R.A., Jung, M.P., Hemmings, Z. & Terblanche, J.S. (2013). Can temperate insects take the heat? A case study of the physiological and behavioural responses in a common ant, *Iridomyrmex purpureus* (Formicidae), with potential climate change. *Journal of Insect Physiology*, **59**, 870–880.

Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J. & Chunco, A.J. (2011). Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, **14**, 677–689.

Araújo, M.B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P.A., Valladares, F. & Chown, S.L. (2013). Heat freezes niche evolution. *Ecology Letters*, **16**, 1206–1219.

Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006). Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, **33**, 1712–1728.

Auffret, A.G., Berg, J. and Cousins, S.A. (2014). The geography of human-mediated dispersal. *Diversity and Distributions*, **20**, 1450–1456.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V.M., Turlure, C. (2013) Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, **88**, 310–326.

Balmer, D.E., Gillings, S., Caffrey, B.J., Swann, R.L., Downie, I.S. & Fuller, R.J. (2014). *Bird Atlas 2007-11: the breeding and wintering birds of Britain and Ireland*. BTO Books, Thetford.

Bates, A.E., Bird, T.J., Stuart-Smith, R.D., Wernberg, T., Sunday, J.M., Barrett, N.S., Edgar, G.J., Frusher, S., Hobday, A.J., Pecl, G.T., & Smale, D.A. (2014). Distinguishing geographical range shifts from artefacts of detectability and sampling effort. *Diversity and Distributions*, **21**, 13–22.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. *Journal of Statistical Software*, **67**, 1–48.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2013). lme4: Linear mixed-effects models using Eigen and S4. *R package version,* **1**, 1–23.

Beckmann, B.C., Purse, B. V., Roy, D.B., Roy, H.E., Sutton, P.G. & Thomas, C.D. (2015). Two species with an unusual combination of traits dominate responses of British grasshoppers and crickets to environmental change. *PLOS ONE*, **10**, 1–25.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.

Berthold, P., Helbig, A.J., Mohr, G. & Querner, U. (1992). Rapid microevolution of migratory behaviour in a wild bird species. *Nature*, **6405**, 668–670.

Boakes, E.H., McGowan, P.J.K., Fuller, R.A., Chang-Qing, D., Clark, N.E., O'Connor, K. & Mace, G.M. (2010). Distorted views of biodiversity: Spatial and temporal bias in species occurrence data. *PLOS Biology*, **8**, e1000385

Bradbury, R.B., Pearce-Higgins, J.W., Wotton, S.R., Conway, G.J. & Grice, P. V. (2011). The influence of climate and topography in patterns of territory establishment in a range-expanding bird. *Ibis*, **153**, 336–344.

Brereton, T. (1998). Pearl-bordered fritillary national survey: 1998 update. *Butterfly Conservation News*, **69.**

Brereton, T., Roy, D.B., Middlebrook, I., Botham, M. & Warren, M. (2011). The development of butterfly indicators in the United Kingdom and assessments in 2010. *Journal of Insect Conservation*, **15**, 139–151.

Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T. & Guisan, A. (2007). Evidence of climatic niche shift during biological invasion. *Ecology Letters*, **10**, 701–709.

Brooks, S.J., Self, A., Powney, G.D., Pearse, W.D., Penn, M. & Paterson, G.L.J. (2016) The influence of life history traits on the phenological response of British butterflies to climate variability since the late-19th century. *Ecography*, **40**, 1152-1165.

Brown, J.H. (1984). On the relationship between abundance and distribution of species. *The American Naturalist*, **124**, 255–279.

Brown, J.H. (2014). Why are there so many species in the tropics? *Journal of Biogeography*, **41**, 8–22.

Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995). Spatial variation in abundance. *Ecology*, **76**, 2028–2043.

Brown, J.H., Stevens, G.C., Kaufman, D.M. (1996). The geographic range: size, shape, boundaries, structure and internal. *Annual Review of Ecology and Systematics*, **27**, 597–623.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media.

Burns, F., Eaton, M.A., Barlow, K.E., Beckmann, B.C., Brereton, T., Brooks, D.R., Brown, P.M.J., Al Fulaij, N., Gent, T., Henderson, I., Noble, D.G., Parsons, M., Powney, G.D., Roy, H.E., Stroh, P., Walker, K., Wilkinson, J.W., Wotton, S.R. & Gregory, R.D. (2016). Agricultural management and climatic change are the major drivers of biodiversity change in the UK. *PLOS ONE*, **11**, e0151595.

Cai, W., Borlace, S., Lengaigne, M., van Rensch, P., Collins, M., Vecchi, G., Timmermann, A., Santoso, A., McPhaden, M.J., Wu, L., England, M.H., Wang, G., Guilyardi, E. & Jin, F.-F. (2014). Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change*, **4**, 111–116.

Carroll, M.J., Heinemeyer, A., Pearce-Higgins, J.W., Dennis, P., West, C., Holden, J., Wallage, Z.E. and Thomas, C.D. (2015). Hydrologically driven ecosystem processes determine the distribution and persistence of ecosystem-specialist predators under climate change. *Nature Communications*, **6**, 1-10.

Cham, S., Nelson, B., Parr, A., Prentice, S., Smallshire, D. & Taylor, P. (2014). *Atlas of Dragonflies in Britain and Ireland*. Field Studies Council, Telford.

Chandler, M., See, L., Copas, K., Bonde, A.M.Z., López, B.C., Danielsen, F., Legind, J.K., Masinde, S., Miller-Rushing, A.J., Newman, G., Rosemartin, A. & Turak, E. (2017).

Contribution of citizen science towards international biodiversity monitoring. *Biological Conservation*, **213**, 280–294.

Chapman, A.D. (2009). *Numbers of Living Species in Australia and the World, 2nd Ed.* Report for the Australian Biological Resources Study, Canberra, 1–19.

Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B. & Sheldon, B.C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, **320**, 800–803.

Chen, I.-C., Hill, J.K., Ohlemuller, R., Roy, D.B. & Thomas, C.D. (2011a). Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.

Chen, I.-C., Hill, J.K., Shiu, H.-J., Holloway, J.D., Benedick, S., Chey, V.K., Barlow, H.S. & Thomas, C.D. (2011b). Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. *Global Ecology and Biogeography*, **20**, 34–45.

Chen, I.-C., Shiu, H., Benedick, S., Holloway, J.D., Khen, V., Barlow, H.S., Hill, J.K. & Thomas, C.D. (2009). Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences*, **106**, 1479–1483.

Chevin, L.-M. & Hoffmann, A.A. (2017). Evolution of phenotypic plasticity in extreme environments. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **372**, 20160138.

Christidis, N., Stott, P.A., Hegerl, G.C. & Betts, R.A. (2013). The role of land use change in the recent warming of daily extreme temperatures. *Geophysical Research Letters*, **40**, 589–594.

Clavero, M., Villero, D. & Brotons, L. (2011). Climate change or land use dynamics: Do we know what climate change indicators indicate? *PLOS ONE*, **6**, e18581.

Comte, L. & Grenouillet, G. (2013). Do stream fish track climate change? Assessing distribution shifts in recent decades. *Ecography*, **36**, 1236–1246.

Cowley, M.J., Thomas, C.D. & Roy, D.B. (2001). Density-distribution relationships in British butterflies. I. The effect of mobility and spatial scale. *Journal of Animal Ecology*, **70**, 410–425.

Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T. and Mynsberge, A.R. (2011). Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, **331**, 324-327.

Daszak, P., Cunningham, A.A. & Hyatt, A.D. (2003). Infectious disease and amphibian population declines. *Diversity and Distributions*, **9**, 141–150.

Davies, Z.G., Wilson, R.J., Coles, S. & Thomas, C.D. (2006). Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology*, **75**, 247–256.

Davis, M.B. & Shaw, R.G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, **292**, 673–679.

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.M. (2011). Beyond predictions: biodiversity conservation in a changing climate. *Science*, **332**, 53–58.

Dennis, R.L. (2012). *A resource-based habitat view for conservation: butterflies in the British landscape.* John Wiley & Sons.

Dennis, R.L.H., Hodgson, J.G., Grenyer, R., Shreeve, T.G. & Roy, D.B. (2004). Host plants and butterfly biology. Do host-plant strategies drive butterfly status? *Ecological Entomology*, **29**, 12–26.

Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. (2008). Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2743–2748.

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., Wynhoff, I. & Jiguet, F. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, **2**, 121–124.

Devictor, V., Whittaker, R.J. & Beltrame, C. (2010). Beyond scarcity: citizen science programmes as useful tools for conservation biogeography. *Diversity and Distributions*, **16**, 354–362.

Dickinson, M.G., Orme, C.D.L., Suttle, K.B. & Mace, G.M. (2014). Separating sensitivity from exposure in assessing extinction risk from climate change. *Scientific Reports*, **4**, 6898.

Dyer, R.J., Gillings, S., Pywell, R.F., Fox, R., Roy, D.B. & Oliver, T.H. (2017). Developing a biodiversity-based indicator for large-scale environmental assessment: a case study of proposed shale gas extraction sites in Britain. *Journal of Applied Ecology*, **54**, 872–882.

Easterling, D.R. (2000). Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068–2074.

Ehrlen, J. & Morris, W.F. (2015). Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters*, **18**, 303–314.

European Environment Agency. (2015). *The State of Nature in the European Union: Results from reporting under the nature directives 2007–2012*. EEA Technical report No. 2/2015.

Foden, W.B., Butchart, S.H.M., Stuart, S.N., Vié, J.C., Akçakaya, H.R., Angulo, A., DeVantier, L.M., Gutsche, A., Turak, E., Cao, L., Donner, S.D., Katariya, V., Bernard, R., Holland, R.A., Hughes, A.F., O'Hanlon, S.E., Garnett, S.T., Şekercioğlu, Ç.H. & Mace, G.M. (2013). Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLOS ONE*, **8**, e65427.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005). Global consequences of land use. *Science*, **309**, 570–574.

Forrest, J.R. (2016). Complex responses of insect phenology to climate change. *Current Opinion in Insect Science*, **17**, 49–54.

Fourcade, Y. & Öckinger, E. (2017). Host plant density and patch isolation drive occupancy and abundance at a butterfly's northern range margin. *Ecology and Evolution*, **7**, 331–345.

Fox, R., Brereton, T.M., Asher, J., August, T.A., Botham, M.S., Bourn, N.A.D., Cruickshanks, K.L., Bulman, C.R., Ellis, S., Harrower, C.A., Middlebrook, I., Noble, D.G., Powney, G.D., Randle, Z., Warren, M.S., Roy, D.B., Brereton, T.M., Asher, J., August, T.A., Botham, M.S., Bourn, N.A.D., Cruickshanks, K.L., Bulman, C.R., Ellis, S., Harrower, C.A., Middlebrook, I., Noble, D.G., Powney, G.D., Randle, Z., Warren, M.S. & Roy, D.B. (2015). *The State of the UK's Butterflies 2015.* Wareham, Dorset, UK.

Fox, J.A., Brereton, T.M., Asher, J., Botham, M.S., Middlebrook, I., Roy, D.B. & Warren, M.S. (2011). *The State of the UK's Butterflies 2011*. Butterfly Conservation and the Centre for Ecology and Hydrology, Wareham, Dorset, UK.

Fox, R., Oliver, T.H., Harrower, C., Parsons, M.S., Thomas, C.D. & Roy, D.B. (2014). Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *Journal of Applied Ecology*, **51**, 949–957.

Fox, R., Parsons, M., Chapman, J., Woiwod, I.P., Warren, M.S. & Brooks, D.R. (2013). *The state of Britain's larger moths 2013*. Wareham, Dorset, UK.

Franco, A.M.A., Hill, J.K., Kitschke, C., Collingham, Y.C., Roy, D.B., Fox, R., Huntley, B. & Thomas, C.D. (2006). Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology*, **12**, 1545–1553.

Frishkoff, L.O., Karp, D.S., Flanders, J.R., Zook, J., Hadly, E.A., Daily, G.C., M'Gonigle, L.K. & Haddad, N. (2016). Climate change and habitat conversion favour the same species. *Ecology Letters*, **19**, 1081–1090.

Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D. & Carter, N. (1995). Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology*, **9**, 1425–1441.

Gallinat, A.S., Primack, R.B. & Wagner, D.L. (2015). Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution*, **30**, 169–176.

Gandiwa, E., Heitkonig, I.M.A., Eilers, P.H.C. & Prins, H.H.T. (2016). Rainfall variability and its impact on large mammal populations in a complex of semi-arid African savanna protected areas. *Tropical Ecology*, **57**, 163–180.

García-Valdés, R., Svenning, J.-C., Zavala, M. A., Purves, D.W. & Araújo, M.B. (2015). Evaluating the combined effects of climate and land-use change on tree species distributions. *Journal of Applied Ecology*, **52**, 902–912.

Gaston, K.J. (2000). Global patterns in biodiversity. *Nature*, **405**, 220–227.

Gaston, K.J. (1996). The multiple forms of the interspecific abundance-distribution relationship. *Oikos*, **76**, 211–220.

Gaston, K.J., Blackburn, T.M., Greenwood, J.D., Gregory, R.D., Quinn, R.M. & Lawton, J.H. (2000). Abundance-occupancy relationships. *Journal of Applied Ecology*, **37**, 39–59.

Geldmann, J., Heilmann-Clausen, J., Holm, T.E., Levinsky, I., Markussen, B., Olsen, K., Rahbek, C. & Tøttrup, A.P. (2016). What determines spatial bias in citizen science? Exploring four recording schemes with different proficiency requirements. *Diversity and Distributions*, **22**, 1139–1149.

Gibbons, D.W., Reid, J.B. & Chapman, R.A. (1993). *The new atlas of breeding birds in Britain and Ireland: 1988-1991*. T & AD Poyser, London.

Gienapp, P., Teplitsky, C., Alho, J.S., Mills, J.A. & Merilä, J. (2008). Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology*, **17**, 167–178.

Gillingham, P.K., Bradbury, R.B., Roy, D.B., Anderson, B.J., Baxter, J.M., Bourn, N.A.D., Crick, H.Q.P., Findon, R.A., Fox, R., Franco, A., Hill, J.K., Hodgson, J.A., Holt, A.R., Morecroft, M.D., O'Hanlon, N.J., Oliver, T.H., Pearce-Higgins, J.W., Procter, D.A., Thomas, J.A., Walker, K.J., Walmsley, C.A., Wilson, R.J. & Thomas, C.D. (2015). The effectiveness of protected areas in the conservation of species with changing geographical ranges. *Biological Journal of the Linnean Society*, **115**, 707–717.

Gillings, S., Balmer, D.E. & Fuller, R.J. (2015). Directionality of recent bird distribution shifts and climate change in Great Britain. *Global Change Biology*, **21**, 2155–2168.

Graham, L.J., Haines-Young, R.H. & Field, R. (2015). Using citizen science data for conservation planning: Methods for quality control and downscaling for use in stochastic patch occupancy modelling. *Biological Conservation*, **192**, 65–73.

Gregory, R.D., Willis, S.G., Jiguet, F., Voříšek, P., Klvaňová, A., van Strien, A., Huntley, B., Collingham, Y.C., Couvet, D. & Green, R.E. (2009). An indicator of the impact of climatic change on European bird populations. *PLOS ONE*, **4**, e4678.

Greven, S. and Kneib, T. (2010). On the behaviour of marginal and conditional AIC in linear mixed models. *Biometrika*, **97**, 773-789.

Hampe, A. & Petit, R.J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, **8**, 461–467.

Hanski, I. (1999). *Metapopulation ecology*. Oxford University Press, New York.

Hanski, I. and Mononen, T. (2011). Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. *Ecology Letters*, **14**, 1025-1034.

Hartley, S. (1998). A positive relationship between local abundance and regional occupancy is almost inevitable (but not all positive relationships are the same). *Journal of Animal Ecology*, **67**, 992–994.

Hayhow, D.B., Burns, F., Eaton, M.A., Al Fulaij, N., August, T.A., Babey, L., Bacon, L., Bingham, C., Boswell, J., Boughey, K.L., Brereton, T., Brookman, E., Brooks, D.R., Bullock, D.J., Burke, O., Collis, M., Corbet, L., Cornish, N., De Massimi, S., Densham, J., Dunn, E., Elliott, S., Gent, T., Godber, J., Hamilton, S., Havery, S., Hawkins, S., Henney, J., Holmes, K., Hutchinson, N., Isaac, N.J.B., Johns, D., Macadam, C.R., Mathews, F., Nicolet, P., Noble, D.G., Outhwaite, C.L., Powney, G.D., Richardson, P., Roy, D.B., Sims, D., Smart, S., Stevenson, K., Stroud, R.A., Walker, K.J., Webb, J.R., Webb, T.J., Wynde, R. & Gregory, R.D. (2016). *The State of Nature*. The State of Nature partnership.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006). The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.

Hickling, R., Roy, D.B., Hill, J.K. & Thomas, C.D. (2005). A northward shift of range margins in British Odonata. *Global Change Biology*, **11**, 502–506.

Hill, M.O. (2012). Local frequency as a key to interpreting species occurrence data when recording effort is not known. *Methods in Ecology and Evolution*, **3**, 195–205.

Hill, J.K., Collingham, Y.C., Thomas, C.D., Blakeley, D.S., Fox, R., Moss, D. & Huntley, B. (2001). Impacts of landscape structure on butterfly range expansion. *Ecology Letters*, **4**, 313–321.

Hill, J.K., Griffiths, H.M. & Thomas, C.D. (2011). Climate change and evolutionary adaptations at species' range margins. *Annual Review of Entomology*, **56**, 143–59.

Hill, M.O. & Preston, C.D. (2015). Disappearance of boreal plants in southern Britain: habitat loss or climate change? *Biological Journal of the Linnean Society*, **115**, 598–610.

Hill, J.K., Thomas, C.D., Fox, R., Telfer, M.G., Willis, S.G., Asher, J. & Huntley, B. (2002). Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 2163–2171.

Hochkirch, A., & Damerau, M. (2009). Rapid range expansion of a wing-dimorphic bush-cricket after the 2003 climatic anomaly. *Biological Journal of the Linnean Society*, **97**, 118-127.

Hodgson, J.C., Baylis, S.M., Mott, R., Herrod, A. & Clarke, R.H. (2016a). Precision wildlife monitoring using unmanned aerial vehicles. *Scientific Reports*, **6**, 22574

Hodgson, J.A., Thomas, C.D., Dytham, C., Travis, J.M.J. & Cornell, S.J. (2012). The speed of range shifts in fragmented landscapes. *PLOS ONE*, **7**, e47141.

Hodgson, J.A., Wallis, D.W., Krishna, R. & Cornell, S.J. (2016b). How to manipulate landscapes to improve the potential for range expansion. *Methods in Ecology and Evolution*, **7**, 1558–1566.

Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P. & Thomas, C.D. (2008). Assisted colonization and rapid climate change. *Science*, **321**, 345–346.

Hollis, D., McCarthy, M. (2017) UKCP09: Met Office gridded and regional land surface climate observation datasets. *UK Met Office, Centre for Environmental Data Analysis*, (available at http://catalogue.ceda.ac.uk/uuid/87f43af9d02e42f483351d79b3d6162a).

Holt, R.D. (2009). Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences*, **106**, 19659–19665.

Holt, R.D., Lawton, J.H., Gaston, K.J. & Blackburn, T.M. (1997). On the relationship between range size and local abundances: back to the basics. *Oikos*, **78**, 183–190.

Holyoak, M. & Heath, S.K. (2016). The integration of climate change, spatial dynamics, and habitat fragmentation: A conceptual overview. *Integrative Zoology*, **11**, 40–59.

Howard, C., Stephens, P.A., Pearce-Higgins, J.W., Gregory, R.D. & Willis, S.G. (2015). The drivers of avian abundance: patterns in the relative importance of climate and land use. *Global Ecology and Biogeography*, **24**, 1249–1260.

Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M. & Williams, S.E. (2012). Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 1665–1679.

Hughes, L. (2000). Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution*, **15**, 56–61.

Huntley, B., Collingham, Y.C., Willis, S.G. & Green, R.E. (2008). Potential impacts of climatic change on European breeding birds. *PLOS ONE*, **3**, e1439.

Hutchinson, G.E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.

Inchausti, P. & Halley, J. (2003). On the relation between temporal variability and time in animal populations persistence. *Journal of Animal Ecology*, **72**, 899–908.

IPCC. (2014a). *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (V.R., Barros, C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea & L.L. White, Eds.). Cambridge University Press, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

IPCC. (2014b). *Climate Change 2014: Mitigation of Climate Change. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York, NY, USA.

IPCC. (2013). *Working Group I Contribution to the IPCC Fifth Assessment Report (AR5), Climate Change 2013: The Physical Science Basis*. Geneva, Switzerland.

Isaac, N.J.B. & Pocock, M.J.O. (2015). Bias and information in biological records. *Biological Journal of the Linnean Society*, **115**, 522–531.

Isaac, N.J.B., van Strien, A.J., August, T.A., de Zeeuw, M.P. & Roy, D.B. (2014). Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution*, **5**, 1052–1060.

IUCN/SSC. (2013). *Guidelines for Reintroductions and Other Conservation Translocations. Version 1.0.* Gland, Switzerland: IUCN Species Survival Commission.

Jackson, S.T., Webb, R.S., Anderson, K.H., Overpeck, J.T., Webb III, T., Williams, J.W. & Hansen, B.C.S. (2000). Vegetation and environment in Eastern North America during the Last Glacial Maximum. *Quaternary Science Reviews*, **19**, 489–508.

Jantz, S.M., Barker, B., Brooks, T.M., Chini, L.P., Huang, Q., Moore, R.M., Noel, J. & Hurtt, G.C. (2015). Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation. *Conservation Biology*, **29**, 1122–1131.

Jenkins, G.J., Perry, M.C. & Prior, M.J. (2008). *The climate of the UK and recent trends*. Met Office Hadley Centre, Exeter, UK.

Jetz, W., Wilcove, D.S. & Dobson, A.P. (2007). Projected impacts of climate and land-use change on the global diversity of birds. *PLOS Biology*, **5**, 1211–1219.

Jiguet, F., Brotons, L. & Devictor, V. (2011). Community responses to extreme climatic conditions. *Current Zoology*, **57**, 406–413.

Julliard, R., Clavel J., Devictor, V., Jiguet, F., Couvet, D. (2006) Spatial segregation of specialists and generalists in bird communities. *Ecology Letters*, **9**, 1237–1244.

Kaisila, J. (1962). Immigration und expansion der Lepidopteren in Finnland in den jahren 1869-1960. *ACTA Entomologica Fennica*, **18**, 1–452.

Kamp, J., Oppel, S., Heldbjerg, H., Nyegaard, T. & Donald, P.F. (2016). Unstructured citizen science data fail to detect long-term population declines of common birds in Denmark. *Diversity and Distributions*, **22**, 1–12.

Karl, T.T.R. & Trenberth, K.E. (2003). Modern global climate change. *Science*, **302**, 1719–1723.

Keeley, A.T.H., Beier, P., Keeley, B.W. & Fagan, M.E. (2017). Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. *Landscape and Urban Planning*, **161**, 90–102.

Kelly, A.E. & Goulden, M.L. (2008). Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11823–11826.

Kendon, E., Roberts, N. & Fowler, H. (2014). Heavier summer downpours with climate change revealed by weather forecast resolution model. *Nature Climate Change*, **4**, 1–7.

Kingsolver, J.G. (1989). Weather and the population dynamics of insects: integrating physiological and population ecology. *Physiological Zoology*, **62**, 314–334.

Knape, J. & de Valpine, P. (2011). Effects of weather and climate on the dynamics of animal population time series. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 985–992.

Kujala, H., Vepsäläinen, V., Zuckerberg, B. & Brommer, J.E. (2013). Range margin shifts of birds revisited - the role of spatiotemporally varying survey effort. *Global Change Biology*, **19**, 420–430.

Kullman, L. (2002). Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, **90**, 68–77.

Lahoz-Monfort, J.J., Guillera-Arroita, G. & Wintle, B.A. (2014). Imperfect detection impacts the performance of species distribution models. *Global Ecology and Biogeography*, **23**, 504–515.

Lawson, C.R., Bennie, J.J., Thomas, C.D., Hodgson, J.A. & Wilson, R.J. (2012). Local and landscape management of an expanding range margin under climate change. *Journal of Applied Ecology*, **49**, 552–561.

Lawton, J.H. (1993). Range, population abundance and conservation. *Trends in Ecology & Evolution*, **8**, 409–413.

Lemoine, N., Bauer, H.G., Peintinger, M. & Bohning-Gaese, K. (2007). Effects of climate and land-use change on species abundance in a central European bird community. *Conservation Biology*, **21**, 495–503.

Lenderink, G. & van Meijgaard, E. (2008). Increase in hourly precipitation extremes beyond expectations from temperature changes. *Nature Geoscience*, **1**, 511–514.

Lenoir, J., Gégout, J.C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N.E., Dullinger, S., Pauli, H., Willner, W. and Svenning, J.C. (2010). Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, **33**, 295-303.

Lenoir, J. & Svenning, J.-C. (2015). Climate-related range shifts - a global multidimensional synthesis and new research directions. *Ecography*, **38**, 15–28.

Lewis, J. & Vandewoude, S. (2015). The effects of urbanization on population density, occupancy, and detection probability of wild felids. *Ecological Applications*, **25**, 1880–1895.

Lhotka, O., Plavcová, E. & Kyselý, J. (2016). Record-breaking 2015 heat waves in Central Europe: how to view them in the climate change context? *EGU General Assembly Conference,* **18**, 7126.

Liang, Y., Duveneck, M.J., Gustafson, E.J., Serra-Diaz, J.M. and Thompson, J.R. (2017). How disturbance, competition and dispersal interact to prevent tree range boundaries from keeping pace with climate change. *Global Change Biology*, **24**, 1-17.

Lynam, C.P., Hay, S.J. & Brierley, A.S. (2004). Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. *Limnology and Oceanography*, **49**, 637–643.

Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J. & Stuart, S.N. (2008). Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, **22**, 1424–1442.

Maclean, I.M.D., Austin, G.E., Rehfisch, M.M., Blew, J., Crowe, O., Delany, S., Devos, K., Deceuninck, B., Günther, K., Laursen, K., Van Roomen, M. & Wahl, J. (2008). Climate change causes rapid changes in the distribution and site abundance of birds in winter. *Global Change Biology*, **14**, 2489–2500.

MacLean, S.A. & Beissinger, S.R. (2017). Species' traits as predictors of range shifts under contemporary climate change: a review and meta-analysis. *Global Change Biology*, **23**, 4094–4105.

Maes, D., Isaac, N.J.B., Harrower, C.A., Collen, B., Strien, A.J. & Roy, D.B. (2015). The use of opportunistic data for IUCN Red List assessments. *Biological Journal of the Linnean Society*, **115**, 690–706.

Mair, L., Hill, J.K., Fox, R., Botham, M., Brereton, T. & Thomas, C.D. (2014). Abundance changes and habitat availability drive species' responses to climate change. *Nature Climate Change*, **4**, 127–131.

Mair, L., Thomas, C.D., Anderson, B.J., Fox, R., Botham, M. & Hill, J.K. (2012). Temporal variation in responses of species to four decades of climate warming. *Global Change Biology*, **18**, 2439–2447.

Malinowska, A.H., Strien, A.J. Van, Verboom, J. & Wallisdevries, M.F. (2014). No evidence of the effect of extreme weather events on annual occurrence of four groups of ectothermic species. *PLOS ONE*, **9**, e110219.

Martay, B., Brewer, M.J., Elston, D.A., Bell, J.R., Harrington, R., Brereton, T.M., Barlow, K.E., Botham, M.S. & Pearce-Higgins, J.W. (2016). Impacts of climate change on national biodiversity population trends. *Ecography*, **40**, 1139–1151.

Mason, S.C., Hill, J.K., Thomas, C.D., Powney, G.D., Fox, R., Brereton, T. & Oliver, T.H. (2017). Population variability in species can be deduced from opportunistic citizen science records: A case study using British butterflies. *Insect Conservation and Diversity*. doi:10.1111/icad.12242

Mason, S.C., Palmer, G., Fox, R., Gillings, S., Hill, J.K., Thomas, C.D. and Oliver, T.H. (2015). Geographical range margins of many taxonomic groups continue to shift polewards. *Biological Journal of the Linnean Society*, **115**, 586-597.

McCain, C., Szewczyk, T. & Bracy Knight, K. (2016). Population variability complicates the accurate detection of climate change responses. *Global Change Biology*, **22**, 2081–2093.

McCarty, J.P. (2001). Ecological Consequences of Recent Climate Change. *Conservation Biology*, **15**, 320–331.

McGeoch, M.A. & Latombe, G. (2016). Characterizing common and range expanding species. *Journal of Biogeography*, **43**, 217–228.

McMahon, S.M., Harrison, S.P., Armbruster, W.S., Bartlein, P.J., Beale, C.M., Edwards, M.E., Kattge, J., Midgley, G., Morin, X. & Prentice, I.C. (2011). Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology & Evolution*, **26**, 249–259.

Menéndez, R., González-Megías, A., Jay-Robert, P. & Marquéz-Ferrando, R. (2014). Climate change and elevational range shifts: evidence from dung beetles in two European mountain ranges. *Global Ecology and Biogeography*, **23**, 646–657.

Menéndez, R., Megías, A.G., Hill, J.K., Braschler, B., Willis, S.G., Collingham, Y., Fox, R., Roy, D.B. & Thomas, C.D. (2006). Species richness changes lag behind climate change. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1465–1470.

Meyer, S., Robertson, B.C., Chilvers, B.L. & Krkošek, M. (2015). Population dynamics reveal conservation priorities of the threatened New Zealand sea lion *Phocarctos hookeri*. *Marine Biology*, **162**, 1587–1596.

Morecroft, M.D., Bealey, C.E., Beaumont, D.A., Benham, S., Brooks, D.R., Burt, T.P., Critchley, C.N.R., Dick, J., Littlewood, N.A., Monteith, D.T., Scott, W.A., Smith, R.I., Walmsley, C. & Watson, H. (2009). The UK Environmental Change Network: Emerging trends in the composition of plant and animal communities and the physical environment. *Biological Conservation*, **142**, 2814–2832.

Mortelliti, A., Sozio, G., Boccacci, F., Ranchelli, E., Cecere, J.G., Battisti, C. & Boitani, L. (2012). Effect of habitat amount, configuration and quality in fragmented landscapes. *Acta Oecologica*, **45**, 1–7.

Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R. and Simpson, I. (2011). *Final Report for LCM2007-the new UK land cover map*. Countryside Survey Technical Report No 11/07.

Murphy, J.M., Sexton, D.M.H., Jenkins, G.J., Boorman, P.M., Booth, B.B.B., Brown, C.C., Clark, R.T., Collins, M., Harris, G.R., Kendon, E.J., Betts, R.A., Brown, S.J., Howard, T.P., Humphrey, K.A., McCarthy, M.P., McDonald, R.E., Stephens, A. & Wallace, R.A. (2009). *UK Climate Projections Science Report: Climate change projections.* Met Office Hadley Centre, Exeter.

NOAA National Centers for Environmental Information. (2017). *State of the Climate: Global Climate Report for June 2017.* Published online July 2017, retrieved on September 1, 2017 from https://www.ncdc.noaa.gov/sotc/global/201706.

Noordwijk, A.J. Van, McCleery, R.H. & Perrins, C.M. (1995). Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *Journal of Animal Ecology*, **64**, 451-458.

Oliver, T.H., Brereton, T. & Roy, D.B. (2013). Population resilience to an extreme drought is influenced by habitat area and fragmentation in the local landscape. *Ecography*, **36**, 579–586.

Oliver, I., Dorrough, J., Doherty, H. & Andrew, N.R. (2016). Additive and synergistic effects of land cover, land use and climate on insect biodiversity. *Landscape Ecology*, **31**, 2415–2431.

Oliver, T.H., Gillings, S., Girardello, M., Rapacciuolo, G., Brereton, T.M., Siriwardena, G.M., Roy, D.B., Pywell, R. & Fuller, R.J. (2012). Population density but not stability can be predicted from species distribution models. *Journal of Applied Ecology*, **49**, 581–590.

Oliver, T., Hill, J.K., Thomas, C.D., Brereton, T. & Roy, D.B. (2009). Changes in habitat specificity of species at their climatic range boundaries. *Ecology Letters*, **12**, 1091–1102.

Oliver, T.H., Isaac, N.J.B., August, T.A., Woodcock, B.A., Roy, D.B. & Bullock, J.M. (2015a). Declining resilience of ecosystem functions under biodiversity loss. *Nature Communications*, **6**, 10122.

Oliver, T.H., Marshall, H.H., Morecroft, M.D., Brereton, T., Prudhomme, C. & Huntingford, C. (2015b). Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change*, **5**, 1–6.

Oliver, T.H. & Morecroft, M.D. (2014). Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. *Wiley Interdisciplinary Reviews: Climate Change*, **5**, 317–335.

Oliver, T.H., Thomas, C.D., Hill, J.K., Brereton, T. and Roy, D.B. (2012). Habitat associations of thermophilous butterflies are reduced despite climatic warming. *Global Change Biology*, **18**, 2720–2729.

Oreskes, N. (2005). The scientific consensus on climate change. *Science*, **306**, 1686-1686

Oxford University News. (2015) Published online May 2015, retrieved on February 11 2017 from http://www.ox.ac.uk/news/2015-05-15-oxford-receives-award-longest-running-weather-station-uk.

Pagel, J., Anderson, B.J., O'Hara, R.B., Cramer, W., Fox, R., Jeltsch, F., Roy, D.B., Thomas, C.D. & Schurr, F.M. (2014). Quantifying range-wide variation in population trends from local abundance surveys and widespread opportunistic occurrence records. *Methods in Ecology and Evolution*, **5**, 751–760.

Palmer, G., Brereton, T., Chapman, J.W., Dytham, C., Fox, R., Pearce-Higgins, J.W., Roy, D.B., Hill, J.K., & Thomas, C.D. (2017). Climate change, climatic variation, and extreme biological responses. *Philosophical transactions of the Royal Society of London, Series B: Biological Sciences*, **372**, 20160144.

Parker, D.E., Legg, T.P. & Folland, C.K. (1992). A new daily central England temperature series, 1772-1991. *International Journal of Climatology*, **12**, 317–342.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Pateman, R.M., Hill, J.K., Roy, D.B., Fox, R. & Thomas, C.D. (2012). Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. *Science*, **336**, 1028–1030.

Pateman, R.M., Thomas, C.D., Hayward, S.A.L. & Hill, J.K. (2016). Macro- and microclimatic interactions can drive variation in species' habitat associations. Global Change Biology, **22**, 556–566.

Pearce, J.L. & Boyce, M.S. (2006). Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology*, **43**, 405–412.

Pearman, P.B., Guisan, A., Broennimann, O. & Randin, C.F. (2008). Niche dynamics in space and time. *Trends in Ecology & Evolution*, **23**, 149–158.

Pescott, O. (2015). Ecological monitoring for citizen science: the design and implementation of schemes for plants in Britain and Ireland. *Biological Journal of the Linnean Society*, **115**, 505–521.

Pescott, O.L., Botham, M., Simkin, J., Dore, A.J., August, T.A. & Randall, Z. (2015). Air pollution and its effects on bryophytes, lichens and cryptogam-feeding Lepidoptera: review and evidence from biological records. *Biological Journal of the Linnean Society*, **115**, 611–635.

Petrovskii, S., Petrovskaya, N. & Bearup, D. (2014). Multiscale approach to pest insect monitoring: Random walks, pattern formation, synchronization, and networks. *Physics of Life Reviews*, **11**, 467–525.

Pimm, S.L., Jones, H. L. & Diamond, J. (1998). On the risk of extinction. *The American Naturalist*, **132**, 757–785.

Pironon, S., Villellas, J., Morris, W.F., Doak, D.F. & García, M.B. (2015). Do geographic, climatic or historical ranges differentiate the performance of central versus peripheral populations? *Global Ecology and Biogeography*, **24**, 611–620.

Pocock, M.J.O., Roy, H.E., Preston, C.D. & Roy, D.B. (2015). The Biological Records Centre: A pioneer of citizen science. *Biological Journal of the Linnean Society*, **115**, 475–493.

Pollard, E. (1988). Temperature, rainfall and butterfly numbers. *Journal of Applied Ecology*, **25**, 819–828.

Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F., Thompson, S.A. & Richardson, A.J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, **3**, 919–925.

Powney, G.D., Broaders, L.K. & Oliver, T.H. (2012). Towards a measure of functional connectivity: local synchrony matches small scale movements in a woodland edge butterfly. *Landscape Ecology*, **27**, 1109–1120.

Prendergast, J.R., Wood, S.N., Lawton, J.H. & Eversham, B.C. (1993). Correcting for variation in recording effort in analyses of diversity hotspots. *Biodiversity Letters*, **1**, 39–53.

Pulido, F. (2007). The genetics and evolution of avian migration. *BioScience*, **57**, 165–174.

Van der Putten, W.H., Macel, M., Visser, M.E. (2010). Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical transactions of the Royal Society of London, B: Biological Sciences*, **365**, 2025–2034.

R Core Team. (2017). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria* (available at https://www.r-project.org/).

R Core Team. (2013). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria* (available at https://www.r-project.org/).

Radinger, J., Hölker, F., Horký, P., Slavík, O., Dendoncker, N. & Wolter, C. (2016). Synergistic and antagonistic interactions of future land use and climate change on river fish assemblages. *Global Change Biology*, **22**, 1505–1522.

Ramankutty, N. & Foley, J.A. (1999). Estimating historical changes in global land cover: Croplands from 1700 to 1992. *Global Biogeochemical Cycles*, **13**, 997–1027.

Rannap, R., Lohmus, A., & Briggs, L. (2009). Restoring ponds for amphibians: a success story. *Hydrobiologia*, **634**, 87-95.

Rapacciuolo, G., Maher, S.P., Schneider, A.C., Hammond, T.T., Jabis, M.D., Walsh, R.E., Iknayan, K.J., Walden, G.K., Oldfather, M.F., Ackerly, D.D. & Beissinger, S.R. (2014). Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. *Global Change Biology*, **20**, 2841–2855.

Reif, J. & Flousek, J. (2012). The role of species' ecological traits in climatically driven altitudinal range shifts of central European birds. *Oikos*, **121**, 1053–1060.

Reif, J., Jiguet, F. & Šťastný, K. (2010). Habitat specialization of birds in the Czech Republic: comparison of objective measures with expert opinion. *Bird Study*, **57**, 197–212.

Robertson, G.S., Bolton, M., Morrison, P. & Monaghan, P. (2015). Variation in population synchrony in a multi-species seabird community: Response to changes in predator abundance. *PLOS ONE*, **10**, 1–15.

Robertson, P.A., Woodburn, M.I.A. & Hill, D.A. (1988). The effects of woodland management for pheasants on the abundance of butterflies in Dorset, England. *Biological Conservation*, **45**, 159–167.

Robillard, C.M., Coristine, L.E., Soares, R.N. and Kerr, J.T. (2015). Facilitating climate-change-induced range shifts across continental land-use barriers. *Conservation Biology*, **29**, 1586-1595.

Roney, N.E., Kuparinen, A. & Hutchings, J.A. (2015). Comparative analysis of abundance-occupancy relationships for species-at-risk at both broad taxonomic and spatial scales. *Canadian Journal of Zoology*, **93**, 515–519.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Rothery, P. & Roy, D.B. (2001). Application of generalized additive models to butterfly transect count data. *Journal of Applied Statistics*, **28**, 897–909.

Roy, D.B., Harding, P.T., Preston, C.D. & Roy, H.E. (eds.) (2014a). *Celebrating 50 years of the Biological Records Centre.*

Roy, H.E., Preston, C.D., Harrower, C.A., Rorke, S.L., Noble, D., Sewell, J., Walker, K., Marchant, J., Seeley, B., Bishop, J., Jukes, A., Musgrove, A. & Pearman, D. (2014b). GB Non-native Species Information Portal: documenting the arrival of non-native species in Britain. *Biological Invasions*, **16**, 2495–2505.

Roy, D.B., Rothery, P., Moss, D., Pollard, E. & Thomas, J.A. (2001). Butterfly numbers and weather: Predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology*, **70**, 201–217.

Sagarin, R.D., Gaines, S.D. & Gaylord, B. (2006). Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology & Evolution*, **21**, 524–530.

Sánchez-Hernández, J., Cobo, F. & Amundsen, P.A. (2015). A simple approach for assigning the conservation status of freshwater fish based on their natural variability - a case study from the Iberian Ecoregion. *Fisheries Management and Ecology*, **22**, 125–133.

Sänger, K., & Helfert, B. (1975) Spontanes Auftreten holopterer Formen von *Tessellana vittata* und *Metrioptera roeseli* (Orthoptera: Tettigoniidae) in Laborzuchten. *Anzeiger der österreichischen Akademie der Wissenschaften (Mathematisch-naturwissenschaftliche Klasse)* **11**, 192–194.

Saura, S., Bodin, Ö. & Fortin, M.J. (2014). Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, **51**, 171–182.

van Schaik, C.P. & van Noordwijk, M.A. (1985). Interannual variability in fruit abundance and the reproductive seasonality in Sumatran Long-tailed macaques (*Macaca fascularis*). *Journal of Zoology*, **206**, 533–549.

Schurr, F.M., Pagel, J., Cabral, J.S., Groeneveld, J., Bykova, O., O'Hara, R.B., Hartig, F., Kissling, W.D., Linder, H.P., Midgley, G.F., Schröder, B., Singer, A. & Zimmermann, N.E. (2012). How to understand species' niches and range dynamics: A demographic research agenda for biogeography. *Journal of Biogeography*, **39**, 2146–2162.

Schweiger, O., Heikkinen, R.K., Harpke, A., Hickler, T., Klotz, S., Kudrna, O., Kühn, I., Pöyry, J. & Settele, J. (2012). Increasing range mismatching of interacting species under global change is related to their ecological characteristics. *Global Ecology and Biogeography*, **21**, 88–99.

Seddon, P.J. (2010). From reintroduction to assisted colonization: moving along the conservation translocation spectrum. *Restoration Ecology*, **18**, 796–802.

Sekercioglu, C.H., Schneider, S.H., Fay, J.P. & Loarie, S.R. (2008). Climate change, elevational range shifts, and bird extinctions. *Conservation Biology*, **22**, 140–150.

Shackleton, N.J. (1987). Oxygen isotopes, ice volume and sea level. *Quaternary Science Reviews*, **6**, 183–190.

Sharrock, J.T.R. (1976). *The atlas of breeding birds in Britain and Ireland*. T & AD Poyser.

Simmons, A.D. & Thomas, C.D. (2004). Changes in dispersal during species' range expansions. *American Naturalist*, **164**, 378–395.

Simpson, R., Page, K.R. & De Roure, D. (2014). Zooniverse: observing the world's largest citizen science platform. *Proceedings of the 23rd International Conference on World Wide Web*, 1049–1054.

La Sorte, F.A. & Jetz, W. (2012). Tracking of climatic niche boundaries under recent climate change. *Journal of Animal Ecology*, **81**, 914–925.

Stanton, J.C., Shoemaker, K.T., Pearson, R.G. & Akçakaya, H.R. (2015). Warning times for species extinctions due to climate change. *Global Change Biology*, **21**, 1066–1077.

Steffen, W., Grinevald, J., Crutzen, P. & McNeill, J. (2011). The Anthropocene: conceptual and historical perspectives. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **369**, 842–867.

Stephens, P.A., Mason, L.R., Green, R.E., Gregory, R.D., Sauer, J.R., Alison, J., Aunins, A., Brotons, L., Butchart, S.H.M., Campedelli, T., Chodkiewicz, T., Chylarecki, P., Crowe, O., Elts, J., Escandell, V., Foppen, R.P.B., Heldberg, H., Herrando, S., Husby, M., Jiguet, F., Lehikoinen, A., Lindström, Å., Noble, D.G., Paquet, J.-Y., Reif, J., Sattler, T., Szép, T., Teufelbauer, N., Trautmann, S., van Strien, A.J., van Turnhout, C.A.M., Vorisek, P. & Willis, S.G. (2016). Consistent response of bird populations to climate change on two continents. *Science*, **352**, 84–87.

Suggitt, A.J., Stefanescu, C., Páramo, F., Oliver, T., Anderson, B.J., Hill, J.K., Roy, D.B., Brereton, T. & Thomas, C.D. (2012). Habitat associations of species show consistent but weak responses to climate. *Biology Letters*, **8**, 590–593.

Suggitt, A.J., Wilson, R.J., August, T.A., Fox, R., Isaac, N.J.B., Macgregor, N.A., Morecroft, M.D. & Maclean, I.M.D. (2015). Microclimate affects landscape level persistence in the British Lepidoptera. *Journal of Insect Conservation*, **19**, 237–253.

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2012). Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, **2**, 686–690.

Sutcliffe, O.L., Thomas, C.D. & Moss, D. (1996). Spatial Synchrony and Asynchrony in Butterfly Population Dynamics. *Journal of Animal Ecology*, **65**, 85–95.

Sutherland, W.J., Clout, M., Côté, I.M., Daszak, P., Depledge, M.H., Fellman, L., Fleishman, E., Garthwaite, R., Gibbons, D.W., De Lurio, J., Impey, A.J., Lickorish, F., Lindenmayer, D., Madgwick, J., Margerison, C., Maynard, T., Peck, L.S., Pretty, J., Prior, S., Redford, K.H., Scharlemann, J.P.W., Spalding, M. & Watkinson, A.R. (2010). A horizon scan of global conservation issues for 2010. *Trends in Ecology & Evolution*, **25**, 1–7.

Sutherland, W.J., Roy, D.B. and Amano, T. (2015). An agenda for the future of biological recording for ecological monitoring and citizen science. *Biological Journal of the Linnean Society*, **115**, 779-784.

Tayleur, C., Caplat, P., Massimino, D., Johnston, A., Jonzén, N., Smith, H.G. & Lindström, Å. (2015). Swedish birds are tracking temperature but not rainfall: evidence from a decade of abundance changes. *Global Ecology and Biogeography*, **24**, 859–872.

Tempel, D.J. & Gutiérrez, R.J. (2013). Relation between occupancy and abundance for a territorial species, the california spotted owl. *Conservation Biology*, **27**, 1087–1095.

Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T.M., Bright, P.W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J.M., Harrington, R., Johns, D., Jones, I.D., Jones, J.T., Leech, D.I., Roy, D.B., Scott, W.A., Smith, M., Smithers, R.J., Winfield, I.J. & Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, **16**, 3304–3313.

Thomas, J.A. (2010). *Butterflies of Britain and Ireland*. British Wildlife Publishing.

Thomas, C.D. (2000). Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 139–145.

Thomas, C.D. (2005). Recent evolutionary effects of climate change, In: *Climate Change and Biodiversity*. (T. E. Lovejoy, L. J.Hannah, Eds.) Yale University Press, 75–88.

Thomas, J.A. (1995). "The ecology and conservation of *Maculinea arion* and other European species of large blue butterfly." *Ecology and Conservation of Butterflies.* Springer, Netherlands. Pp 180–197.

Thomas, C.D. (2011). Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends in Ecology & Evolution*, **26**, 216–221.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M. & Conradt, L. (2001). Ecological and evolutionary processes at expanding range margins. *Nature*, **411**, 577–581.

Thomas, C.D., Franco, A.M.A. & Hill, J.K. (2006). Range retractions and extinction in the face of climate warming. *Trends in Ecology & Evolution*, **21**, 415–416.

Thomas, C.D. & Gillingham, P.K. (2015). The performance of protected areas for biodiversity under climate change. *Biological Journal of the Linnean Society*, **115**, 718–730.

Thomas, C.D., Gillingham, P.K., Bradbury, R.B., Roy, D.B., Anderson, B.J., Baxter, J.M., Bourn, N.A.D., Crick, H.Q.P., Findon, R. A., Fox, R., Hodgson, J. A., Holt, A.R., Morecroft, M.D., O'Hanlon, N.J., Oliver, T.H., Pearce-Higgins, J.W., Procter, D. A., Thomas, J. A., Walker, K.J., Walmsley, C. A., Wilson, R.J. & Hill, J.K. (2012). Protected areas facilitate species' range expansions. *Proceedings of the National Academy of Sciences*, **109**, 14063–14068.

Thomas, C.D. & Jones, T.M. (1993). Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges: lessons for conservation in a fragmented landscape. *Journal of Animal Ecology*, **62**, 472–481.

Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clarke, R.T. & Lawton, J.H. (2004). Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science*, **303**, 1879–1881.

Thuiller, W., Lavorel, S. & Araújo, M.B. (2005). Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, **14**, 347–357.

Tingley, M.W. & Beissinger, S.R. (2009). Detecting range shifts from historical species occurrences: new perspectives on old data. *Trends in Ecology & Evolution*, **24**, 625–633.

Tingley, R., Vallinoto, M., Sequeira, F. & Kearney, M.R. (2014). Realized niche shift during a global biological invasion. *Proceedings of the National Academy of Sciences*, **111**, 10233–10238.

Tischendorf, L. & Fahrig, L. (2000). On the usage and measurement of landscape connectivity. *Oikos*, **90**, 7–19.

Titeux, N., Henle, K., Mihoub, J.B., Regos, A., Geijzendorffer, I.R., Cramer, W., Verburg, P.H. & Brotons, L. (2016). Biodiversity scenarios neglect future land-use changes. *Global Change Biology*, **22**, 2505–2515.

Tulloch, A.I.T., Possingham, H.P., Joseph, L.N., Szabo, J. & Martin, T.G. (2013). Realising the full potential of citizen science monitoring programs. *Biological Conservation*, **165**, 128–138.

Turner, B.L., Meyer, W.B. & Skole, D.L. (1994). Global land-use land-cover change - towards an integrated study. *Ambio*, **23**, 91–95.

Ummenhofer, C.C. & Meehl, G.A. (2017). Extreme weather and climate events with ecological relevance: a review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **372**, 20160135.

United Nations (2017). *World Population Prospects: The 2017 Revision, Key Findings and Advance Tables.* Working Paper No. ESA/P/WP/248.

Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M.B., Balaguer, L., Benito-Garzón, M., Cornwell, W., Gianoli, E., van Kleunen, M., Naya, D.E., Nicotra, A.B., Poorter, H. & Zavala, M.A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters*, **17**, 1–14.

Vázquez, D.P., Gianoli, E., Morris, W.F. & Bozinovic, F. (2017). Ecological and evolutionary impacts of changing climatic variability. *Biological Reviews*, **92**, 22–42.

Vedder, O., Bouwhuis, S. & Sheldon, B.C. (2013). Quantitative assessment of the importance of phenotypic plasticity in adaptation to climate change in wild bird populations. *PLOS Biology*, **11**, 1–10.

Visser, M.E., Holleman, L.J.M. & Gienapp, P. (2006). Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia*, **147**, 164–72.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997). Human domination of earth's ecosystems. *Science*, **277**, 494–499.

Vucetich, J.A., Waite, T.A., Qvarnemark, L. & Ibargüen, S. (2000). Population variability and extinction risk. *Conservation Biology*, **14**, 1704–1714.

Wade, A.A., Hand, B.K., Kovach, R.P., Muhlfeld, C.C., Waples, R.S. & Luikart, G. (2017). Assessments of species' vulnerability to climate change: from pseudo to science. *Biodiversity and Conservation*, **26**, 223–229.

WallisDeVries, M.F., Baxter, W. & van Vliet, A.J.H. (2011). Beyond climate envelopes: effects of weather on regional population trends in butterflies. *Oecologia*, **167**, 559–571.

Walther, G.-R. (2010). Community and ecosystem responses to recent climate change. *Philosophical transactions of the Royal Society of London, Series B: Biological Sciences*, **365**, 2019–2024.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.

Waters, C.N., Zalasiewicz, J., Summerhayes, C., Barnosky, A.D., Poirier, C., Gałuszka, A., Cearreta, A., Edgeworth, M., Ellis, E.C., Ellis, M., Jeandel, C., Leinfelder, R., McNeill, J.R., Richter, D. D., Steffen, W., Syvitski, J., Vidas, D., Wagreich, M., Williams, M., Zhisheng, A., Grinevald, J., Odada, E., Oreskes, N. & Wolfe, A.P. (2016). The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science*, **351**, aad2622.

Webb, T.J., Freckleton, R.P. & Gaston, K.J. (2012). Characterizing abundance-occupancy relationships: there is no artefact. *Global Ecology and Biogeography*, **21**, 952–957.

Weiss-Lehman, C., Hufbauer, R.A. and Melbourne, B.A. (2017). Rapid trait evolution drives increased speed and variance in experimental range expansions. *Nature Communications*, **8**, 14303.

Wiens, J.J. (2016). Climate-related local extinctions are already widespread among plant and animal species. *PLOS Biology*, **14**, e2001104

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A. A. & Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLOS Biology*, **6**, 2621–2626.

Wilson, R.J., Bennie, J., Lawson, C.R., Pearson, D., Ortúzar-Ugarte, G. & Gutiérrez, D. (2015). Population turnover, habitat use and microclimate at the contracting range margin of a butterfly. *Journal of Insect Conservation*, **19**, 205–216.

Wilson, R.J., Davies, Z.G. and Thomas, C.D., (2009). Modelling the effect of habitat fragmentation on range expansion in a butterfly. *Proceedings of the Royal Society B: Biological Sciences,* **276**, 1421–1427.

Wilson, J.W., Thomas, C.D., Fox, R., Roy, D.B. & Kunin, W.E. (2004). Spatial patterns in species distribution reveal biodiversity change. *Nature*, **432**, 393–396.

Woodcock, B.A., Harrower, C., Redhead, J., Edwards, M., Vanbergen, A.J., Heard, M.S., Roy, D.B. & Pywell, R.F. (2014). National patterns of functional diversity and redundancy in predatory ground beetles and bees associated with key UK arable crops. *Journal of Applied Ecology*, **51**, 142–151.

Yackulic, C.B., Nichols, J.D., Reid, J. & Der, R. (2015). To predict the niche, model colonization and extinction. *Ecology*, **96**, 16–23.

Zuckerberg, B., Porter, W.F. & Corwin, K. (2009). The consistency and stability of abundance–occupancy relationships in large-scale population dynamics. *Journal of Animal Ecology*, **78**, 172–181.