Changes to plant distributions in Britain

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Abstract

Species distributions always have and will change, and there are a number of controlling factors involved in their overall distribution. Climate is considered one of the strongest drivers of changes to species distributions, and due to historical climate change, has played an important part in current species distributions. A large number of species have changed their distributions in the past century, which can largely be attributed to current anthropogenic climate change. This study uses the Botanical Society of Britain and Ireland (BSBI) vascular plant database to explore changes which are occurring to native plant species distributions in Britain. Studies are carried out to assess how and where plant species distributions are changing. Initially the northern range margin of southerly distributed native plant species were used to determine if there was a poleward shift as would be expected with a warming climate. Results show that, unlike animal species which have advanced north, plant species are not advancing towards the pole and a large number are in fact retracting at their northern edge. This is a clear indication that although the climate is changing, other factors are having a stronger influence on many plant species distributions in Britain. As it is known historically that plant species will follow climate change it is likely that human disturbance such as agricultural intensification and urbanisation are stronger drivers of distribution changes in Britain. Natural dispersal mechanisms are no longer facilitating spread in a large number of species due to these barriers. However, human mediated dispersal may become the main disperser in the future by carrying seeds beyond their natural range. There is however evidence that Bee orchids (*Ophrys apifera* Huds.*)*, a species which is wind dispersed, with seeds carried on currents due to the dust like seeds, are successful in spreading and have in recent years been occurring in a broader range of habitats to where they are considered to traditionally occur. This is likely to be an example of a species that is benefiting from the warmer climate and has facilitated its spread into previously un-colonised areas. Therefore I conclude that at present the majority of species distributions used in this study have not responded to climate as expected due to other anthropogenic factors, however humans may become the most important disperser, facilitating species spread into new locations and some species may start to infill in their range and spread by natural means if propagules are easily dispersed long distances.

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Declaration

I declare the work carried out in this thesis is my own work and has been written by me with the exception of the distribution data used which was provided by the Botanical Society of Britain and Ireland and where used this is specified in the text.

1. General introduction

Humans are changing the environment on earth at an unprecedented rate and this is affecting nearly all forms of life. A vast amount of research has been carried out on how these anthropogenic influences are affecting species in a variety of ways such as their ecology, distribution, morphology and life histories. As many of these human caused impacts are having adverse effects on the world's biota, these anthropogenic influences need careful study in order to assess the changes that are occurring. This information feeds into the growing body of evidence on how we can best conserve species in the changing environments on earth.

This chapter is intended to give an overview of environmental changes, extinction and conservation, and then of British plants as a study group and the data available for this research. Following this introduction chapter there will be two data chapters. Chapter two concentrates on northern range margin changes of southerly distributed native plant species in Britain and looks at what may be affecting these changes. Chapter three takes Bee orchids (*Ophrys apifera* Huds.) as a case study species which has shown recent changes which are likely to be as a result of the warming trend in Britain and looks at habitat changes associated with this. The final chapter (Chapter four) will bring the two data chapters together and suggest future avenues for related research.

1.1. Environmental change

Environmental drivers such as nitrogen deposition, land use change, and climate change are likely to have the greatest affect on terrestrial ecosystems (Sala et al., 2000), largely down to anthropogenic influences. Humans have caused substantial increases in atmospheric carbon dioxide, methane and nitrous oxide since around the 1800s (IPCC, 2013). This change in environmental conditions has been shown to have affected many different species of plants and animals, and continuing environmental changes, which are predicted to continue into the future, will change the distributions, life cycles, ecosystems and in some cases cause the extinction of species. This section briefly summarises these environmental changes and provides an overview of the impact on plants.

1.1.1 Climate change

Climate has throughout the history of the planet been changing and will continue to do so. This fluctuation in climatic conditions, such as temperature and precipitation, is caused by a number of different factors, but the over-riding drivers are Milankovitch cycles (Grubic, 2006). There are however, other influences on climatic which include sun spot activity, volcanic gasses, ocean currents and greenhouse emissions. The next three sections will briefly cover historic climate, post industrial revolution climate (from 1750) including future climate predictions and a section on current and predicted future changes of climate in the UK.

1.1.1.1. **Historic climate change**

Our understanding of historic climate systems are based on observations which go back hundreds of thousands of years and help inform on how the climate reacts to different naturally occurring events (IPCC, 2013). This information in combination with other anthropogenic factors is important in determining how humans are affecting the climate and what the future may hold for climatic conditions on earth.

The strongest influence on the earth's climate is changes to the angle and orbit of the earth in relation to the sun. There are 3 cycles (collectively termed the Milankovitch Cycles) (Grubic, 2006) which have strong influences on glacial and interglacial cycles and the seasons (i.e., the differences between summer and winter temperature). The eccentricity of the Earth's orbit varies with periods of 100,000 and 400,000 year cycles which changes from an elliptic to a more circular orbit. The obliquity of the earth has a 40,000year cycle and the tilt of the earth varies from about a 21° tilt to a 24.5° tilt during this cycle. The precession of the earth has a 21,000 year cycle and this relates to the wobble of the earth and is caused by the earth's axis rotating in a circular motion. Over the past 500,000 years there has been a series of glacial and interglacial cycles and these cycles last about 100,000 years and can be linked to the eccentricity of the Earth's orbit. Over 1 million years ago there were cycles of 41,000 years which ties in with the obliquity of the earth. In between these time periods the climate has shown intermediate behaviour. The obliquity and precession also creates our seasons and how large the difference is between summer and winter temperatures (Robert, 2003).

When the eccentricity, obliquity and precession are all in alignment then the northern hemisphere receives the least amount of summer insolation, thereby allowing snow to accumulate in winter and summer. This causes the icesheets to advance thereby increasing the potential for an ice age to occur (Robert, 2003).

The close correlation between historical Antarctic temperatures and atmospheric CO_2 and CH_4 concentrations suggest that they are important amplifiers of temperature and, along with the initial orbital forcing, are important in glacial-interglacial changes (Genthon et al., 1987, Lorius et al., 1990, Raynaud et al., 1993, Petit et al., 1999). Over the history of the earth there have been many dramatic changes in global temperature and concentrations of different gasses in the atmosphere. During the middle Pliocene (3.3 to 3.0 million years ago), during warm intervals, global mean surface temperatures were between 2-3.5 °C warmer than temperatures of the pre-industrial climate with CO_2 levels thought to be between 250-450 ppm (IPCC, 2013). Around 52 to 48 million years ago, during the Early Eocene, CO_2 levels in the atmosphere exceeded ~1000 ppm and global mean surface temperatures were thought to be about 9-14°C higher than pre-industrial conditions. The last interglacial period occurred 129,000 to 116,000 years ago and global mean temperatures were no higher than 2°C above pre industrial levels (IPCC, 2013). Over the past ~ 11,000 years, known as the Holocene, which represents the current interglacial, the climate has been relatively stable (Barnosky et al., 2012). However, current climate change, which is strongly linked with anthropogenic activities, is altering the natural environment, including greenhouse gas composition, habitat structures and composition and land uses particularly rapidly.

1.1.1.2. Current/anthropogenic and future climate change

It is certain that the global mean surface temperature has warmed since the late 19th century (Brohan et al., 2006, Hansen et al., 2010). The past three decades have all been warmer than previous decades as far back as instrumental records go, with the 2000’s decade being the warmest, and the global average temperature has warmed by 0.6 °C between 1951-2010. There is evidence that the number of cold days and nights (as defined by the IPCC 2014) has decreased and the number of warm days and nights (as defined by the IPCC 2014) has increased on the global scale since the 1950’s and there is evidence of changes to rainfall and drought on a regional and global scale. This increase in temperature is due to an imbalance in radiative forcing since around the 1970s with more energy from the sun entering than exiting the top of the atmosphere.

The largest proportion of the heat which is retained from radiative forcing is absorbed by the ocean which in turn causes increased sea ice melt (Levitus *et al*., 2000, Hegerl and Bindoff, 2005, Levitus *et al.,* 2005). This increase in ocean temperatures is set to continue over the 21st Century and for a number of centuries to come due to heat transfer happening over a long time scale from the surface to the depth, even if greenhouse gas emissions remain the same or are reduced (IPCC 2014).

This radiative forcing increase, which leads to global climate changes, has been shown with consistency of modelled and observed changes across climatic systems to mainly be the result of anthropogenic increases in greenhouse gas concentrations (Hansen *et al.*, 2005, IPCC, 2014). Until recently the three largest radiative forcing gasses which were influenced by anthropogenic activities were CO_2, CH_4 and CFC-12. The latter gas has seen decreases as the Montreal Protocol has caused CFC-12 to have emissions phased out. This has lead to nitrous oxide (N_2O) now being likely to be the third largest contributor to radiative forcing. The other main anthropogenic contributors of radiative forcing are ozone (O_3) and atmospheric water vapour, both short lived greenhouse gasses.

Information is available for the past 800,000 years on atmospheric greenhouse gases, carbon dioxide, methane and nitrous oxide, concentrations which are determined from polar ice cores (EPICA community members, 2004, Lüthi *et al.,* 2008). Concentrations of these gasses in 2011 exceeded concentrations known from ice core data. The current rate of the rise in concentrations of these three gasses (and increases in radiative forcing associated with this) are unprecedented over the last 22,000 years, and are likely to be unprecedented compared to the past 800,000 years although the resolution of the latter time period is lower.

Radiative forcing does change naturally, with solar activity and large volcanic eruptions having an impact on the global climate, but these do not explain the rate of climate change that is currently being observed. The natural carbon cycle has been disrupted since around the 1750's (considered the beginning of the industrial revolution) due to anthropogenic release of CO_2 from fossil sources into the atmosphere. From 1750 to present day there has been a continual rise in CO_2 concentrations which has resulted largely from combustion of fossil fuels, cement production and land use change emissions. Between the dates 1750 and 2011 there has been about 545 PgC released into the atmosphere (IPCC, 2013). Of this 240 PgC has accumulated in the atmosphere with an increase in CO_2 concentrations from 278 ppm in 1750 to 390.5 ppm in 2011. The atmospheric CO_2 concentrations increase on average with latitude over industrialized countries north of the equator which clearly demonstrates that the distribution is driven by anthropogenic emissions. The remaining carbon released by fossil fuels, cement production and land use change has been re-absorbed and stored into the terrestrial ecosystem and ocean (Battle *et al.,* 2000, Rayner *et al.,* 1999) with 150 PgC accumulated in natural terrestrial ecosystems (not affected by land use change) between 1750 to 2010 (IPCC, 2013).

As well as CO_2 being released in large quantities by anthropogenic activities, methane (CH_4) has also increased since pre-industrial times by a factor of 2.5. CH_4 rose from 720 ppb in 1750 to 1803 ppb in 2011 (IPCC, 2013). This rise in CH_4 is largely due to increase in ruminant number, rice paddy agriculture expansion, emissions from waste and landfills and emissions from fossil fuel extraction and its use. Emissions from these and other anthropogenic sources account for between 50 to 65 % of total emissions. Methane is not only released by human activities but is also produced naturally by wetlands. Models and ecosystem warming experiments have shown that methane emissions will increase from wetlands in warmer climates. It is uncertain, however, the amount of methane that will be released as precipitation will also dictate the rate of methane emissions. This casts uncertainty in how warmer climates will affect wetlands. It is also likely that, due to future warming, release of carbon stored in the permafrost will occur, leading to increased global warming gasses in the atmosphere. Release of greenhouse gases are not the only warming impact that humans are having on the climate. Black carbon, such as soot, on snow and ice is also responsible for an increase in radiative forcing. This is because forcing energy is directly deposited into the cryosphere and this drives a positive albedo feedback on the climate and can represent a significant forcing mechanism in ice or snow covered regions such as the Arctic.

There have been large advances in predictive modelling of future climate. However, there are still many uncertainties and it is not possible to predict solar irradiance (except for the 11 year solar cycle) or volcanic eruptions. Therefore, these elements of natural forcing are difficult to include in predictive models of near and long term climate change and are often not included in assessments due to these difficulties. Climate models have shown that they can reproduce the general features of mean surface temperature changes (global and annual) over historical periods, including the immediate cooling following large volcanic eruptions and the warming in the second half of the 20th century, but they perform less well for precipitation (Meehl *et al.,* 2007, IPCC, 2013). Predictive climate model projections indicates that much of what is currently occurring will continue to increase in strength. Previous global climate change predictions have been shown not to have exaggerated the change, and in some instances, such as sea level change, have underestimated this change (Rahmstorf *et al.*, 2015). There is likely to be an increased number of heat waves and extreme hot temperatures, changes to precipitation with wetter areas tending to become wetter and drier areas becoming drier, changes in water vapour in the atmosphere (which has radiative forcing implications), alterations to atmospheric circulation (such as the Hadley Circulation and the Southern Hemisphere Mid-latitude Westerlies shifting poleward) and the temperature is set to continue rising with predictions of a 1.5-4.5°C rise by 2100. Recent research by Sherwood et al (2014) has indicated that global temperature is likely to be at the higher end of the predictions due to calculating in radiative forcing resulting from cloud formation.

Due to current levels of greenhouse gases in the atmosphere, mitigation efforts will not have a large impact on the next 30 years' climate change outcomes according to different modelled scenarios. However, longer term climate change (post mid-21st Century) show different outcomes depending on action taken to mitigate anthropogenic greenhouse gasses. This near term future warming from past emissions cannot be avoided due to thermal inertia of the oceans and will continue with the ongoing emissions of greenhouse gasses over the near term (IPCC, 2013).

Climate is one of the most important factors in determining where species can occur, influencing advancement and retraction of species ranges. The climate must be suitable for them to grow, reproduce and spread and Grinnell (1917; see Parmesan, 2006) highlighted the importance of these climate thresholds in species range margins. Current and predicted future changes to the environment, especially climate change, will have a large impact on nearly all of earth's species. Sections within 1.1.2 will go into more detail about how current and future changes to the environment will impact on species.

1.1.1.3. **British climate and climate change**

It is known that changes to climate will differ in different regions of the earth and so how climate has and will affect the United Kingdom (UK) will have important implications for many aspects of biodiversity in the region. The UK experiences maritime influences to the climate, with westerlies from the Atlantic dominating. Between the south and the north the climate is dominated by high pressure to the south and the Icelandic low to the north. There are also areas of high ground in Wales, north-west England and Scotland (mountains reaching up to 1344 m above sea level). From the Atlantic comes the Gulf Stream, an ocean current which has a warming effect on the UK. This is particularly important as for the latitude of the UK it results in mild winters. Mean temperatures in the UK decrease with increases in latitude and altitude. As well as a temperature gradient with altitude and latitude there is also a distinct west-east pattern to average rainfall amounts with higher rainfall in west Scotland, north-west England and north Wales, and relatively cool summers and warm winters in the west (Met Office, 2011).

Climate is an important factor in determining the composition of the flora in the UK. The flora being the result of thousands of years of climate change as well as changes to vegetation and land use. In recent times (geologically speaking) the most dramatic change has been during the Pleiostocene (which began 2.3 million years ago) with successive glacial and inter-glacial periods. The most recent started 120,000 years ago and reached maximum development 25,000 and 18,000 years ago, finishing about 16,000 and 11,500 before present (BP). Trees were absent from the UK during this time although some vegetation did exist south of the ice sheet. The late glacial period saw the recolonization of trees and temperate vegetation, dominated by trees, had already become established in the low lands by 9,000 BP and these native tree species are still common in Britain today (Preston *et al.,* 2002).

Since the 1960’s temperature across the UK has increased, consistent with a warming signal with the trend for winter temperatures having increased by 0.23°C per decade and summer temperatures having increased by 0.28°C per decade between 1960-2010 (Met Office, 2011). There have been fewer cool nights and cool days, and warm days and warm nights have increased in number and the warming in summer is greater than that in winter (Met Office, 2011). This warming trend is set to continue and by 2100 is predicted that the south of the UK will see an increase of 3° C with moderate agreement between models, whereas the north increase of 2.5° C is predicted with low agreement between models (Met Office, 2011). Additional to temperature increases there are also precipitation changes projected to occur with an increase of up to 10% in the UK, although in some southern parts there may be decreases of up to 5% experienced (Met office, 2011). These changes in climate across the UK will alter the environment for all species in the UK and so species distributions, species compositions and habitats are predicted to change as will be discussed in the following sections.

1.1.2. Anthropogenic environmental impacts on plants

Since the beginning of the last interglacial period (~ 11,000 years ago) humans have migrated across the globe (Barnosky et al., 2012) and over the past 500 years disturbance to vegetation as a result of human activities has affected the ecology of many ecosystems on the planet (Russell and Davis, 2001). Humans have dramatically altered the earth, with between one-third and one-half of the land surface having been transformed by the action of humans. Humans have fixed more atmospheric nitrogen than all natural terrestrial sources combined and humans have put to use over half of all accessible surface fresh water (Vitousek et al., 1997). In recent history, almost everywhere will have experienced changes in climate. These changes which have occurred over the past century, particularly in the past 4 decades (the time period which has seen the most rapid climate warming), can be seen in the responses of a large number of taxa. Both plants and animals have exhibited changes in their phenology, latitudinal range, and altitudinal range, and it is likely that it has and will continue to lead to the extinction of many species (Williams et al., 2003, Parmesan, 2006). Each of these topics is discussed briefly in the following sections.

1.1.2.1. **Phenology**

Plant phenology (such as flowering, leafing and leaf fall) is affected by climatic changes. Phenological changes to plants currently provide the best documented biological response to current anthropogenic climate change. Not only does warmer weather, which is associated with climatic warming, advance phenological events (Chmielewski and Rotzer, 2001, Fitter and Fitter, 2002, Menzel et al., 2006, Doi and Katano, 2008, Jeong et al., 2011, Ziello et al., 2012, Molnar et al., 2012, Li et al., 2013), but warmer winters can mean that chilling which some species require to break bud dormancy may not be sufficient, resulting in abnormal or delayed bud burst (Morin et al., 2009). Also warmer climates can delay phenological events at the end of the growing season, and Sherry et al. (2007) showed that reproduction was delayed in species which started flowering after peak temperatures in the middle of the season. Large numbers of species have advanced their flowering times by several days as a result of increased temperature (Fitter and Fitter, 2002, Menzel et al., 2006, Ziello et al., 2012, Molnar et al., 2012, Li et al., 2013). This phenological change in flowering time will have important implications for the survival of some species, including insects that have seasonal emergence times and plant species which are reliant on these organisms for pollination. *Corydalis ambigua*, a species reliant on pollination by bumble bees (*Bombus spp.*), has been shown to have low seed set when spring arrived early as emergence of the pollinator was later than flowering; and therefore some of these early flowering events are already being shown to interfere with plant pollinator interactions (Kudo and Ida, 2013). There is, however, evidence that at least some insect species emergence times may keep up with changes to flowering time (Bartomeus et al., 2011).

Amongst plants, flowering time is not the only change in phenology which has responded to the environmental change, especially climate warming, in the past few decades. Time of leafing in spring (start of growing season) has been brought forward and there has been a delay of leaf fall at the end of growing season in many species, which have been linked to warmer spring and autumn temperatures respectively. In Europe, it was shown that an increase in temperature of 1 °C in early spring (Feb-April) caused an advance in the start of the growing season of 7 days (Chmielewski and Rotzer, 2001).

Phenology can also affect the range margins of a species if the ability of a plant to spread at its range margin is linked to its ability to reproduce due to phonological changes (Chuine, 2010). For example, Chapman et al (2014) used climate and phenology to predict future distributions of *Ambrosia artemisiifolia* L., a native plant in North America but occurring as an invasive as a crop weed in Europe. The research showed that phenology can be key in determining the species' range margins in relation to latitude and altitude.

1.1.2.2. Distribution change

There are a number of factors involved in determining species distributions. The distribution of the species as a whole will change as a result of the cumulative effect of many individual population changes. Some populations will expand or increase in number and some populations will see a reduction in number of individuals or the population may cease to exist and therefore the species will become locally extinct. Some of these changes are natural. However, humans have become one of the biggest drivers in changes to the distribution of the world's biota, such as changes in the landscape over the past 5000 years in central England due to the transition of man from hunting to shepherding or herding livestock (e.g. Armstrong 1956; see Hodgson et al., 2005). Although there are many causes of distribution changes, one of the strongest drivers of the distribution of different species is climate (Walther et al., 2002).

As the climate is now warming, largely due to anthropogenic influences (see Section 2.1.1.2), populations are changing, which results in the shift of the species distribution to new localities, adaptation or extinction (Huntley et al., 1995, Erasmus et al., 2002, Peterson et al., 2002, Thuiller, 2004, Parmesan, 2006). Although it is certain that species will change their distributions with climate change there are many uncertainties in predictive distribution models. It has been shown that when modelling species distributions, finer scale climate models reveal more climate refugia than coarser scale models, however, coarse scale models have been more commonly used when predicting future distributions of species (Franklin et al., 2013). Soil properties and dispersal ability are also important in determining how and where species will disperse, as well as climate, and therefore they have been incorporated into some climate based predictive models (Condit et al., 2013, Dubuis et al., 2013, Snell, 2014). A number of studies have shown that distribution changes in many taxa have already taken place (Hughes, 2000). There is also evidence that a substantial number of species risk extinction over the 21st century (Thomas et al., 2004), particularly species growing on mountains (Thuiller et al., 2005) as well as coastal species which will have limited habitat available space as the climate changes and sea level rises, but are constrained by human infrastructure and ecosystem alterations further inland (Mendoza-Gonzalez et al., 2013). There are two main distributional changes, poleward shift (latitudinal change) and altitudinal range shift which will be dealt with in the following sections.

1.1.2.2.1. Historical distribution change

Throughout the history of the Earth species have changed their distributions in response to climatic changes. Over the past 500 years, humans have influenced changes in vegetation (Russell and Davis, 2001) but prior to this other driving factors influenced changes in distributions. These historic changes in distribution are important to study as they provide a useful insight into how current climate change may affect species distributions and assemblages (Williams et al., 2001). Human disturbance, which was not present in responses to historic climate change, will play in important part in how vegetation will change in future climates.

Fossil pollen records in un-glaciated regions can span hundreds of thousands of years and therefore provide information of the former distributions of species (Tzedakis, 1993, Allen et al., 1999). Climate changes have been shown to have had dramatic affects on plant associations causing the migration of plant species and vegetation changes with distributions of some species increasing in warmer or drier times and other species becoming dominant in drier or cooler time periods (Singer et al., 1996, Allen et al., 1999, Prentice et al., 2000, Shuman et al., 2002b, Shuman et al., 2004, Williams et al., 2004). Pathogen/insect outbreaks have been linked to Hemlock (*Tsuga*) decline in the Upper Peninsula Michigan, USA around 5500 to 4500 cal. Yr BP, which has also been linked to changes in climate around that time therefore, likely weakening Hemlock growth and meaning an increased susceptibility to pathogens and insects (Calcote, 2003). Some of these changes in abundance and distribution, such as the *Populus* increase in abundance in the late glacial to present in North America, may be down to the climate changes affecting some species' major competitors and therefore increased space available for the species rather than the climate having a direct effect on the species itself (Peros et al., 2008). Precipitation has also played an important part in species distribution along with temperature (Lloyd and Graumlich, 1997, Shuman et al., 2002a) and soil texture, and therefore its water holding capacity, can play an important role in vegetation composition (Ewing, 2002). Plant migration and refugia are associated with ecological preferences for different soil acidities and therefore bedrock types during the Holocene in the last glacial era (and subsequent climate variations) (Alvarez et al., 2009). One element of responses of plant communities to historic climate change, which will be important to conservation with current anthropogenic climate change, is that historical climate change has led to what is termed “Non-Analogous Communities”. This is defined as communities that are different in species composition from communities that can be recognised from selected reference points in time (Keith et al., 2009). This subject is reviewed by Stewart (2009). The dynamic nature of plant communities needs to be taken into account with future conservation planning.

Natural treelines are sensitive to climate and it has been shown that historically they have increased in elevation in warmer time periods and have retracted down mountain sides in cooler time periods (Helama et al., 2004, Paus, 2010, Kullman, 2013). Evidence such as subfossil wood remains (e.g. Kullman, 1998), plant macrofossils such as seeds, pine needles and other plant fragments (e.g. Tinner and Kaltenrieder, 2005) and megafossils including tree ring data (e.g. Lloyd and Fastie, 2002) have been used to show this trend. Changes in climate during the Holocene had very strong influences on the treeline with many studies demonstrating that the tree line was significantly higher in elevation during the ‘climatic optimum’ during the present interglacial (ca 4500 years BP) as is discussed by Grace et al (2002). Much research has been carried out in northern Scandinavia looking at tree line changes in the Holocene as megafossils of tree remains have been preserved above the modern tree line under glacier ice, peat and lakes. The use of radiocarbon-dating to date these megafossils giving a good picture of where the tree line has changed (e.g. Karlen, 1976, Kullman, 1995, Kullman and Kjallgren, 2000, Helama et al., 2004, Kullman and Kjallgren, 2006, Paus, 2010). In the late Pleistocene and Holocene periods when climate was periodically changing, changes to the distribution and altitudinal range of species in USA such as limber pine (*Pirus flexilis*), whitebark pines (*P. albicaulis*), bristlecone (*P. longaeva*) and junipers (*Juniperus occidentalis* and *J. osteosperma*) have been found with the species moving in line with changes to climate and increasing in elevation by hundreds of metres as temperatures changed (Westfall and Millar, 2004).

1.1.2.2.2. Latitudinal range shift (north shift)

Plants are immobile for most of their lifecycle and therefore in order to expand into new climatically suitable space, the population must move when propagues such as seeds, spores and dethatched plant fragments are dispersed. This contrasts with the trailing edge of their distribution, where the plants will fail to regenerate as this area will become climatically unsuitable for growth and or reproduction, although the plants may persist for some time after. There is a large body of literature on latitudinal shifts towards the poles at the warm margins of species' distributions (Walther et al., 2002, Parmesan and Yohe, 2003, Hickling et al., 2006, Chen et al., 2011, Mair et al., 2012, Mantyka-Pringle et al., 2012, Chessman, 2012, Feeley, 2012, Groom, 2013), as would be expected with warming climates, however, the majority of these relate to animal distributional changes. The literature on plant latitudinal range shifts is more limited. Of course, not all movement will be poleward (or increase in altitude discussed in section 1.1.2.3) when it comes to climate induced range movement of species. Climatically suitable space may have been created for some species in directions which are not poleward such as has been found in Australia. A multi-directional distribution shift is likely to occur when temperature and precipitation interactions are modelled and the fingerprint of climate change is underestimated if only looking at poleward movement (VanDerWal et al., 2013).

As the future climate is set to continue warming (IPCC, 2013), latitudinal shifts in species distributions will continue as new climatically suitable habitat opens up. In the tropics many species are at risk as they already live at or near the highest temperatures on earth prior to current global warming and they are also often isolated from cool refuges which they could migrate to as the temperature rises (Wright et al., 2009), however, tropical climates are not changing as rapidly as other cooler areas of the planate. In the Amazon rainforest, in order to track temperature changes, species are likely to have to move nearly 300 km and if precipitation is also included in the equation the distance is over 475 km by 2050 (Feeley and Rehm, 2012). This could lead to serious threats to many species if deforested areas act as a dispersal barrier. As a result of human disturbance on the landscape it may not be possible for species to migrate into new localities due to inability to disperse past barriers into the new climatically suitable space. Many of these barriers to dispersal (particularly in plants which rely on chance to carry the seed to a suitable habitat) are caused by changes to the landscape by anthropogenic activities such as urbanisation, conversion to land for agricultural use and deforestation, causing increasing distance between suitable habitat and therefore blocking species movement.

The question of whether plant species are tracking climate at their latitudinal range margin has seen little attention. This is important not only to determine whether plant species are tracking climate but also as plants form the basis of many habitats and ecosystems. They are important as food sources for a large proportion of animal species and many animal species are reliant on a specific or small group of plant species. It is hoped that this work will go some way to addressing this question in order to determine how plants are responding to changes in climate, which have been shown to have affected animals range margins in a number of countries.

1.1.2.2.3. Altitudinal shift

Plants growing on mountain sides experience a much steeper temperature gradient as the decreases in temperature on an altitudinal gradient are much steeper than latitudinal temperature gradients. Due to recent climate change there has been strong interest in how global warming has and will affect plants in mountain communities as the more compressed temperature gradient may facilitate distributional changes. Due to the sensitivity of montane floras to climate change and their distributions being largely controlled by ecological factors relating to climate, mountains are regarded as important observation sites for tracing the impacts of climate change on plant communities (Diaz et al., 2003). There have now been a number of studies which have shown increases in altitude of a number of plant species as the climate warms (Grabherr et al., 1994, Walther et al., 2005, Beckage et al., 2008, Kelly and Goulden, 2008, Telwala et al., 2013). There is evidence that plant species with faster life history traits such as those with shorter life cycles, faster maturation and smaller size at maturity are showing more increase in shift in altitude than trees and shrubs which possess slower life history traits (Lenoir et al., 2008).

Although this shift in altitude of species is evident in many plants there are also plant species which have either not shifted or reduced in altitude (Rabasa et al., 2013, Baessler et al., 2013), which Crimmins et al (2011) attributed to water deficits. Species richness is expected to increase the most in response to warming at high elevations, as climatically suitable space further up becomes available to plants that were constrained by the climate at these elevations. However, declines in precipitation, which are much harder to predict, are likely to drive most projected decreases in species richness (Venevskaia et al., 2013). In tropical regions increasing temperatures based on global studies suggest that there will be an upslope shift in distribution of vegetation zones, leading to potential extinction of the current high-altitude species as well as putting at risk a large number of highly specialized species in respect to particular temperature and moisture conditions (Williams et al., 2007, Colwell et al., 2008). Trees may be more likely to advance in altitude at the tree line where different zones meet (from tree to shrub zone) and tree species growing at lower elevations below the tree line may not advance at their upper margin as rapidly as was found in a study by Ettinger and Hille Ris Lamberts (2013).

1.1.2.2.4. Alpine flora

Grabherr et al (1994) showed a trend in elevation increases in the alpine nival flora in the Austrian mountains, which suggested that global warming was already having a significant affect in some plant communities. Although this showed that the flora was responding to temperature changes, the migration rate was much slower than the rate at which isotherms have migrated over the same time period, with the Alps warming by about 1°C over the past century (e.g. Grabherr et al., 1994, Grabherr et al., 2000, Kullman, 2002, Pauli et al., 2007, Erschbamer et al., 2009). It became obvious that climate was having an effect on alpine ecosystems and there was a demand for research to continue in this area to provide information on environmental change and help inform decision making. The GLORIA (A Global Observation Research Initiative in Alpine Environments) project was initiated in order to satisfy the demand for this knowledge (Grabherr et al., 2000). Alpine regions are considered to be good indicators of climate change for a number of reasons: they are generally considered sensitive to climate warming, they have a comparatively low ecological complexity, they may be more influenced by climatic factors than biotic factors and human land use changes are often less influential in these regions than they are in low land regions (Grabherr et al., 2000). Since Grabherr et al. (1994) and subsequently the GLORIA project was initiated, a large number of papers have been published on the subject of global warming and alpine and alpine-nival areas (Keller et al., 2000, Walther et al., 2005, Lenoir et al., 2008, Ross et al., 2012, Telwala et al., 2013). There has been an increase in simulated climatic change experiments in alpine regions (Zhang and Welker, 1996, Price and Waser, 2000) and predictive modelling for future distribution of vegetation patterns (Gottfried et al., 1998, Zimmermann and Kienast, 1999, Carlson et al., 2013). It has been suggested in a number of studies that alpine plants have evolved adaptations from the Pleistocene to late Holocene epochs in response to long term climate change (Schonswetter et al., 2005, Harris, 2007), and so many of these plant species which are adapted for colder climates may be at risk as the climate warms. As discussed in section 2.1.2.3, decreasing precipitation and increasing temperatures, which is likely to occur in some areas, may have an adverse affect on some species and this may particularly negatively impact on wetland alpine ecosystems (Wu et al., 2013) as well as other alpine plants and may promote expansion of subalpine species (Kopp and Cleland, 2014).

1.1.2.2.5. Treelines

Alpine treelines are often used when looking at climatic affects on plant distributions in alpine regions (Walther, 2004). The alpine treeline (hear after termed just treelines) is of importance because denser forested areas below the treeline or advancing treelines will exclude species which occur in the alpine and arctic regions beyond the treeline changing the montane landscape and possibly ousting rare species and disturbing plant communities. Where treelines are found is largely governed by temperature decreases associated with altitude and latitude, the closer to the poles the area, the lower the treeline until when close to the poles the treeline is near sea level. This treeline is where the forest margin finishes and there will be what is often termed the struggle zone (or zampfzone) above this where isolated trees exist decreasing in size as the elevation increased (Thomas and Packman, 2007). The treeline location in temperature terms does not have a strict lowest temperature limit that trees can grow at as other climatic variables also affect the treeline such as wind speed, moisture etc. The threshold air temperature for trees to grow (in terms of tree tissue growth and development) is higher than 3°C but lower than 10°C (Korner, 1998).

With global mean surface temperatures having increased by 0.72°C between 1951 and 2012 (IPCC, 2013) a number of papers have shown this temperature rise has triggered increases in altitude and densities at treelines globally (Szeicz and Macdonald, 1995, MacDonald et al., 1998, Klasner and Fagre, 2002, Camarero and Gutierrez, 2004, Walther, 2004, Kharuk et al., 2006, Danby and Hik, 2007, Devi et al., 2008, Elliott and Kipfmueller, 2011, Liang et al., 2011, Kirdyanov et al., 2012). There are many other factors as well as temperature increases which also affect the treeline position such as precipitation (Daniels and Veblen, 2003, Daniels and Veblen, 2004, Wang et al., 2006), disturbance (Gehrig-Fasel et al., 2007, Ameztegui et al., 2010), or plant-plant interactions (Germino et al., 2002, Bekker, 2005) and over the past century the advances of treelines are not consistent. Many studies showing that the treeline has either remained stable or advanced over the past century (Harsch et al., 2009).There have also been observations that only in exceptionally warm summers are viable seed actually produced at high elevations with seed viability falling as elevation increases (Barclay and Crawford, 1984, Holm, 1994, Cuevas, 2000). During paleoperiods with temperature differences between 2-3°C the treeline changed in elevation by less than 100 m (Petersson., 1998 but see: Grace et al., 2002) and McConnell (McConnell 1996. but see Grace et al., 2002) showed a similar slow treeline advance over the past 1000 years in the Cairngorms of Scotland. It appears that although treelines in many areas are affected by changing temperatures because of the slow rate of growth at these elevations it may take much longer for some treelines to respond to temperature increases and there are many other factors which influence their growth, some of which, such as grazing by wild mammals or domestic stock, may adversely affect the ability of treelines to advance.

1.1.2.2.6. Distribution infilling

There is clear evidence for distributional changes of many plant species, although not all species are responding in the same way and some are not shifting at all. The apparent lack of range advancement response of many species may in part be down to habitat within dispersal distance not being suitable to colonise or barriers being present such as urban or agricultural landscapes which prevent dispersal to suitable habitats. However, many species are restricted to a small set of locations or habitats near their range boundaries (Lennon et al., 1997), and there is the potential for them to spread into nearby habitats within the existing range boundary, a phenomenon that can be termed range infilling. Limited literature exists on the topic of infilling of distributions and there has been much less attention paid to it than has been dedicated to range expansion (Warren et al., 2013). As discussed in section 2.1.2.3.2 there is clear evidence that the number of trees at the treeline has increased, even if the altitudinal range has not advanced. There are limited numbers of studies which show infilling of distributions such as studies looking at non-native plants (Warren et al., 2013). This can be seen with microfossil evidence of infilling when fire opens up more available space which facilities space for infilling of the range of another local species (Weppner et al., 2013). There can also be increase in woody vegetation cover (Tremblay et al., 2012) such as forests infilling where savannah was originally present (Rackham, 2008). There is also evidence that climate will not just increase the densities of populations as some species will be adversely affected by the changing climate and may cause populations to decrease in density (Levine et al., 2008). The infilling of a species' range should be studied as this may provide information on how species distributions are changing with the climate, and which species are responding positively (increasing densities or number of populations within the current range) and which species are not (reduction in densities or number of populations within the current range).

1.1.2.3. Increased CO_2 and global warming

Atmospheric CO_2 concentrations (essential for plant photosynthesis) have been increasing globally due to the burning of fossil fuels and forest clearing, and are set to continue increasing for at least the next several decades. Since the pre-industrial period there has been a 30% increase in concentrations of CO_2 and trees which are currently living may experience a doubling in CO_2 concentrations over their lifetimes (IPCC 2014). On an evolutionary time scale this represents an instantaneous change.

Although much larger atmospheric CO_2 concentration changes have taken place on a greater time scale (e.g. in the Triassic, Jurassic and Cretaceous periods there is evidence that atmospheric concentrations of CO_2 were four to eight times greater than at present) the present-day rapid change in CO_2 concentrations will increase photosynthesis of C_3 and C_4 plants and CO_2 concentrations are often artificially increased in commercial greenhouses whilst growing crops to increase their yield (Mortensen, 1987).

It is known that elevated atmospheric CO_2 concentrations lead to increased leaf photosynthesis and a reduction in canopy transpiration (Way *et al.* 2015). It also leads to an increase in water use efficiency and a reduction in fluxes of surface latent heat (IPCC, 2013). A large number of studies have been published on long term free-air CO_2 enrichment (FACE) experiments which have fed into the growing body of evidence on how plants respond to atmospheric CO_2 increases such as nutrient uptake and accumulation, photosynthesis, stomata size and biomass production (Leakey et al., 2009, Norby and Zak, 2011, Ellsworth et al., 2012, Jin et al., 2012, De Kauwe et al., 2013, Tausz-Posch et al., 2013, Zhang et al., 2013). Plant responses to increased CO_2 are an important part of understanding how plants, both in an ecological and agricultural sense, will be affected by changes to CO_2 which are currently underway and experimental research and has also raised awareness of where the many uncertainties lie. Direct evidence of increased water use efficiency and photosynthesis rates are available from field experiments of plants growing under elevated CO_2. A doubling of CO_2 from pre-industrial concentrations has shown to increase net primary production of plant species by 20-25% in two-thirds of experiments (IPCC, 2013), however, not all plants responded in the same way. For example Ainsworthy and Long (2005) demonstrated trees proved the most responsive to increased CO_2 compared with herbaceous species, and Wang et al (2012) showed differing temperature treatments produce different results between different C_4 plant species, but C_3 species showed enhanced net photosynthesis and among these legumes had a greater increase in net photosynthesis than non-legumes. It is believed likely that the primary driver of the evolution of C_4 plant species occurred due to reductions in atmospheric CO_2 after the Cretaceous period (Begon et al., 2006) and so C_3 and C_4 plant species are likely to react differently to elevated CO_2 such as differences in growth rate and drought tolerance. It is clear that there are still many uncertainties as to how increased atmospheric CO_2 will affect plants' net primary production but the CO_2 fertilisation effect will lead to enhanced net primary production with uncertainties in the magnitude of this effect (IPCC, 2013).

1.1.2.4. Nitrogen deposition effects on plants and interactions with sulphur

As well as acceleration of the global carbon cycle as a result of increasing atmospheric CO_2, humans have also accelerated the nitrogen, phosphorus and sulphur cycles (Falkowski et al., 2000). Along with climate change and habitat conversion, atmospheric deposition of reactive nitrogen is one of the most important threats to biodiversity on a global scale (Sala et al., 2000). Changes to the availability of one of these elements influences biological productivity as well as the requirements and availability of other elements (Gruber and Galloway, 2008). Atmospheric deposition of nitrogen compounds as a result of fossil fuel combustion and agriculture saw a dramatic increase in Europe in the second half of the 20_{th} century (Galloway et al., 2004). Prior to the industrial era, the conversion of reactive nitrogen from non-reactive atmospheric nitrogen mainly occurred as a result of two natural processes, lightning and biological nitrogen fixation (microbial mediated processes convert N_2 into ammonia) (IPCC, 2013). Human creation of reactive nitrogen was at least two times larger in 2010 than the rate of natural terrestrial creation. The human creation of reactive nitrogen is caused mainly by the production of ammonia for fertilizer and industry as well as from combustion of fossil fuels and legume cultivation. It is also likely that $N0_2$ and N_20 emissions will increase from soils due to the demand for nitrogen fertilizers which agriculture is reliant on and the increasing demand for food/feed (IPCC, 2013).

Nitrogen is an essential component of living organisms. Despite its abundance in the atmosphere it is in short supply in a form which can be absorbed by plants and as a result plays a critical role in the control of primary production on earth. Without the availability of nitrogenous fertilizers which have increased hugely, large increases in food production over the past century to sustain the increasing global population would not have been possible (Gruber and Galloway, 2008). The increase in reactive nitrogen being released has strongly impacted on plants through direct foliar damage and therefore affected vegetation diversity (Hallingback, 1992, Pearson and Stewart, 1993, Krupa, 2003, Dise et al., 2011), acidification (Vanbreemen et al., 1982, Roelofs et al., 1985, Dise et al., 2011), susceptibility to secondary stress (Brunsting and Heil, 1985, Throop and Lerdau, 2004, Dise et al., 2011) and eutrophication (Bobbink et al., 1998, Suding et al., 2005, Dise et al., 2011). Communities or species which experience the most sensitivity to the chronic elevation of reactive nitrogen are those adapted to low nutrient levels, or species that are poorly buffered against acidification (Dise et al., 2011). There is evidence that nitrogen deposition affects many habitats showing changes in plant richness, abundance or composition and reductions in plant species richness (e.g. Jones et al., 2004, Mitchell et al., 2005, Nordin et al., 2006, Stevens et al., 2006, Bassin et al., 2007, Maskell et al., 2010, Edmondson et al., 2010).

Sulphur, like Nitrogen, has an acidifying effect on the soil and water and may lead to some of the same pathway changes. This causes difficulty in separating the effects in areas where the deposition of both the pollutants are high. The increase in sulphur and nitrogen may cause increases in acid resistant species and acid sensitive species may decline in areas affected by one or both of these pollutants. In Europe, sulphur deposition peaked in the 1980’s and has declined dramatically since then across the continent. There are, however, some soils in high impact ecosystems which have continued to show elevated levels of heavy metals and acidity and a reduced concentration of basic cations. This can have a synergistic effect with nitrogen deposition, causing the effects of nitrogen deposition to have stronger impacts in soils which have been depleted of basic cations (Dise et al., 2011).

It is clear that the increase in nitrogen deposition has strong effects on the environment and in addition with previous sulphur increases many habitats will incur lasting damage resulting in a serious threat to a large number of species and habitats. Therefore, it is reasonable to suppose that different distribution changes might be observed for species with different nitrogen and pH requirements.

1.1.2.5. **Habitat loss and fragmentation**

Land use change has been shown to cause habitat loss, fragmentation, and degradation, which in turn change the biodiversity of an area (Puetz et al., 2011). Landscape fragmentation has been shown to interrupt some of the key ecological processes, including seed dispersal (With and King, 1999), colonization (Collingham and Huntley, 2000) and gene flow (Neve et al., 2008). Human action has had a huge impact on the earth, affecting in some way all areas of land (Vitousek et al., 1997). Although many uncertainties exist as to the exact figure of how much natural habitat has been lost due to human activities, it has been shown that between a third and a half of the land surface on earth has been transformed or degraded by human activities (Vitousek et al., 1986). In 1997 figures included between 10-15% of the earth’s land surface being used for urban-industrial areas or row-crop agriculture and 6-8% having been converted to pastureland (Olson et al., 1997) and these figures are likely to have seen increases since then. This represents significant areas of habitat loss for a large number of species and even though these figures include many uncertainties, it is certain that this figure is large (Vitousek et al., 1997). The threat to species in biodiversity hot spots was quantified by Myers et al. (2000), showing that 25 biogeographically distinctive hotspots, which make up only 1.4% of the land surface on earth, contained as many as 44% of all species of vascular plant and 35% of all species in four vertebrate groups. Out of these 25 hotspots, no more than one third of their pristine habitat remains.

Fragmentation, which results in smaller populations with increased spatial isolation, causes risks of extinction to many plant species. This is due to effects such as inbreeding, genetic drift and gene flow on genetic diversity and fitness and this is particularly so with species which are already rare or endangered (Ellstrand and Elam, 1993). Some of these fragmented habitats, as land is converted for use by humans such as agriculture, will likely disappear resulting in total loss of some habitats. However, fragmentation events do not always result in these risks, and in some circumstances fragmentation appears to increase gene flow among remnant populations, breaking down local genetic structure (Young et al., 1996). The presence of scattered vegetation such as individual trees may facilitate the migration and gene flow in response to climate change as it provides connectivity across a fragmented landscape (Breed et al., 2011).

Current climate and climate change are important factors in the determination of the negative effects of habitat loss on the diversity and/or density of species (Mantyka-Pringle et al., 2012). Mantyka-Pringle et al. (2012) in a study which looked at the effects of habitat loss and fragmentation along with climatic conditions showed the effects of habitat loss and fragmentation were largest in areas which had high maximum temperatures and lowest in areas where average rainfall has increased over time. Although habitat loss and fragmentation by themselves have huge impacts on many species, with recent impacts that are stronger than responses to climate warming (Sala et al., 2000, Warren et al., 2001, Jetz et al., 2007), their relative impacts may switch over time, and climate change may become the largest contributor to population trends (Lemoine et al., 2007).

1.1.2.6. Habitat invasion and invasive species

In order for a species to spread into a new area, the species must be able to colonise the area, survive and reproduce and then spread more widely. In this regard, the lessons from invasion biology may help us to understand the likely long-term impacts of climate change. Due to human movement around the world, which often includes the transportation of plant material and soil, either deliberately or accidently, the number of non-native species in all geographical regions has risen hugely (discussed by Auffret *et al.*, 2014). However, although many species escape from locations such as gardens, they do not all succeed in reproducing and spreading; only a small number of the non-native plants, comparaed to the actual number plants growing outside their native range, are considered invasive (Richardson et al., 2000b, Kolar and Lodge, 2001). Research into which species have or may become invasive and which will not is of importance not only due to environmental impacts of invasive species, but also from an economic view point as control of invasive species is a costly process. Approximately $137 billion dollars each year is spent in the United States due to the major environmental damage and losses caused by non native species to the country (Pimentel et al., 2000).

Research into invasion biology is vast and there are a number of hypotheses in the literature as to why a species moves from a non-invasive state to an invasive state and how to predict which species will become invaders and which will not (Kolar and Lodge, 2001, Mitchell et al., 2006).

It is argued by some that when a species is introduced to an area outside of its native range, many of the pathogens and insect herbivores from its native range will not be present and therefore a reduction in natural enemies will provide the species with the ability to attain a greater abundance. This hypothesis is termed the enemy release hypothesis (e.g. Keane and Crawley, 2002, DeWalt et al., 2004, Torchin and Mitchell, 2004, Mitchell et al., 2006). Although many studies have been carried out showing the reduction in pests and diseases on non native species in the introduced range, not all species consistently show less damage from natural enemies than do the native resident species, and the process underlying biological invasion is likely not to be a simple enemy release relationship but a far more complex process, as reviewed by Colautti et al (2004).

A second hypothesis concerns mutualist species, a subject reviewed by Richardson et al. (2000a). When a species moves from its current range to a new location, it loses its original association with mutualist species. It is often therefore essential for the species to have this lost mutualist association replaced by different mutualist species in the new area in order for the species to establish and spread in the new location. This is termed the mutualist facilitation hypothesis (Richardson et al., 2000a). There are several categories of mutualist species which facilitate plant species establishment, growth and spread. These include animal aided pollination, seed dispersal by animals, mycorrhizal fungi and the symbiosis between plants and nitrogen-fixing bacteria (Richardson et al., 2000a). Some species when in a new habitat may not succeed in colonising the new site due to an absence of mutualist species which it depends upon (Nadel et al., 1992). There are three main plant groups (*Ficus, Yucca* and some orchids) which are highly reliant on specific pollinators and therefore, in the absence of these pollinators, the species will not be able to reproduce sexually (Bond, 1994). Nonetheless, the majority of plant species do not possess this specific interaction with single species and are associated with a number of different species which often are from wide taxonomic origins, and hence likely already to be present in the region of establishment (Richardson et al., 2000a).

The empty niche hypothesis suggests that the success of invaders is due to the species' abilities to acquire resources by avoiding competition. Species can take advantage of resources which are not utilised by current species and therefore leads to the species success (Mitchell et al., 2006). Within the species' native range this would mean that other species also utilise that resource and therefore the species is not able to proliferate as successfully in the native as opposed to the introduced range.

Like the empty niche hypothesis, the novel weapons hypothesis uses the argument that the success of invaders is due to the species' ability to acquire resources by avoiding competition. Some plant species produce root exudates, which may be relatively ineffective against other co-adapted plant species in the native habitat, but in the new habitat this may inhibit the growth of plants, giving the introduced species a competitive advantage (Callaway and Ridenour, 2004).

These factors may interact, and there are, of course, many more factors which will affect how and where species will become invasive. Some of these factors will be more influential than others with different species in different habitats. It is likely that a combination of factors will culminate in a species becoming invasive and factors such as climate, habitat, land use, the species currently present in a habitat, will enable them to establish. Whichever the specific or combined mechanism, increasing amounts of global movement of plant material, which increases propagule pressure, can be expected to give rise to increased changes to species composition and increased numbers of invasive species. Given the lessons of invasive species biology, it is valuable to consider the role of transport by humans in determining the distribution changes of species at otherwise 'natural' range boundaries.

1.2. Extinction of species

Extinctions have occurred throughout earth's history, and out of the estimated four billion species thought to have evolved over the past 3.5 billion years at least 99% are now extinct (Novacek 2001 but see Barnosky et al., 2011). Although species have and will continue to evolve and go extinct, current rates of species loss globally indicate that we may be heading into a mass extinction, something which has happened only 5 times in the past c. 540 million years (Barnosky et al., 2011). The estimated rate of extinction of species today is 100 to 1,000 times more than is considered natural (Rockstrom et al., 2009). Recovery from mass extinction episodes probably only occurs on a timescale of millions of years (Lu et al., 2006, Alroy, 2008) and therefore recovery from current biodiversity loss is not likely to happen on a timescale which is meaningful to people. The number of species which have been documented as extinct in recent history as a result of human influences is likely to be a large underestimation as the majority of species have not yet been formally described (Dirzo and Raven, 2003, Joppa et al., 2011). Predicting which species are likely to become extinct is important for conservation efforts although there is much variation with projected future extinction rates, primarily due to four factors: an uncertain degree of land use change, the level of climate change, a lack of understanding of species ecology, and variation due to different modelling approaches. Despite uncertainty, extinction rates are predicted to rise considerably during the 21st Century (Pereira et al., 2010). The prelude to species extinction is the disappearance of populations and large numbers of populations have been shown to have been lost (Hughes et al., 1997, Ceballos and Ehrlich, 2002). There are a number of factors influencing the extinction of populations and thence species, although the the main driver is ultimately humans. As such, efforts to conserve biodiversity are increasingly important.

1.3. Conservation and biodiversity loss

As discussed, humans may be in the process of generating the 6th mass extinction. Habitat loss (see section 1.1.2.5) and climate change (see section 1.1.2.3) are two of the largest threats to biodiversity today and much of the research which has been carried out on these subjects is important in determining how funds are best spent on conserving biodiversity and reducing losses. New protected areas, connectivity, managed relocation, ex situ conservation and adaptive management have all been identified as necessary elements of conservation strategies in light of climate change (Heller and Zavaleta, 2009, Mawdsley et al., 2009). In order to effectively conserve a species, it is likely to be necessary to conserve the genetic diversity of the species as this assists in the ability of a species to adapt both in the short and long term to changing environmental conditions (Jump et al., 2009, Doi et al., 2010).

Protected areas were the classical leading conservation tools prior to climate change gaining attention and they will continue to be an effective measure in conserving species in a warming climate. However, in order for species to cope with climate change, new protected areas will need to be created in most, if not all parts of the world (Hannah et al., 2007). Connectivity of protected areas (with migration corridors and climatic cross gradient corridors) is also an important part of conserving species as some reserves may not be large enough to sustain some species and ecosystem function in isolation (Hannah, 2011).

Although efforts in increasing protected areas and ensuring connectivity between populations and habitats is an essential part of conservation, there will still be some species which will not migrate rapidly enough or are unable to migrate to new suitable habitats. As such it may prove that in some instances assisted migration may be necessary (McLachlan et al., 2007). However, the movement of species outside of its native range is often considered a contentious issue. It is known that some species when introduced into new localities become invasive. The risk of introductions to new areas in order to assist migration becoming invasive is small, however, if the species does become invasive, effects on the local ecosystem could have large detrimental impacts on the local flora and fauna (Mueller and Hellmann, 2008). Ex-situ conservation measures will be important if all else fails and there is the need to re-introduce the species, but re-introduction of species into the wild has only had limited success (Fischer and Lindenmayer, 2000, Armstrong and Seddon, 2008). Both assisted migration and ex-situ conservation are generally only considered when other types of conservation action is not possible or has failed and therefore funding projects involved with protective areas and increasing connectivity between populations/habitats is likely to be the most effective method of conservation (Hannah, 2011). In north west Europe, investment in conservation efforts appear to have been paying off with the negative trend of biodiversity loss having slowed or partially reversed for some taxa (Carvalheiro et al., 2013) however, this may in part be to do with the economics of farming. Food production imports into north west Europe in countries where workers are paid low wedges will produce cheaper food and so less land will be needed for food production in north west Europe, reducing pressure on the natural resources in the area.

1.4. Plant life history

The responses of populations and species to all of these pressures are likely to depend on a number of their characteristics, such as their life histories. Plant life histories can be classified in a number of ways, one of which is the difference between being monocarpic or polycarpic. The former contains species such as many annual species, including weeds of arable crops, which grow from seed to mature plant then have a single, distinct period of flowering within their life and concentrate nearly all of resources into seed production and then the plant dies. In contrast, individuals of a polycarpic species have a number of flowering events within their life (which may merge together to give an extended continuous flowering), such as perennial plants which flower and bear fruit year after year and some annual which continues to grow and produces flowers throughout the year until it is killed by the first hard frost of winter or perennial species, and it continues to invest resources into survival and growth in order to ensure survival to reproduce again. Within long lived polycarpic species there is often a rhythm of flowering which ties in with the seasons as flowering is often triggered by day length, temperature or precipitation.

These differences in life history strategies are associated with a number of functional traits. Large seeded species, those with long lived leaves or dense wood have been shown to have slow life histories meaning that the population growth rates is influenced more strongly by survival than growth and reproduction (Adler et al., 2014). Species with fast life histories tend to be small seeded species, those with short-lived leaves, or soft wood (Adler et al., 2014). Looking at life history stage of species has also been used to explore a number of ecological patterns and evolutionary questions (e.g. Goldberg et al., 2001, Warner and Cushman, 2002, Williams, 2008, Muola et al., 2010, Hempel et al., 2013). Fast species, and those with effective dispersal mechanisms, are likely to extend their leading-edge range boundaries in response to climate warming more rapidly than are species with slow reproduction and limited dispersal.

1.4.1. Habitats and geology

There has been a number of habitat classifications put forward (Begon et al., 2006) and, as part of the UK Biodiversity Action Plan, a Broad Habitat classification was developed which provided 27 Broad Habitats in the UK such as calcareous grassland, broadleaved, mixed and yew woodland, rivers and streams, fen marsh and swamp etc (Carey et al., 2009). It is useful to be able to classify habitats as this provides much of the knowledge needed in order to assess habitat threats and changes over time if habitat types are mapped and assessed for degradation; if this information feeds into the legal framework providing protection for habitats under threat (JNCC, 2014). There are basic elements of habitat which are important to a species in order for the organism to be able to colonise an area and therefore find suitable conditions. As previously discussed in Section 1.1.2.3, climate is an extremely important factor in where plant species are able to colonise and there are also many human influences on the surroundings which influence the habitat. Soil is very important in determining where plants can and cannot grow such as pH, availability of nutrients, availability of soil moisture, soil structure and type etc, and the nature of the bedrock has strong influences on the overlying soil. There are many species of plant and animal which are typical of certain soil types and therefore typical of certain bedrock types (British Geological Survey) and the bedrock has a distinctive effect on vegetation patterns (Kruckeberg, 1969, Strahler, 1978). Although it is know that the bedrock strongly influences the overlying soil due to weathering, overlying soils can also be determined by superficial deposits which are made of sediments reworked during periods of climatic instability such as acidification, flooding and glaciations (Martignier et al., 2013). Soil type is of course a consequence of both the physical and biological systems, and soils under different vegetation types on the same bedrock can diverge markedly. Knowledge of the soil and geological requirements of species, and how they are influenced by climate, is important information if we are to understand the nature of the habitat available to a colonizing species, and hence the connectivity of the landscape through which it is spreading.

1.4.1.1. Ellenberg indicator values

Mapping the specific habitats of large numbers of species is difficult, and hence it is useful to use proxies for the requirements of each species. In Britain and many European countries, plant species have been assigned Ellenberg indicator values (EIV) which helps classify the habitat when a species list is compiled. The EIV can be used in research for many purposes, such as providing indications of overall change in the characteristics of plant species in areas, to aid in the comparison of habitats and vegetation and to assist in describing vegetation associations (Hill, 1999). A number of research papers have used EIV in their research for such purposes (e.g. Hawkes et al., 1997, Hill and Carey, 1997, Dzwonko, 2001, Jones et al., 2007, Delgado and Ederra, 2013).

The principle behind EIV is to be able to provide information using a certain range of tolerances that plants have, and therefore provide ecological niche information on where those species occur. The flora of a site provides a considerable amount of information on the ecological conditions of sites and the EIV encapsulate this information. The values are not direct measurements; e.g. EIV for soil pH, termed "reaction" is a numerical scale from 1-9, and not actual pH values. EIV scores are available for light (L), moisture (F), reaction (R), nitrogen (N), salt (S), temperature (T) and continentality (K) (Hill, 1999). However, generally only the first 5 of these 7 EIV are used regularly in Britain as T and K are considered unreliable in oceanic climates such as Britain (Hill, 1999).

1.4.1.2. Functional groups

In addition to the EIV proxies for the niche dimensions of species, it is useful to classify organisms for study using functional groupings when carrying out ecological studies as it aids the description of the function and structure of the ecosystem, and facilitates research into how different elements of the ecosystem respond to different environmental factors. Functional traits offer good insight into general predictive understanding of ecosystems and communities (Venable, 1992, Lavorel and Garnier, 2002, Wright et al., 2004, Moles and Westoby, 2006, McGill et al., 2006, Chave et al., 2009) and this trait-based approach is now being used for predictive purposes to answer many questions (Scholze et al., 2006, Shipley et al., 2006, Lavorel and Garnier, 2002, Laughlin et al., 2012, Diaz and Cabido, 2001, Eviner and Chapin, 2003).

Plant functional classifications have been a matter for debate since the 1960s and a number of different concepts and variations on classifications have been proposed by different authors. The differences in classifications lie in the characteristics of species they use to determine groups, such as: environmental resource use, phylogenetic origins, analogous genetic characteristics, biotic components of ecosystems that perform the same function/set of functions, morphology and physiology and groups of closely interacting species. Different authors have come up with different names for their systems but Smith (1998) has generally divided the systems into two sets of ideas: guilds (first used by Root (1967)), which are grouped according to which resource they use, and functional types (coined initially by Cummins (1974) for aquatic invertebrates), which are grouped according to how they respond to specified outside influences. There has, however, been much overlap in the way these two groupings have been used. This allows a simplified context specific way of grouping organisms in order to facilitate predications of dynamics of the systems, or components of these systems (Smith et al., 1998).

1.4.2. Plant dispersal

The ability of plants to disperse to new locations is essential for the success of any plant species, in the context of climate change. Species exhibit a wide range of adaptations to facilitate the movement of the seeds, and there are many structural adaptations to seeds and seed pods which aid their dispersal. These adaptations take many forms, including differing fruit colours, chemical compositions and sizes which attract animal dispersers, sticky surfaces and appendages adapted to attach to animals, morphological characteristics such as flat surfaces and small sizes to facilitate dispersal by wind, appendages which aim to attract ants, air pockets and waxy surfaces with allow flotation of the seeds, and thick tough surfaces in order to protect the seed when passing through an animal’s gut (Cousens et al., 2008). Some seeds themselves have no obvious dispersal mechanism or disperse initially in a ballistic manner but this will only throw the seeds a matter of a metre or so from the parent plant. Seeds are often of a small size, allowing them to be carried to new localities in mud that has stuck to an animal. Although many species have specialised dispersal mechanisms, the majority of dispersal events may not be carried out by the intended disperser or the seeds may have duel methods of dispersal such as seeds with wings which aid dispersal by wind may also float more easily and so are able to be carried to new locations by water. Many dispersal events also occur by means for which there is no seed adaptation, and it is merely by chance that the seed is carried to a new location. In principle, it may be possible to predict the trajectory of a dispersal event, even if the propagule is not obviously adapted for that method of dispersal, by estimating both the strength and direction of the vector over the duration of dispersal events (Cousens et al., 2008).

A number of factors are involved in where a plant propagule will land and whether it will be successful in germinating and maturing into an adult plant, of which habitat is likely to be particularly important. Hence, a number of dispersal modes tend disproportionately to deliver the seeds into potentially suitable habitat. For example, Carlo et al (2013) showed that the seeds of *Ilex aquifolium* and *Crataegus monogyna*, both bird dispersed plants which produce red fruit, disperse disproportionately to similar habitats to the parent plant. Despite a number of elaborate adaptations for dispersal, the most frequent distance of dispersal in most plant species is generally a very short distance, often directly under the parent plant (Cain et al., 2000). Although long distance dispersal events are considered rare, these events are likely to be the most important dispersal events in determining distribution changes (Nathan, 2006). These are however, very difficult to study as it is very difficult to track seeds long distances and these long distance dispersal events are rare. There are however a number of new methods which provide new insight into long distance dispersal of plant diaspores due to miniaturization of tracking devices (attached to vectors), genetic analysis, mechanistic model refinements and elaboration of stable isotope analysis (Nathan et al., 2003).

Humans have had large impacts on plant species distributions throughout history and this has seen acceleration in the rate of human mediated dispersal recently (Hodkinson and Thompson, 1997). Some plants dispersed by animals are being adversely affected due to human disturbance, causing the animals not to visit the plants when in fruit and disperse the seeds to new locations (Markl et al., 2012). Also, livestock which graze the grassland areas of Europe, and therefore have traditionally been important for the dispersal of many grassland species, have seen limitations in their movement due to land use changes and changes to the ability of livestock to roam (Auffret, 2011). Although the negative impacts of humans have had a large impact on species' distributions, humans are now one of the largest dispersers of many plant species, not only to new localities within countries but also on a global scale. In some cases, this dispersal is deliberate, as many aspects of our lives are reliant on plants such as crops, clothing, building materials, fuel, drugs and purely for our own enjoyment such as garden plants. We also act as dispersal vectors by accidently carrying propagules to new localities such as seeds stuck on clothing and footwear, ingestion and defecation, mud which contains seeds stuck to machinery and vehicles and accidental transport of seeds in other plant material such as pot plants (Cousens et al., 2008). Interest in human mediated dispersal has grown over recent years, in part due to the increase in non-native species to most parts of the world and the risk posed by invasive species which can have devastating effects on the native ecology. The tourist industry is seeing large numbers of people travelling globally, and is involved in the dispersal of many weed seeds carried on clothing and equipment (Pickering and Mount, 2010). Studies have shown that seeds can be carried 5 km or more on the shoes, socks and trousers of humans (Wichmann et al., 2009, Pickering et al., 2011). The link between spread of species and roads has also been studied as species often spread along road networks and vehicles can act as the disperser (Lavoie et al., 2007, Taylor et al., 2012, von der Lippe et al., 2013).

Human dispersal of plants has had large impacts on species compositions within ecosystems and distributions of species globally, but most of the research has concentrated on the negative impacts of humans dispersing plant propagules. As humans are now one of the most common dispersers of many plant species, it may be that this human mediated dispersal could facilitate the spread of native plant species and become the primary long distance disperser, potentially becoming the main means by which species can colonise new climatically suitable areas which the species would struggle to reach by natural dispersal.

1.5. Plant collectors and plant distribution data

Understanding changes to the distributions of species requires knowledge of past distributions. There has been a long history of plant collecting and much of the historical data that exists today regarding the distribution of plants is as a result of plant collectors.

Herbarium specimens, which often contain valuable information on collection location, and therefore provide distribution information, have been collected for hundreds of years as tools for identifying species. Within the collections of herbarium specimens at the Oxford University Herbarium, established in 1621, there are some of the oldest specimens in the world (Oxford University Herbarium website). The information contained within these herbarium specimens is used to aid the production of many publications such as monographs and floras and is often used in many areas of research. In more recent years the accuracy of where herbarium specimens were collected has increased dramatically with records now regularly giving GPS locations within 10 m of the collection point. The Botanical Society of Britain and Ireland (BSBI) plant distribution database contains information from a wide range of sources including herbariums and floras and so this historical collection of data is of importance to aiding in the knowledge of distribution of species in Britain as well as on a global basis. The plant distribution data and the BSBI will be discussed in more detail in the next section (Section 1.5.1)

1.5.1. Botanical Society of Britain and Ireland and plant distribution data

The Botanical Society of Britain & Ireland (formerly the Botanical Society of the British Isles, BSBI) is a long established charity dedicated to the study and conservation of wild plants, and the society can trace its origins back to 1836 when it was founded under the name Botanical Society of London. The society is involved in many areas of botany including training, research and the study of plants throughout Britain and Ireland, organisation of meetings, conferences and publications, but most relevant to the present study, it has co-ordinated the mapping of plant distributions in recent decades.

In the 1950s the Distribution Maps Scheme was launched and continues to this day. This is one of the longest running natural history distribution mapping projects in the world, being constantly updated and improved. This is carried out by mainly by amateur botanists, including vice-county recorders, volunteers and taxonomic referees and is a valuable resource to government bodies, conservationists and scientists with the data providing information on range, changes in distributions and abundance of all charophytes and vascular plants that occur in the British Isles. The Mapping Scheme resulted in the publication of the first Atlas of the British and Irish flora in 1962 (Perring and Walters, 1962) with all species mapped at the hectad scale (10x10 km square). This was followed by the New Atlas of the British and Irish Flora in 2002 (Preston et al., 2002) based on a repeat survey of hectads between 1987 and 1999, but covering all records in the following dateclasses: before 1930, 1930-1969, 1970-1986 and 1987-1999. There have since been two subsequent date classes , 2000-2009 and 2010-2019, and these will form the basis of the third atlas due to be produced around 2020. This data forms the basis of this thesis and is used throughout.

1.6. Knowledge gaps and objectives

Despite the range of literature available on environmental impacts of humans on the world's biota, as described above, there are still a considerable number of knowledge gaps. The following sections outlines some of these gaps and how this thesis aims to cover these areas.

1.6.1. Chapter 2: Northern range margin shift and how humans have impacted on dispersal

Despite considerable knowledge of the northwards range margin shifts of animals in the northern hemisphere, there is little conclusive evidence of latitudinal shifts in plant species distributions. It might be expected that plant species would be advancing further north or towards the cooler regions, here in Britain, as temperatures warm, but this has not been demonstrated, however with the BSBI plant distribution data available it is possible to assess changes to the northern range limits of British plant species.

The rates of range expansion (or retraction) might be expected to be affected by the attributes of species, but progress in this area has also been modest. There are a range of plant traits which might be expected to facilitate or impede the speed at which plant species are spreading at their northern range. As such, traits such as Ellenberg values and dispersal mode could help explain the changes of northern range margin of different plant species and so help understand changes which are occurring. Dispersal of plant propagules can broadly be split into two large categories, these being natural methods of dispersal (although there are also broadly speaking 3 large categories amongst natural dispersal: animal, wind and non-specialised) and human assisted dispersal. The BSBI data have been categorized for the two atlases as native and introduced occurrences (see chapter 2.4.1 for definition), the latter being records of a species growing in a location where humans are thought to have been responsible for its transport. No previous attempt has been made to contrast the dynamics of range margins of plants using records believed to be native and those which are considered introduced. This method of using the data may provide important information not only on how climate has affected plant distributions but the implications of how human mediated dispersal has affected the distribution of species.

1.6.1.1. Aims and hypothesis

Chapter 2 aims to determine:

- if species' northern range margins have shifted northwards.
- if the rate of movement in plants is similar to that of animals
- what effect introduced records has on the rate of northern range margin change
- whether "introduced" and "native" records at northern range margins persist over time
- whether plant traits can help explain the northern range margin shift

1.6.2. Chapter 3: Distribution infilling and habitat change: a case study using the Bee Orchid *Ophrys apifera*

The majority of research into distribution changes has concentrated on range margin shifts and changes in overall range size, and there is a lack of research on whether distribution infilling is taking place at the leading-edges of distributions, where species have usually been very localised in the past. Treelines have shown to have become denser in tree species, but there is a gap in the literature looking at the infilling of plant distributions away from treelines. Some habitats which were previously unsuitable for colonisation may have become suitable for colonisation in more recent years, due to climate warming. This may have facilitated the spread of some species into new areas and potentially, in some cases, into types of habitat which were not traditionally colonised by the species. The Bee orchid (*Ophrys apifera*) is the study species selected for this analysis because it seems likely to be exhibiting the effects of a warming climate. The BSBI county recorders have recently observed this species growing in a number of new locations, although there is no published research demonstrating either distribution infilling or shifts in habitat association, which might facilitate this.

1.6.2.1. Aims and hypothesis

The aims of chapter 3 are to determine if:

- Bee orchid populations are being observed in new locations within their former, broad-scale geographic distribution (infilling)
- the nature of the habitat within the sites can explain why Bee orchids are localised within most sites, especially on non-calcareous substrates
- long established Bee orchid sites differ from newly colonised sites, indicating a climate-driven niche shift that could facilitate infilling, and
- recently colonised Bee orchid sites are more likely to be on non-calcareous areas than calcareous areas compared to old sites using BSBI data, again testing whether a habitat change is enabling the species to infill its distribution.

2. Northern Range Margin change

2.1. Abstract

There is published evidence that changes in climate have caused the distribution of many animal species globally to change. Although there is published evidence that plant species have moved to higher altitudes, there are few studies on poleward shifts in the distribution of plants. In Britain the Botanical Society of the British Isles (BSBI) (and before that as the Botanical Society of London) have been collecting distribution data for British plant species distributions since the early part of the 20th century. Additionally, records have also been collected from a variety of other sources including herbarium specimens and publications dating back to the fifteenth Century. These data have been used to calculate the northern range margin of southerly distributed British native plant species, comparing an earlier (pre 1930) and later (1984-1999) time period. Three main conclusions were drawn from the research. 1: On average southerly distributed plant species in Britain are retracting their distributions at their northern range margins. 2: More species are contracting than expanding their overall distribution sizes. 3: introduced populations may facilitate future north shift of species as they often occur further north than the northernmost populations considered to be native. These results suggest that climate is not the predominant driving factor determining changes at northern range margins in Britain. Factors such as agricultural intensification and, to a lesser extent, urbanisation are likely to be stronger driving factors in determining distribution shifts, and dispersal by humans is likely to be the predominant means of long-distance movement.

2.2. Introduction

Due to current climatic warming, distribution change research has been the focus of many studies as the changing climate has widespread implications for all forms of life. Some studies look at the expansion and contraction of species distributions using fossil records, which follow ancient upheavals in the climate (Graumlich and Davis, 1993, Pitelka et al., 1997, Hewitt, 1999). There is evidence that temporal variation in climate can cause adaptive evolution of species over long time periods (Reu et al., 2011, Franks et al., 2012) and a species can exhibit adaptive evolution with population differentiation in relation to climate tolerance across current day ranges as is discussed by Shaw and Etterson (2012). Species introduced to areas outside of their native range have been subject to an increase in research, questioning why some species became invasive and alter the native biota, and other species never seem to reproduce or spread (Blossey and Notzold, 1995, Williamson and Fitter, 1996, Peterson, 2003, Maron et al., 2004, Callaway and Maron, 2006, Dietz and Edwards, 2006, Broennimann et al., 2007, Elliott and Cornell, 2012). Range changes of native species had also become an important topic for research with anthropogenic climate change increasing temperatures, which organisms may then either adapt to or move to more favourable conditions (Parmesan, 1996, Parmesan et al., 1999, Warren et al., 2001, Thomas et al., 2001, Kullman, 2002, Root et al., 2003, Hickling et al., 2006, Parolo and Rossi, 2008, Hofgaard et al., 2009, Erschbamer et al., 2009, Melles et al., 2011, Chen et al., 2011, Mair et al., 2012). These shifts may cause the extinction of species (Thomas et al., 2004, McClean et al., 2005, Malcolm et al., 2006) and changes to temperature and precipitation have been implicated in the extinction of a number of frog species, such as *Bufo periglenes*, the golden toad from Costa Rica, although introduced pathogens have also had a strong influence on frog species decline (Pounds et al., 1999, Pounds et al., 2006). Climate change has and will continue to affect the survival of organisms, whether directly or in many cases indirectly as a result of changes to the ecology of an ecosystem and range of a species. This means research must be done on how these changes will occur in order to provide the best advice on how to conserve habitats and species. Most species are not found globally and occur in small geographical range sizes and therefore have a measurable range margin (Gaston, 1996). The range margin can be used to assess if there are changes occurring and if this can be attributed to climate change.

Animal taxa in the northern hemisphere are shifting their distributions north as would be expected as the climate warms (Hill et al., 1999, Parmesan et al., 1999, Thomas and Lennon, 1999, Hickling et al., 2006, Chen et al., 2011). A method that has proved successful in demonstrating northward shifts has been to compare the average of 10 most northerly records from an earlier and a later time period and then compare the two averages to see if a shift has occurred. Hickling et al. (2006), who used this method and provided the most complete analysis to date, demonstrated that there is a significant northward shift in the northern range margin of a large number of animal taxa from differing taxonomic groups in Britain, including damselflies, lacewings, butterflies, spiders, freshwater fish, mammals, woodlice, birds and millipedes. Most plant based range change studies have examined altitudinal change (e.g. Grabherr et al., 1994, Grabherr et al., 2000, Kullman, 2002, Pauli et al., 2007, Erschbamer et al., 2009) or relative changes in range size (Telfer et al., 2002). Only two studies of the distribution changes of multiple plant species in Britain have been published to date, these being Doxford and Freckleton (2012) and Groom (2013). Doxford and Freckleton (2012) showed that most species only colonised areas adjacent to the existing distribution and only if suitable habitat is available; short distance dispersal is the main method of spread. A climate signal was also evident in just under half of the species used in the study with rainfall and temperature having separate affects on the species distributions. The data used in this paper did not differentiate between native and introduced records for native species, or apparently between native and introduced species, the latter potentially expanding their distributions in all directions (including northwards) as a result of their recent establishment, rather than because of climate change. Furthermore, introduced species were seriously under-recorded in earlier time periods. Groom (2013) took a subsample of more consistent data, and examined poleward movement of British native plant species, using the centre of mass of each species distribution to detect the range change rather than the leading northern edge. Groom split Britain into 4 geographic regions (Scotland, Wales, north England and south England) for analysis and species, with expanding ranges analysed separately to species which are declining in their ranges. The study looks at the direction of movement of each species central mass which picks up which direction the central mass is moving. Groom demonstrates that there is a small but significant movement north in species with expanding ranges (which is to be expected because most plant species have southerly distributions) but not with species with declining ranges. There is little if any evidence of a climate signal in this study, however. Neither of these papers explicitly examines changes to the distribution margins of plants in a similar way to previous studies of animal species. The study in this chapter I apply a method similar to that used by Hickling et al (2006) to test whether the northernmost range

margins of southerly-distributed plant species in Britain are advancing northwards, with the warming climate.
Another aspect of plant movement relates to how humans move plants around the country. Many of the native plants in Britain are deliberately or accidently introduced to areas outside their natural range, allowing them to spread via seed or vegetative propagule to new areas. This facilitates their spread and can give an increased rate of spread for many of the species, as can be seen in Dehnen-Schmutz et al. (2007) which demonstrates that exotic species are more likely to become established if trade in these species is increased. Incorporating records that are considered introduced into an area would provide information as to whether humans are the dominant method of dispersal to new areas and facilitate colonization in areas which would not be possible by natural means. Additionally the 10 most northern native records and the 10 most northern introduced records from both time periods can be compared to see if the records are persisting.

The Botanical Society of Britain and Ireland’s (BSBI) distribution database possesses data for all species occurring Britain and Ireland was used to create ‘The New Atlas of the British and Irish Flora’ (Preston et al., 2002a).This data was used to assess changes in southerly distributed plant species northern range margin in Great Britain. The analysis was carried out twice, once including and once excluding records considered introduced.

2.3. Aims

To determine:

- if species’ northern range margins have shifted northwards.
- if the rate of movement in plants is similar to that of animals
- what effect introduced records has on the rate of northern range margin change
- whether “introduced” and “native” records at northern range margins persist over time
- whether plant traits can help explain the northern range margin shift

2.4. Method

2.4.1. North range margin shift

Only fully checked and verified data from the Vascular Plant database (VPDB) of the BSBI were used for analysis in this chapter, which includes all records used to produce the maps in the New Atlas of the British and Irish Flora (Preston et al., 2002a). This atlas was organised so that species records fell into three date classes, these being pre 1970, 1970-1986 and 1987-1999. Additionally all records are classified as either native or introduced to the 10 x 10 km square, (here on in referred to as 10 km square). A 10 km square which was classified as 'native' according to the atlas when one or more records for that 10 km square was considered to have occurred naturally without human assistance. A 10 km square which was considered 'introduced' in the second atlas is a 10 km square where one or more occurrences of a species in that 10 km square were considered to have occurred there due to human assistance. If a 10 km square is classified as 'introduced' then that means that no 'native' records occur within that 10 km square. Whether a species has been introduced is derived from information supplied by vice-county recorders combined with other sources of literature such as floras (see p 10-11 Preston et al., 2002a). The set of criteria established and followed in order to extract a set of species for use in this study are:

- Species are southerly distributed: Most 10 km native squares should occur south of the Scottish border with a cut-off level of 5 native squares occurring north of this boundary
- Species must have no more than a third of the 10 km squares recorded as introduced. The introduced 10 km squares can occur anywhere in Britain
- The species must occupy 10 or more 10 km squares in both date classes in mainland Britain

The application of these criteria resulted in 196 taxa with a measurable northerly range margin in Britain.

2.4.2. Data filtering and date classes

Date class 1 (DC1) includes all records pre 1970 and date class 2 (DC2) spans from 1984-1999. These dates correspond roughly to the New Atlas of the British and Irish Flora (Preston et al., 2002a) date classes. However they do not exactly correspond. A number of problems were encountered when initial analysis of the data was carried out, given that there appeared to be inconsistencies between the maps of some plant species, for some date classes, using the raw data when compared with the maps in the New Atlas of the British and Irish Flora (Preston et al., 2002a). Initially it was decided that the date classes 1930-1960 and 1987-1999 would be used as these dates correspond to collecting periods for the Atlas of the British Flora (Perring and Walters, 1962) and the New Atlas of the British and Irish Flora (Preston et al., 2002a). From here on in the Atlas of the British Flora (Perring and Walters, 1962) will be referred to as the "first atlas" and the New atlas of the and Irish British flora will be referred to as the "second atlas".

The data for analysis were split into two classes, pre 1970 and 1984-1999, because the underlying data were not exactly consistent with the two Atlas recording periods; for reasons discussed below. There were several elements to the data which caused problems with analysis and so the data had to be cleaned several times and repeatedly checked before it was ready for the final analysis. Some aspects of the data, which were not known prior to analysis, meant that the distribution would not have accurately represented species distributions at their northern range in an earlier and later time period. The following process was carried out in order to ensure the data used were as close to the new atlas maps as possible. Two example species have been mapped to show the progression of how these following steps cleaned the data in order to provide distribution data which gave unambiguous northern range margins to be analysed (Figure 2.1, 2.2).

Steps of data cleaning

1) Once each species data were extracted from the VPDB BSBI database all Irish records and records from Channel Islands were removed as these were not to be used in analysis (Figure 2.1 a,e and Figure 2.2 a,e).

2) Within the data were two columns, one for “Ident” (Identification) and one for “Status” (native or introduced; see below). The Ident column was coded according to whether the species identification was considered correct in the record or whether there was doubt over its identification (e.g. dubious (needs confirmation), misidentified, hybrid etc.). The Status column was coded according to whether it was considered native (coded 1) or introduced (all other numbers) (e.g. deliberate introduction, naturalised escapee, migrant, casual, surviving but not spreading etc.). It was advised that if there was no code in the Ident column it could be assumed it was correctly identified and a native occurrence. All introduced records and records with doubt over their identification were removed which left those records classified as correctly identified and native and those with the Ident column left blank which is discussed in the following paragraph (Figure 2.1 b,f and Figure 2.2 b,f).

3) Once mapped it was noted that some species distribution maps did not match the second atlas maps with records appearing further north than expected. Some records which had not been assigned an Ident status had been entered after completion of the second atlas into the VPDB database and these records had not yet been assigned a status. David Pearman (ex-chair of BSBI Records and Research Committee (retired Feb 2014) and co-author of the New Atlas of the British and Irish Flora (Preston *et al.*, 2002)) was contacted to establish the status of any northern records which did not match 10 x 10 km squares from the new atlas distribution maps. Records which fell in the southern or middle part of a species range were not queried as these would not affect the northern range margin of the species. David Pearman classified many of the additional northern records (i.e. in the data but not on the published maps) as incorectly identified, in which case they were removed, but new correctly identified native records were retained (e.g., new records collected during the second data period, but added to the database after the second atlas had been published) (Figure 2.1 c,g, and Figure 2.2 c,g).

4) It was found that some species still showed large differences between the distributions mapped from extracted data and the second atlas maps of the species, particularly in the earlier date class (1930-1960). It was noted that many records from the VPDB BSBI database had collection dates which span many years for a single record. Therefore, if you were to use data from 1930-1960 then a record that possessed a date range for collection of 1920-1950 would be excluded from analysis but these data make up an important part of the earlier date class distribution; excluding them would give an inaccurate representation of a species distribution in the earlier time period. The second atlas used pre 1970 as their earlier time period and, as a large number of records in the database had a collecting date of 1500-1969, it seemed appropriate to use the same earlier date class as the second atlas. The records with a collecting period range of over 400 years (1500-1969) was data that when input into the VBDB database did not have an exact date of collection but a latest possible date of collection was known and therefore a wide collecting period date was allocated to all this data. Note that Doxford and Freckleton (2012) used a date class “1930-60” for distribution records, but did not provide information on how this period in their analysis relates to the underlying data. The second atlas includes two later date classes, 1970-1986, and then 1987-1999. After the underlying data had been extracted, it was noticed that some records were allocated to a time period which spanned these two periods: the start of the date class starting just before 1987, in some cases. Expert advice provided by the BSBI informed us that these data would have been included in the 1987-1999 data for the purposes of the atlas. Therefore, to ensure that the data were entirely consistent, the second date class was extended to 1984-1999. The species were again mapped in order to check the distributions closely matched those found in the new atlas (Figure 2.1 d,h and Figure 2.2 d,h). The above method of extracting and checking the data had to be repeated for the re-extracted data with the expanded date classes. This step added more records to the analysis which more accurate reflected the distributions of the earlier date class in the New Atlas of the British and Irish Flora as can be seen in Figure 2.1d.

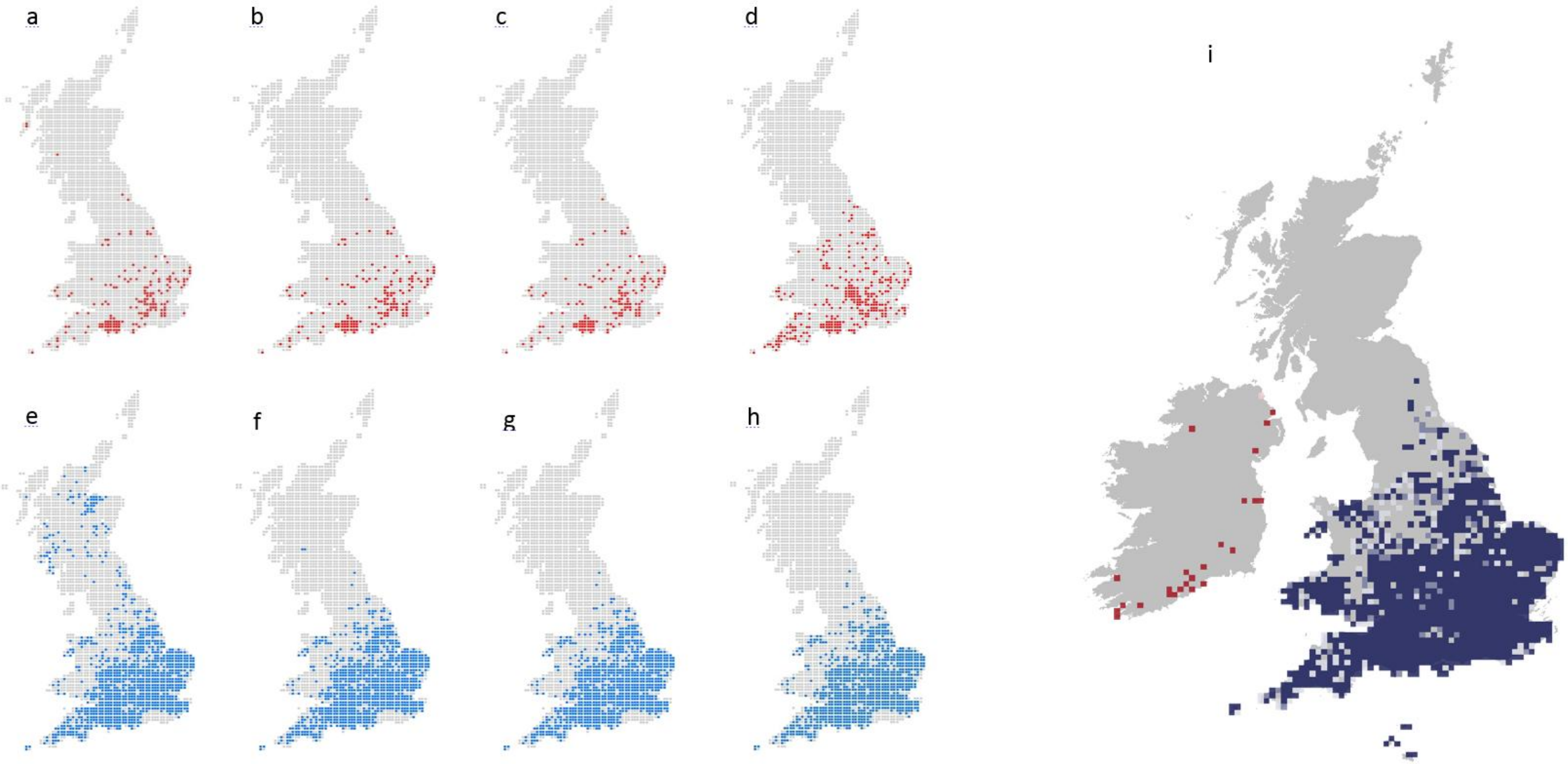


Figure 2.1: Distribution maps of *Epilobium tetragonum*. a) DC1 showing distribution after step 1 of data cleaning, b) DC1 showing distribution after step 2 of data cleaning, c) DC1 showing distribution after step 3 of data cleaning, d) DC1 showing distribution after step 4 of data cleaning, e) DC2 showing distribution after step 1 of data cleaning, f) DC2 showing distribution after step 2 of data cleaning, g) DC2 showing distribution after step 3 of data cleaning, h) DC2 showing distribution after step 4 of data cleaning, i) map of *Epilobium tetragonum* taken from New Atlas of the British and Irish flora (Preston *et al.* 2002)

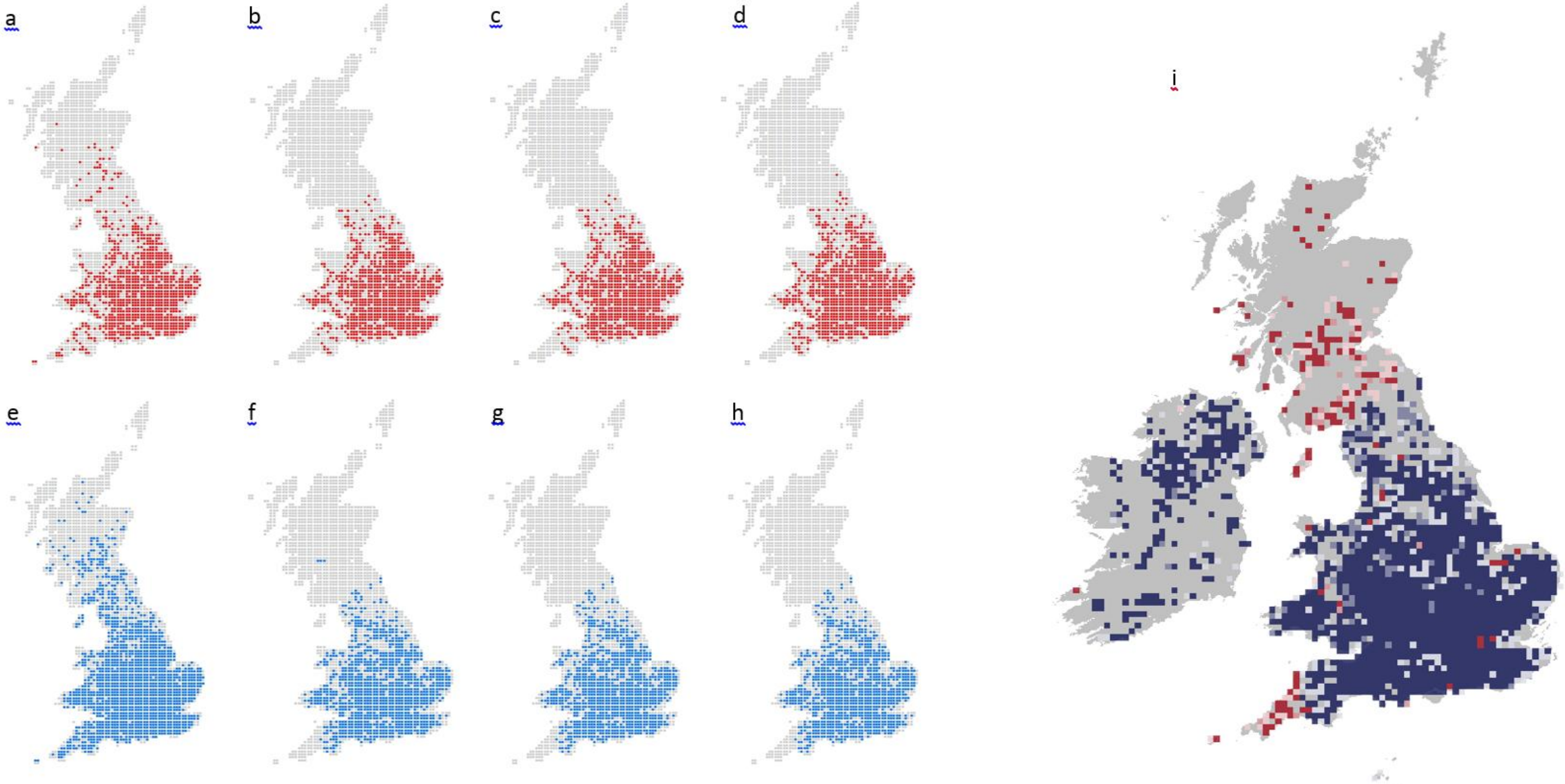


Figure 2.2: Distribution maps of *Lysimachia nummularia*. a) DC1 showing distribution after step 1 of data cleaning, b) DC1 showing distribution after step 2 of data cleaning, c) DC1 showing distribution after step 3 of data cleaning, d) DC1 showing distribution after step 4 of data cleaning, e) DC2 showing distribution after step 1 of data cleaning, f) DC2 showing distribution after step 2 of data cleaning, g) DC2 showing distribution after step 3 of data cleaning, h) DC2 showing distribution after step 4 of data cleaning, i) map of *Epilobium tetragonum* taken from New Atlas of the British and Irish flora (Preston *et al.* 2002)

2.4.3. Calculating the northern range margin

An assessment of northwards shift was calculated by extracting the 10 most northerly 10 km square records (on the Ordnance Survey grid) from DC1 and DC2 for each species and the mean was calculated for each date class. The difference between the mean of DC1 and DC2 is the range margin shift of the northern range margin. Two shifts were estimated for each species, one using native only records and one also including records considered introduced. Wilcoxon signed rank tests were carried out to determine if there was a significant shift of the northern range margin of the species used in the study. The raw data were not normally distributed and so in an attempt to transform the data into a normal distribution it was transformed using $\log_{10}$ and square root but neither was successful, therefore it was decided to use a non-parametric statistical test.

2.4.4. Phylogenetic influences

It is important to know if related species change their distributions in similar ways, perhaps for reasons other than responding to climate change. Therefore, analysis was also carried out at the family level rather than species level. This was done as it transforms the initial data into values which are more statistically independent than the original data as some species will be more closely related than others. Ideally an independent contrasts method of testing phylogenetic influences would have been preferred but analysis was completed prior to the publication of a full phylogeny of UK plants which was completed late 2012 (Durka and Michalski, 2012). The method used to test if results remained the same at the family level was to take the average northern range margin for each family, calculated by averaging the northern range margin of all southern species in the family for each date class. There are some families represented by only one or two species and these species had to be excluded from this family level analysis. Analysis was carried out twice, once using families containing a minimum of three species (Family 3) and once using families with a minimum of five species (Family 5).

2.4.5. Accounting for recorder effort

It is recognized that there is often biases in recorder effort over time (Dennis et al., 1999, Rocchini et al., 2011). As such, recorder effort must be taken into account when carrying out any analysis of distribution data over time. In order to take this into account, a similar method to Hicking et al. (2006) was employed. The number of species recorded in each 10 km squares was counted for DC1 and DC2. These are classified into two levels of recorder effort and these were “recorded” and “well recorded”. Recorded squares were classified as those squares that contained records of 1 or more plant species for both date classes; those that failed these criteria were excluded from analysis. Well recorded squares were those that that possess at least 10% (281 spp) of all native British plant species. 37 10x10km squares failed to meet the criterion for recorded squares and 618 squares failed to achieve the well recorded category criterion, and were excluded from the respective analysis. These squares were mainly Scottish squares or squares that fell on the coast (Figure 2.3) and may be areas which do not possess ≥10% of the British flora, but as most of the records used in this analysis are not present in these squares it did not have a large effect on the results.

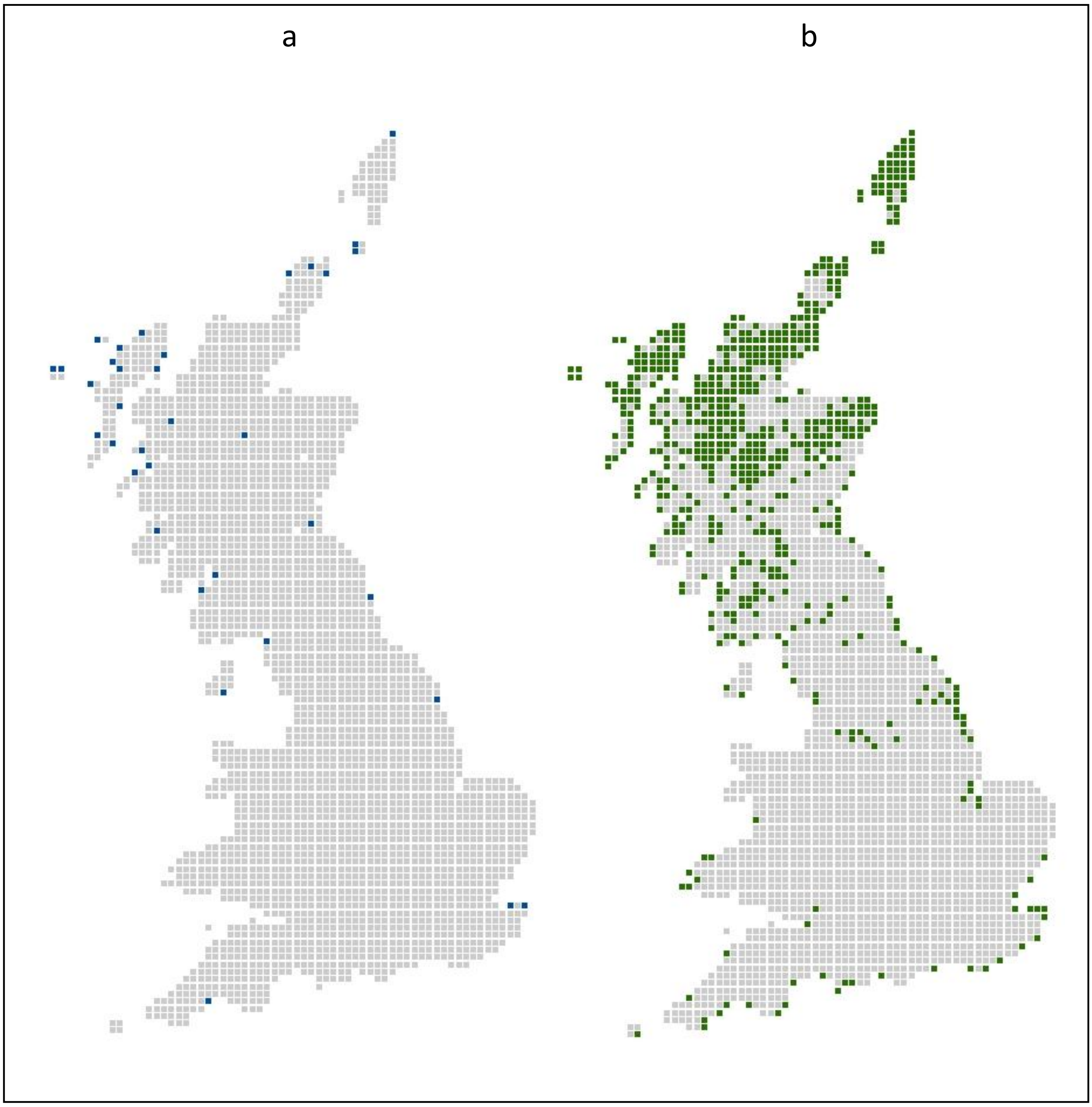


Figure 2.3: Maps showing 10x10 km squares with limited recorder effort: a) squares with <1 British species recorded in one or both of the date classes in blue (not Recorded squares), and b) squares with <10% of British species recorded in one or both of the date classes in green (not Well Recorded squares)

2.4.6. Ellenberg values

Ellenberg values for light, moisture, nitrogen, reaction and salt were available for all species from PLANTATT (Hill et al., 2004a). In order to determine if any of these traits explained the shift in northern range margin, Spearman's rank correlation between Ellenberg values and northern range margin shift was carried out. The analysis was repeated four times: for native only records, including introduced records, and for the family-level analyses, Family 3 and Family 5.

2.4.7. Dispersal

The mode of dispersal for each taxon was assigned based on seed morphology and literature searches, identifying the commonest method of short distance and commonest mode of long distance dispersal (Table 2.1, Appendix II). Of course, the majority of dispersal propagules will fall directly below the parent plant (Cousens et al., 2008) but a large proportion of plant species has adaptations which will aid longer-distance dispersal to new sites. The method of dispersal assigned to each taxon was the commonest method of long distance dispersal, as this classification reflects the longest likely dispersal event. For some species it was not clear, based on the available literature what dispersal method was most likely to be used and so these were classified as “Unknown”. Dispersal method was split into long and short dispersal so that the analysis could be done using both dispersal modes. It is largely unknown how far an individual propagule is likely to travel as there are a large number of factors involved in a dispersal event as is discussed in section 1.4.2. However, some dispersal types are likely to be able to transport a propagule further than others. As such a “long” and “short” classification was created. Species were assigned to “long” dispersal if their propagules may travel a hundred or more meters away from the parent plant, including dispersal by animals such as birds or large mammals (highly mobile organisms), rivers carrying the seed down waterways, or tiny dust like seeds are carried on the wind for long distances. Plant species were allocated to the “short” dispersal class if their seeds normally travel only a few cm or meters away from the parent plant, examples including ants carrying seeds, ballistic seed dispersal mechanisms, large seeds with small wings, or seeds which merely drop and roll. A Kruskal-Wallis rank sum test was performed using the dispersal classes to determine if there was a pattern between species which advanced or retracted at the northern range margin and dispersal method. Human dispersal was considered in relation to “native” and “introduced” records of each species in section 2.4.1.

Table 2.1: Number of taxa in each dispersal type and dispersal types likely length of travel

Dispersal type	Example	Long or short dispersal	Number of species
Seed/veg: Bird (external)	Aquatic seed (stick to water birds feathers and legs)	Long	2
Seed/veg: Water	Buoyant seed	Long	19
Seed: Ant	Eliasomes	Short	8
Seed: Ballistic	Explosive seed pod	Short	4
Seed: Bird (internal)	Fruits containing seeds	Long	21
Seed: Gravity only	No explicit means of dispersal	Short	61
Seed: Mammal (external)	Burr	Long	8
Seed: Mammal (internal)	Nuts caches by rodents	Long	2
Seed: Wind (long)	Light seeds with arils	Long	29
Seed: Wind (short)	Parachute only	Short	16
Veg: Attached spreading	Stolons	Short	6
Veg: Detached fragments	Regeneration from fragments	Short	6
Unknown		Unknown	14

2.4.8. Persistence

In order to assess how long populations are persisting at the northern edge of their range with and without humans as a disperser, the 5 most northerly 10 km squares for data which was classified as introduced in the BSBI database, and the 5 most northerly 10 km squares for data which was classified as native in the BSBI database were extracted for DC1 and DC2 for each species with ≥5 introduced records. This gave two northern range margins for each data class, one for introduced 10 km squares and one for native 10 km squares. These 10 km squares were compared to data from DC2 for introduced and native records to determine if sites persist between the two time periods or if the northern most sites are normally transitional in their occurrences. The number of 10 km squares that were persisting between DC1 and DC2 for native only 10 km squares and including introduced records were compared to determine if native or introduced 10 km squares were most likely to persist. This analysis was then repeated using the 10 most northern 10 km squares.

2.5. Results

2.5.1. Northern range margin shift

196 taxa were analysed for northern range margin shift. Results from analysis using recorded and well recorded data for each date class were very similar (see Table 2.2 and Figure 2.4), indicating that the relative positions of range boundaries were not strongly dependent on recording effort.

Table 2.2: Correlation coefficients for comparisons between recorded and well recorded northern range margins (n=196)

	R^2	p
DC1 native, recorded v well recorded	0.9914	<0.0001
DC2 native, recorded v well recorded	0.9966	<0.0001
DC1 inc. introduced, recorded v well recorded	0.9938	<0.0001
DC2 inc. introduced, recorded v well recorded	0.9953	<0.0001

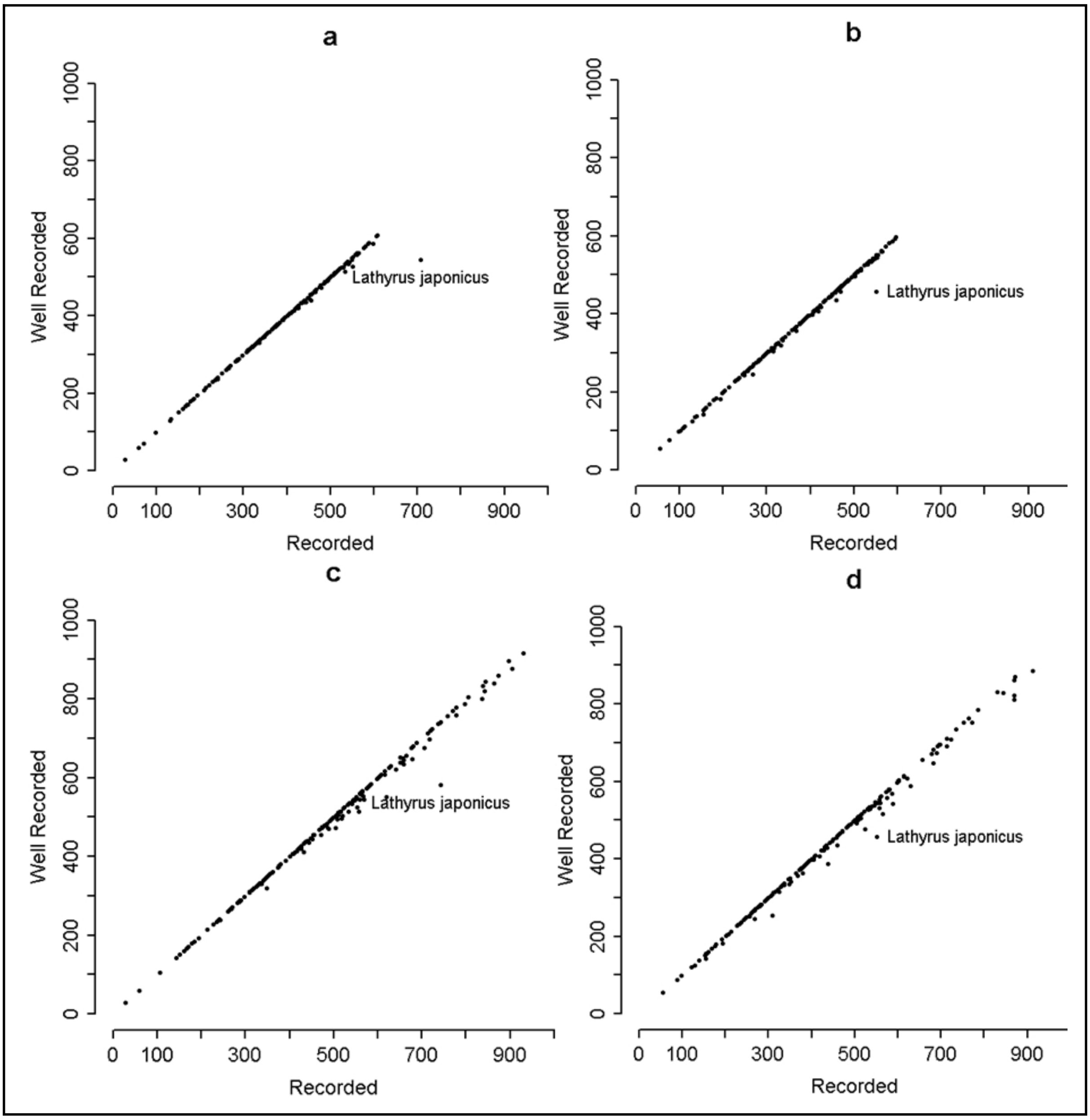


Figure 2.4: Scatter plots showing northern range margin (km north on UK Ordnance Survey grid) of taxa on the x and y axis, plotting results from recorded against well recorded squares for a) native only records for DC1, b) native only records for DC2, c) incorporating introduced records for DC1, d) incorporating introduced records for DC2.

Using native only (as defined by the BSBI) recorded records the northern range margin of 133 taxa retracted south, 59 taxa advanced north and 4 taxa were unchanged and there was a significant difference between date class 1 (DC1) and date class 2 (DC2) (Wilcoxon signed rank test V = 14413.5, *p*=<0.0001) with the average shift being south (mean= -29.10, SD = 56.48, max 101 km, min: -308 km) (Figure 2.5a). Using native well recorded records 134 taxa retracted south, 58 taxa advanced north and 4 taxa were unchanged and there was a significant difference between DC1 and DC2 (Wilcoxon signed rank test V = 14526.5, *p*=<0.0001) with an average shift being south (mean= -29.08, SD = 55.56, max 101 km, min: -308 km) (Figure 2.5b). Incorporation of introduced records for recorded records meant that the northern range margin of 143 taxa retracted south and 53 taxa advanced north and there was a significant difference between DC1 and DC2 (Wilcoxon signed rank test V = 15305, *p*=<0.0001) with the average shift being south (mean= -48.60, SD = 97.97, max 279 km, min: -473 km) (Figure 2.5c). Incorporating introduced well recorded records meant 144 taxa retracted south and 52 advanced north and maximum expansion and there was a significant difference between DC1 and DC2 (Wilcoxon signed rank test V = 15481, *p*=<0.0001) with the average shift being south (mean= -46.11, SD = 95.87, max 279 km, min: -473 km) (Figure 2.5d).

Regardless of whether only native records were used or if introduced records were incorporated, the overall change of the northern range margin for southerly distributed British native plant taxa remained southwards.

To avoid repetition, all analyses from here on use only the recorded data as the data and results when using recorded and well recorded squares were so similar.

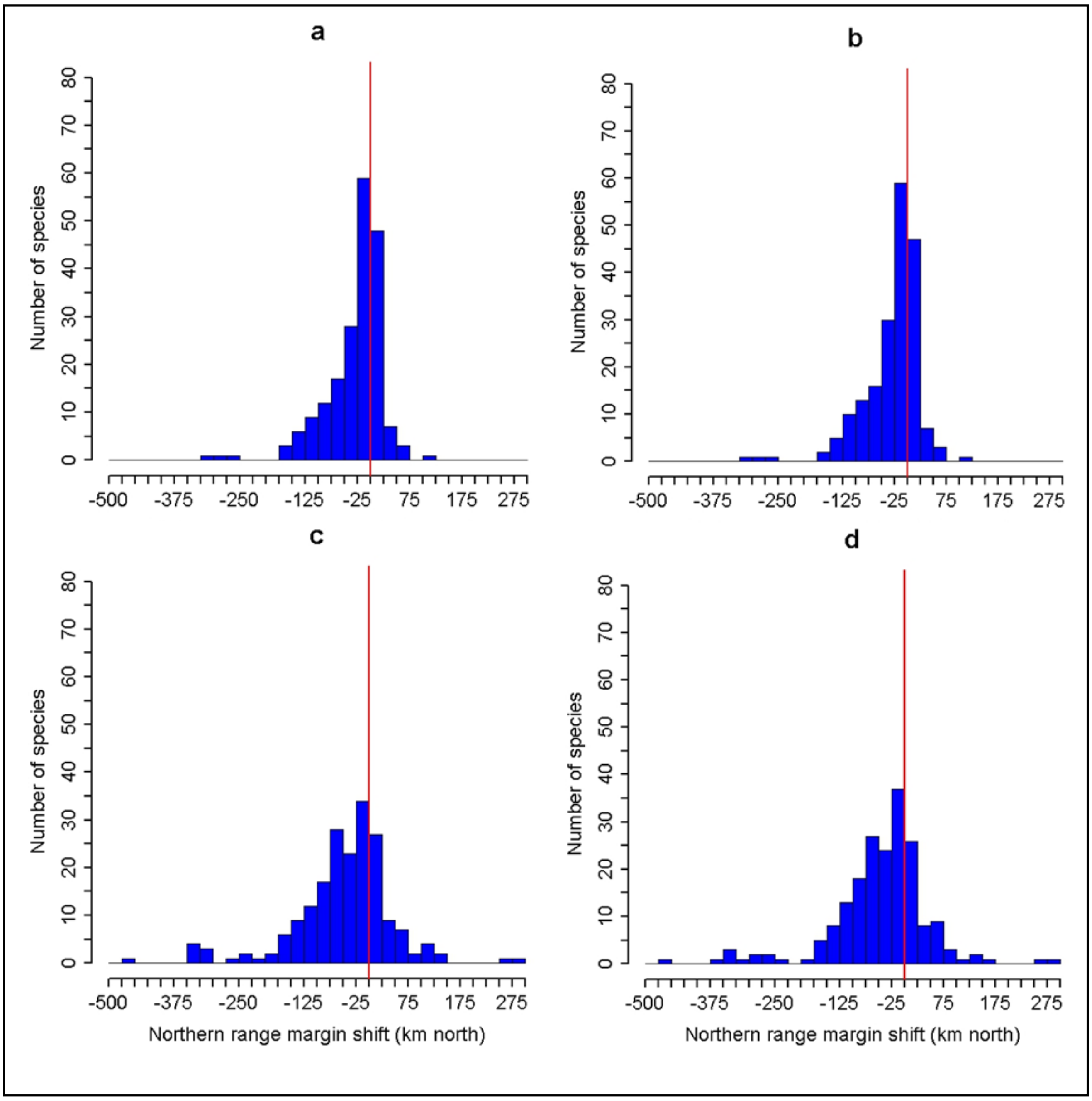


Figure 2.5: Histograms: Northern range margin retraction southwards (negative values) or advance northwards (positive) for a) native only records using recorded squares, b) native only records using well recorded squares, c) incorporation of introduced records using recorded squares, d) incorporation of introduced records using well recorded squares. Red line indicates 0 km shift.

2.5.2. Phylogenetic influences

It is important to know if analysis is robust at the family level to ensure that the overall conclusion is not driven by a few species-rich groups. When analysis was carried out using all families with a minimum of 3 species, a total of 22 families was included in the analysis, incorporating 149 species from the original 196. The 47 species which were excluded spanned 39 families. When analysis was carried out using all families with a minimum of 5 species, a total of 11 families was included in the analysis, incorporating

113 species from the original 196. The 83 species excluded using this criterion spanned 50 families. There was a significant difference between DC1 and DC2 for the minimum of 3 species per family level analysis for native taxa (Wilcoxon signed rank test V = 252, *p*=<0.0001) with the average shift being south (mean= -35.15 km, SD = 24.23 km, max = 5.33km, min = -88.50 km) and there was a significant difference between DC1 and DC2 for introduced records (Wilcoxon signed rank test V = 245, *p*=<0.0001) with the average shift being south (mean = -50.52 km, SD = 39.84 km, max = 46 km, min = -156.7 km). There was a significant difference between DC1 and DC2 when analysis was carried out using a minimum of 5 species per family for native only data (Wilcoxon signed rank test V = 66, *p*=<0.0009) with the average shift being south (mean = -36.80 km, SD = 21.67 km, max = -9.60 km, min = -88.50 km). The same analysis when including introduced data also gave a significant difference between DC1 and DC2 (Wilcoxon signed rank test V = 66, *p*=<0.0009) with the average shift being south (mean = -59.30, SD = 37.83, max = -11.44 km, min = -156.7 km). Thus, the family-level analyses were consistent with those that treated individual species as data points. With a little more time it would good to repeat the phylogenetic analysis using the phylogeny published by Durka and Michalski (2012) which was published after completion of this chapter. However, I believe that as results obtained from the family level analysis did not change the conclusion that overall species are retracting at their northern edge and therefore believe that a repeat analysis using the phylogeny would not change the results found here.

2.5.3. Comparison of native only records and incorporation of introduced records

If the difference in the change to the northern range margin of each taxon from the native only data is plotted against data incorporating introduced records, it can be seen that some taxon have retracted or advanced at their northern range margin at different rates (Figure 2.6). The average range shift of the northern range margin using native only records is -29.1km and the average range shift if introduced records are incorporated is -48.6km over the period of analysis. However, the northern range margin of DC1 using native only records was compared with DC1 where introduced records are incorporated it can be seen that the introduced records advance the northern range margin by an average of 78.4km and for DC2 the advance is 58.9km (Figure 2.7). Thus, the northern boundaries of introduced records are further north than those shown by native-only records, but consideration of both types of record lead to the conclusion that the overall marginal range shift is towards the south (Figure 2.7). Out of the 196 taxa which were included in the analysis in DC1, 147 included ≥1 introduced records and out of these 114 advanced north when compared to DC1 using native only data. In DC2 166 out of the 196 taxa included ≥1 introduced records and out of these 112 advanced north when compared to DC2 native only.

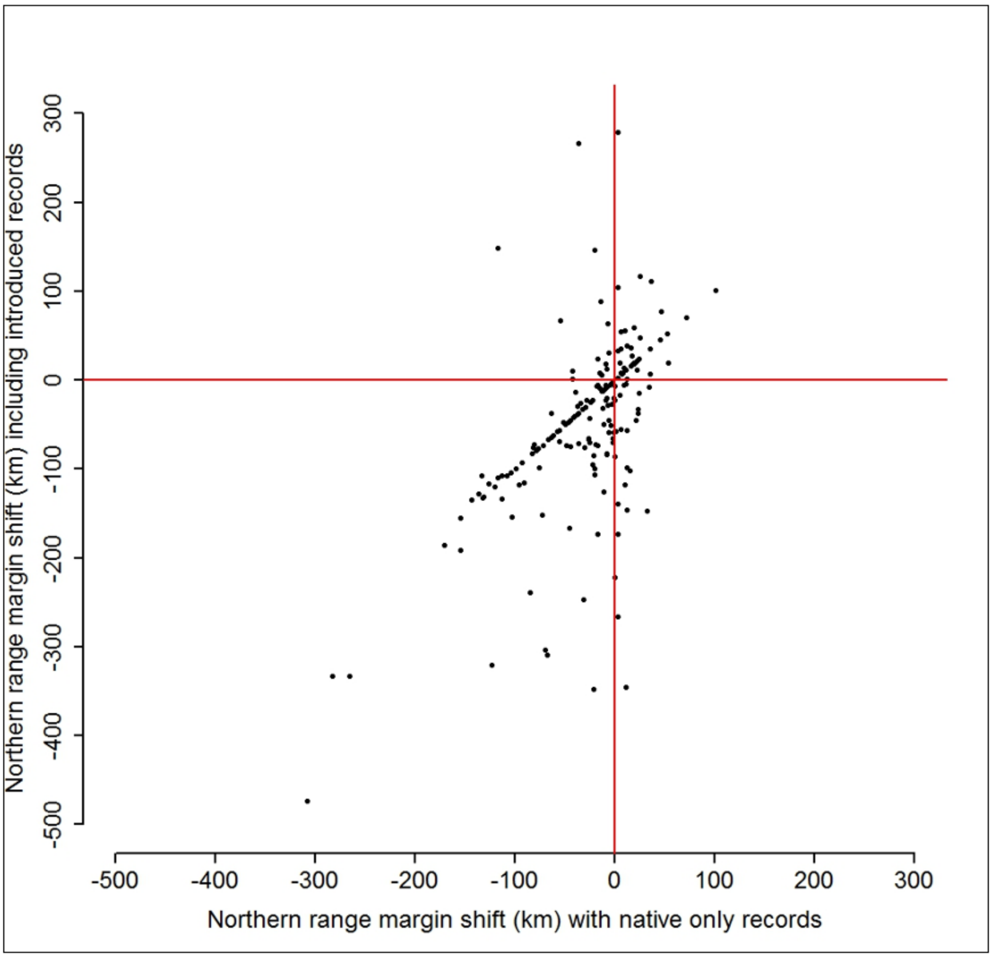


Figure 2.6: Scatter plot: Differences between northern range margin shift for incorporation of introduced records plotted against native only recorded records

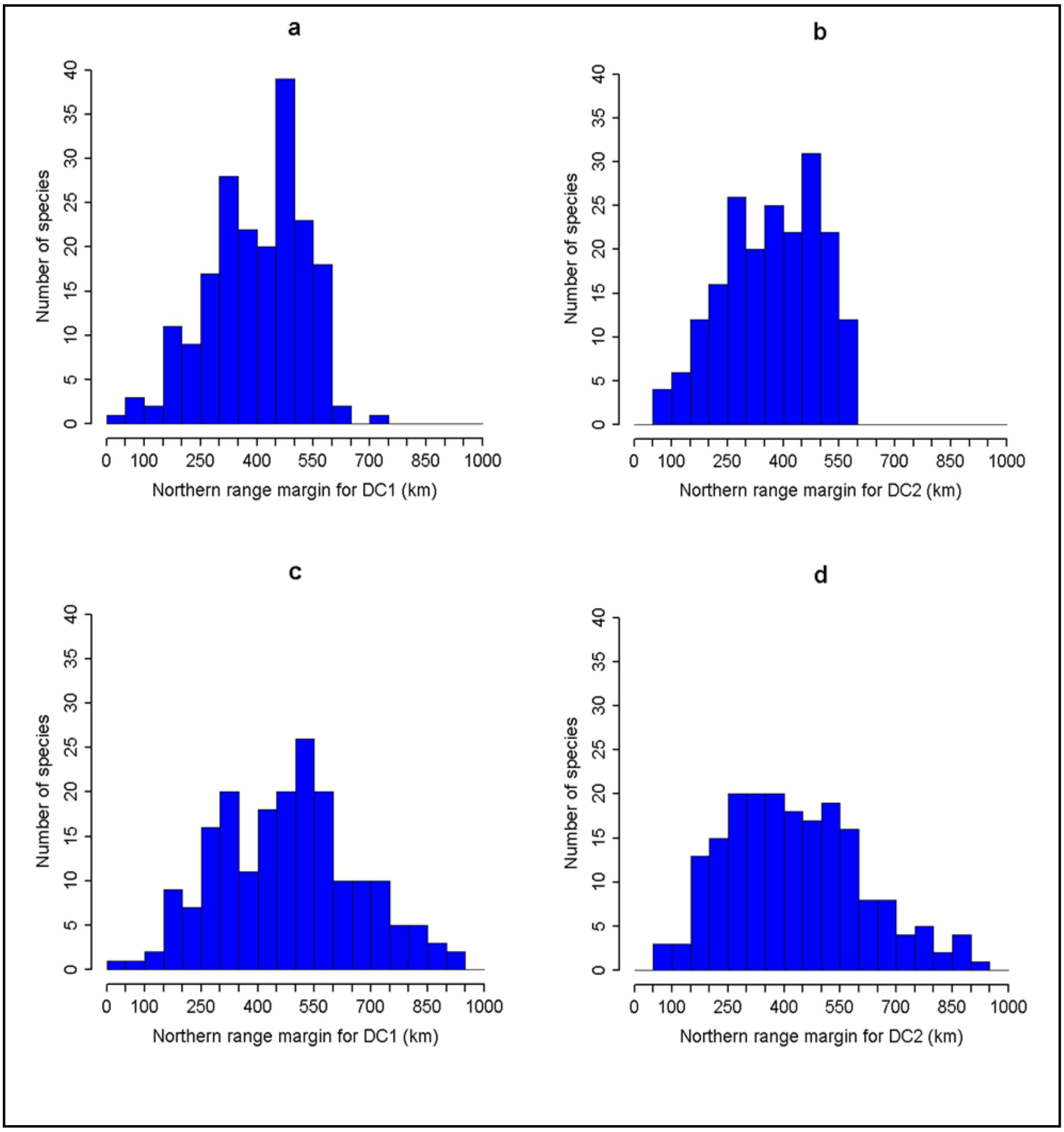


Figure 2.7: Histograms showing northern range margin a) native only records for DC1, b) native only records for DC2, c) including introduced records for DC1 and d) including introduced records for DC2

2.5.4. Comparing northern range margin shift with change in range size

The majority of species which have had a negative change in status, (change in status being $\log_{10}$ of the difference in number of squares between DC1 and DC2 for each species) have shifted in their northern range margin south when both native records and introduced records are compared (Table 2.3, Table 2.4). Out of the 124 taxa with a negative status change (reduction in overall 10x10 km squares from DC1 to DC2) using native only records, 85.5% also contracted south at the northern range margin, 12.9 %

advanced north at the northern range margin and 1.6% did not change at the northern range margin (Table 2.3). When introduced records were incorporated into the data out of the 120 records with a negative status change, 86.7% contracted south at the northern range margin and 13.3% advanced north at the northern range margin (Table 2.4). Species which have a positive status change (increased their overall range between DC1 to DC2), however, have often shown a strong shift north, as would be expected. Out of the 70 taxa with a positive status change using native only records, 58.6% advanced north at the northern range margin, 38.6% contracted south at the northern range margin and 2.9% showed no northern range margin change. When introduced records were incorporated into the data out of the 74 taxa with a positive status change, 48.6% advanced north at the northern range margin and 51.4% contracted south at the northern range margin. These results are consistent with the northern range margin on average contracting between the two date classes.

Table 2.3: Change in status versus northern range margin shift for native records

NATIVE	No status change	Expanding range	Contracting range
North shift	2	41	16
South shift	0	27	106
No change	0	2	2

Table 2.4: Change in status versus northern range margin shift for data incorporating introduced records

INTRODUCED	No status change	Expanding range	Contracting range
North shift	1	36	16
South shift	1	38	104
No change	0	0	0

Scatter plots were created with change in range margin plotted against change in status. The x = 0 intercept in Figure 2.8a, which is using data with native only records, shows a shift south of -12.101 km (SE = 3.565, t value = -3.395, n=196, *p*= <0.001; equation for regression line: y=-12.101+175.195x). Figure 2.8b with the x=0 intercept (and uses data including introduced records) shows a southwards shift of -25.498 km

(SE = 6.901, t value = -3.695, n=196, *p*= <0.001; equation for regression line: y=-25.498+234.337x). Thus, there appears to be a slight southwards retraction, on average, even when accounting for changes in overall distribution size.

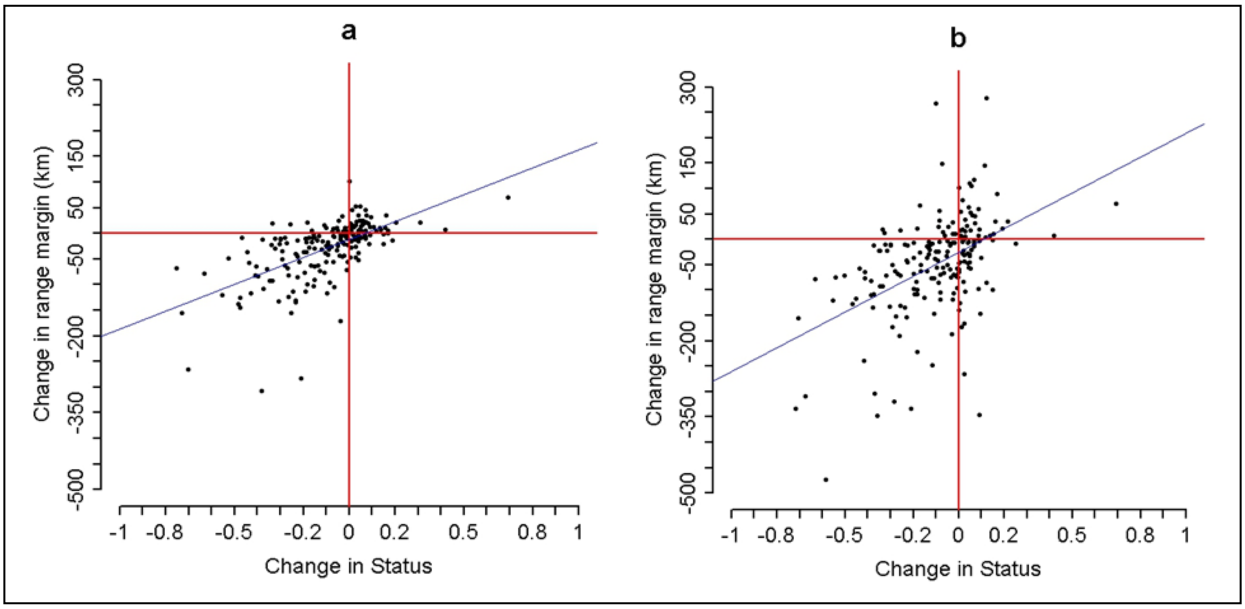


Figure 2.8: Change in range margin of species plotted against change in status ($\log_{10}$ of change in number of squares occupied between DC1 and DC2) for a) native records only, b) including introduced records.

2.5.5. Taxa trait data, Ellenberg values

Ellenberg values for light, moisture, nitrogen, salt and reaction for each taxa (extracted from: Hill et al., 2004b) were used to determine if any traits gave some insight into why some species have advanced north and why others have retracted south at their northern range margin. Spearman rank correlations were used to determine if any of these traits were associated with advances or contractions at the northern range margin for both native only records and incorporation of introduced records (Table 2.5), using recorded data.

Table 2.5: Spearman's rank correlations between northern range margin shift and Ellenberg values when analysed at species level.

Ellenberg	Native r_s, value	*p* value	Including introduced r_s, value	*p* value
Light	-0.264	0.000183	-0.190	0.0076
Moisture	0.100	0.163	0.147	0.0397
Reaction (pH)	-0.170	0.0175	-0.130	0.0697
Nitrogen	0.0464	0.475	-0.051	0.518
Salt	-0.228	0.00130	-0.188	0.009

Out of the 5 Ellenberg indicator values which were used in the analyses, light, reaction (pH) and salt provided significant results when native only records were used (Table 2.5). This indicates that species with high light level requirements, higher soil pH requirements and higher salt tolerance have retracted the most. When introduced records were included, light, moisture and salt produced significant results, whereas the reaction results were marginal (Table 2.5). This indicates that species with high light level requirements, species growing in more arid soil and higher salt tolerances have retracted the most. The analysis was carried out to determine if the results were maintained at family level and so Spearman's Rank Correlation was carried out on results for plant families with ≥3 species per family (Table 2.6) and ≥5 species per family (Table 2.7). Ellenberg indicator value for each family used was calculated by taking the average Ellenberg indicator value. For ≥3 species per family, only light provided a significant result using data including introduced records, with families preferring higher light level requirements having retracted the most. For ≥5 species per family, only salt provided a significant result using data, excluding introduced data, with species with a higher salt tolerance having retracted the most. Graphs comparing Ellenberg values with north shift for species level, family 3 level and family 5 level analysis can be found in Appendix I. The family-level results, therefore, suggest that caution should be taken when interpreting the role of plant characteristics, as represented by their Ellenberg scores.

Table 2.6: Spearman's rank correlations between northern range margin shift and Ellenberg values when analysed at family level with a minimum of 3 taxa per family

Ellenberg	Native r_s, value	*p* value	Including introduced r_s, value	*p* value
Light	-0.381	0.080	-0.500	0.0178
Moisture	-0.0334	0.883	-0.0277	0.9026
Reaction (pH)	-0.396	0.0678	-0.144	0.522
Nitrogen	-0.0113	0.960	-0.0469	0.836
Salt	0.221	0.324	0.0459	0.839

Table 2.7: Spearman's rank correlations between northern range margin shift and Ellenberg values when analysed at family level with a minimum of 5 taxa per family

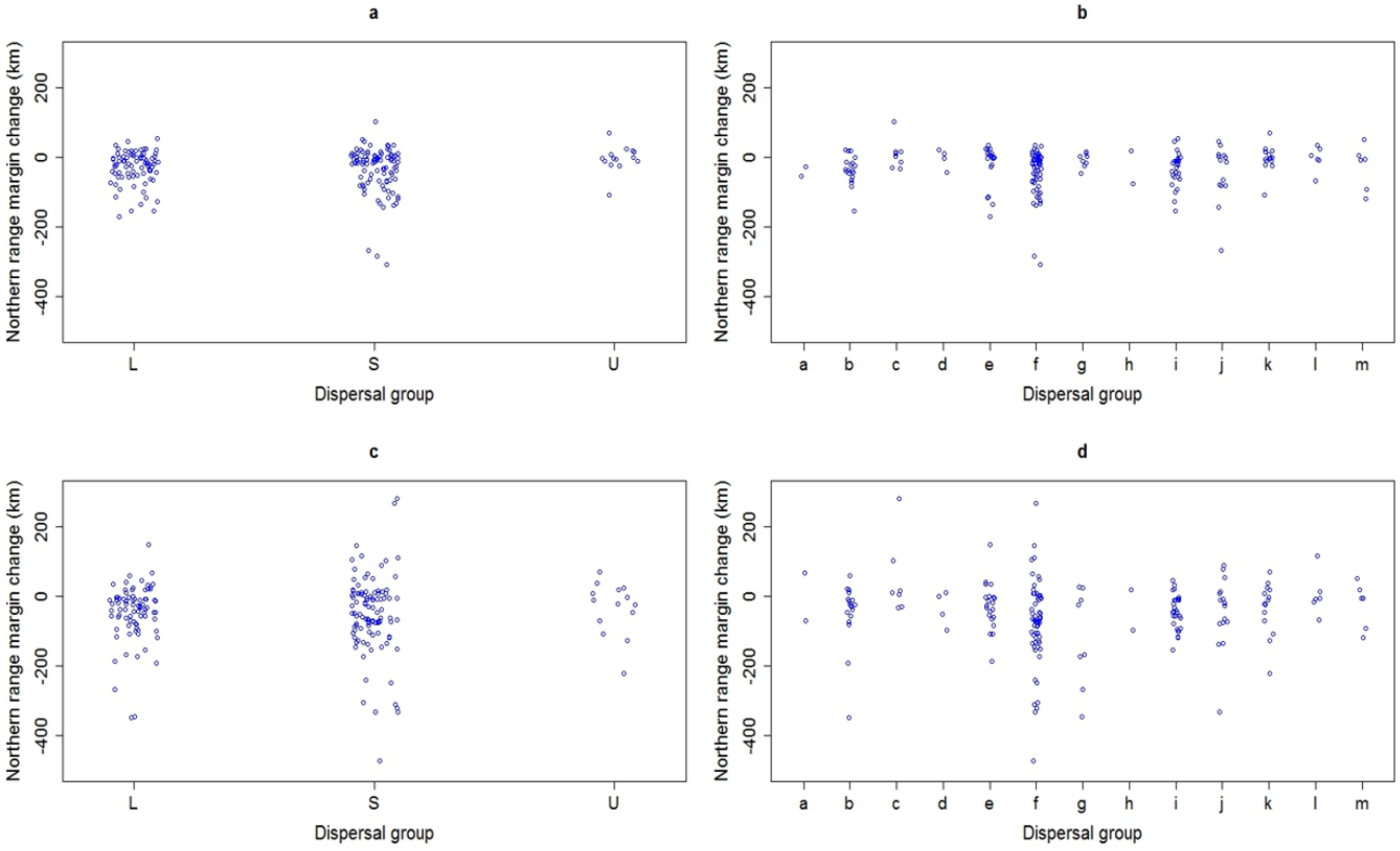
Ellenberg	Native r_s, value	*p* value	Including introduced r_s, value	*p* value
Light	0.0636	0.860	-0.346	0.299
Moisture	0.473	0.146	0	1
Reaction (pH)	-0.0818	0.818	0.336	0.313
Nitrogen	0.118	0.734	-0.282	0.402
Salt	0.610	0.0461	0.0191	0.956

2.5.6. Taxa trait data, dispersal

Kruskal-Wallis tests were carried out for shift in northern range margin as a function of dispersal method and for long/short dispersal. Irrespective of whether native only data was used or including introduced data, the results were not significant for both dispersal method and long/short dispersal (Table 2.8, Figure 2.9).

Table 2.8: Table gives results for Kruskal-Wallis test

	Native only	Including introduced
Dispersal group	Kruskal-Wallis chi-squared = 19.6 df = 12 *p* = 0.075	Kruskal-Wallis chi-squared = 19.3 df = 12 *p* = 0.081
Long/short dispersal	Kruskal-Wallis chi-squared = 3.5725 df = 2 *p* = 0.17	Kruskal-Wallis chi-squared = 1.0545 df = 2 *p* =0.59



	Dispersal vector
a	Seed/Veg: Bird (external)
b	Seed/Veg: Water
c	Seed: Ant
d	Seed: Ballistic
e	Seed: Bird (internal)
f	Seed: Gravity
g	Seed: Mammal (external)
h	Seed: Mammal (internal)
i	Seed: Wind (long)
j	Seed: Wind (short)
k	Unknown
l	Veg: Attached spreading
m	Veg: Detached fragments
L	Long
S	Short
U	Unknown

Figure 2.9: Scatter graphs showing northern range margin shift against a) long/short distance dispersal for analysis using native only data, b) dispersal vector using native only data, c) long/short distance dispersal for analysis using data including introduced records, d) dispersal vector using data including introduced records.

2.5.7. Persistence

The survival of the northernmost native and introduced records of species were compared, to evaluate whether the introduction of species beyond the northern edges of their native ranges is resulting in a persistent extension to the range. 81 species possessed ≥5 introduced records and so could be used in analysis for persistence of the 5 most northerly records. Out of the five 10 km squares present in DC1 which were still occupied in DC2, native records showed a significantly higher number of records persisting between the two time periods than introduced records (Wilcoxon signed rank test V =1643, *p*=<0.001, n=81). It can clearly be seen that native records are more likely to persist at the northern edge than introduced records (Figure 2.10, Table 2.9). 87.7% of the species either had zero or one of their five most northerly introduced records persisting between the two time periods, whereas the corresponding figure for native records was 48.1%. The median was zero survival for the introduced records of species, but 2 out of 5 surviving for native records.

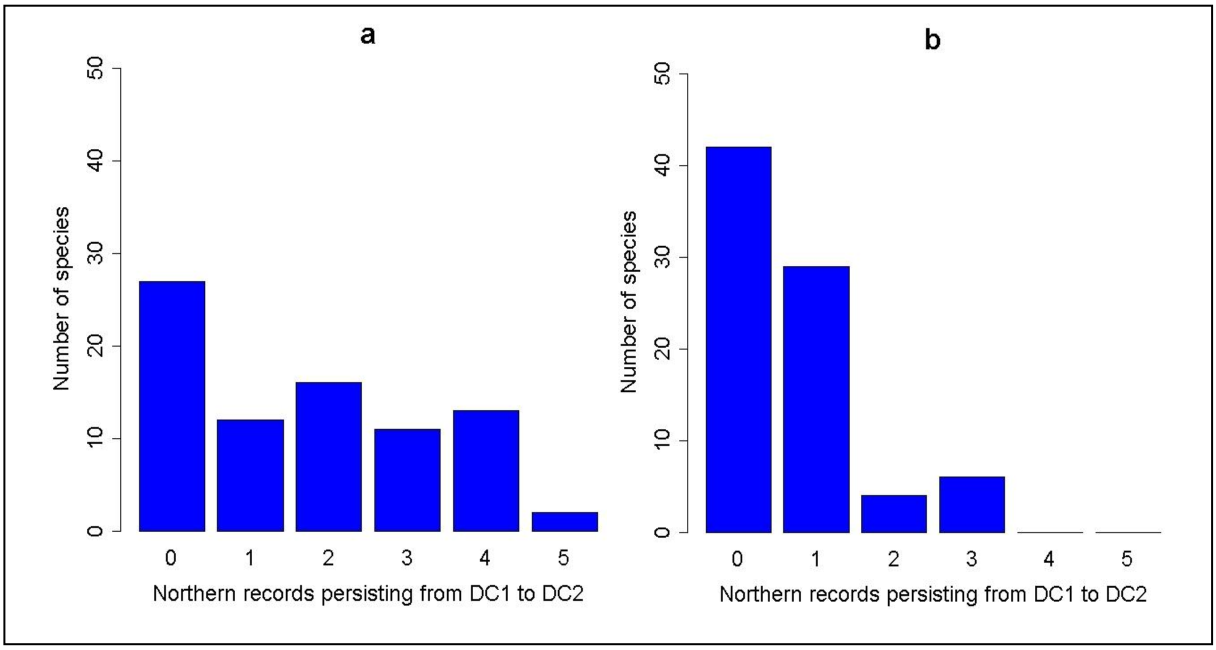


Figure 2.10: Histogram showing number of records which persisted in DC2 that occurred in DC1 using the 5 most northerly records from DC1 for a) native records b) introduced records

Table 2.9: Persistence between DC1 and DC2 for the 5 most northerly native records and 5 most northerly introduced records.

	0 records persisting into DC2	1 records persisting into DC2	2 records persisting into DC2	3 records persisting into DC2	4 records persisting into DC2	5 records persisting into DC2
Percentage of Native records persisting	33.3%	14.8%	19.8%	13.6%	16%	2.5%
Percentage of Introduced records persisting	51.9%	35.8%	4.9%	7.4%	0%	0%

The analysis was repeated for the subset of 52 species that possessed ≥10 introduced records. Out of the 10 km squares present in DC1 which were still occupied in DC2, native records showed a significantly higher number of records persisting between the two time periods than introduced records (Wilcoxon signed rank test V =885, *p*=<0.001, n=52); native records are more likely to persist at the northern edge than introduced records (Figure 2.11, Table 2.9). The medians were only 1 out of 10 introduced records of a species surviving, but 4 of 10 native records surviving.

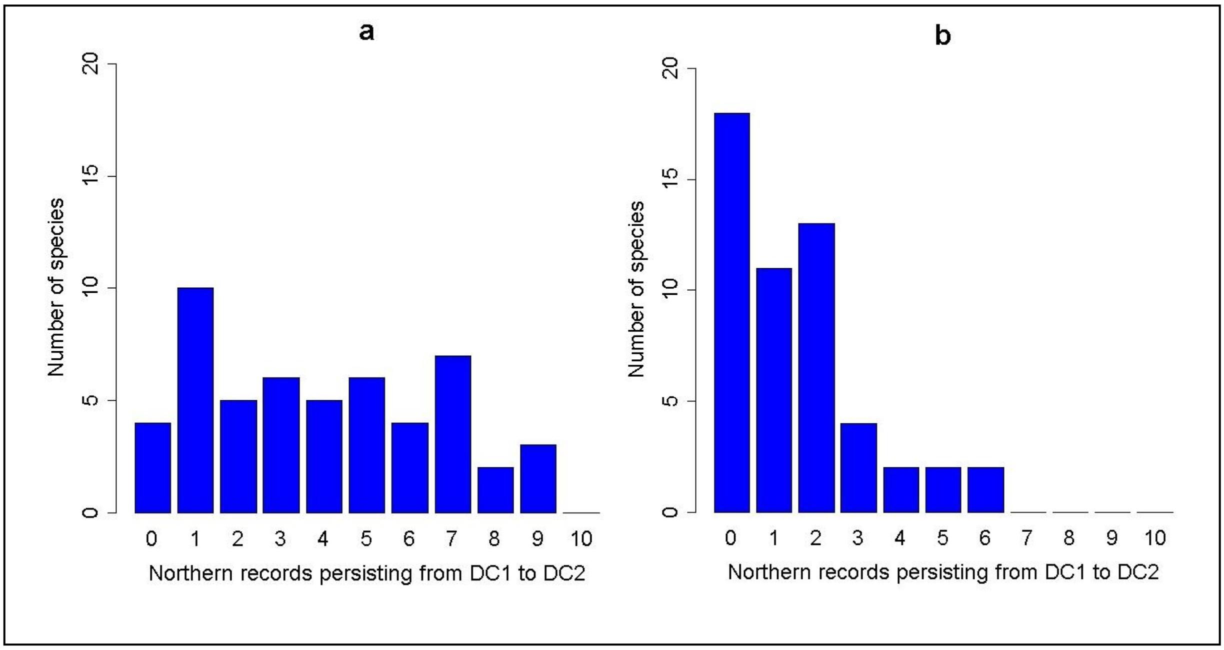


Figure 2.11: Histogram showing number of records which persisted in DC2 that occurred in DC1 using the 10 most northerly records from DC1 for a) Native records b) Introduced records

Table 2.10: Persistence between DC1 and DC2 for the 5 most northerly native records and 5 most northerly introduced records.

	0 records persisting in DC2	1 records persisting in DC2	2 records persisting in DC2	3 records persisting in DC2	4 records persisting in DC2	5 records persisting in DC2	6 records persisting in DC2	7 records persisting in DC2	8 records persisting in DC2	9 records persisting in DC2	10 records persisting in DC2
Percentage of Native records persisting	7.7%	19.2%	9.6%	11.5%	9.6%	11.5%	7.5%	13.5%	3.9%	5.8%	0%
Percentage of Introduced records persisting	34.6%	21.2%	25%	7.7%	3.8%	3.8%	3.8%	0%	0%	0%	0%

2.6. Discussion

2.6.1. Northern range margin shift

Hickling et al. (2006) and later Chen et al. (2011) showed that there is strong evidence that anthropogenic climate change has caused a range of animal species to shift north at the northern edge of their distribution. Results from this study of plants' northern range margins showed that British plants are not following this trend. Significantly more species have retracted at their northern edge than have advanced and this trend is evident irrespective of whether introduced records are included or excluded from analysis. This implies that, unlike many animal species, climate is not the main driving factor of shift in the northern range margin of plant species in Britain and other factors are having stronger influences. Over the past 50 years in Britain there have been dramatic changes to the landscape with agricultural intensification changing the landscape in an unprecedented way (Fuller, 1987, Robinson and Sutherland, 2002). Urban areas have also grown substantially in the past 20 years (Grimm et al., 2008), however agricultural intensification is likely to be the main barrier to dispersal as outside of London the expansions of cities is likely not to be sufficient to block dispersal and so urbanisation will be a less significant barrier to dispersal. These changes are likely to underlie the declines, and retractions away from range boundaries, of the majority of species, and may also prevent potential expansions. It may be that species are unable to travel the distances needed to colonise new more northerly localities due to barriers such as urban or agricultural land. These may also prevent the movement of animal species, which may act as dispersal vectors for the plants. Habitat further north may also not be suitable for colonisation either due to changes to the landscape such as agriculture change, or that the preferred habitat of that species does not exist further north. Even if there is a seed rain to the north of existing distributions, the likelihood of it falling in locations suitable for population establishment may be very small. This begs the question that if the habitat is not suitable further north, can species adapt to new habitats, something that will be considered further in Chapter 3.

As well as dramatically altering the landscape, humans have also had dramatic effects on local biodiversity by moving plant material on a local and global scale (Weber, 1997). Within Britain, many species occur in locations considered outside their natural range as a result of this and this can often occur when plant material is moved either accidentally such as through movement of soil, or deliberately, which can be as a result of the species possessing desirable horticultural characteristics or other functional use. *Acer campestre* (Field Maple) is often planted as a parkland tree, *Arum maculatum* (Lords-and-Ladies) is used as an ornamental in traditional or woodland shade gardens and *Humulus lupulus* (Hop) is often planted for use in beer making. All these species have a northern range margin much further north that they would otherwise have due to human movement of them to new locations. Although the distribution of introduced records was not further north in the second time period than in the first, introductions were responsible for the northern margin being considerably further north (on average by 78.4 km for DC1 and 58.9 km for DC2) than it would have been in the absence of introductions (Figure 2.7). However, these introduced records at the northern edge of the distribution have not persisted between the two time periods, as well as native occurrences species have (Figure 2.10, Figure 2.11). This could either be if many of the introductions have been to sub-optimal habitat where individuals can survive for a while, but where positive population growth is not possible, or they have been introduced to areas where the climate is not suitable. However, as the climate warms, these introduced plants may act as long distance dispersal events which will help the species colonise further north at a faster rate than would otherwise be possible. Given the failure of dispersal traits to explain significant variation in northern range margin shifts, it would appear that human-mediated dispersal is likely to be the predominant mode of dispersal in future plant range shifts.

A retraction at the range margin has still occurred (although the retraction is smaller) with species which have shown to have a stable overall distribution size (Figure 2.6). It is likely that this reflects the original density of the populations at the northern edge of the distribution, as the northernmost 10 km squares will likely have contained fewer populations due to the area being climatically marginal. This will have impacted on the likelihood of a 10 km square losing all its populations with the land use changes. Therefore, a higher proportion of the northernmost squares would have experienced a complete disappearance of the species.

2.6.2. Ellenberg values

Plant tolerances to certain environmental conditions are a key to survival of a species in certain landscapes and have the ability to govern where plants can and can’t grow. When Ellenberg values for species used in this study along with north shift were compared in a Spearman Rank Correlation, three of the five traits showed significance when both native only and including introduced records were used. Significance for Ellenberg values was generally lost when analysis was carried out at the family level (Appendix I).

Salt showed a significant result at species level. However, as can be seen from the graph the majority of species are not tolerant of salt and have an Ellenberg value of 0 (Table 2.5): 85% of the British flora have an Ellenberg value of 0. The results indicate there is a negative slope and therefore more salt tolerant species are less likely to have retracted as far as those that are less salt tolerant. The graph in Appendix I Figure 5a and 5b shows the abnormality of the data and most salt tolerant species are still retracting at their northern edge. It is possible that the salt tolerant species are retracting marginally less than those with no salt tolerance due to salting roads which provides a suitable habitat for the species inland which would not ordinarily occur there (Sera, 2010). However, this trend is not evident based on maps of those species with salt tolerance (Ellenberg values 1-6) (Appendix II). The weak effect of salt tolerance, and the fact that the trend is likely to be driven by a few species that have invaded salted road-margins (e.g. *Atriplex litoralis*, *Cochlearia danica*, *Puccinellia distans*), suggest that this is a habitat (and perhaps transport) effect, rather than an impact of climate change. Because these few species are largely colonising , starting from originally coastal areas, these expansions do not necessarily affect the northern boundaries of the species.

Light tolerance also had significant results with a negative correlation with north shift (Table 2.5). This implies that species which occur in shadier areas are more likely to have either shifted north or, rather, not retracted as far south as species which occur in areas with high light levels such as open grasslands. Part of the reason for this may be due degradation of southern grasslands such as many chalk grasslands which are traditionally more open, and therefore species which prefer higher light levels are more likely to have lost habitat. There has been an increased effort to conserve these habitats over recent years which may in future studies reverse this trend. Conservation efforts in lowland calcareous grassland is on the UK Biodiversity Action Plan (BAP) list of priority habitats (JNCC, 2013). Again, this appears to be an effect associated with land use, rather than climate or climate change.

Reaction, which is a measure of soil pH, showed a significant negative correlation with north shift using native only records, but was not significant when introduced records were incorporated into the analysis (Table 2.5). This would imply that species growing in more acid conditions are less likely to have shifted as far south. The possible reason for species which prefer higher pH having retracted further than those which occur on more acidic conditions may be in part because of the decline in chalk grasslands (which typically have a pH of 6 or above) in the past century. Chalk grasslands contain many plant species which have a strong association with this habitat and so this decline in habitat will likely have caused a decline the species distribution and a larger retraction at the northern edge of their range.

Ellenberg values for moisture had a significant positive effect on slope when introduced records were incorporated. However, the effect was not significant for data using native only records. This would imply that when introduced records were incorporated it showed that aquatic plants and plants which grew in moister conditions were either advancing or not contracting as much at the northern edge when compared to species which grow in arid conditions. It is possible that dispersal may have played a part in this as plants which have propagules which are transported by water are able to float down waterways, unimpeded by urbanisation and therefore barriers which may exist for other plants are less likely to affect the movement of aquatic species. However as most rivers run east-west across Britain water birds may offer a better explanation as to why plants from wetter conditions more likely to either advance north or not contract as far south. Water birds often travel between different water bodies and therefore may externally carry propagules to new areas on their legs or in feathers. It is difficult to see however why this would only be the case for populations which are considered introduced and the same story is not told for native populations. However, the most plausible explanation is that humans are the main vector, given that the result was only significant for introduced records and that aquatics are often planted out in somewhat naturalistic settings.

2.6.3. Dispersal

Although it is often stated that dispersal is an important factor in the spread of species' distributions, none of the results from this analysis gave significant results when dispersal method or dispersal distance was used with northern range margin shift. It can be concluded from these results that methods of dispersal which are considered to disperse species long distances are not facilitating species spread north in the taxa used in this study , presumably because the factors stated above far outweigh any dispersal that may be occurring (e.g. habitat loss). This might not be expected during a period of general distribution decline, when the predominant process of relevance is local extinction rather than colonisation. Corlett (2009) looked at tropical seed dispersal and results indicated that plants had the potential to track temperature changes in areas with a steep altitudinal gradient but in lowland areas temperature and rainfall gradients are much shallower and so species will not be able shift to new locations tracking temperature changes as a result of global warming. Nearly all of the species used in this study occurred in low altitude areas and therefore are not able spread in order to track the changes in temperature which Britain is experiencing.

2.6.4. Persistence

The results for inclusion or exclusion of introduced records into the analysis both tell the same story, the northern range margin of southerly distributed species are retracting and not advancing as would be expected with a warming climate. It was hypothesized that when introduced records were included in the analysis species would show an increased north shift and less of a retraction as humans would be facilitating the shift north. This however was not the case when the data were analysed. This is likely to be due to persistence. It can clearly be seen that out of the species which possessed enough introduced data, whether using the 5 or 10 most northerly records, the introduced records are not persisting as long as those that have occurred there naturally. However, the northern margin for individual date classes moved north when introduced records are incorporated. These introduced records, although not persisting over the time frame of the data used in this study, may provide the opportunity for north shift of many species as the climate increases in temperature.

2.7. Conclusion

The overall result of this study, that most southerly distributed plant species are retreating southwards rather than migrating northwards, has implications for the conservation of native plant species in Britain. It seems likely, based on these results, that climatic warming has not been the primary driving factor of range changes over recent decades which have influenced the northern range margins of southerly distributed native plant species. Other anthropogenic factors such as habitat loss, fragmentation, and modification are likely to have been far more influential in any changes to distributions of species, and some species have been shown not to be tracking climate change due to these non climatic influences (Hill et al., 2001). There is also sometimes a lag in northern range margin shift, as has been implied by Mair et al. (2012). This study encompassed the most rapid warming time period but further studies using the next 10 years of data may give an insight into whether plants are yet beginning to shift their margins northwards. Because most plant species are extremely localised within specific habitats, it may be that the rain of natural and human-assisted propagules (introductions) to the north of the existing northern range margin may be insufficient for it to be likely for the propagules to arrive in suitable habitats and for populations to establish.

Study into the changes in the northern range margin of animals has shown that as the climate is warming their northern range is shifting north in Britain (Hickling et al., 2006) and globally (Chen et al., 2011). The results here have shown that this is not the case for native plants in Britain and that more species are retracting at their northern edge than advancing (Figure 2.5). These results are the same for both analyses, regardless of whether introduced records are incorporated or excluded. The fact that more taxa are retracting than advancing at their northern range margin, regardless of the data used, implies that introduced populations are suffering the same (or even worse) fate in the landscape as the native populations. The retraction of the northern range margin is larger when introduced records are incorporated into the analysis. It has been shown that if species are introduced to an area in larger quantities outside their native country that it is more likely the species would persist than if only small numbers of plants are available (Dehnen-Schmutz et al., 2007). This may be why species are retracting further when introduced records are incorporated. The introductions further north are likely to only be short lived as they may represent only small populations or individual plants.

Many factors are involved in the retraction of the northern range margin. A likely cause for the retraction may be as a result of habitat loss and degradation, which has been associated with may declines in species and extinctions (Sih et al., 2000, Hughes et al., 1997). Due to the mobile nature of animals, it may be that they are succeeding in advancing where plants are failing to due to their mobility. The ability of animals actively to select suitable habitats for reproduction when they arrive in a new region (whereas plant propagules lie where they fall) may be particularly important. The dispersal mechanisms employed by plants may no longer be able to spread to new locations due to the fragmented nature of the land and the distances it must cross. This advance of animals may mean that species with particular host plants could be facing a future where their advancement starts to slow due to a lack of host plant availability or they may need to adapt to a new host plant. If the native only data are compared with data incorporating introduced records from the same time period the introduced records would substantially advance the northern range margin (Figure 2.7) by an average of 78.4 km for DC1 and 58.9 km for DC2. These records, in principle, represent long distance dispersal events, most of which are likely to have been carried out by humans, although some of them may be so far outside the formerly known range that they are treated as introductions in the 'New Atlas of the British and Irish Flora' (Preston et al., 2002b), even though the dispersal vector was not known. This implies that there is a scattering of records which represent dispersal much further north than the rest of the distribution. These may be available for future expansion of the range and it is likely that the primary disperser will be humans.

3. Habitat change, distribution infilling and bee orchids

3.1. Abstract

Species have been shown to respond to climate change in many ways such as changes in distribution, phenology and abundance. Some species in introduced ranges outside their native country have been shown to have successfully adapted to new climates and habitats, but there is limited information on changes to the habitat preferences within a species native range. *Ophrys apifera* (bee orchid), which is considered a species of calcareous grassland, has shown distribution infilling and expansion further north at their northern edge. Botanical Society of Britain and Ireland (BSBI) county records have observed that it appears to have been occurring in a broader range of habitats away from its traditional association with calcareous grassland. It was determined whether populations of bee orchid from a more recent time period are occurring in a boarder range of habitats compared to populations in an older time period using the BSBI plant database, underlying geology, and habitat data from field work. Three main conclusions can be drawn from this research. 1: There is little difference between where bee orchids are and are not occurring within sites where field work was carried out. 2) Newly colonised bee orchid sites exhibit a broader range of habitat types compared to old established sites based on field work analysis. 3) bee orchids have exhibited an infilling of their distribution with old established sites more likely to occur over a calcareous bedrock and newly established sites occurring over a broader range of bedrock types. These results show that bee orchids have been able to spread to new habitats away from the calcareous soil association in more recent years. This broadening of habitats that bee orchids occur in is likely to be facilitated by a warming climate, allowing the species to shift to new climatically suitable space, and an ease of dispersal due to the light windblown seeds.

3.2. Introduction

3.2.1. Niche shift

It is well know that many species occupy specific habitat niches and are associated with a restricted number of vegetation communities (e.g. Rodwell, 1991-2000, Gottfried et al., 1999, Blake et al., 2003, Eyre et al., 2003, Eyre, 2006, Anthes et al., 2008, Oliver et al., 2010, Gillingham et al., 2012) such as *Thymus polytrichus* and *Linum catharticum* which are associated with calcareous grassland communities and *Armeria maritima* and *Plantago coronopus* which are associated with maritime grassland communities (Rodwell, 1991-2000). Plant habitat specialists are often species associated with nutrient-poor habitats, whereas species which occur in a wider ecological niche are more likely to be species growing in nutrient rich areas (Fajmonova et al., 2013). With anthropogenic climate change now influencing distributions of species, there is a need to understand how habitat associations will affect the distribution of species and if the habitat tolerance of a species may change in light of changes to climate. Changes to habitat associations will affect that availability of habitats to species, and hence determine whether the species are able to relocate to higher latitudes and elevations (Thomas et al., 2001). These changes may facilitate the range expansion of species that experience increases in their realised niches at their cold range boundaries.

Most species distribution models assume specific niches, habitats or sets of habitats for the modelled species (Guisan and Zimmermann, 2000). However there is evidence that species can adapt to new habitats as the climate changes in long time scales (Shaw and Etterson, 2012). Reviews on the subject have shown that biota responds to climate change in a diversity of different ways. Some species have undertaken evolutionary changes, other have changed their geographical locations, and some species have become extinct (Hoffmann and Sgro, 2011, Shaw and Etterson, 2012). A broad range of literature exists on the ability of species to adapt or evolve to new environmental conditions, such as morphological changes with stomatal guard cell size changes (Franks et al., 2012), rapid adaptation to tolerate heavy metal contaminated soils (McNeilly, 1968, Antonovi.J and Bradshaw, 1970, Antonovics, 2006), evolved resistance to herbicides used in agriculture (Weed Science, 2013), and adaptive evolution to climatic differences across geographical ranges with population differentiation relating to climate (Rehfeldt et al., 1999). Species with different fundamental prior adaptations may also differ in their responses. For example, the evolution of C_3 and C_4 photosynthesis pathways generates different responses to changing CO_2 levels, temperature and water deficit (Sage, 2004, Cerling et al., 1997, Edwards et al., 2010), such that C_4 plants may become more invasive under current day conditions (Chuine et al., 2012).

There have been studies which look at climatic and habitat niche shifts between the native and non-native species range (Broennimann et al., 2007, Essl et al., 2009, Gallagher et al., 2010, Alexander and Edwards, 2010, Mandle et al., 2010, Mukherjee et al., 2012). These studies look at species outside of their native range where other factors such as release from pests and diseases will influence the ability of the species grow and spread (Mitchell and Power, 2003, DeWalt et al., 2004, Callaway and Maron, 2006, Mitchell et al., 2006) and therefore cannot be directly compared to niche shift within native range. Phenotypic plasticity also can be important in allowing plants to cope with changing environmental conditions, but this plasticity may also be maladaptive and could hinder a plant's ability to cope with environmental changes (Bradshaw, 2006). Although this demonstrates the potential of plants to adaptation to rapid environmental changes, there are many more species which have failed to adapt to novel environments, such as areas contaminated as a result of mining causing heavy metals in the soil (Bradshaw, 1991). As a result of humans influence on the earth's climate due to release of greenhouse gasses the climate is changing, causing rapid warming of the planet (IPCC, 2013) and it is not yet clear if plants and populations of plants will be able to adapt fast enough to keep up with the changing conditions. The complexities of climate change and both the ecological and evolutionary responses of species make predicting plants' responses to a changing climate extremely challenging.

Climate and ecological niches are important to species distributions and are often used in distribution models when predicting future distribution (e.g. Peterson et al., 2002, McClean et al., 2005, Schwartz et al., 2006, Coudun and Gegout, 2007, Morin et al., 2008, Normand et al., 2013). However, these models typically ignore potential climate-associated changes to the habitat associations of species, which will affect whether the projected new range contains suitable habitats, as well as suitable climates. It is therefore necessary to know if the habitat preference of a species will remain the same and if the species can only move to similar habitat types or if species may broaden or change their habitat preference as they migrate with climate warming. Such information is needed to advise on appropriate conservation strategies for a species.

Little attention has been paid to whether native plant species will change or broaden the habitat associations as the climate warms, and therefore opens up more suitable space for colonisation, although there are anecdotal reports of such changes. For example, it has been reported in observations by BSBI county recorders (Walker *pers com*. 2011) that the bee orchid, *Ophrys apifera* Huds., may be broadening its habitat tolerance, but no study has been carried out to test this observation. Therefore, it was decided to use *Ophrys apifera* data both from the BSBI database and data collected from the field to test this hypothesis. A study of orchid distribution change in Britain has been carried out by Kull and Hutchings (2006) at a 10x10 km level, and this revealed that the ranges of orchids have contracted between 1930-1969 and 1987-1999, especially in calcareous grassland and woodland. Nonetheless, there has been a marked expansion of *Ophrys apifera* in the past c.10 years and there is some question whether higher resolution data might reveal higher rates of local expansion than a 10 km resolution analysis.

3.2.2. *Ophrys apifera* Huds. life history and background information

One of the advantages of using *Ophrys apifera* as a study species is that the *Orchidaceae* family as a whole have been very well recorded in Britain, so good distribution data are available. This is, in part, due to the unusual flower structure and diverse range of pollination mechanism in the *Orchidaceae*, which has been of interest to the scientific community for 200 years or more. Darwin was so interested in the subject that he wrote the book “The Various Contrivances by which Orchids are Fertilised by Insects” which was first published in 1862. In this he discusses the various methods of orchid pollination and *Ophrys apifera* pollination is written about over several pages, detailing how unlike most other orchid species, *Ophrys apifera* is self pollinated (Darwin, 1904), although there is evidence that occasional pollination does occur by male B

bees (Pedersen & Faurholdt 2007). Also because of the strong interest in Orchids people deliberately search for orchid populations and there is a very active and dedicated society for hardy orchids in Britain (The Hardy Orchid Society), which meets regularly (in 2013 there were 14 meetings) and has a strong interest in British orchid species, being involved in several conservation projects of British orchids (Hardy Orchid Society website). There are also a number of books which have been published specifically on British orchid species and where and when to find them (e.g. Lang, 2004, Harrap and Harrap, 2007). As such high levels of records exist for this plant family in Britain, new sites are noted and recorded with a high level of dedication.

There is much disagreement about how many species the genus *Ophrys* L. has and numbers vary between around 19 species (Pedersen and Faurholdt, 2007) to around 253 species (Delforge, 2006), and this disagreement depends on which taxonomy you choose to follow. In Britain it is widely agreed that there are 4 species of *Ophrys* (Stace, 2010) with *Ophrys apifera* (here on in referred to as bee orchid) being the most widespread species (Preston et al., 2002). The number of flowering plants within *Ophrys* populations varies from year to year as well as between species (Pridgeon et al., 2001) and plants can remain underground for up to two years (Pedersen and Faurholdt, 2007). Therefore, in a single year a number of individuals in a population cannot be detected. On average 30% of any *Ophrys sphegodes* population will remain dormant with a dormancy period of on average less than 2.25 years (Jacquemyn and Hutchings, 2010). In an average year, only 27% of bee orchids in a population actually produce flowers (Wells and Cox 1989, but see Pridgeon et al., 2001).

Orchidaceae species all have tiny seeds, which are normally made up of a c.120-celled embryo encased in a thin paper-like testa (Arditti & Clements 1988; see Yoder et al., 2010). The dust-like seeds are adapted for dispersal by wind. However, the seeds often do not spread far from the parent plant in terrestrial orchid species. *Spiranthes spiralis* seed rarely to travels further than a few tens of centimetres from the maternal parent (Jacquemyn and Hutchings, 2010) and *Orchis mascula* seeds normally only travel between 0.01 and 7.21 m from the parent plant (Jacquemyn et al., 2009). This means that recently established populations are likely be confined to a relatively small space in a site as the population will not have had time to spread out. Having said this, there is the potential for these tiny seeds to occasionally travel long distances and therefore colonise new sites many kilometres from the parent plant. This applies to the bee orchid and, due to the self-pollinating method of fertilisation, large numbers of seeds will be produced and dispersed, and new colonies can potentially establish following the arrival of a single seed in a suitable location.

The bee orchid grows from a fleshy underground tuberoid which is replaced annually. Each year, a new tuberoid starts to grow from the stem above the old tuber and this starts in the autumn of the previous year after the aerial part has died down and seed has set and dispersed. This growth continues slowly during winter but will increase rapidly during spring. By the time the plant flowers this new tuberoid can be as large as or larger than the old one. The old tuberoid will start to whither as the food reserves are used up creating the new tuberoid and vegetative parts.

The bee orchid is a temperate species with a widespread distribution throughout Macaronesia, Europe to Caucasus, and the Mediterranean to South Turkmenistan (WCSP, 2014) and has a mainly south east distribution across Britain (Preston et al., 2002). It is a species for which its local range appears to be expanding, infilling the gaps within its former British range (Figure 3.1, Figure 3.2) with records from around the past 15 years showing an advance at the northern edge of its distribution (Figure 3.3). This was not picked up in the northern shift analysis in chapter 2, as most of the new northern populations were found after 1999, the last date in DC2. As such, this species makes an interesting case study to look at habitat shifts in its range.

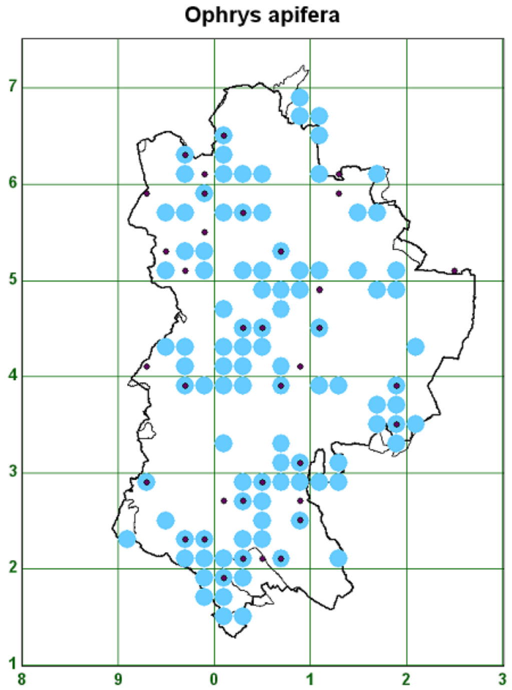
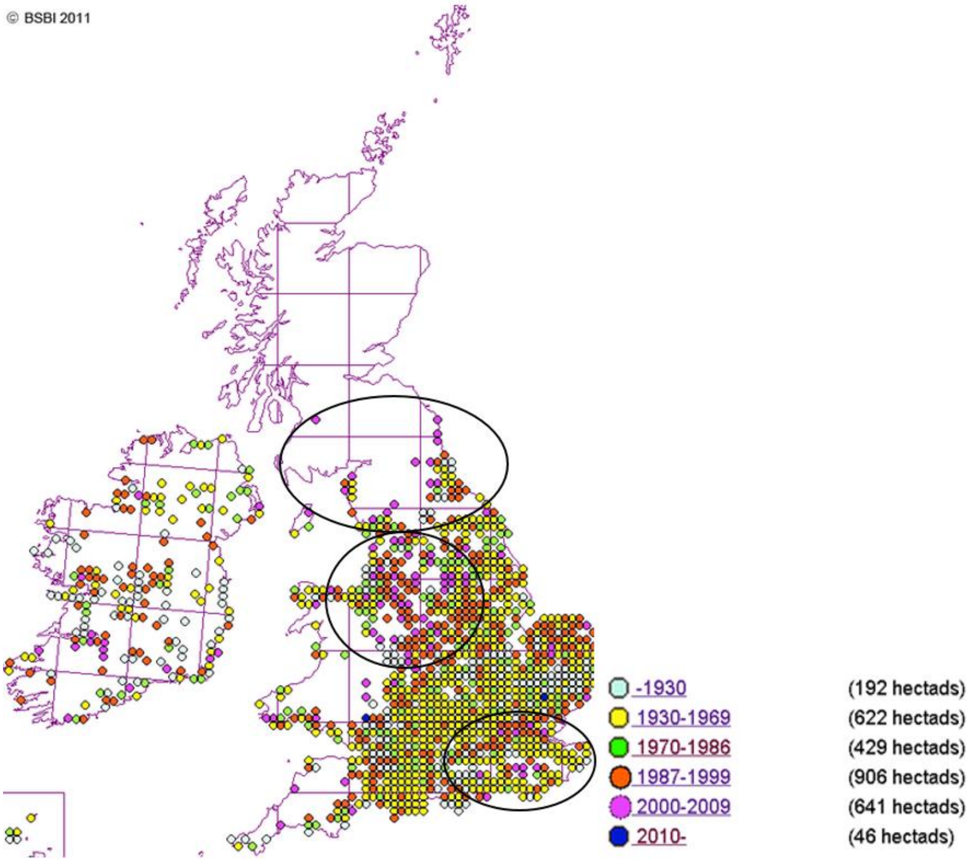


Figure 3.1: Infilling of *Ophrys apifera* in Bedfordshire with the dark blue smaller spots being 1970-1976 & pale blue larger circles records from post 1987. Each circle represents a 2 x 2 km square[1]



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[1] Map from BOON, C. R. & ALAN, R. 2011. *Flora of Bedfordshire*, Bedfordshire Natural History Society.

Figure 3.2: BSBI map of Britain showing oldest records on top. Each circle represents 10 x 10 km^2. Black ovals represent areas where 10 x 10 km^2 have been occupied post 1999 (infilling and expansion of range)

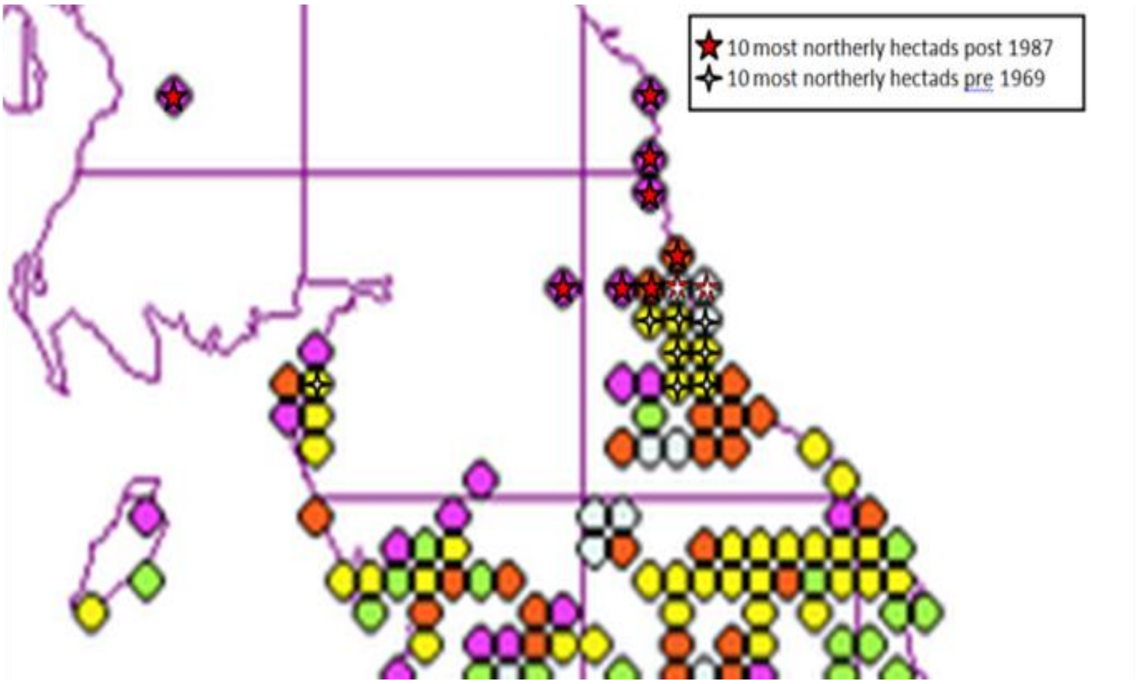

Figure 3.3: Distribution map of the northern edge of *Ophrys apifera's* range with oldest records on top. Red stars indicate the 10 most northerly 10x10 km squares in the later time period and crosses show the 10 most northerly occurrences pre 1970 [2]

The habitat of the bee orchid is normally regarded as calcareous, well drained soils within habitats such as railway banks, scrub, grasslands, sand dunes, limestone pavement and roadsides, as well as more disturbed sites such as gravel-pits, quarries and industrial waste ground (Preston et al., 2002). With changes in climate, there may be populations able to grow in different habitats than would previously be observed for the species, and some county recorders have made the observation that they appear to be occurring on sites with a more clayish soil (K. Walker *pers. comm.*, 2011). In order to assess if a change had occurred, a detailed analysis of high resolution data were carried out and field work was planned to complement this by surveying a number of both old and recently colonised sites.

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[2] Map from http://www.bsbimaps.org.uk/atlas/main.php viewed: 17/01/2011

3.3. Aim

The aim is to:

1. evaluate if in-site variation in habitat can explain occurrence of bee orchids, especially in non-calcareous sites
2. use field work data to test whether the habitat type of long-established sites differs from the conditions on newly-colonised sites
3. examine, using BSBI data, whether recently-colonised bee orchid sites are more likely than long-established populations to be found in non-calcareous sites, and to assess whether bee orchids are occurring in a broader range of habitats.

3.4. Method

3.4.1. 2011 Field Work: in site variation, comparisons between quadrats with and without bee orchids.

3.4.1.1. Field work

In order to determine if bee orchids were occurring in specific microhabitats within a site, new and old sites were selected to search for bee orchids according to the following set of criteria:

Old site

- At least one pre-1980 record (old) and one post-1990 record (new)
- At least one of the old and one of the new records needed to be at 100 x 100 m resolution
- New and old record a maximum of 500 m apart, such that the records could be deemed to belong to the same population

New Site

- At least one record post-1990 and no pre-1990 record
- Nearest pre-1990 record ≥ 800m away
- Site recorded at 100 x 100 m resolution

The aim was to quantify the habitat characteristics of the locations where bee orchids were, and were not, occurring *within* each of these sites. Field work was carried out across Hertfordshire and Bedfordshire, two vice counties which had repeat floras (Pryor, 1987, Dony, 1953, Dony, 1967, Dony, 1978, James, 2009, Boon and Alan, 2011) and therefore data are available at a higher resolution than other parts of the country.

44 sites were found using the above criteria stated above (Appendix IIIi) and searched for bee orchids which included 28 new sites and 16 old sites. Length of time spent searching each site was based on site size (Table 3.1). Site size was determined once the site had been located and a Google satellite map was used as a guide, based on the area of vegetation similar to where the orchid was found. If a bee orchid was found on a site then the search was extended (Table 3.1).

Table 3.1: Time spent at each site based on site approximate size

	sites ≤ 0.01 ha	sites between 0.01 and 1 ha	sites ≥ 1 ha
Initial site search: give up time	20 min	40 min	1.2 hours
Site search time if bee orchid found	40 min	1 hour	2 hours

Site underlying bedrock was classified by plotting each grid reference for each site over a British geological map obtained (British Geological Society) and sites were classed as calcareous/chalk or not calcareous/chalk (referred to as "chalk" and "not chalk" sites throughout this document, see Appendix IIIi for list of chalk and not chalk sites). All sites which fit the criteria in the survey area were searched for Bee orchids. Out of the 28 new sites, 13 had an underlying bedrock of chalk and 15 had an underlying bedrock which was not chalk. Out of the 16 old sites, 14 had underlying bedrock of chalk and 2 were not chalk. All sites were visited and it was hoped that the survey work could be carried out on 2 old chalk, 2 old not chalk, 2 new chalk and 2 new not chalk and that ≥20 bee orchids could be found at each site to collect data. However, dry early summer conditions resulted in a very low flowering frequency on many sites, reducing sample sizes. It was planned to collect data from 20 1 x 2 meter quadrats with a bee orchid in the centre square (square 13 from (Figure 3.4) and 20 1 x 1 meter quadrats without a bee orchid. Each quadrat was, at its centre point, ≥1.5 m away from the centre of the next nearest bee orchid quadrat. The non-bee orchid quadrats were selected by walking 20 m away from each bee orchid quadrat in a random direction. The data collected for each quadrat were, species present (% cover), bare ground (% cover), aspect, GPS co-ordinate and vegetation height (cm). There were some plants which could only be identified down to family or genera level, as often it proved difficult to identify accurately species which only had a small quantity of plant material to identify or were not in flower, and indeed some species are impossible to identify without flowers, such as *Carex* spp., for which it is essential to have ripe fruit to key out the species (Stace, 2010). As such these were identified as far as possible (family/genus) and then included for analysis based on this along with the site (e.g. Asteraceae N3 which would stand for Asteraceae found on new site 3). Vegetation height was measured at tallest leaf in squares 3, 7, 9, 11, 13, 15, 17, 19 and 23 (Figure 3.4). A basic pH meter and a theta probe for moisture were both brought along to try to collect pH and moisture readings, but both pieces of equipment failed and so it was not possible to collect these data.

The number of sites used and the number of quadrats taken had to be revised due to insufficient number of bee orchids on each site. No old non-chalk sites were found to have bee orchids on so it was not possible to take quadrat data for this group of sites. It was possible to collect quadrat data for two new chalk sites (one with 17 orchid quadrats possible, one with one orchid quadrat possible), two new non-chalk sites (one with 20 orchid quadrats possible, one with six orchid quadrats possible) and two old chalk sites (one with eight orchid quadrats possible, one with six orchid quadrats possible).

Sites representing old traditional sites (chalk site) and new non-traditional sites (not chalk) had soil samples collected and it was hoped that two sites each with 20 bee orchid quadrats for 1) old chalk and 2) new not chalk could be found but this was not possible as there were insufficient bee orchid numbers present on the old chalk sites. The method was amended so that samples were collected from two new non-chalk sites and two old chalk sites. 28 soil samples were collected from old chalk sites (14 quadrats with a bee orchid and 14 quadrats without a bee orchid present) and 30 soil samples were collected from new not chalk sites (15 quadrats with a bee orchid and 15 quadrats without a bee orchid present). Each soil sample consisted of four soil cores which were 20 cm away from the centre of the quadrat in squares 8, 12, 14 and 18 (Figure 3.4) which were stored in a labelled clear plastic bag, stored in an cooled ice box and collected for analysis within 24 hours of collection. This was done by removing the vegetation directly on top of the sample area and using a soil corer to a depth of 15 cm to collect the core. Analysis was carried out by NMR Ltd and each sample was analysed for organic matter using the Walkley-Black method (% w/w) (Walkley and Black, 1934), available phosphorus (mg/l), available potassium (mg/l), available magnesium (mg/l), sand 2.00-0.063 mm (% w/w), silt 0.063-0.002 mm (% w/w), clay <0.002 mm (% w/w), nitrate nitrogen (mg/kg), ammonium nitrogen (mg/kg), ammonium nitrogen (mg/kg), dry matter (%), textural class, and available nitrogen at 15 cm depth (kgN/ha).

1	2	3	4	5
6	7	8	9	10
11	12	13	14	15
16	17	18	19	20
21	22	23	24	25

Figure 3.4: representation of a 1 x 1 meter quadrat divided into 25.

3.4.1.2. Statistical analysis

3.4.1.3. Detrended Correspondence Analysis

Once data had been collected it was input into a spreadsheet ready for analysis. Initially, a Detrended Correspondence Analysis (DCA) was carried in R (version 3.1.3) using decorana in the vegan package. Variables used for analysis were: 132 taxa (% cover), bare ground (% cover), average vegetation height (cm) and elevation (m). DCA scores 1-4 of the DCA output were used for further analysis as variables to determine if orchid and non-orchid quadrats were separated along the axes. The DCA site scores from the DCA output were used to determine if any of the variables used in the analysis were particularly important in separating out orchid and non-orchid quadrats. The DCA was repeated using a sub set of the quadrat data which also had soil samples taken. Soil sample variables were: Organic matter Walkley-Black method (% w/w), available phosphorus (mg/l), available potassium (mg/l), available magnesium (mg/l), sand 2.00-0.063 mm (% w/w), silt 0.063-0.002 mm (% w/w), clay <0.002 mm (% w/w), nitrate nitrogen (mg/kg), ammonium nitrogen (mg/kg), ammonium nitrogen (mg/kg), dry matter (%), available N at 15 cm depth (kgN/ha).

3.4.1.4. Logistic Regression

Logistic regression was used using a General Linear Mixed Model (GLMM) to determine if the DCA site scores 1-4 and new/old sites showed any significance in relation to bee orchid/non bee orchid quadrats. DCA scores 1-4 were used as independent continuous (predictor) variables, new and old sites as independent categorical (predictor) variable, site as a random variable and bee orchid/non bee orchid quadrats were used as the dependent (response) variable which were given the binary code orchid quadrat = 1, non-orchid quadrat = 0. This was carried out using the General Linear Mixed Model (glmer) function in R (version 3.1.3). This analysis was repeated on the bee orchid data which included soil samples.

3.4.2. Underlying bedrock change in old and new sites using BSBI data

3.4.2.1. Classification of sites by age and underlying bedrock

In order to assess if bee orchids were occurring in a broader range of habitat to what is considered their traditional habitat, old and new sites were compared using the underlying bedrock as an indication of the overlying soil and habitat type. This was to determine if bee orchids in more recent years are occurring outside of the traditional chalk/limestone areas of Britain.

All bee orchid records were extracted from the online BSBI Distribution database (BSBI distribution database) and records with grid references to a precision of 100 x 100 m (=site) or higher resolution were sorted into old and new sites. The new sites had two levels, one “strict” level which possessed fewer records and one “broad” level with a larger number of records. The records were classified using the following criteria:

Old site

- Records recorded in 1980 or before
- If grid references were ≤500 m away from another old record then they were considered same site

New site “broad”

- Record after 1990
- No pre 1991 records with a grid reference resolution of less than 10 x10 km within a 900 m radius of the new record
- **If the new site fell within a pre-1991 10 x 10 km grid reference it was still included in the analysis for the broad new site category**

- If grid references were ≤500 m away from another new record then they were considered same site

New site "strict"

- Records recorded after 1990
- **Strictly no pre-1991 records with a 900 m radius of the new record (site were excluded if they fell into a 10 x 10 km (i.e., tetrad, 1 km or finer resolution) grid square with a pre-1991 record)**
- If grid references were ≤500 m away from another new record then they were considered same new site

This gave 284 old sites, 980 broad new sites and 149 strict new sites. The reason behind the decision to have two levels of new site was because many new sites (colonisations) will have taken place within 10 x 10 km grid squares where Bee orchids had previously been recorded at other sites within the same 10 km grid square. This would represent infilling of the distribution and in a large proportion of these occurrences the site would have been a genuine new occurrence. However, as there was a pre-1991 10 x 10 km record occurred for the whole 10 km grid square, it could not be guaranteed that the site was new (if the location of the older record in the 10 x 10 km square was not specified in the data base). In contrast, the "strict" new sites had no nearby historical (pre-1991) record at any resolution, and hence they are more likely to be genuine colonisations. The three lists of sites represent old sites, new sites and infilling of distribution in recent years. These sites were plotted on a geology map of Britain (British Geological Society), which showed the underlying bedrock across Britain. Each site was classed as limestone/chalk or not limestone/chalk (Appendix VII). The underlying geology of old and new sites were then compared in geological associations between old records to new records.

Maps were created in ArcMap (version 9.2) to display distribution of old sites, new strict sites and new broad sites and proportions of chalk and not chalk for each age class were calculated.

3.4.2.2. Statistical analysis

Chi squared tests were initially carried out to determine if there was a significant difference between old sites and new strict sites, and old sites and new broad sites.

A logistic regression was carried out to determine if the underlying bedrock of a site (chalk = 0, not chalk = 1) could be predicted on the basis distance north of a site and age (new=1, old=0) of the site. The interaction between distance north and age was also tested. This was done in R (version 2.15) using the function general linear model (glm) and the family quasibinomial which allows for over dispersion of residuals.

3.4.3. 2012 Field work: Comparisons between new and old bee orchids sites

In order to determine if there was a difference in the habitat of new and old bee orchid sites, sites were selected initially for quadrat surveys according to the following set of criteria:

Old site

- Two records, one pre 1980, one post 1990
- At least one old and one new record at 100 x 100 m resolution
- New and old record maximum of 500m apart

New Site

- First recorded post 1990
- Nearest pre 1990 site ≥ 800m away
- Site recorded at 100 x 100 m resolution

As it was not possible to survey every field site with bee orchids records across Britain fitting the above criteria due to time constraints, it was decided that sites selected would be from two 200 km wide bands across Britain, one representing the core of bee orchids distribution in the south and one representing the northern edge of their distribution (Figure 3.5).

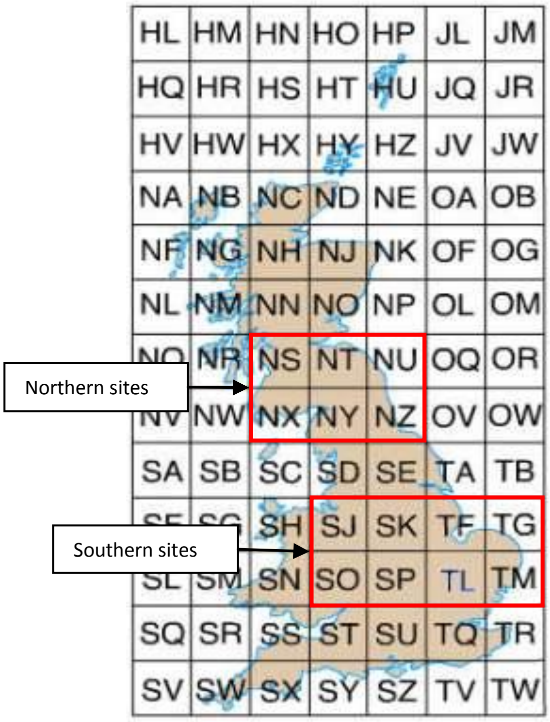


Figure 3.5: Map showing Ordnance Survey squares over Britain with northern and southern field work sites falling in the areas outlined in Red

The aim was to see if the field data showed a difference in traditional bee orchid sites and sites which had occurred in more recent years in relation to their habitat. Initially only six old northern sites could be found using the original criteria so in order to increase the number of sites visited for the old northern class, it was decided that all six figure grid reference sites with an old record (pre 1980), irrespective of if there was a new record present, would be searched for bee orchids increasing the number of old northern sites to 10. The opposite problem was encountered with new southern sites as a total of 57 sites were identified as possible areas to carry out field work. There was only limited time available to carry out field work, as it could only be done whilst bee orchids were in flower, which is from June to July and if too many sites were identified then it would not be possible to visit all sites. It was decided that this figure needed to be reduced in order to make it more feasible to visit all sites within the time available. Initially it was decided to only have one site from each 10 x 10 km square in the new southern area and the oldest sites were the ones which were eliminated leaving just the newest site in the 10 x 10 km square. If there were two sites with the same date then the most southerly one was selected. This left 38 new south sites, 20 old south sites, 21 new north sites and 10 old north sites (see Appendix IIIii for complete list of sites visited).

Once sites were selected two maps of each sites were printed (one MAGIC map and one Google map) so that upon arrival it was already evident how to access the site and the approximate size based on the Google map aerial photo. All sites were searched for bee orchids starting with southern sites as the south sites would be flowering first. Time spent on a site was calculated according to site size (Table 3.1).

All 89 sites were visited and every site where bee orchids were found had quadrat data collected. A maximum of five quadrats was taken from each of these sites. The quadrat was placed with the bee orchid in the centre square of the quadrat (square 13 from Figure 3.4). If more than five quadrats were possible on a site as there were more than five bee orchids sufficiently spaced to collect data, then each bee orchid was marked with a numbered marker and numbers were written on paper. Five numbers were then picked out of the hat and were the ones selected to take quadrat data of. The data collected for each quadrat were; species present (% cover), bare ground (% cover), aspect, GPS co-ordinate, vegetation height, shade (% cover) and a soil sample was collected from each quadrat to obtain pH using a pHep pH/Temperature tester (model number HI 98128) and soil texture class. The pH was taken at the end of each day and the sample was left to air dry and soil texture class was done after the field season had finished due to time constraints. This was done using the soil texture by feel method (Thien 1979 but see Presley and Thien, 2008). Vegetation height was measured at tallest leaf in squares 3, 7, 9, 11, 13, 15, 17, 19 and 23 and the average of these squares was used for analysis. The soil was taken from two areas approximately 20 cm away from square 13 (Figure 3.4). This was done by removing the vegetation directly on top of the sample area and soil removed with a small hand trowel to a depth of 15cm. The sample was then left to air dry for soil texture class to be taken upon return to the lab in York.

3.4.3.1. Statistical analysis

3.4.3.1.1. Detrended Correspondence analysis

Once the data had been collected it was initially analysed using Detrended Correspondence Analysis (DCA) carried in R (version 3.1.3) using decorana in the vegan package. Variables used for analysis were: 164 taxa variables (% cover), bare ground (% cover), moss (% cover), average vegetation height (cm), shade and elevation (m). DCA scores 1-4 of the DCA output were used for further analysis as variables to determine if new and old sites quadrats were clustering separately in any of the PC's. The DCA site scores from the DCA output were used to determine if any of the variables used in the analysis were particularly important in separating out old and new sites.

3.4.3.1.2. Logistic Regression

A logistic regression was carried out using a General Linear Mixed Model (GLMM) to determine if the DCA site scores for DCA site scores 1-4 showed any significance in relation to new and old sites. This was repeated using chalk/not chalk underlying bedrock as the dependent variable to see if any of the DCA sites scores relate to chalk/not-chalk underlying bed rock. . This was carried out using the General Linear Mixed Model (glmer) function in R (version 3.1.3).

3.5. Results

3.5.1. 2011 field work: Results

3.5.1.1. All quadrat analysis (without soil analysis data)

In 2011 out of the 44 sites which were searched for bee orchids, plants were only found on 10 sites (see Appendix IIIi). The six sites which contained the highest number of bee orchid plants for each category (chalk old, chalk new, not chalk new) were selected, as no old non-chalk sites could be found with bee orchids on they could not be represented in the analysis. The sites represent two new chalk sites, two old chalk sites and two new not chalk sites (Table 3.2). The chalk sites were in the Chiltern Hills, and the not chalk sites were nearby, to the NNW (Figure 3.6). Some quadrats at each site contained Bee orchids, and these were compared with quadrats in the same sites which did not; i.e., to evaluate within-site predictors of the occurrence of the orchids.

Table 3.2: sites where quadrat data were collected. Site locations and grid references can be found in Appendix IIIi.

Site	Chalk site	Site age category	Number of orchid quadrats	Number of non-orchid quadrats
Site 3	Chalk	New	17	17
Site 5	Chalk	New	1	1
Site 38	Not chalk	New	20	20
Site 39	Not chalk	New	6	6
Site 4	Chalk	Old	8	8
Site 20	Chalk	Old	6	6

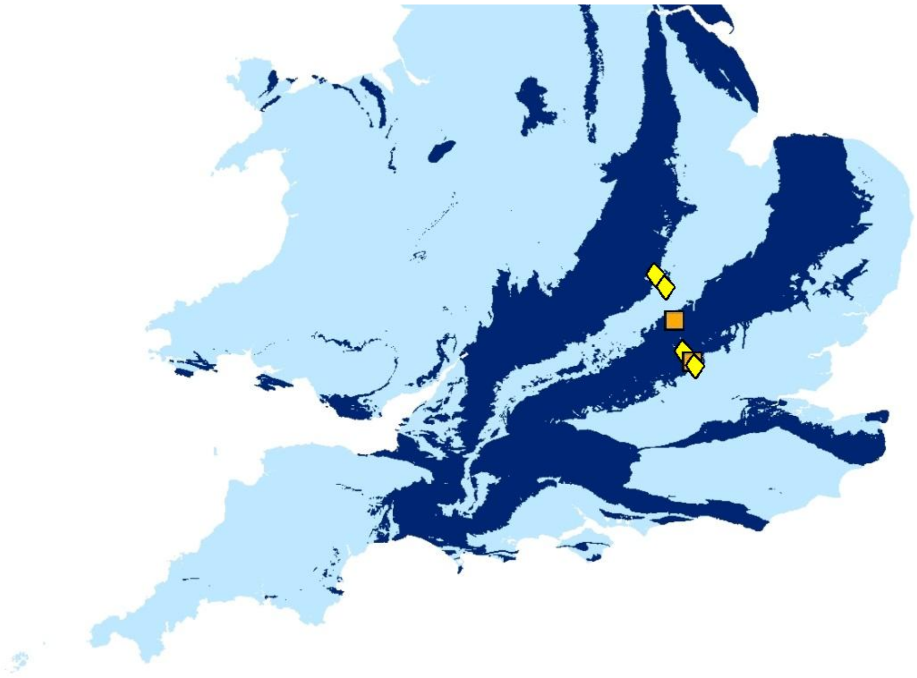


Figure 3.6: Map of field work sites for 2011. Underlying bedrock geology with chalk or limestone areas in dark blue and other in light blue. Yellow diamond: new site, orange square: old site.

DCA was carried out using the variables collected from each quadrat. There is a clear site effect visible in the results, with the different coloured symbols in Figure 3.7 (representing different types of sites) separating along the axes: DCA scores 1 and 2 explain much of the between site variation (Figure 3.7a).

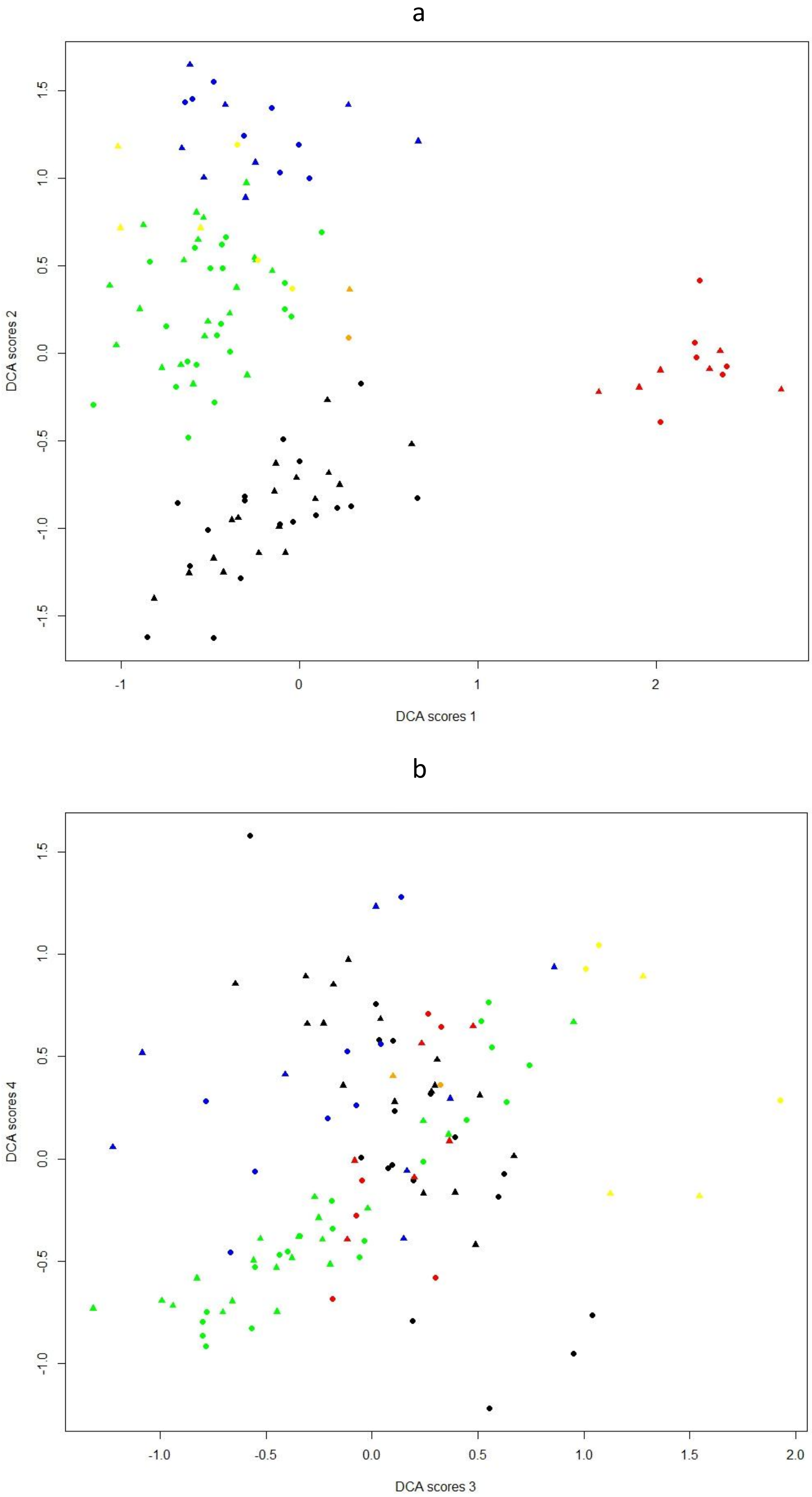


Figure 3.7: DCA scores based on quadrat data for six field work sites in Hertfordshire and Bedfordshire for a) DCA scores 1 and 2 and b) DCA scores 3 and 4. Quadrats are either bee orchid present (circle) or bee orchid absent (triangle). Sites are represented in the following colours: site 3 = black, site 4 = blue, site 5 = orange, site 20 = red, site 38 = green, site = 39 yellow.

Logistic regression using a GLMM with orchid/non orchid as the dependent (response) variable, DCA scores 1-4 included as continuous independent (predictor) variables, old and new sites as independent categorical (fixed) variable and site as a random factor showed no significance for any of the predictor variables, indicating that orchid and non-orchid quadrats show no difference habitat/vegetation within sites (Table 3.3).

Table 3.3: Output of the general linear mixed model using the model binomial for orchid/non orchid quadrats as the predictor variable, the DCA scores as continuous fixed factors and new old site as a categorical fixed factors and site as a random factor.

Principal component	Slope estimate	Standard error	z value	*p* value
Intercept	0.161	0.570	0.282	0.778
DCA1	0.025	0.32	0.079	0.937
DCA2	-0.098	0.332	-0.293	0.769
DCA3	0.524	0.372	1.409	0.159
DCA4	-0.414	0.385	-1.076	0.282
New/Old	-0.21	0.735	-0.286	0.775

3.5.1.2. Analysis for subset of samples with soil sample data

16 soil samples were taken at site 4 (old chalk site, 8 quadrats with and 8 quadrats without a bee orchid), 12 soil samples taken at site 20 (old chalk, 6 quadrats with and 6 quadrats without a bee orchid), 24 soil samples taken at site 38 (new clay, 12 quadrats with and 12 quadrats without a bee orchid) and 6 soil samples taken at site 39 (new clay, 3 quadrats with and 3 quadrats without a bee orchid). A total of 58 quadrats had soil samples collected and analyzed. The soil sample results for each quadrat were added to the other variables, and the used for DCA analysis was repeated. The first two DCA site scores explained the most variation in the data. A clear site effect be seen in the scatter graphs, particularly PC1 and 2, which explain the largest percent of the variation (Figure 3.8a).

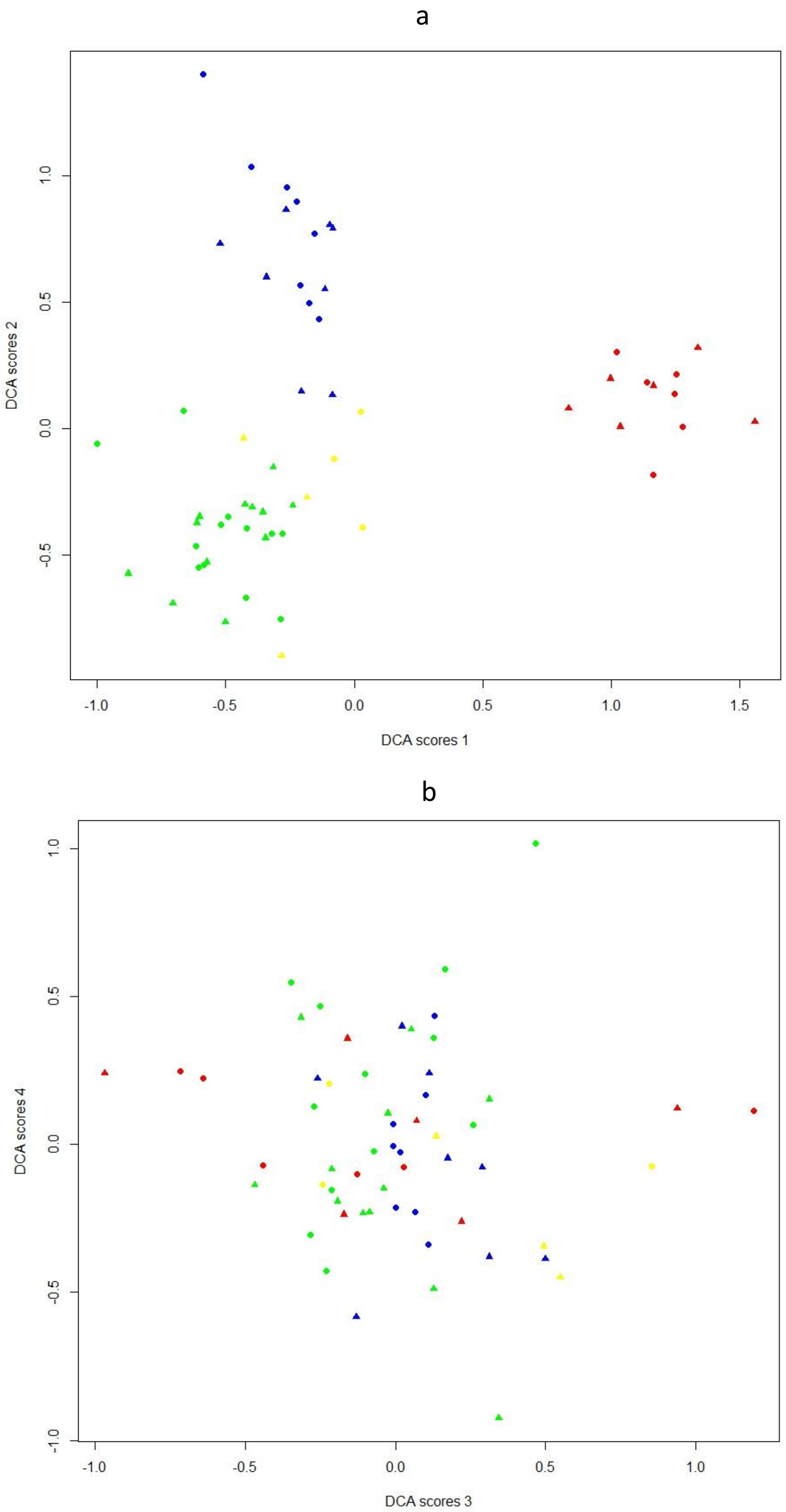


Figure 3.8 DCA site scores based on quadrat data for four field work sites with soil analysis in Hertfordshire and Bedfordshire for a) DCA site scores 1 and 2 and b) DCA site scores 3 and 4. Quadrats are either bee orchid present (circle) or bee orchid absent (triangle). Sites are represented in the following colours: site 4 = blue, site 20 = red, site 38 = green, site = 39 yellow.

Logistic regression using a GLMM with orchid/non orchid as the dependent (response) variable, DCA scores 1-4 included as continuous independent (predictor) variables, old and new sites as independent categorical (fixed) variable and site as a random factor showed no significance any of the predictor variables, indicating that orchid and non-orchid quadrats show no difference habitat/vegetation with sites where soil was collected and analysis carried out (Table 3.4). Thus, the biological conclusion did not change with the inclusion of soil data.

Table 3.4: Output of the general linear mixed model using the model binomial for orchid/non orchid quadrats as the dependent variable, the DCA scores as continuous independent variables and new old site as independent categorical variable.

Principal component	Slope estimate	Standard error	z value	*p* value
Intercept	-0.8822	0.8136	-1.084	0.2782
DCA1	0.4795	0.6811	0.704	0.4814
DCA2	1.6135	1.1682	1.381	0.1672
DCA3	-0.4958	0.7686	-0.645	0.5189
DCA4	1.6567	0.9404	1.762	0.0781
New/Old	1.7007	1.4982	1.135	0.2563

3.5.2. Underlying bedrock data analysis

The second set of analyses examine whether there have been large-scale and long-term changes in the associations of bee orchids with chalk and limestone, the traditional habitat of this species in Britain. Older records of bee orchids were more strongly association with chalk than were the newer records, whether looking at the new broad records or the new strict records (Figure 3.9). Out of 281 old sites, 60 (21%) sites were over areas which did not have chalk/limestone as the underlying bedrock (Figure 3.10a) and 221 (79%) sites were over areas with the underlying bedrock as chalk (Figure 3.10b). Out of the 931 broad new sites, 469 (50%) were over areas which did not have chalk/limestone as the underlying bedrock (Figure 3.10c) and 462 (50%) sites were over areas which had the underlying bedrock of chalk/limestone (Figure 3.10d). Out of the 147 new strict sites, 101 (69%) were over areas which did not have chalk/limestone as the underlying bedrock (Figure 3.10e) and 46 (31%) were over areas which had the underlying bedrock of chalk/limestone (Figure 3.10f).

There was a significant difference between the associations of old and new records with chalk and limestone, compared to other substrates, regardless of whether old records were compared with new broad sites ($X^2 = 73.9$, df = 1, $p < 0.00001$) or new strict sites ($X^2 = 92.2$, df = 1, $p < 0.00001$). In both comparisons, the new records are less associated with chalk and limestone.

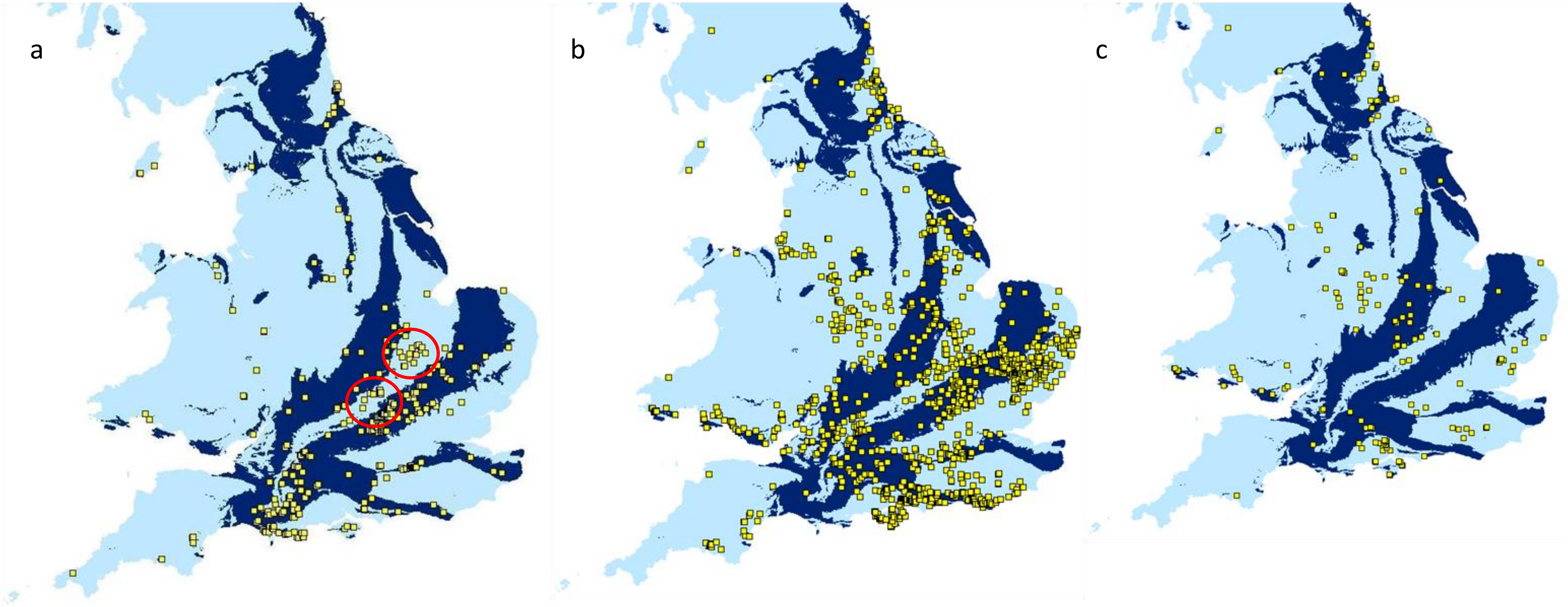
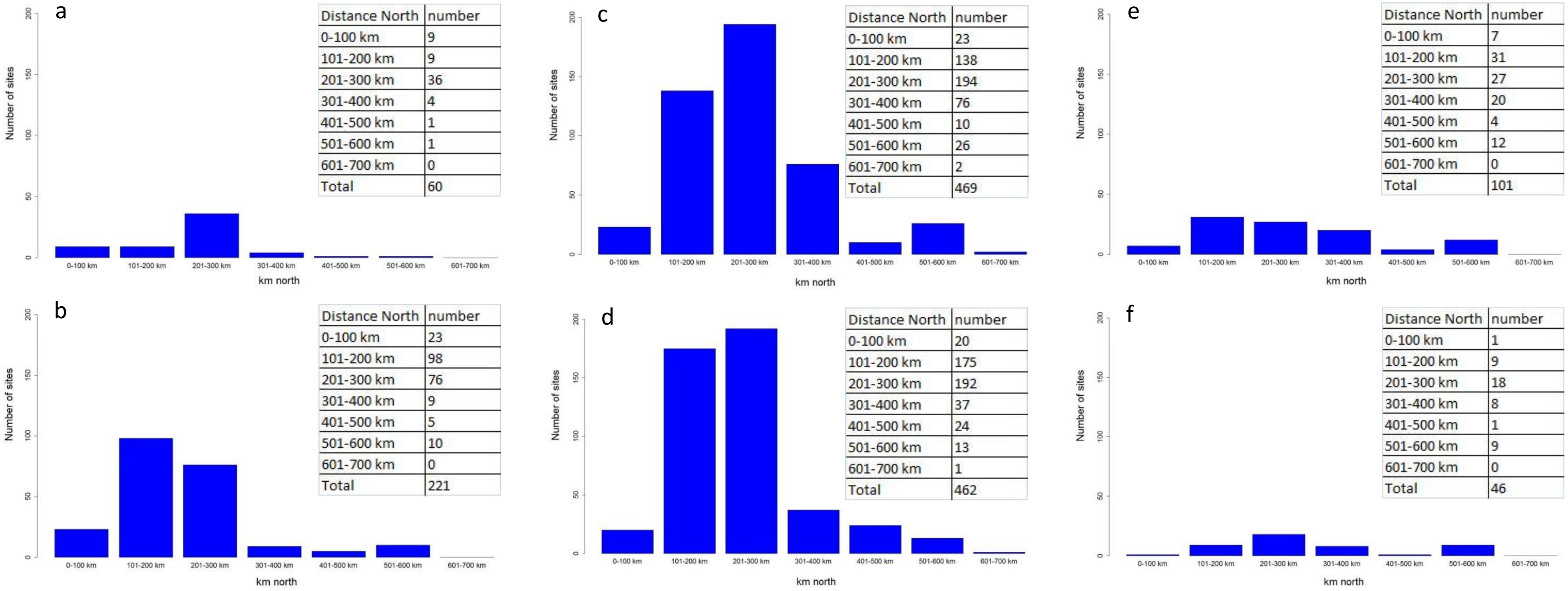


Figure 3.9: Underlying bedrock geology with chalk or limestone areas in dark blue and other in light blue with a) Old 100 m^2 sites across Britain. Red circles indicating populations mainly on "mudstone, siltstone and sandstone", b) new broad 100 m^2 sites across Britain and c) new strict 100 m^2 sites across Britain.



Distance North	number
0-100 km	9
101-200 km	9
201-300 km	36
301-400 km	4
401-500 km	1
501-600 km	1
601-700 km	0
Total	60

Distance North	number
0-100 km	23
101-200 km	98
201-300 km	76
301-400 km	9
401-500 km	5
501-600 km	10
601-700 km	0
Total	221

Distance North	number
0-100 km	23
101-200 km	138
201-300 km	194
301-400 km	76
401-500 km	10
501-600 km	26
601-700 km	2
Total	469

Distance North	number
0-100 km	20
101-200 km	175
201-300 km	192
301-400 km	37
401-500 km	24
501-600 km	13
601-700 km	1
Total	462

Distance North	number
0-100 km	7
101-200 km	31
201-300 km	27
301-400 km	20
401-500 km	4
501-600 km	12
601-700 km	0
Total	101

Distance North	number
0-100 km	1
101-200 km	9
201-300 km	18
301-400 km	8
401-500 km	1
501-600 km	9
601-700 km	0
Total	46

Figure 3.10: Number of sites against site location north in Britain for a) old sites on non-chalk/limestone underlying bedrock, b) old sites on chalk/limestone underlying bedrock, c) new broad sites on non-chalk/limestone underlying bedrock, d) new broad on chalk/limestone underlying bedrock, e) new strict sites on non-chalk/limestone underlying bedrock, f) new strict sites on chalk/limestone underlying bedrock

The logistic regression showed a positive relationship between age and chalk (*z* value = 3.186, *p* = 0.002), indicating that new sites were more likely to be on non-chalk areas. There was no significant relationship between northing and age and no interaction between northing and age (Table 3.5), suggesting that the observed range changes reflect a general shift away from limestone and chalk, rather than spread northwards northwards (there was spread at all latitudes considered) or spread away from chalk and limestone only in the south (in the most favourable climates).

Table 3.5: Output of logistic regression with bedrock as dependent variable and age and northing and age with northing as the predictor variables

Coefficients:	Estimate	Standard Error	z value	*p value*
(Intercept)	-1.673	0.324	-5.159	<0.001***
Age	1.149	0.361	3.186	0.002**
Northing	<0.001	<0.001	1.231	0.219
Age: northing	<0.001	<0.001	0.449	0.653

A possible complication could be that chalk and limestone are not equally represented in the landscape at all latitudes (Figure 3.11, solid line), and hence shifts in latitude and occurrence of different bedrocks could be confused. Within each 100 km band of Britain chalk and limestone makes up between 12 % and 40 % of the underlying bedrock (Figure 3.11), with somewhat reduced availability in the south-west peninsula in the far south (Figure 3.9). The percentages of old records on chalk and limestone for each 100 km band ranges from 68 % to 92 %, and largely mirror the availability of these geological substrates (Figure 3.11), except in the furthest north where the number of orchid sites is very small (Figure 3.9). There was a significant difference between the numbers of old records on chalk and limestone and the availability of these bedrocks in each latitudinal band (Wilcoxon signed rank test V = 21, df = 5, *p*=0.031), showing that bee orchids were more likely to occur on this substrate than would be expected by chance. The new broad category records range from 33 % to 71 % of sites on chalk for each 100 km band, less strongly associated with chalk than the old records, but still significantly more so than at random (Wilcoxon signed rank test V = 21, df = 5 *p*=0.031). In contrast, the new strict records, which represent new parts of the orchid distribution, rather than infilling, were not more associated with chalk and limestone than at random (Wilcoxon signed rank test V = 12, df = 5, *p*=0.8438), with 13 % to 43 % of records associated with this substrate (Figure 3.11). Thus, bee orchids have shifted away from their historically strong association with chalk.

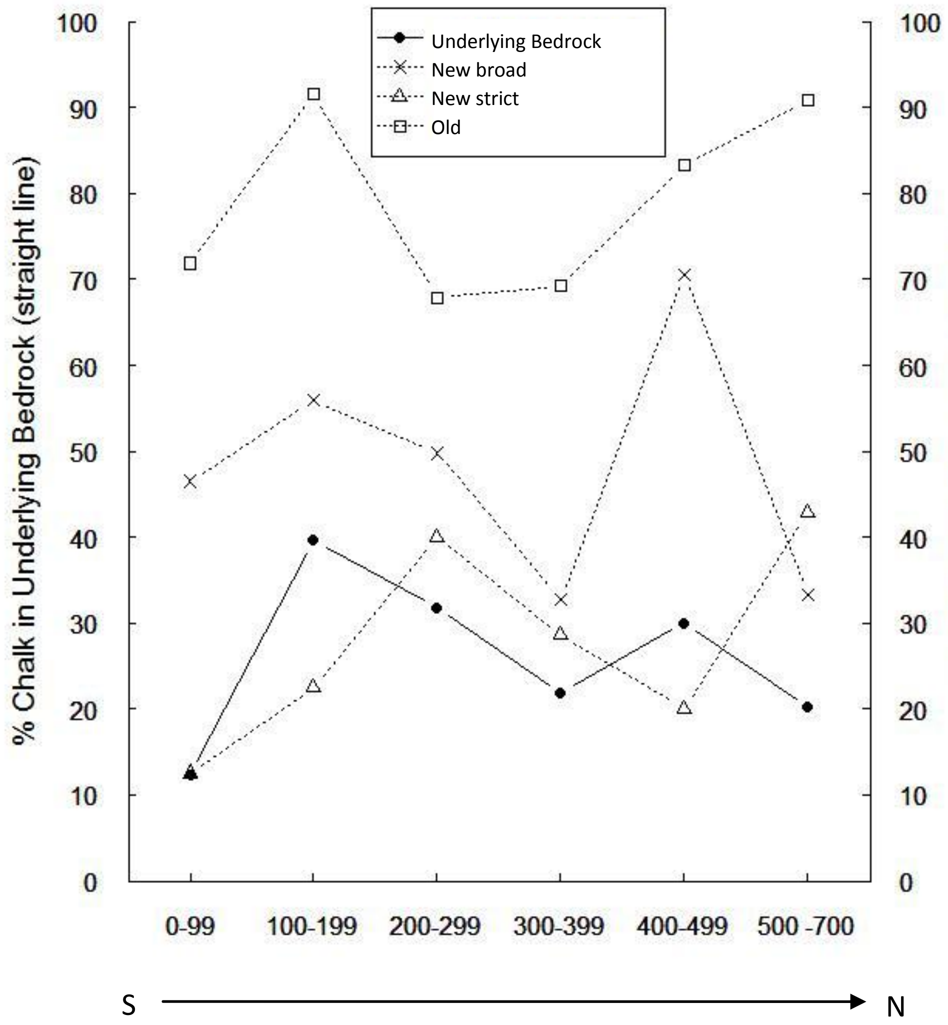


Figure 3.11: Graph showing % chalk and limestone and % of sites on chalk in 100 km bands across Britain for new broad sites, new strict sites and old sites. % underling bedrock which was chalk was also plotted.

3.5.3. Results for 2012 field work: comparing old and new bee orchid habitat

In 2012, all quadrats considered contained bee orchids, concentrating on comparisons among sites. 18 sites contained bee orchids out of the 89 searched (see Appendix IIIii). Out of these, five were old south sites with 15 quadrats taken, five were new south sites with 25 quadrats taken, two were old north sites with 10 quadrats taken and five were new north sites with 20 quadrats obtained (Table 3.6, Figure 3.12).

Table 3.6: sites selected to collect quadrat data with site information and number of bee orchid quadrats taken at each site. Site locations and grid references can be found in Appendix IIIi.

Site	North or south	Site age category	Number of bee orchid quadrats
Site 2	South	Old	1
Site 5	South	Old	5
Site 11	South	Old	5
Site 12	South	Old	2
Site 17	South	Old	2
Site 25	South	New	4
Site 28	South	New	5
Site 40	South	New	1
Site 43	South	New	5
Site 49	South	New	5
Site 54	South	New	5

Site 64	North	Old	5
Site 68	North	Old	5
Site 72	North	New	2
Site 76	North	New	5
Site 79	North	New	3
Site 81	North	New	5
Site 82	North	New	5

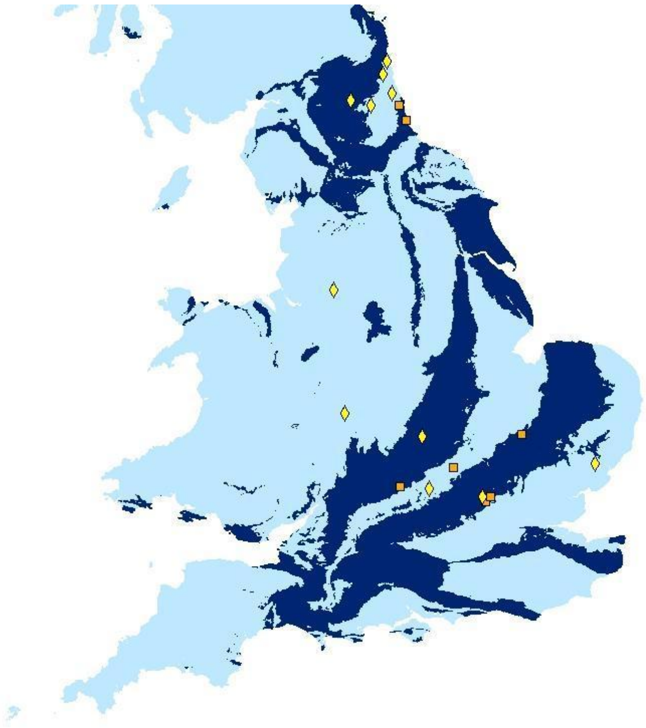


Figure 3.12: Map of northern and southern sites from 2012 field work season. Underlying bedrock geology with chalk or limestone areas in dark blue and other in light blue. Yellow diamonds: new sites, orange square: old site.

DCA was carried out and the first 4 DCA site scores extracted (Appendix VIiii). When the scatter plots were created from the DCA scores 1-4 sites in the north and south appear to cluster together and this is particular evident in the graph plotting scores 1 and 2 (Figure 3.13), as would be expected as many species within the vegetation quadrats do not occur across the whole country; some are specific or more common in the northern areas of Britain and some specific or more common in the southern areas.

The data points for each site usually cluster together (different symbols and colours for each site in Figure 3.13), but this was not as obvious as for the 2011 field work sites because there were 18 sites with ≤5 quadrats at each site in 2012.

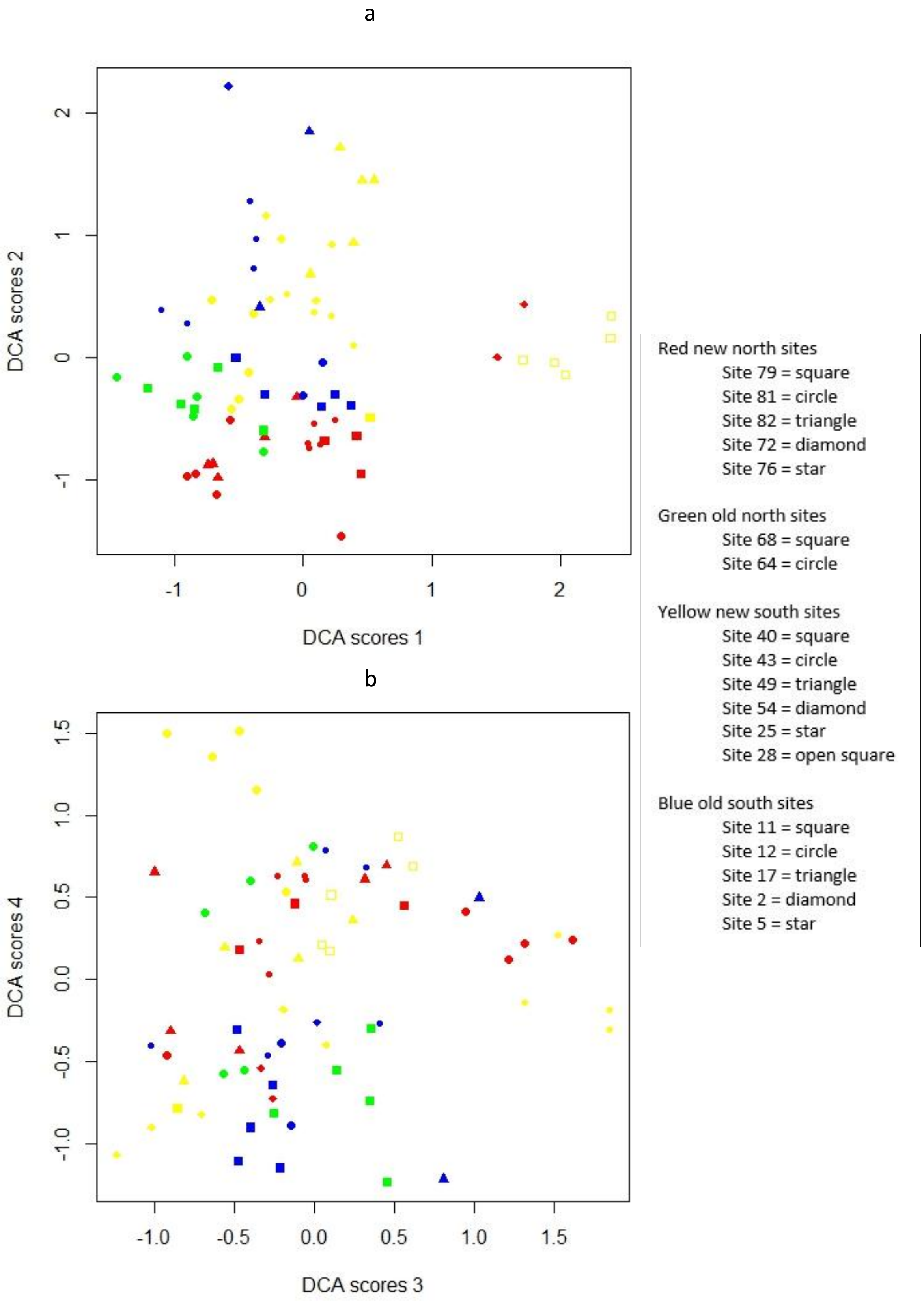


Figure 3.13: DCA scores based on quadrat data for all quadrats from 2012 field work for a) DCA scores 1 and 2 and b) DCA scores 3 and 4. Quadrats are coded according to age, location and site number. See key for details

Logistic regression using GLMM with north/south as the dependent (response) variable, DCA scores 1-4 included as continuous independent (predictor) variables, old and new sites as independent categorical (fixed) variable and site as a random factor showed a significant difference for DCA scores 2 (Table 3.7).

Table 3.7: W and *p* values from the General Linear Mixed Modal carried out using DCA scores 1-4 with the predictor variables north(1) and south (0)

DCA Site scores	Slope estimate	Standard error	z value	*p* value
Intercept	-1.19404	0.49797	-2.398	0.017
DCA1	-0.69630	0.51880	-1.342	0.18
DCA2	-4.70580	1.24586	-3.777	<0.001
DCA3	0.72413	0.65742	1.101	0.271
DCA4	-0.03922	0.48952	-0.080	0.936

Logistic regression using GLMM with old/new site as the dependent (response) variable, DCA scores 1-4 included as continuous independent (predictor) variables, north/south sites as independent categorical (fixed) variable and site as a random factor showed a link between the age of sites (old/new sites) and DCA site scores 1 and 4 (Table 3.8) implying old and new sights can be differentiated using the data collected. Old sites appear to be associated with more negative DCA site scores and new sites associated with more positive DCA site scores in DCA site scores 1 and 4 (Table 9, Table 10).

Table 3.8: Output of the General Linear Mixed Modal using the family binomial for old versus new sites as the predictor variable and the DCA scores 1-4 as continuous fixed factors.

DCA Site scores	Slope estimate	Standard error	z value	*p* value
Intercept	1.44279	0.44539	3.239	0.001
DCA1	2.88380	0.83003	3.474	<0.001
DCA2	-0.75755	0.44181	-1.715	0.086
DCA3	0.05456	0.43110	0.127	0.899
DCA4	1.85552	0.58387	3.178	0.001

Table 3.9: Number of old and new sites with positive and negative DCA site scores in DCA 1

	Negative DCA site scores	Positive DCA site scores	Total number of sites
Old sites	20 (80%)	5 (20%)	25
New sites	18 (40%)	27 (60%)	45

Table 3.10: Number of old and new sites with positive and negative DCA site scores in DCA 4

	Negative DCA site scores	Positive DCA site scores	Total number of sites
Old sites	19 (76%)	6 (24%)	25
New sites	15 (33%)	30 (67%)	45

Spearman rank correlations were used to determine if DCA values 1 and 4, which were significant linked to site age (Table 3.8), were linked to the Ellenberg values of the species associated with these axes (Table 3.11). Ellenberg Reaction indicator values were positively associated with DCA species scores 1. For DCA species scores 4 moisture and nitrogen were both negatively associated (Table 3.11; Figure 3.14).

Table 3.11: Spearman's rank correlations between DCA values 1 and 4 and Ellenberg values

Ellenberg	DCA 1 value r_s, value	DCA 1 value *p*-value	DCA 4 value r_s, value	DCA 4 value *p*-value
Light	-0.1201	0.1554	0.109	0.2
Moisture	0.069	0.4171	-0.2256	0.007
Reaction (pH)	0.314	<0.001	0.047	0.582
Nitrogen	0.153	0.0712	-0.359	<0.001
Salt	0.015	0.860	-0.050	0.556

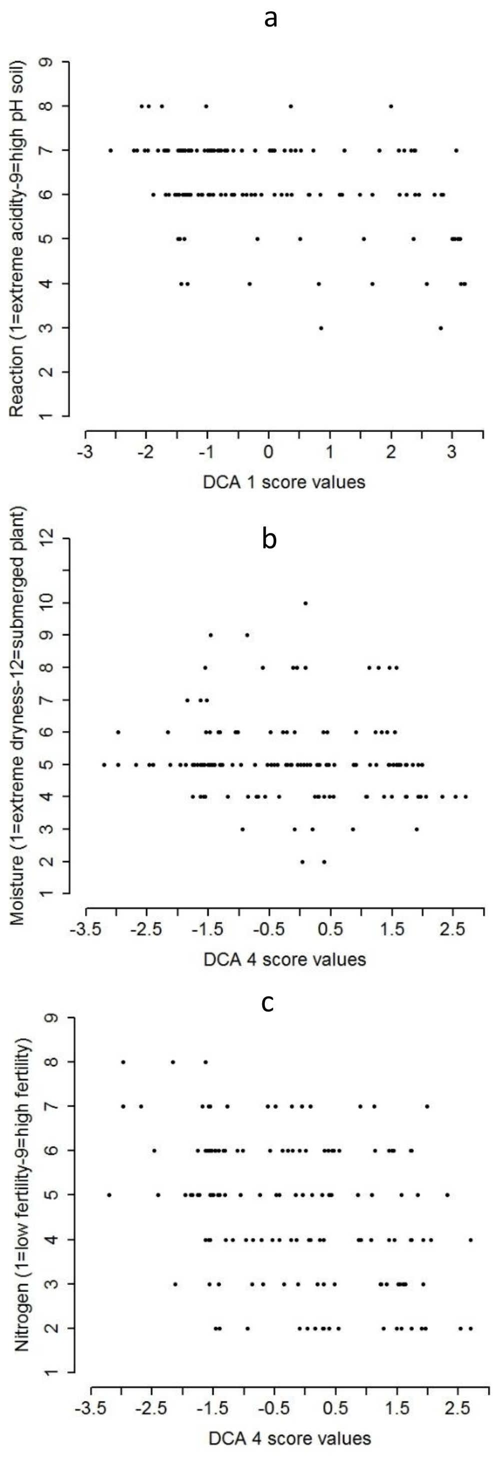


Figure 3.14: Ellenberg values plotted against DCA species scores for those with significant results from GLMM (Table 3.8) for a) Ellenberg indicator reaction with DCA 1 species scores, b) Ellenberg indicator moisture with DCA 4 species scores, c) Ellenberg indicator nitrogen with DCA 4 species scores.

The importance of Ellenberg values for Reaction (a measure of pH) is confirmed by the significant difference between pH for old and new sites (Figure 3.15; Kruskal-Wallis chi-squared = 19.4232, df = 1, *p*-value = <0.001), showing that new site quadrats have a much broader, and more acidic, pH range than old sites quadrats.

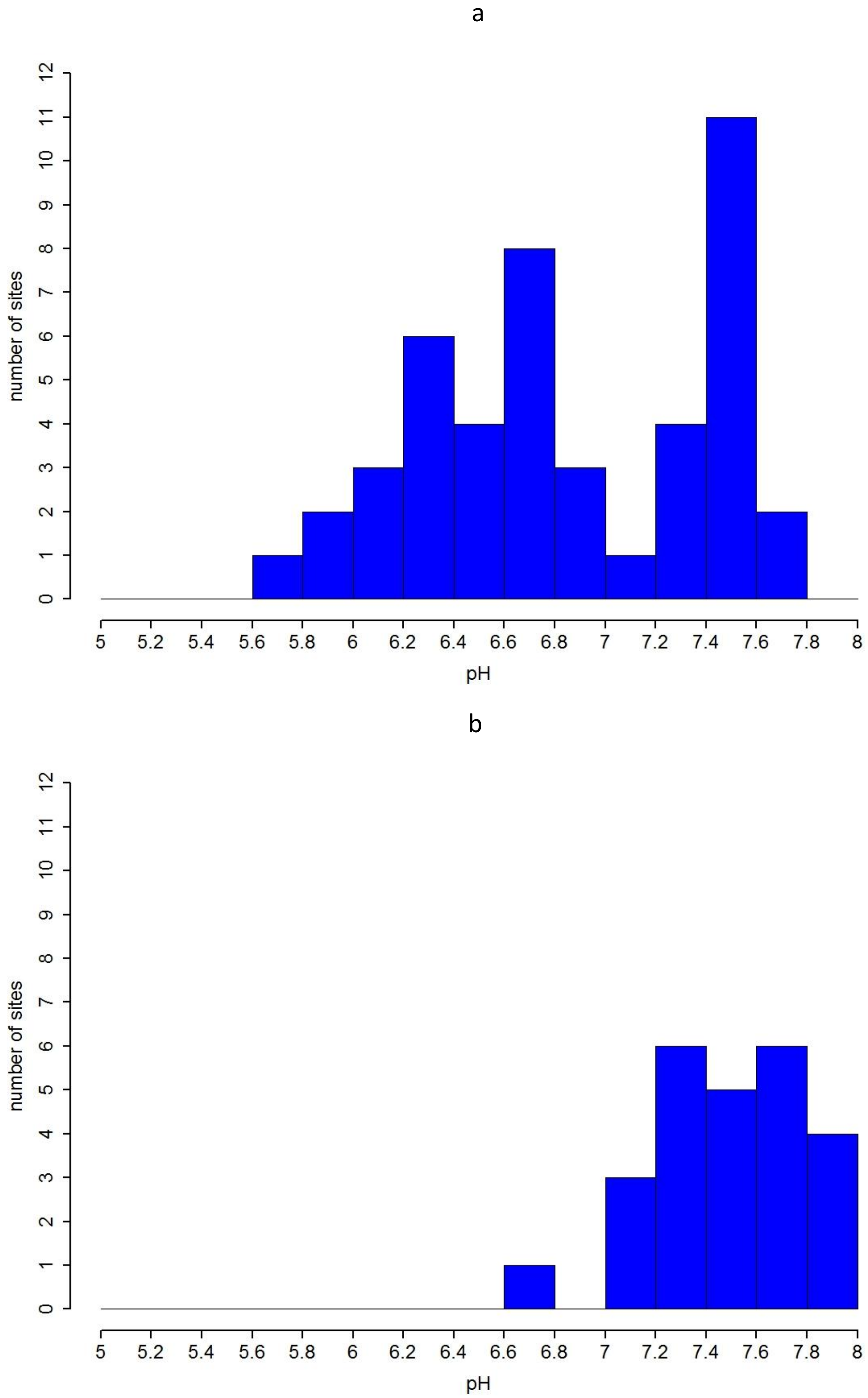
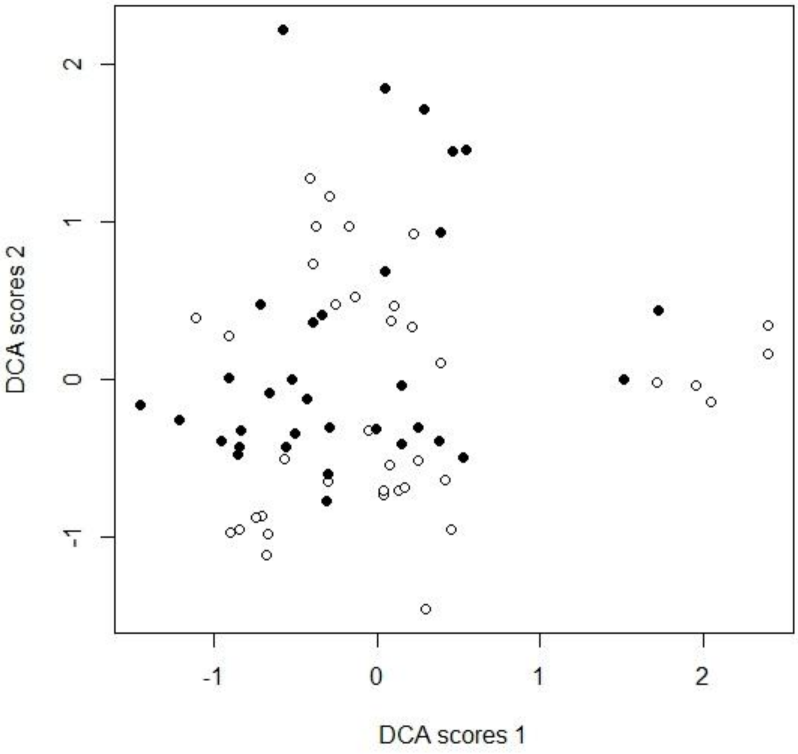


Figure 3.15: showing pH for a) new sites and b) old sites

Chalk and non-chalk underlying bedrock were distinguished in logistic regressions principally by their associations with DCA site scores 3, having a negative slope (Table 3.12, Figure 16). Thus, the underlying bedrock affects the vegetation and soil the sites.

Table 3.12: Output of the general linear mixed model using the family binomial for chalk and non-chalk sites as the predictor variable, DCA scores as continuous fixed factor, old and new sites as categorical fixed factor and site as a random factor.

DCA Site scores	Slope estimate	Standard error	z value	*p* value
Intercept	0.125	0.886	0.141	0.888
DCA1	0.018	0.408	0.044	0.965
DCA2	0.568	0.387	1.469	0.142
DCA3	-1.057	0.522	-2.023	0.043
DCA4	0.124	0.456	0.273	0.785



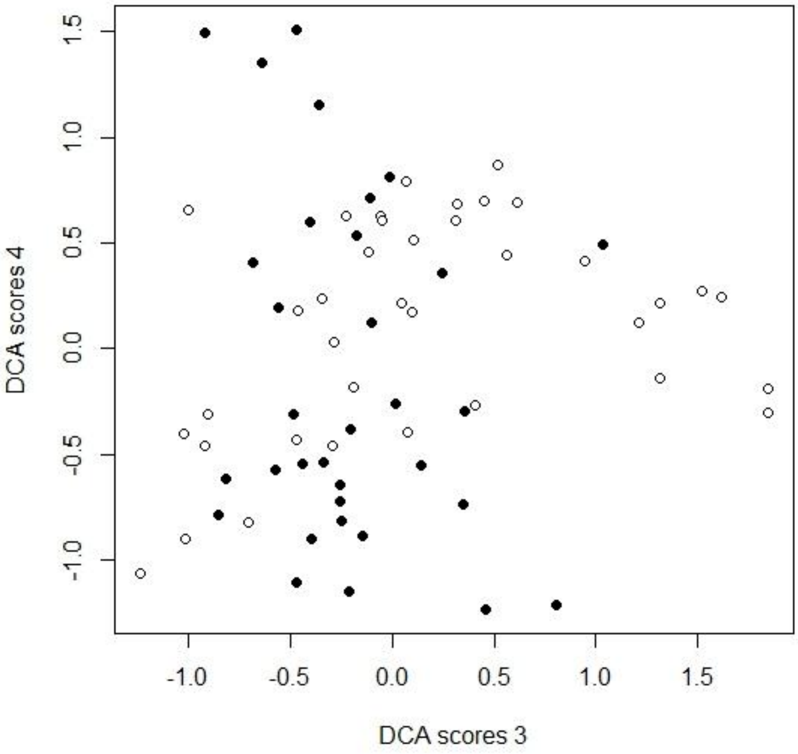


Figure 3.16: DCA site scores based on quadrat data for all quadrats from 2012 field work for a) DCA site scores 1 and 2 and b) DCA 3 and 4. Quadrats are coded according to chalk (black circle) or non chalk (open circle).

3.6. Discussion

3.6.1. 2011 Field season

3.6.1.1. Without soil analysis

3.6.1.1.1. Field work

The aim of field work in 2011 was to determine if bee orchids were occurring in specific microhabitats within sites and if it was in-site variation that dictated where bee orchids grew. One of the problems encountered was that bee orchids did not occur in sufficient numbers. Therefore it was not possible to collect data from 20 orchid and 20 non orchid quadrats from each site as was initially planned. Bee orchids were only found on a small number of the sites (less than ¼ of sites) and only one site had more than 20 bee orchids present. *Ophrys* plants do not flower every year and many plants remain in the non-flowering state within a population (Pridgeon et al., 2001). The proportion of flowering bee orchid plants in an average year is around 27% of the population (Wells and Cox 1986 but see Pridgeon et al., 2001) and so if there is only a small number of plants present at a site then it may be that none were flowering when the field work took place. This low number of plants found may also, in part, be due to a low rainfall from March-May which is when bee orchids will start to grow and initiate flower spikes (plants are very difficult to spot and identify without the flower spike present). bee orchids have an Ellenberg score of 4 for moisture (Hill et al., 2004a) (1 being extreme dryness and 12 being plants submerged in water) which indicates that although this is the drier end of the Ellenberg scale it does indicate that it prefers areas which have at least some moisture (4 indicates a moderate dryness tolerance (Hill, 1999)). The average rainfall for the months March-May for 2001-2010 was 168 mm for the south of England but in 2011 the average rainfall of these three months was 54 mm and this represents the lowest average March-May rainfall in the data available from the Met Office for the south of England going back to 1910 (Metoffice website, 2013). This low rainfall is likely to have affected the flower development in the bee orchids that year causing senescence of the flower spike. It has been shown that drought can cause some plants not to flower such as has been found to be the case in *Microstegium vimineum* (Gibson et al., 2002). It was shown by Wells and Cox (1989 but see Pridgeon et al., 2001) that drought can also prevent the formation of the inflorescence and Neiland (1994 but see Pridgeon et al., 2001) found that it can cause premature floral senescence. This is likely to be in order to conserve energy as flower and seed production is an expensive process on plant energy reserves (Inghe and Tamm, 1988), with the plants potentially ensuring that energy goes into production of the next year's tuber, as the all species from the genus *Ophrys* have underground tubers and roots which are replaced each year (Pridgeon et al., 2001). There is also the possibility that plants may have flowered earlier than expected as drought early on in the season for many plants can cause the early onset of flowering (Franke et al., 2006). However, there was no evidence of old inflorescence spike found on any of the sites searched. Although it is likely that the plants still occurred on many of the sites visited, it was very unlikely they would be spotted if they were not in flower. The local bee orchid population on the University of York campus showed no signs of flower spike initiation in early June when they were checked and only the basal rosette of leaves could be found. It was decided to try to obtain data from as close to the initial field work plan as possible. With these results it was still possible to assess within site variation and determine if bee orchids were occurring in specific microhabitats within a site or if there was very little difference between where they were and were not occurring.

3.6.1.1.2. Analysis

The first two DCA site scores explained much of the variation between sites, most likely due to differences such as different management. The DCA did not detect any difference between where orchids were and were not occurring in the first four DCA site scores (the decorana function in R. only finds the first four axes as these represent the largest percent of the variation). When soil analysis was added in the result was the same.

3.6.2. Underlying bedrock data analysis

The association of bee orchids mainly with the chalk/limestone areas of Britain before 1981 is obvious when old high resolution bee orchid sites are plotted over the geological map of Britain (Figure 3.9a). Over ¾ of all records from before 1981 occur on areas of Britain with chalk/limestone underlying bedrock. Most of the species from the genus *Ophrys* occur on calcareous sites and the bee orchid habitat is considered to be on wet to dry calcareous soil throughout its range (Pedersen and Faurholdt, 2007). There were two notable populations which did not fall on the areas classed as chalk or limestone areas (circled in red Figure 3.9) and the underlying bedrock was mudstone, siltstone and sandstone. This indicates that although traditionally bee orchids grow on calcareous sites, they have the ability to grow on non-chalk sites.

There has been significant expansion of the bee orchid (Figure 3.2 and Figure 3.9). Although some of these “new broad” sites may represent old sites which were only recorded at the 10 x 10 km resolution, some of these sites will also be newly recorded sites and it is clear that there has been a broadening of their range in Britain. Roughly half of these have occurred on areas outside of the chalk/limestone areas of Britain. The “new strict” sites show a strong change in underlying bedrock association with just over $^2/_3$ occurring in areas which do not have chalk/limestone as the underlying bedrock. Climate is a strong factor in where species are and are not able to occur (Singer et al., 1996, Allen et al., 1999, Prentice et al., 2000, Shuman et al., 2002, Shuman et al., 2004, Williams et al., 2004), but soil association and surrounding species composition also play a strong role in where a species will grow (British Geological Survey, Kruckeberg, 1969, Strahler, 1978). Bee orchids which appear to have originally been strongly associated with chalk/limestone areas of Britain do appear to have broadened their association in recent years. It is clear that many species shifted their distributions with recent climate change (Chen et al., 2011, Hickling et al., 2006, Groom, 2013), expanding their ranges to occupy areas which have recently become climatically suitable. As discussed by Huntley (Huntley, 1991), the normal response for plants to climate change is migration rather than evolutionary adaptation but with current climatic warming being particularly fast, and habitat being highly fragmented due to urbanisation and agricultural intensification, relying on migration it is likely to leave many plant species struggling for survival and widespread extinction is likely to happen. However, like other orchids, bee orchids have tiny, dust-like seeds and this will have increased the likelihood that they will disperse long distances, and colonise new sites. Colonisation may also be facilitated by the species’ ability to self, an extremely rare trait within the genus *Ophrys*, and hence for isolated individuals originating from a single colonising seed to generate further seed in the next generation.

There are instances where plants have adapted or evolved to new habitats or changed their tolerance to temperature (Sage, 2004, Franks et al., 2012) and sometimes this has occurred within a small number of generations (McNeilly, 1968, Antonovics, 2006). Based on the results presented here, the bee orchid appears to have broadened its habitat tolerance, no longer being predominantly confined to chalk/limestone areas of Britain. It maybe that the traditional association with chalk/limestone was not due to the soil composition, as traditionally supposed, but due to their preference for drier areas of grassland and chalk/limestone grassland, which fits this niche. In order to determine if bee orchids are genuinely broadening their habitat types or if it is just that the new sites, although not on chalk/limestone, are still very similar in their characteristics to old sites the second years field work was carried out in 2012 comparing new and old sites.

3.6.3. 2012 Field season

The field work in 2012 concentrated on testing whether there were differences between sites in the north and south, and on sites with different ages (new and old). As in 2011, it proved extremely difficult to locate bee orchids at each site in 2012. Plants were found at just over $^1/_5$ of sites searched. Some of the problems may be down to a low number of flowering plants as a result of low rainfall in the south the previous year which was discussed in section 2.5.1 However, northern areas of England did not have unusually low rain fall in the months running up to flowering in 2012, according to the met office data (Metoffice website, 2013), and so the low number of sites with bee orchids found may just be that on a single year only a small number of sites which have bee orchids present actually have flowering plants.

Results showed that there was a south north difference in the data collected from field work (DCA site scores 2) as a result of the changes in vegetation from the south to the north of Britain, which was not unexpected as it is well know that northern parts of Britain have many species which do not occur further south and vice versa (Preston et al., 2002). It is well documented that different species occur in different parts of Britain due to temperature and rainfall differences and species maps in the “New Atlas of the British and Irish Flora” (Preston et al., 2002) show a large number of species can be seen to only occur in the north (e.g. *Ajuga pyramidalis*, *Alchemilla alpine*, *Carex pauciflora*) or the south (e.g. *Carex strigosa*, *Centaurium pulchellum*, *Cirsium acaule*) of Britain, or only in certain regions. It is also well known that in the United Kingdom there is a north-west to south-east climatic gradient. In the north-west there are wetter and cooler climatic conditions; to the south-east it is drier, sunnier and warmer. These differences are as a result of a combination of factors including latitude, prevailing tracks of pressure systems, proximity to the European continental land mass and from the transition of upland areas in the north-west to lowland in the south-east (Mayes, 2000).

A difference could also be detected in results between old and new sites (DCA site scores 1 and 4). Two sites on DCA site scores axes 1 separated out from the rest of the scores, new south site 28 and new north site 72. New south site 28 was a disturbed open site with sandy soil and new north site 72 was a disturbed area by a track behind industrial estate buildings.

Ellenberg values (which relate to habitat) provided a valuable insight into how the species composition of new and old sites differed. Moisture, Reaction (a measure of pH) and Nitrogen showed a strong relationship . The species associated with new sites are associated with more acidic, drier soil and lower nitrogen although the latter is not a strong correlation. The chalk/limestone grassland association for old sites was likely to be because typically chalk grassland sites are historically drier. Climatic warming will have resulted in drier areas available off chalk grassland and this may have combined with disturbance of land, likely to be largely because of human caused disturbance (Metoffice, 2011), to make more habitat available to colonise off their traditional chalk grassland sites. Bee orchids have an Ellenberg value for Reaction of 8 (indicating they prefer more acidic soil), moisture of 4 (indicating they prefer drier areas) and nitrogen of 3 (indicating they prefer lower nutrient availability in the soil) and results here suggest that this has not changed. However, changes to the environment have enabled bee orchids to grow in a wider range of habitats. It has been found that for introduced plant species it is the habitat generalists or species that prefer disturbed habitats that are more likely to thrive, become invasive and be able to grow in a broader range of habitat conditions than in their native distribution (Bradshaw et al., 2008). It seems likely that the fact that bee orchids are showing a marked increase in distribution may be in part down to their ability to colonise disturbed areas of land and much like many introduced species (Maskell et al., 2006a, Maskell et al., 2006b, Sadlo et al., 2007, Chytry et al., 2008, Khan et al., 2008). Bee orchids are able to colonise habitat which has been disturbed as a result of anthropogenic activities.

3.7. Conclusion

Although there are many complexities associated with where bee orchids occur and do not occur, and differences between new and old sites, a clear general pattern can be seen. Bee orchids have broadened their habitat niche. Bee orchids have spread to locations which are outside of their traditional habitat (chalk and limestone grasslands) and it seems likely that their historical association with chalk grassland was due to a preference for dry open and nutrient poor habitats. Furthermore, it appears that calcareous soil was not a specific prerequisite for bee orchid presence. Climate warming, along with possible habitat disturbance associated with anthropogenic activities, has facilitated the spread of the bee orchid into an increasing amount of dry habitat, much of it no longer on chalk and limestone geological substrates. This spread may also be facilitated by the tiny dust like wind dispersed seeds which are produced in vast quantities by bee orchids and so facilitates their spread to new localities. It seems likely that other species with similar associations with dry open habitat may also be provided with new habitat to colonise in Britain, although many of these species may have dispersal limitations.

4. General discussion

4.1. Overview of findings

The initial focus of this thesis was to examine how climate has affected plant distributions, specifically, whether climate change has been altering plant distributions as would be expected, and as has been demonstrated in a large number of animal taxa (e.g. Hickling et al., 2006, Chen et al., 2011).

The first data chapter (chapter two) looked at latitudinal shifts in southerly distributed plant species in Britain and aimed to determine if plants' northern range margins were advancing as they frequently are in animal species. It also considered the extent to which human mediated dispersal affected range margins, and whether plant traits could help explain the observed changes. Despite Britain having warmed by 0.25°C per decade between 1960-2010 (Met Office, 2011) as a result of anthropogenic climate change, the northern range margins of plant species were not found to be advancing, making it clear that climate was not the main factor influencing their northern distributional margins. Land use change is likely to have been the main driving factor. It was, however, possible to show that human influences have aided the dispersal of a number of southerly distributed plant species at the northern edge of their distribution; populations that are classified as introduced (not occurred via natural dispersal) by Preston et al. (2002) may aid the poleward movement of these species in the future. However, these introduced northern populations have not persisted well during the study period. The plant traits which were used to try to determine whether species with particular propagule dispersal types were showing different levels of distribution change did not provide any conclusive results. This is perhaps not surprising. Propagule type might be expected to explain some variation in rates of expansion, but not necessarily explain variation in rates of retraction, the predominant type of distribution change that was observed. Ellenberg values indicated that some species' retractions may be due to degradation of calcareous grasslands and marginal land because the species associated with open sites and high pH were retracting further. This again indicates a link with land use changes.

The second data chapter (chapter 3) used bee orchids as a study species as it has been noted by some BSBI county recorders that Bee orchids appeared to be occurring in non-calcareous sites (calcareous sites being their traditional habitat), that there had been infilling of the range of the species and, particularly in the past decade, a distinct northward shift in their distribution. Thus, whilst it is not representative of southerly plant species in general, it illustrates some of the changes taking place in an exemplar species that is expanding its range northwards, and that is apparently being successful in the warmer climate. Bee orchids belong to a well-studied taxonomic group, and all 10 x 10 km squares are native occurrences (i.e., introductions are not thought to have affected the distribution). Thus, they provided a useful opportunity to assess the positive responses of one species to a warmer climate, using a combination of field work and BSBI data.

In order to assess if the hypothesised change in habitat was real, the research was split into three sections. The first was to determine if the occurrence of bee orchids within a site was as a result of small patches of suitable habitat amongst unsuitable habitat. This was particularly important to assess whether habitat change was as a result of small calcareous deposits within a site (e.g., associated with previous human activities) or whether bee orchids were genuinely growing successfully on non-calcareous substrates. It was demonstrated that there was no consistent in-site variation in where plants were and were not found growing, indicating that the overall habitat type and bedrock was a reliable metric of habitat. The second year's field work aimed to assess if new sites differed in the habitat type compared to the old sites, and it could be seen that this was indeed the case. Old sites tended to be conventional calcareous sites whereas new sites were far broader in terms of the geological substrate and habitat where the bee orchids were occurring. This revealed that bee orchids occurring in a broader range of habitat types in their more recent distribution with newer sites showing a broader range of pH and older sites having a more basic pH. Thirdly, BSBI data for all sites which fell in the older time period were mapped over a geological map of the underlying bedrock of Britain and all newly established sites were also mapped over the same map. It could clearly be seen that older sites occurred mainly over calcareous areas of Britain but in the newer sites there was a clear shift to non-calcareous regions. The apparent success of bee orchids could be attributed to both their habitat associations and their dispersal. Their ability to colonise disturbed areas would facilitate their spread as humans have caused disturbance to many areas. Traditionally they are considered to prefer calcareous grassland habitats but this association may be as consequence of a preference for drier areas. As the climate has warmed, increasing evapotranspiration, an increase in drier areas are likely to have facilitated their spread. They are also self pollinated and produce large numbers of dustlike seed which can be carried long distances on the wind. This will facilitate their dispersal. No pollinator is necessary for seed production, so even isolated individuals can reproduce successfully, and seeds can be carried over some of the barriers (unsuitable habitats) which humans have created in the landscape.

4.2. Distribution changes

When this research was originally started, there was an obvious knowledge gap in terms of research on northern range margin shifts in plants. It is well established in the literature that the northern range margin of animal taxa are advancing north, as would be expected in a warming climate (e.g. Hickling et al., 2006, Chen et al., 2011) but the majority of literature which exists for the leading edges of plant distributions is concentrated on elevation increases at the upper range limits of plant species, particularly at the tree line and in the alpine zone (Walther et al., 2005, Parolo and Rossi, 2008, Harsch et al., 2009, Frei et al., 2010). The BSBI data which contains distribution data on all native British plant species is ideal for research into distribution of plants and has been used in a number of published papers (e.g. Kull and Hutchings, 2006, Jackson et al., 2009, Groom, 2013, Powney et al., 2014), but the northern range margin had not been studied to see if plants are also tracking climate in the same way as animals. Considering the importance of northern populations in facilitating the spread of species to keep pace with climate, this was an important knowledge gap that needed filling. The status, and in some cases survival, or plant species will depend on the capacity of northern populations to spread into the newly available space. This research has shown that most plant taxa are in fact not advancing at their northern range margin in Britain, contrary to expectation. Most taxa are either retracting or remaining the same at their northern edge. It was originally thought that plant species would be advancing at their northern range margin, even if land use was resulting in reductions within the cores of their distributions, this has clearly not been the case. It is likely that the lack of northwards shift is down to the huge impact humans have had on the landscape with agricultural intensification and urbanisation leading to a generally unsuitable habitats for most species, with the remaining suitable habitats being highly fragmented (Vitousek et al., 1997) and therefore hindering species dispersal via natural means.

These results bring up some stark questions about the future of British plant species. If they are not able to move north into the newly available climatically suitable habitat, many species will decline, as the current area of distribution becomes less favourable. The lack of northwards expansion at plant species' northern range margins (chapter two) is coupled with a general decline in the number of occupied 10 x 10 km squares for a large numbers of the taxa, resulting in widespread declines. This reduction in overall distribution has previously been demonstrated in orchid species in the UK (Kull and Hutchings, 2006), but the work reported in chapter 2 shows that this reduction of distribution is clearly affecting a wide range of plant taxa. An avenue of research which would be extremely useful, from a conservation view point, would be to examine changes to the status of species in different parts of their distributions, as this would facilitate conservation efforts in areas where species are experiencing a higher rate of decline and identify where species distributions are stable. Although insects and other animals have been spreading northwards in recent decades, there may eventually be consequences of a failure of plant species to shift their distributions. Many insects are often highly dependent on specific plant taxa, which could mean that the northwards expansion rates of animals will slow if suitable host plants are not be available. It is know that insects are responsive to climate alterations as temperature influences much of their life history, but the insects are also strongly affected by the availability and quality of their plant food supply (Pelini et al., 2009). Hence, the lack of northwards shifts in plants is likely to have knock-on effects for many other species. If the average ranges sizes of plant species decrease, or, plant growth is negatively affected, then negative implications for other organisms reliant on these plants are likely to follow. Hence, the observed mismatch in the distribution changes of animals and plants may be greater than previously realised. Previous work suggested that plants and insects disperse at different speeds, so during climate change range shifts could differ substantially, leading to mismatches between ranges (Schweiger et al., 2008). For example, insects, such as a number of butterflies, have been shown to shift their distributions poleward or to higher elevation. Parmesan *et al.* (1999) demonstrated shifts in Butterfly species of up to 240 km over 30 years whereas trees are expected to track climate change at a rate of just 20-40 km per century, far below the rate which would be needed to keep pace with current climate change (Davis and Shaw, 2001). This issue of mismatches between animal and plant distributions has been illustrated using bird assemblages and their association with woody plants. Kissling et al. (2010) demonstrated that bird loss as a result of climate change would be significantly higher due to lag time of woody species when lag time of woody plants and the birds associated with them were modelled. The work reported here suggests that the situation may be even worse. The previous studies assumed that the plants would respond, just more slowly, whereas the results in chapter 2 indicates that they may fail to expand at all. Animals and plants are actually going in opposite directions. An interesting avenue for future research would be to take the species covered in chapter 2 and identify which of them is an important host plant to specific animal species; and then to assess whether any of these animal species have datasets which would enable comparisons between changes to the distributions of the hosts and herbivores. These disassociations may also have negative effects for some plant species if specialist pollinators are lost or if the above ground/below ground interaction is affected and there is already evidence that of some parallel decline of pollinator insects and insect pollinated plants in the Netherlands and Britain (Biesmeijer et al., 2006). Plant species are strongly linked to below-ground terrestrial assemblages such as microhorizal fungi and detritovores. Mismatches between the rates at plant species ranges shift and the below-ground biota changes could affect plant distributions and diversity. This may explain why some species become rare and some more abundant in their new ranges (Van der Putten et al., 2010).

Another element of range shift is changes to the densities and abundances of some species. This has been shown to be occurring as tree density increased at the higher elevations of some alpine treelines in recent years, even if the treeline is not advancing higher to altitude (e.g. Szeicz and Macdonald, 1995, MacDonald et al., 1998, Klasner and Fagre, 2002, Danby and Hik, 2007). Infilling of shrubs in arctic regions has also been observed using historical and present day aerial photography to compare areas (Sturm et al., 2001) and liana’s in tropical forests have also been shown to be increasing in number abundance, which has been linked to climate change and increased CO_2 as well as disturbance (reviewed by Schnitzer and Bongers, 2011). Increase in densities at the northernmost edge or in the core of species’ distributions may be occurring in plant taxa; and Groom (2013) demonstrated that there has been a change in the latitudinal weighting of species distribution records, although different time periods were used to those used in chapter two.

Despite the lack of a northwards shift at the northern range in plants, some species are not declining in their distributions, based on observations from the BSBI atlas information, (Preston et al., 2002), and a number of these may be exhibiting an infilling of the distribution. This has happened with the bee orchid (see chapter 3). They have not only successfully colonised new habitats but are also colonising habitats which are not traditionally considered suitable for the species. This infilling of range may also be evident in species which have a stable distribution but where higher resolution data would be required to identify whether infilling is taking place. For example, it would be possible to take species which have relatively stable or positive change index values and look at higher resolution data for particular vice counties where repeat floras have been published (e.g. Bedfordshire, Hertfordshire etc).

4.3. Dispersal

The ability to disperse is essential if a species is to spread and colonise suitable habitats, and utilise suitable environmental space (Cousens et al., 2008). How far a plant propagule is able to travel is likely to influence its chances of colonising new habitats. Factors such as seed size and mass can often determine the likely distance travelled, plants with heavy seeds generally not dispersing far, their seeds dropping next to the parent plant; whereas light seeds such as those dispersed by wind are able to move kilometres from the parent plant (Venable and Brown, 1988; Greene and Johnson, 1993; Muller-Landau et al., 2008; Soons and Bullock, 2008). In order to determine if there was a difference between the northern margin range change in species with propagules which facilitate long distance dispersal, compared to those with short distance dispersal methods, dispersal modes were considered in chapter two. The results did not show any relationship between dispersal mode and range margin shift. In Northwest Europe there is known to be an ongoing decline in many plant species and it has been found that species adapted to water and fur assisted dispersal are over represented amongst declining species whilst species dispersed by wind and bird are underrepresented indicating a dispersal link the region (Ozinga et al., 2009), however, this link to dispersal method was not evident in this research. It is known that plant species were able to disperse to new localities, during historic climatic changes, such as during the onset of the Holocene, when areas were freed from ice, for example travelling great distances to reach Northeast Greenland and colonise the newly available space (Klein et al., 2008). The absence of a link between range shifts and dispersal method/distance is likely to be due to changes in land use between the first and second time period. It is well know that there have been dramatic changes to the landscape due to urbanisation and agricultural intensification in the 20th century (Vitousek et al., 1997) and so these artificial barriers will have impacted on the ability of plants to disperse. Dispersal mode is only likely to be an important predictor of differences in rates of expansion during periods when ranges are expanding, which was not the case for most of the British plants. On the other hand, a small number of species which are capable of long distance dispersal may be expanding, as exemplified by the Bee orchid (chapter 3). Although dispersal method has been explored in chapter two, seed weight has not, and so a future avenue which could be explored would be to look at seed weight in relation to the range of species. It is possible that lighter seeds, which may be more easily picked up on the fur and feet of passing animals as well as human shoes and vehicles, as well as having the capacity to be blown, may have more stable or expanding distributions than those with larger seeds that lack specific transport mechanisms.

Bee orchids (*Ophrys apifera*) have shifted northwards in Britain, particularly in the past decade, and this may be in part be down to the easily-dispersed dust-like seeds, which are adapted for long distance wind dispersal (Pridgeon et al., 2001). Unusually for an *Ophrys*, the bee orchid is mainly self pollinating in Britain (Darwin, 1904) which will mean there is an abundance of fertile seed available and pollinators are not required to produce viable seed. suggested that self pollinating species may have a competitive advantage over those that have specific plant-pollinator interactions as both the plant and the pollinator will need to spread in order for them to be successful in colonising new sites (e.g. Baker 1955, 1974; Klein et al. 2008), and so this may be part of the reason for the success of the Bee orchid in the UK. A single plant originating from a wind-blown seed and colonising a new site would itself be able to set seed, consolidate a population in the new site, and potentially send out more propagules to continue the colonisation process. There are three other species of *Ophrys* native to the UK (*O. fuciflora, O. insectifera* and *O. sphegodes*) all of which have seen declines in their distribution over the past century and this has been put down largely to land use changes (Preston et al., 2002). It may also be that there may be a link with pollinators as all three species have specific pollinator associations and so the species are reliant on presence of pollinators for seed production (Vereecken et al., 2011). The failure of these species to expand may be because of this requirement, an example of an Allee effect, whereby very small populations tend to decline even if the environment is generally suitable for population growth.

When looking at dispersal distance for individual plant propagules there are many difficulties in determining the fate of seeds after leaving the parent plant (Wang and Smith, 2002). Although species may have evolved dispersal methods that facilitate the spread of their propagules, it is also the case that the very longest distance dispersal events may be brought about by other mechanisms (Cousens et al., 2008). The ‘rain’ of long-distance propagules is hard to detect. Almost all of the propagules are likely to fall in locations where the habitat is unsuitable for a given species, so they will not grow into plants that will be recorded by botanists. Unlike dispersing animals, the propagules of plants have little (unless transported by an animal) or no capacity to select suitable target habitats for colonisation. This difference could underlie why animals are spreading northwards whereas plants are not. Despite the apparent lack of north movement of plant species in Britain, species are still managing to occur in new locations as a result of human-mediated dispersal. This is likely to become one of the most important dispersal methods of plant species in future.

4.4. Human mediated dispersal

Anthropogenic influences are clearly having and will continue to have an impact on species in many ways, including negative impacts on the ecosystem due to land use changes (Sala et al., 2000). The way humans utilise the land in urban and agricultural landscapes has generated considerable reductions in habitat availability for many species, and hence large dispersal barriers (Vitousek et al., 1997), but not all human actions will have negative impacts on species' distributions. The movement of plant species around the world has had a high level of impact on many ecosystems. Some of these impacts may be negative such as the damage caused by many species of plant which are considered invasive outside their native range (e.g. Rejmanek and Richardson, 2013). For example, *Falopia japonica* is considered an aggressive invader in Europe, the North America (Aguilera et al., 2010). Research on human-mediated dispersal is concentrated on non-native species and their invasion or potential to invade countries far outside of their native ranges, due to the negative impact on both human and natural systems (Mack et al., 2000). However, from the perspective of these plants, human-mediated dispersal has increased their ranges. Human-mediated dispersal also has the potential to have large impacts on the distributions, in the context of climate change, facilitating their movements towards the poles. This was observed in the northern range margin chapter (chapter 2), which demonstrates that the northernmost 'introduced' 10 x 10 km records of species are much further north than the 'native' occurrences of the same species. The scattering 'introduced' northern records of species, due to human movement of plant material, represents long distance dispersal events which have the potential to facilitate northwards distribution shift and overcome human-created habitat barriers. It may be that in the future, with temperature changes to the climate occurring, human intervention may become essential in facilitating species spread to suitable areas On the other hand, the apparently very low survival of these human-generated populations suggests that most of this transported material is ending up in locations that are not suitable for long-term population establishment.

4.5. Habitat and environmental conditions

Vascular plants are good indicators of the effects of environmental change on biodiversity in general and are key components of nearly all terrestrial ecosystems (Godefroid, 2001, Landsberg and Crowley, 2004). The habitat preference of a plant species is an important factor in where species are able to colonise. Along with climatic factors, habitat is important in the distribution of species as habitat availability is important in changes to distributions of species. Ellenberg values, which give indications of habitat associations, have been assigned to plant species in Britain (Hill et al., 2004) and plant atlases and floras often provide information on the particular habitat associations of the species listed (e.g. Preston et al., 2002). It is known that different character traits and habitat associations can have significant effects on species distributions and survival (Fisher and Owens, 2004, Koh et al., 2004, Cardillo et al., 2005, Powney et al., 2014) but the extent to which these requirements change through time (as the climate changes) is less well known. Changes in the realised niche of the Bee orchid (chapter three) was revealed by its occurrence in a broader range of habitats in more recent years than in historical records, when it was almost entirely restricted to calcareous substrates. This ability to occur in a wider range of habitats may be one of the reasons for the expansion of the Bee orchid in Britain, which might otherwise have been expected to decline, given that this has been the trend for most plant species which are specialised to use open, dry habitats, characterised by high pH soils; most of these species having declined due to the intensifications of agriculture (Powney et al., 2014). This intensification of agriculture in the southern parts of Britain may also explain the poleward shift in central mass of British plants shown by Groom (2013), even though the northern range margins of most of these species have retreated (chapter two). Higher levels of agricultural intensification in the south than in the north of Britain would cause the central masses of species to shift northwards, even if they had also declined in the north.

4.6. Climate and plants

Temperatures in the UK range from warmer areas in the south of Britain to cooler areas in the north, as well as there being a north west-south east gradient in rainfall with the west experiencing higher rainfall than the east (http://www.metoffice.gov.uk/climate/uk/averages/ukmapavge.html, viewed 24 March 2014). Britain’s climate has warmed and is set to continue increasing in temperature across the country. By 2100, temperatures are predicted to increase by 3°C in the south of Britain and 2.5°C in the north and there is likely to be an increase in average rainfall by 2100, despite potentially more severe summer droughts in some years (Metoffice, 2011). The northern range margins of southerly distributed plant species would be predicted to be moving north, but the reverse was observed. It is well known that changes in climate (temperature and rainfall) are predicted to drive changes to the distributions of plant species, as has happened historically in times of climate change (Morgan et al., 2014). The observed retreats do not imply that British plant populations have been unaffected by the climate. They may be declining throughout Britain, but potentially less so in regions where the climate is improving the most. Therefore, a further step in assessing changes to plant species distributions would be to incorporate bioclimatic variables into the analysis, for example using average and change values from met office data (Metoffice regional values web page) for growing degree days over 5°C (GDD5), mean temperature of the coldest month in °C (MTCO), mean temperature of the warmest month in °C (MTWO), summer June to August precipitation in mm (SPRE), winter December to February precipitation in mm (WPRE) (Metoffice regional values web page) and ratio of actual to potential evapotranspiration (APET) (Prentice et al., 1992, Huntley et al., 1995). These data are available for each 10 x 10 km square in Britain and could be used in an analysis in a similar way to latitudinal information in order to assess if species have expanded or retreated along climatic gradients, both for temperature and moisture. Inclusion of climatic gradients into the analyses may reveal patterns not detected in the latitudinal analysis (http://www.metoffice.gov.uk/climate/uk/averages/ukmapavge.html, viewed 24 March 2014).

4.7. Conservation implications

Plants are essential to life on Earth as the foundation of food webs, as habitat and shelter for a wide range or organisms and they play an important role in removing carbon dioxide from the atmosphere. Vascular plants are, therefore, good indicators of environmental changes in biodiversity (Godefroid, 2001, Landsberg and Crowley, 2004). As such, the general trend for retractions at the northern range boundaries of the majority of species could have large implications for many other organisms, both above and below ground.

Species distribution models, which predict species distributions under climate change scenarios, often assume no change to land use in estimating future distributions of species when land use variables are incorporated (e.g. Pearson et al., 2004, Thuiller et al., 2004, Luoto et al., 2007, Titeux et al., 2009). Not incorporating land use change as a dynamic variable in the species distribution modelling may mean that the results from many of these models do not give an accurate indication of future distributions of species. However, evidence suggests that in order for land use changes to be used to aid in predicting future distributions of species with climate change results are improved mainly when high resolution data is used (Martin et al., 2013) with climate being a large scale determinant of future species distributions and land cover being more important at the finer scale resolution (Luoto et al., 2007). It is clear from research carried out in this thesis that land use has played the main driving factor in plant species distributions over the past century and due to the apparent dispersal failure of many plant species in Britain. The species used in chapter 2 demonstrate a failure to disperse further north to track climate and therefore it is likely that land use change should be considered as an important contributing factor in predictive modelling of plant species distributions. Pompe et al. (2008) demonstrated that when land use change and climate were used to model plant species projected distributions that species losses at the local scale will occur for 15-19% of plant species.

As the climate changes, the composition and abundances of species in biological communities will change, and the ranges of species will move. In Britain, land use changes are apparently dominating changes to the distributions of plant species, and presumably many of the other species that are associated with them. However, climate change can also generate risks to plants and their associated species, particularly when changes to the abundances and distributions of plants alter the nature of habitats. It is clear that there are changes occurring with increases in densities and advancement of the treeline (reviewed in chapter 1.2.2.5) and was initially shown by Grabherr (1994) and lead to the GLORIA project (Grabherr et al., 2000) in order to monitor these changes. This advancement will threaten species living above the tree line, as the increase in densities and advancement of the treeline occurs. Rocky Mountain Apollo butterfly (*Parnassius smintheus*) larvae are reliant a host plant (*Sedum lanceolatum*) growing above the treeline, and feed most intensively on the plants that grow furthest away from the treeline. Therefore, if the treeline continues to encroach, as it already has, on the higher elevation space the larvae will be adversely affected by these change, and the butterfly population threatened (Illerbrun and Roland, 2011). This is encroachment of the treeline into alpine areas is also likely to put many alpine plant species at risk, such as Australian alpine regions where there is a lack of nival zone which would facilitate altitudinal succession of alpine plant species into higher altitudes (Pickering et al., 2008) or there may be no available space to colonise (Chou et al., 2011). The research carried out in chapter 2 does not look at altitudinal shift but the poleward shift of plant species and so the knock on effect of treeline advancement resulting in habitat encroachment will not occur. However, other detrimental knock on effects will be evident, as a result of the failure of many plant species to advance poleward, many animal species that are dependent on these species and associated habitats struggling to advance polewards to the newly available climatically suitable habitat.

This thesis has shown that, although some plant species are faring well, in particular the Bee orchid, a large number of species do not appear to be keeping pace with the warming climate. How to prevent further losses, and potentially enable species to expand northwards, will be an important element in policy-making in the future. An increase in protected areas, as well as an increase in connectivity between habitats, will likely be needed in order to facilitate north movement of plant species and protected areas have been shown to be important in facilitating range expansion in bird and butterfly species in Britain (Thomas et al., 2012). It is, however, clear from results in chapter 2 (northern range margin shift) that these protected areas in Britain are not enough to allow range expansion in plants. It is uncertain whether enough habitat, of the types that will be used by most of these declining plant species, can be restored or created to permit natural colonisation. It may be that humans will become the most important disperser of plant species due to movement of seed and soil to new locations and an increasing amount of literature exists on methods of human mediated dispersal such as seeds carried on shoes, clothing and vehicles (Wichmann et al., 2009, Pickering and Mount, 2010, Pickering et al., 2011, Taylor et al., 2012, von der Lippe et al., 2013). However, accidental introductions by humans may not be sufficient to allow species to keep track with climate warming, given that most of the accidentally introduced populations seem to fail, perhaps because the introduced propagules do not arrive in appropriate habitats as can be seen in persistence of introduced populations compared with native populations at the northern edge of plant species distributions demonstrated and discussed in chapter 2. It may therefore be necessary for humans to deliberately introduce species to areas poleward of their current distribution, if conservation organisations aim to ensure the long-term persistence of species.

4.8. Synopsis and concluding remarks

Overall this thesis has shown that human influences on the landscape are likely to have caused, and will most probably continue to cause, large declines to the overall distribution sizes of species. However, a small number of species have the capacity to expand. The example studied here was the Bee orchid, potentially benefitting from a warmer climate, which has enabled it to expand its habitat range, coupled with an ability to produce large quantities of highly dispersable seed due by self-pollination. For many plant species, human mediated dispersal is likely to be one of the most important dispersal modes in the future of species distributions, bridging human caused gaps of unsuitable habitat in the landscape. Human-mediated dispersal may eventually be seen as a benefit to plants, whereas it is currently seen as predominantly negative, associated with the arrival of invasive species in new areas. Over the next century, climate will continue to warm across Britain (as well as globally) and so conservation strategies need increasingly to include strategies to ensure that species' distributions are able to move to the newly available climatically suitable space.

Chapter 2: Appendix I

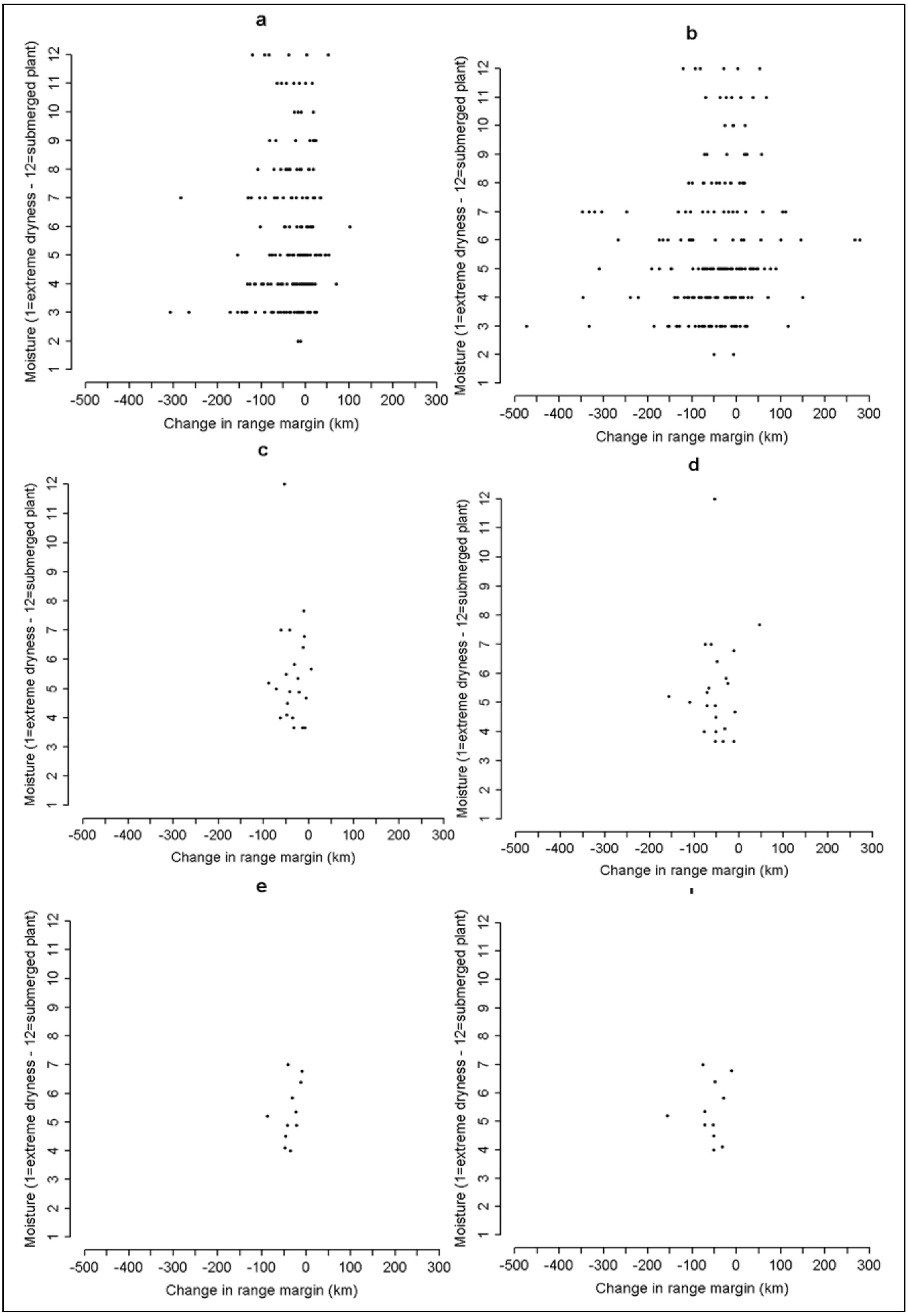


Figure 1: Change in northern range margin plotted against Ellenberg indicator value for moisture using a) native records only for all species, b) including introduced records for all species, c) native records only using family 3, d) including introduced records using family 3, e) native records only using family 5, f) including introduced records using family 5.

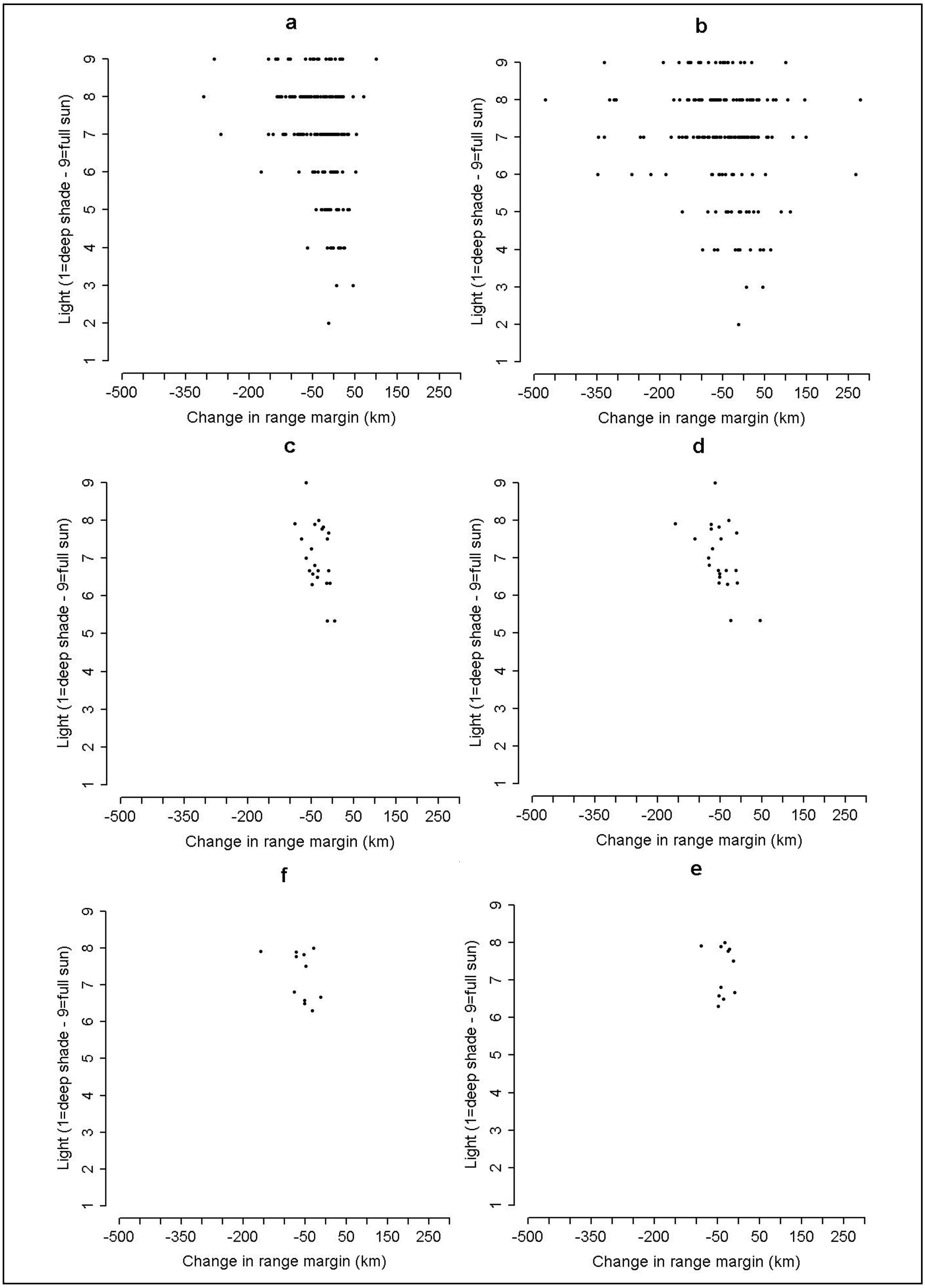


Figure 2: Change in northern range margin plotted against Ellenberg indicator value for light using a) native records only for all species, b) including introduced records for all species, c) native records only using family 3, d) including introduced records using family 3, e) native records only using family 5, f) including introduced records using family 5.

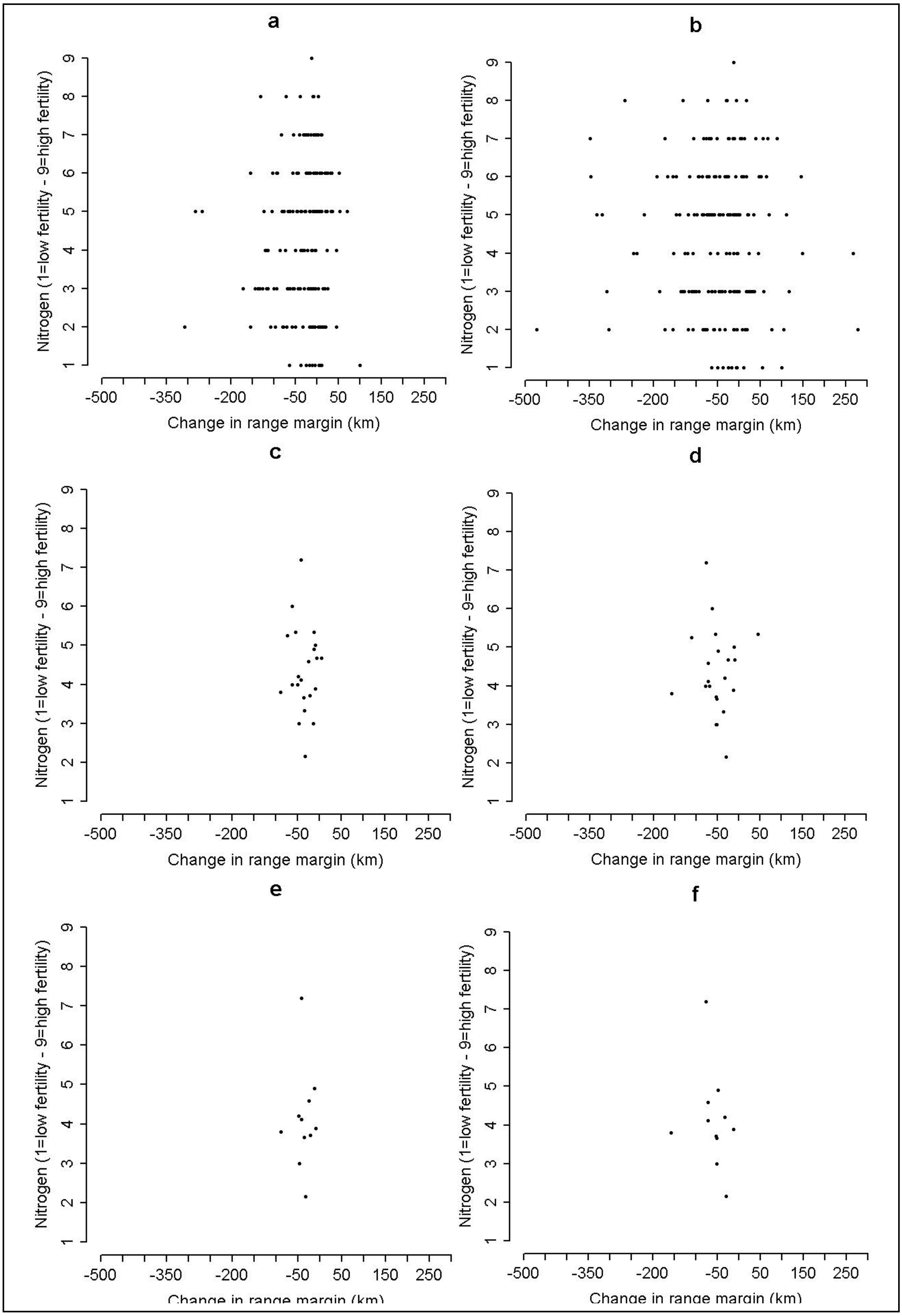


Figure 3: Change in northern range margin plotted against Ellenberg indicator value for nitrogen using a) native records only for all species, b) including introduced records for all species, c) native records only using family 3, d) including introduced records using family 3, e) native records only using family 5, f) including introduced records using family 5

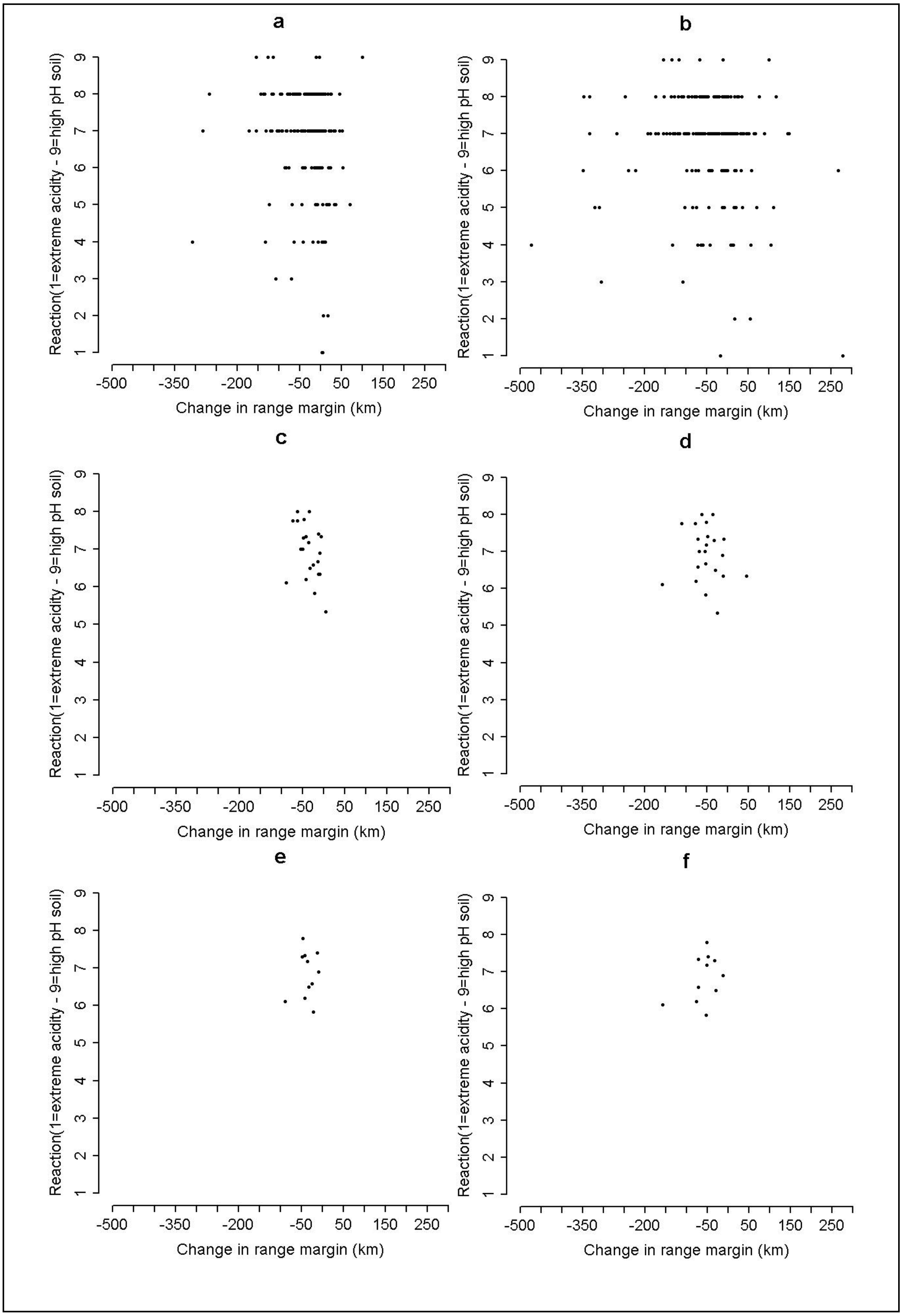


Figure 4: Change in northern range margin plotted against Ellenberg indicator value for reaction using a) native records only for all species, b) including introduced records for all species, c) native records only using family 3, d) including introduced records using family 3, e) native records only using family 5, f) including introduced records using family 5

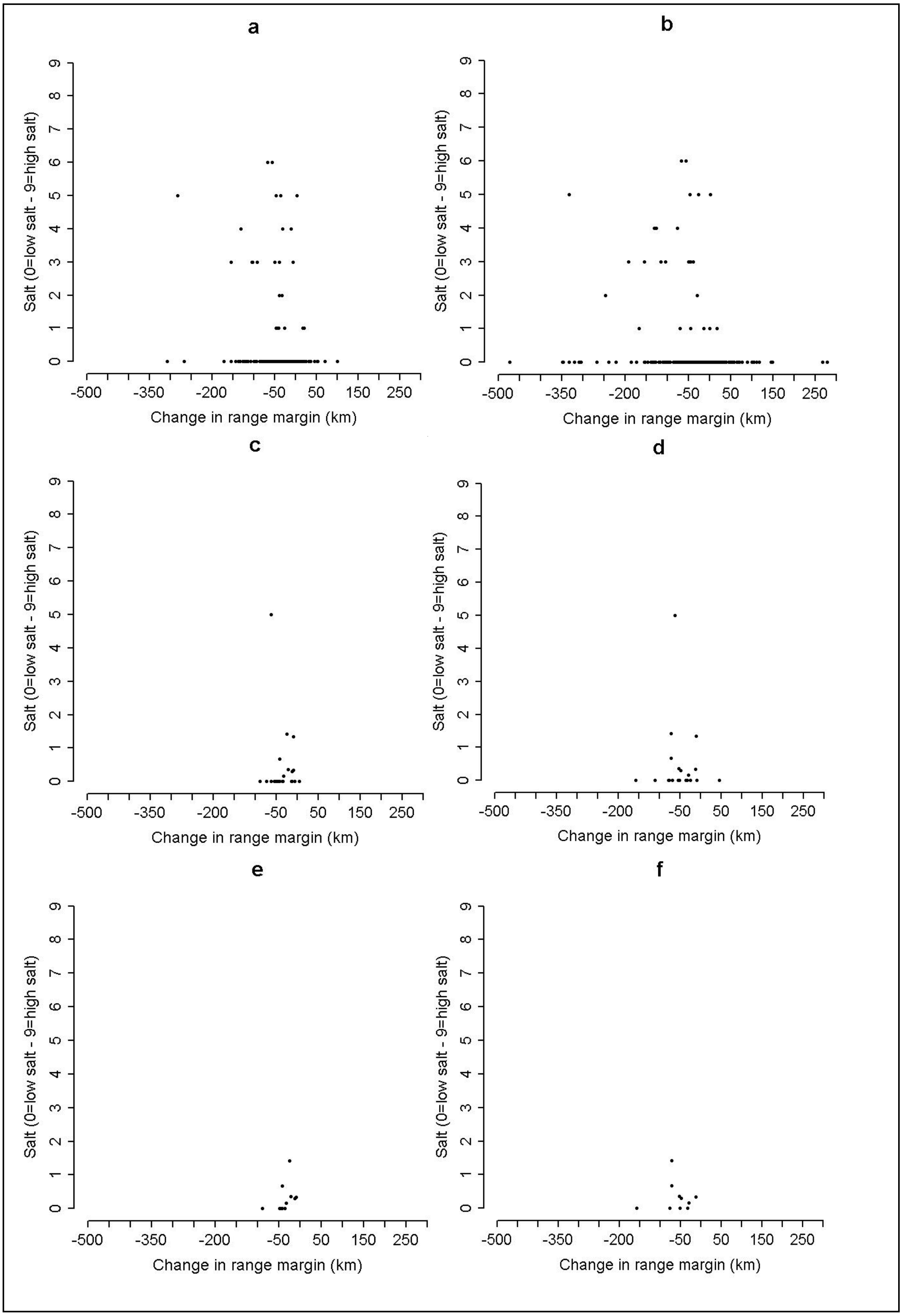


Figure 5: Change in northern range margin plotted against Ellenberg indicator value for salt using a) native records only for all species, b) including introduced records for all species, c) native records only using family 3, d) including introduced records using family 3, e) native records only using family 5, f) including introduced records using family 5

Chapter 2: Appendix II

Table of species used giving dispersal information

Species	Dispersal method	Long Short method	Reference
Acer campestre	Seed: Wind (short)	Short	(Fitter and Peat, 1994, Jones, 1945)
Aceras anthropophorum	Seed: Wind (long)	Long	(Fitter and Peat, 1994, Pridgeon et al., 2001)
Agrostis curtisii	Seed: Wind (short)	Short	(Fitter and Peat, 1994, Cope and Gray, 2009)
Alopecurus aequalis	Seed: Gravity	Short	(Cope and Gray, 2009, Hubbard, 1992)
Alopecurus bulbosus	Seed: Gravity	Short	(Rose, 1989)
Althaea officinalis	Seed: Gravity	Short	(Stace, 2010)
Arabis glabra (Turritis glabera according to Stace)	Seed: Wind (short)	Short	(Walker, Unpublished data set)
Arum maculatum	Seed: Bird (internal)	Long	(Sowter, 1949, Fitter and Peat, 1994)
Asperula cynanchica	Seed: Gravity	Short	(Walker, Unpublished data set)
Asplenium obovatum	Seed: Wind (Long)	Long	(Raus, 1988)
Atropa belladonna	Seed: Bird (internal)	Long	(Butcher, 1947)
Blackstonia perfoliata	Seed: Wind (short)	Short	(Fitter and Peat, 1994, Walker, Unpublished data set)
Brachypodium pinnatum s.l	Veg: Attached spreading	Short	(Cope and Gray, 2009)
Bromopsis erecta (Cope=Bromus erectus)	Seed: mammal (external)		(Walker, Unpublished data set)
Bromus commutatus	Seed: mammal (external)		(Carlquist and Pauly, 1985; Walker, Unpublished data set)
Bromus racemosus	Seed: mammal (external)		(Royal Botanic Gardens Kew Seed Information Database (SID), 2014; Walker, Unpublished data set)
Bryonia dioica	Seed: Bird (internal)		(Walker, Unpublished data set)(Fitter and Peat, 1994, Royal Botanic Gardens Kew Seed Information Database (SID), 2014)
Bunium bulbocastanum	Seed: Gravity		(Stace, 2010)
Bupleurum tenuissimum	Seed: Gravity		(Stace, 2010)

Butomus umbellatus	Seed/veg: Water		(Fitter and Peat, 1994, Hroudova and Zakravsky, 1993)
Callitriche truncate	Seed: Gravity		(Barry and Wade, 1986)
Campanula patula	Seed: Gravity		(Thome, 1885)*
Campanula trachelium	Seed: Gravity		(Emorsgate Seeds website, 2014)
Cardamine impatiens	Seed: Balistic		(Royal Botanic Gardens Kew Seed Information Database (SID), 2014, Fitter and Peat, 1994, Stace, 2010)
Carex appropinquata	Unknown		
Carex digitata	Seed: Ant		(Czarnecka, 2005, Dzwonko and Loster, 1992)
Carex divisa	Seed: Gravity		(Stace, 2010)
Carex elata	Seed/veg: Water		(Cappers, 1993)
Carex ericetorum	Veg: Attached spreading		(Fitter and Peat, 1994, Preston et al., 2002)
Carex humilis	Veg: Detached fragments		(Fitter and Peat, 1994)
Carex montana	Seed: Ant		(Walker, Unpublished data set)
Carex pseudocyperus	Seed/veg: Water		Walker K. 2010 pers com.
Carex strigosa	Unknown		
Centaurium pulchellum	Seed: mammal (internal)		(Bakker et al., 2008)
Cephalanthera damasonium	Seed: Wind (Long)		(Pridgeon et al., 2001)
Cerastium pumilum	Seed: Gravity		Andersen U. 1993
Ceratophyllum submersum	Seed/veg: Water		(Fitter and Peat, 1994, Preston et al., 2002)
Chamaemelum nobile	Seed: Gravity		(Walker, Unpublished data set)
Chenopodium chenopodioides	Seed: Gravity		(Digital Seed Atlas of the Netherlands online, 2006)
Cicendia filiformis	Unknown		
Cirsium acaule	Seed: Wind (Long)		(Fitter and Peat, 1994)(Walker, Unpublished data set)
Cirsium eriophorum	Seed: Wind (Long)		(Fitter and Peat, 1994)(Walker, Unpublished data set)
Clematis vitalba	Seed: Wind (Long)		(Fitter and Peat, 1994)(Walker, Unpublished data set)(Royal Botanic Gardens Kew Seed Information Database (SID), 2014)
Clinopodium ascendens	Seed: Gravity		(Walker, Unpublished data set)
Clinopodium calamintha	Seed: Gravity		(Walker, Unpublished data set)
Colchicum autumnale	Seed: Gravity		(Fitter and Peat, 1994)(Walker, Unpublished data set)(Butcher, 1954)
Cornus sanguine	Seed: Bird		(Fitter and Peat, 1994, Krusi and Debussche, 1988)

	(internal)		
Crassula tillaea	Seed: Gravity		(Walker, Unpublished data set)
Crataegus laevigata	Seed: Bird (internal)		(Garcia et al., 2007)
Cuscuta europaea	Seed/veg: Water		(Fitter and Peat, 1994, Puustinen et al., 2004, Verdcourt, 1948)
Dactylorhiza praetermissa	Seed: Wind (Long)		(Pridgeon et al., 2001)(Walker, Unpublished data set)
Daphne laureola	Seed: Bird (internal)		(Fitter and Peat, 1994, Alonso and Herrera, 2011)
Dianthus armeria	Seed: Gravity		(Thompson and Hodgson, 1996, United States Department of Agriculture)
Dipsacus pilosus	Seed: Gravity		(Romermann et al., 2005, Caputo et al., 2004)
Epilobium lanceolatum	Seed: Wind (Long)		(Stace, 2010)
Epilobium tetragonum	Seed: Wind (Long)		(Stace, 2010; Walker, Unpublished data set)
Epipactis phyllanthes	Seed: Wind (Long)		(Pridgeon et al., 2001)
Epipactis purpurata	Seed: Wind (Long)		(Pridgeon et al., 2001)
Erica ciliaris	Veg: Attached spreading		Rose (1996) Journal of Ecology
Erigeron acer	Seed: Wind (Long)		(Fitter and Peat, 1994; Walker, Unpublished data set)
Erodium maritimum	Unknown		
Euphorbia amygdaloides	Unknown		
Euphrasia anglica	Seed: Gravity		(Stace, 2010)
Euphrasia pseudokerneri	Seed: Gravity		(Stace, 2010)
Fallopia dumetorum	Seed: Wind (short)		(Stace, 2010)
Frangula alnus	Seed: Gravity		(Godwin, 1943a)
Frankenia laevis	Seed/veg: Water		(Brightmore, 1979)
Fumaria occidentalis	Unknown		
Galium pumilum	Seed: Gravity		(Walker, Unpublished data set)
Gentiana pneumonanthe	Seed: Wind (short)		(Fitter and Peat, 1994, Simmonds, 1946)
Gentianella anglica	Seed: Wind (short)		(Walker, Unpublished data set)
Gentianella germanica	Seed: Wind (short)		(Fitter and Peat, 1994; Walker, Unpublished data set)
Geranium purpureum	Seed: Balistic		(Fitter and Peat, 1994, Herrera, 1991)
Geranium rotundifolium	Seed: Balistic		(Fitter and Peat, 1994)
Gymnocarpium robertianum	Seed: Wind (Long)		(Stace, 2010) spores therefore wind
Helianthemum oelandicum	Unknown		

Herminium monorchis	Seed: Wind (Long)		(Fitter and Peat, 1994) (Pridgeon et al., 2001; Walker, Unpublished data set)
Himantoglossum hircinum	Seed: Wind (Long)		(Fitter and Peat, 1994, Pridgeon et al., 2001; Walker, Unpublished data set)
Hippocrepis comosa	Seed: Gravity		(Fitter and Peat, 1994; Walker, Unpublished data set)
Hordelymus europaeus	Seed: mammal (external)		(Graae, 2002)
Hordeum secalinum	Seed: mammal (external)		(Walker, Unpublished data set)
Hornungia petraea	Seed: Gravity		(Fitter and Peat, 1994, Ratcliffe, 1959)
Hottonia palustris	Seed/veg: Water		(BarratSegretain, 1996)
Humulus lupulus	Seed: Wind (short)		(Fitter and Peat, 1994, Hodgson et al., 1995)
Hydrocharis morsus-ranae	Seed/Veg: Bird (external)		(Global Invasive Species Database)
Hypericum montanum	Seed: Wind (short)		(Fitter and Peat, 1994, Bojňanský and Fargašová, 2007; Walker, Unpublished data set)
Hypericum undulatum	Seed: Wind (short)		(Fitter and Peat, 1994; Walker, Unpublished data set)
Illecebrum verticillatum	Seed: Gravity		(Bojňanský and Fargašová, 2007)
Inula conyzae	Seed: Wind (Long)		(Fitter and Peat, 1994; Walker, Unpublished data set)
Inula crithmoides	Seed: Wind (Long)		(Stace, 2010): genera has papas so considered wind dispersed
Iris foetidissima	Seed: Bird (internal)		(Herrera, 1982, Fitter and Peat, 1994)
Juncus acutus	Seed/veg: Water		(Fitter and Peat, 1994)
Lathyrus japonicas	Seed/veg: Water		(Andersen, 1993)
Lathyrus nissolia	Seed: Gravity		(Walker, Unpublished data set)
Lathyrus palustris	Unknown		
Ligustrum vulgare	Seed: Bird (internal)		(Fitter and Peat, 1994, Hodgson et al., 1995)
Linum bienne	Seed: Gravity		(Discover Life image)
Lotus angustissimus	Seed: Gravity		(Walker, Unpublished data set)
Lotus subbiflorus	Seed: Gravity		(Walker, Unpublished data set)
Luronium natans	Unknown		
Luzula forsteri	Seed: Ant		(Fitter and Peat, 1994)
Lysimachia nummularia	Seed: Gravity		(Fitter and Peat, 1994, Hodgson et al., 1995)

Medicago Arabica	Seed: Gravity		Oba (2000) Field Crop Research
Melampyrum cristatum	Seed: Gravity		Horrill (1972) Journal of Ecology
Melittis melissophyllum	Seed: Gravity		(Sturm, 1796)
Minuartia hybrida	Seed: Gravity		(Stace, 2010): capsule has tiny seeds
Moenchia erecta	Seed: Gravity		(Flora Vascular website)
Myosoton aquaticum	Seed: Gravity		(Stace, 2010)
Myriophyllum verticillatum	Seed/veg: Water		(Fitter and Peat, 1994, Caffrey and Monahan, 2006)
Oenanthe fluviatilis	Seed/veg: Water		(Preston et al., 2002b)
Oenanthe pimpinelloides	Seed/veg: Water		(Walker, Unpublished data set)
Oenanthe silaifolia	Seed/veg: Water		(Walker, Unpublished data set)
Ophrys apifera	Seed: Wind (Long)		(Fitter and Peat, 1994, Pridgeon et al., 2001;Walker, Unpublished data set)
Ophrys insectifera	Seed: Wind (Long)		(Pridgeon et al., 2001; Walker, Unpublished data set)
Ophrys sphegodes	Seed: Wind (Long)		(Pridgeon et al., 2001; Walker, Unpublished data set)
Orchis morio	Seed: Wind (Long)		(Fitter and Peat, 1994; Walker, Unpublished data set, Hodgson et al., 1995, Pridgeon et al., 2001)
Orchis purpurea	Seed: Wind (Long)		(Fitter and Peat, 1994, Pridgeon et al., 2001; Walker, Unpublished data set)
Orchis ustulata	Seed: Wind (Long)		(Pridgeon et al., 2001; Walker, Unpublished data set)
Ornithogalum pyrenaicum	Seed: Gravity		(Fitter and Peat, 1994, Hill and Price, 2000)
Orobanche elatior	Seed: Wind (Long)		(Fitter and Peat, 1994; Walker, Unpublished data set)
Orobanche hederae	Seed: Wind (Long)		(Preston et al., 2002b)
Orobanche minor	Seed: Wind (Long)		(Fitter and Peat, 1994; Walker, Unpublished data set)
Parapholis incurve	Unknown		
Pastinaca sativa	Seed: Wind (short)		(Jongejans and Telenius, 2001; Walker, Unpublished data set)
Persicaria mitis	Unknown		
Petroselinum segetum	Seed: Gravity		(Stace, 2010)
Peucedanum palustre	Seed: Wind (short)		(Fitter and Peat, 1994)
Phleum phleoides	Seed: mammal (external)		(Walker, Unpublished data set)
Phyteuma orbiculare	Seed: Gravity		(Walker, Unpublished data set)
Picris hieracioides	Seed: Wind (Long)		(Fitter and Peat, 1994; Walker, Unpublished data set)
Pimpinella major	Seed: Gravity		(Stace, 2010; Walker, Unpublished data set)
Poa bulbosa	Veg: Detached		(Fitter and Peat, 1994, Ofir and Kigel, 2003)

	fragments		
Poa infirma	Unknown		
Polygala amarelle	Seed: Ant		(Walker, Unpublished data set)
Polygala calcarea	Seed: Ant		(Walker, Unpublished data set)
Polygonatum odoratum	Seed: mammal (external)		(Eriksson and Ehrlen, 1991)
Potamogeton acutifolius	Veg: Detached fragments		(Fitter and Peat, 1994)
Potamogeton compressus	Veg: Detached fragments		(Fitter and Peat, 1994)
Potamogeton trichoides	Veg: Detached fragments		(Fitter and Peat, 1994)
Primula elatior	Seed: Gravity		(Van Rossum and Triest, 2006)
Puccinellia fasciculate	Seed: Gravity		(Cope and Gray, 2009)
Puccinellia rupestris	Seed: Gravity		(Cope and Gray, 2009)
Pulmonaria longifolia	Unknown		
Pulsatilla vulgaris	Seed: Wind (short)		(Wells and Barling, 1971, Fitter and Peat, 1994; Walker, Unpublished data set)
Ranunculus parviflorus	Seed: mammal (internal)		(Malo and Suarez, 1995)
Ranunculus tripartitus	Unknown		
Rhamnus cathartica	Seed: Bird (internal)		(Godwin, 1943b)
Rorippa amphibian	Veg: Detached fragments		(Preston et al., 2002b)
Rosa agrestis	Seed: Bird (internal)		(Grime, 1979; Walker, Unpublished data set)
Rosa arvensis	Seed: Bird (internal)		(Grime, 1979; Walker, Unpublished data set)
Rosa micrantha	Seed: Bird (internal)		(Grime, 1979; Walker, Unpublished data set)
Rosa obtusifolia	Seed: Bird (internal)		(Grime, 1979)
Rosa stylosa	Seed: Bird		(Grime, 1979)

	(internal)		
Rosa tomentosa	Seed: Bird (internal)		(Grime, 1979; Walker, Unpublished data set)
Rubia peregrine	Seed: Bird (internal)		(Debussche and Isenmann, 1994)
Rumex palustris	Seed/veg: Water		(Fitter and Peat, 1994)
Rumex pulcher	Seed: mammal (external)		(Fitter and Peat, 1994; Walker, Unpublished data set)
Rumex rupestris	Seed/veg: Water		(Fitter and Peat, 1994)
Sagittaria sagittifolia	Seed/veg: Water		(Fitter and Peat, 1994)
Sarcocornia perennis	Seed/veg: Water		(Davy et al., 2006)
Scilla autumnalis	Seed: Gravity		(Fitter and Peat, 1994)
Sibthorpia europaea	Veg: Attached spreading		(Fitter and Peat, 1994)
Silene conica	Seed: Gravity		(Watson and Dallwitz, 1992 onwards)
Silene nutans	Seed: Gravity		(Hepper, 1956, Fitter and Peat, 1994)
Sison amomum	Seed: Gravity		(Stace, 2010)
Sonchus palustris	Seed/veg: Water		(Fitter and Peat, 1994)
Sorbus anglica	Seed: Bird (internal)		(Chester et al., 2007)
Sorbus porrigentiformis	Seed: Bird (internal)		(Chester et al., 2007)
Sorbus torminalis	Seed: Bird (internal)		(Chester et al., 2007)
Spartina maritime	Veg: Attached spreading		(Marchant and Goodman, 1969)
Spiranthes spiralis	Seed: Wind (Long)		(Fitter and Peat, 1994; Walker, Unpublished data set)
Spirodela polyrhiza	Seed/Veg: Bird (external)		Jacobs (1947) Ecological Monographs
Suaeda vera	Seed: Gravity		(Stace, 2010)
Tamus communis	Seed: Bird (internal)		(Fitter and Peat, 1994, Hodgson et al., 1995, Preston et al., 2002a)
Tephroseris integrifolia subsp. Integrifolia	Seed: Wind (Long)		(Fitter and Peat, 1994; Walker, Unpublished data set)

Thesium humifusum	Seed: Gravity		(Stace, 2010; Walker, Unpublished data set)
Thymus pulegioides	Seed: Gravity		(Fitter and Peat, 1994)
Trifolium glomeratum	Seed: Gravity		(Walker, Unpublished data set)
Trifolium ochroleucon	Seed: Gravity		(Walker, Unpublished data set)
Trifolium ornithopodioides	Seed: Gravity		(Walker, Unpublished data set)
Trifolium squamosum	Seed: Gravity		(Walker, Unpublished data set)
Trifolium subterraneum	Seed: Gravity		(Walker, Unpublished data set)
Trifolium suffocatum	Seed: Gravity		(Walker, Unpublished data set)
Ulex minor	Seed: Ant		(Gammans et al., 2005; Walker, Unpublished data set)
Ulmus minor	Seed: Wind (short)		(Fitter and Peat, 1994, Lopez-Almansa et al., 2004)
Ulmus plotii	Veg: Attached spreading		(Lopez-Almansa et al., 2004)
Verbascum nigrum	Seed: Wind (short)		(Czarnecka, 2005)
Viburnum lantana	Seed: Bird (internal)		(Fitter and Peat, 1994)
Vicia bithynica	Seed: Gravity		(Walker, Unpublished data set)
Vicia parviflora	Seed: Gravity		(Walker, Unpublished data set)
Vicia tetrasperma	Seed: Gravity		(Walker, Unpublished data set)
Viola lacteal	Seed: Ant		(Moore, 1958, Fitter and Peat, 1994)
Viola odorata	Seed: Ant		(Fitter and Peat, 1994, Hodgson et al., 1995)
Viola reichenbachiana	Seed: Balistic		(Fitter and Peat, 1994)
Vulpia fasciculate	Seed: Gravity		(Watkinson, 1978)
Wolffia arrhiza	Seed/veg: Water		(Fitter and Peat, 1994)

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Chapter 3: Appendix III

Appendix IIIi

Table of sites selected to search for Bee orchids 2011

Sight	Location	10 x 10 km square	Full grid reference	Year range records collected	Chalk/ not chalk	No. orchids found
Site 1	Sandhouse Lane Pit (S) NR and Double Arches Pit CWS	42/92	42/936--298-- 42/939--297-- 42/937--287--	1977-1999	Not chalk	0
Site 2	Brogborough Pit	42/93	42/969--389-- 42/9690438878	1949-2003	Not chalk	0
Site 3	Verulamium Park: rough grass	52/10	52/134067	2000	Chalk	23
Site 4	By Old Parkbury Fishing Lakes: filled pit area AND Park Street Gravel Pits	52/10	52/161025 52/161027 52/163025	1977-2000	Chalk	21
Site 5	London Colney: former Model farm	52/10	52/173014	2000	Chalk	5
Site 6	Totternhoe Knolls SSSI	42/92	42/978--222-- 42/9783-2218- 42/979--221--	1976-2005	Chalk	2
Site 7	Turvey - Bromham Disused Railway CWS	42/95	42/997523	2002-2005	Not chalk	0
Site 8	Stewartby Lake CWS	52/04	52/008471	2004	Not chalk	0
Site 9	Studham (v.c. 30), Holywell Road, E section	52/01	52/018-167- 52/01831673	2002-2006	Chalk	0
Site 10	Ampthill	52/03	52/022383	2006	Not chalk	0
Site 11	Great Gaddesden: meadow by Hoo Wood	52/01	52/030-126- 52/031-126- 52/031-127-	1979-1998	Chalk	0

Site 12	Sheethanger Common: chalk slopes	52/00	52/035053 52/036053	1970-1993	Chalk	0
Site 13	Cut Throat Lane Allotments, Bedford	52/05	52/03575070 52/036-506- 52/036-508- 52/03645117	2000	Not chalk	0
Site 14	Luton, SKF(UK) Factory	52/02	52/050256	2002	Chalk	0
Site 15	Smithcombe, Sharpenhoe and Sundon Hills SSSI	52/03	52/065-303- 52/06573033 52/067-303-	1977-2002	Chalk	0
Site 16	Near Langleybury: bank of lane	52/00	52/079004	2000	Chalk	0
Site 17	Barton Hills SSSI	52/03 52/02	52/085-301- 52/089-302- 52/0889629931 52/090--298--	1949-2003	Chalk	0
Site 18	Pertenhall - A village	52/16	52/102660	2003	Not chalk	0
Site 19	Pertenhall, Hoo Farm Reservoir	52/16	52/103649	2003	Not chalk	0
Site 20	Sundon Chalk Pits CWS	52/02	52/041--284-- 52/042--283--	1979-1998	Chalk	11
Site 21	Bedford - Sandy Disused Railway	52/15	52/10675018	2003	Not chalk	1
Site 22	Tingley Wood: West Down	52/13	52/135--304--	1979-2003	Chalk	0
Site 23	Chawston, Manor Farm	52/15	52/154-561-	2004	Not chalk	0
Site 24	Wyboston - A village	52/15	52/16855790	2005	Not chalk	4
Site 25	Cox Hill	52/14	52/17814973 52/18024970	2006	Not chalk	0
Site 26	London Colney: bank of M25 by 'Savacentre'	52/10	52/184031	2000	Chalk	0
Site 27	Sleapshyde Gravel Pits, Colney Heath	52/20	52/203-065- 52/202-065-	1972-1998	Chalk	7
Site 28	Stotfold - Town	52/23	52/21403596	2004	Chalk	0

Site 29	Norton Common, Letchworth, Letchworth: Westholm	52/23	52/217-333- 52/219-337-	1977-2005	Chalk	0
Site 30	Near Hinxworth: 'Farrowby Farm', meadow	52/23	52/226-385-	2001	Chalk	0
Site 31	Letchworth: Woolgrove School, grounds	52/23	52/232-326-	2005	Chalk	0
Site 32	Mardley Heath	52/21	52/245182 52/243184	1968-1998	Chalk	0
Site 33	Mill Green: by The Commons and The Commons Open Space	52/21	52/254105 52/257108	1977-1997	Chalk	0
Site 34	Tewin Upper Green: old orchard	52/21	52/272144	2001	Chalk	0
Site 35	Luffenhall: garden - village	52/22	52/292285	2001	Chalk	0
Site 36	Bayford: Parkfield, near cricket field	52/30	52/310090	2001	Not chalk	0
Site 37	Bayfordbury: by science block	52/31	52/314104 52/315103	1978-1994	Chalk	0
Site 38	Turvey, Picts Hill Estate Woodland and Pictshill Farm	42/95	42/965522 42/965525	2003-2002	Not chalk	20
Site 39	Harrold Country Park CWS	42/95	42/960570 42/961568	2000-2004	Not chalk	6
Site 40	Stanstead Abbotts - village : near Ryegate Farm, field	52/31	52/389112	2005	Chalk	0
Site 41	Near Meesden: ditch and bank by path	52/43	52/422323	2004	Chalk	0
Site 42	Bury Green Farm	52/42	52/450211	2005	Not chalk	0

Site 43	Therfield Heath: Pen & Church Hills, Fox Covert: clearing, Jubilee Wood: plantation, Therfield Heath	52/33	52/331396 52/332395 52/332397 52/333396 52/333397 52/334396 52/334398 52/335396 52/336398	1966-1992	Chalk	0
Site 44	Rye House Power Station site: near pylon	52/30	52/389087	2005	Not chalk	0

sites shaded in pale gray were used to collect data used in analysis

Appendix IIIii

Table of sites selected to search for Bee orchids 2012

Site	Location	vc	10 x 10 km square	Full grid reference	Year range records collected	age class	north/south	Number of orchids found
Site 1	Llanymynech Hill	47	SJ/22	SJ/267--220-- SJ/264--216-- SJ/268--217-- SJ/265--218-- SJ/267--218-- SJ/2674-2187- SJ/2677-2189- SJ/268--219--	1978-2009	old	south	0
Site 2	Stonesfield	23	SP/31	SP/393--165-- SP/3916-1642-	1950-2006	old	south	1

Site 3	Pilch Field SSSI & Pilch Farm	24	SP/73	SP/747--322--	1973-1999	old	south	0
Site 4	Jubilee Works : Spoilheap and Jubilee pit	24	SP/83	SP/867--314-- SP/868--312-- SP/869--311-- SP/869--312--	1973-2001	old	south	0
Site 5	Blue Lagoon LNR	24	SP/83	SP/867--329-- SP/868--326-- SP/868--328	1973-2001	old	south	5
Site 6	St. Michael and All Angels Churchyard, Halton	24	SP/81	SP/874--101--	1976-1998	old	south	0
Site 7	Aston Clinton Ragpits SSSI	24	SP/81	SP/887--108-- SP/888--108--	1900-1999	old	south	0
Site 8	Ivinghoe Beacon & Ivinghoe Hills SSSI	24	SP/91	SP/959--164-- SP/959--165-- SP/959--168-- SP/961--159-- SP/963--159-- SP/960--160-- SP/960--163--	1900-2004	old	south	0
Site 9	Dunstable: 'California', old chalk pit & Spoondell CWS	30 & 20	TL/02	TL/008--209-- TL/011--208--	1979-1999	old	south	0
Site 10	Collyweston Quarry SSSI	32	TF/00	TF/004--037-- TF/004--038--	1953-1996	old	south	0
Site 11	By Old Parkbury Fishing Lakes: filled pit area	20	TL/10	TL/161--025-- TL/161--027--	1977-2000	old	south	5
Site 12	Sleapshyde Gravel Pit	20	TL/20	TL/203--065-- TL/202--065--	1972-1998	old	south	2
Site 13	Great Paxton, nr Bankside	31	TL/26	TL/217--653--	1979-1999	old	south	0

Site 14	Letchworth: Westholm	20	TL/23	TL/217--333-- TL/219--337--	1977-2005	old	south	0
Site 15	The Commons Open Space	20	TL/21	TL/254--105-- TL/257--108-- TL/262--108--	1977-1997	old	south	0
Site 16	Ware: Chauncy School, playing field (old pit)	20	TL/31	TL/348--147-- TL/347--150--	1979-1991	old	south	0
Site 17	Milton Country Park	29	TL/46	TL/478--623-- TL/479--622--	1975-2006	old	south	2
Site 18	Fulbourn SSSI 3	29	TL/55	TL/531--561-- TL/532--560--	1960-2008	old	south	0
Site 19	Weybread	25	TM/28	TM/243--816-- TM/247--815--	1958-1992	old	south	0
Site 20	Calvert Jubilee & Extension	24	SP/62	SP/684--250-- SP/684--254--	1900-1998	old	south	0
Site 21	Blaenavon Railway Museum Car Park	35	SO/20	SO/2363-0955-	2010	new	south	0
Site 22	Moss Side	58	SJ/58	SJ/5640-8485-	2001	new	south	0
Site 23	Higher Whitley	58	SJ/68	SJ/615--815--	2005	new	south	0
Site 24	Barnton	58	SJ/67	SJ/6370-7460-	2000	new	south	0
Site 25	Bethell's Tip	58	SJ/79	SJ/796--928--	2007-2008	new	south	4
Site 26	Weston	58	SJ/75	SJ/729--511--	2004	new	south	0
Site 27	SO89Q	39	SO/89	SO/874--916--	2002	new	south	0
Site 28	VC39 Staffordshire	39	SO/88	SO/887--815--	2004	new	south	5
Site 29	Astonfields	39	SJ/92	SJ/927--253-- SJ/926--252--	2001-2009	new	south	0
Site 30	VC39 Staffordshire	39	SK/15	SK/138--544--	1998	new	south	0
Site 31	SK10J	39	SK/10	SK/133--083--	2009	new	south	0
Site 32	VC39 Staffordshire	39	SP/19	SP/149--993--	2003	new	south	0
Site 33	Widney Road	38	SP/17	SP/153--774--	1993	new	south	0

Site 34	Coleshill M6/A452 verge	38	SP/28	SP/202--865--	1997	new	south	0
Site 35	Foleshill Gasworks	38	SP/38	SP/346--834--	1998	new	south	0
Site 36	Ashby Woulds	55	SK/31	SK/300--165--	2006	new	south	0
Site 37	Nettle Hill	38	SP/48	SP/418--826--	1996	new	south	0
Site 38	Evenley, Northamptonshire	32	SP/53	SP/586--348--	2008	new	south	0
Site 39	Helmdon Station	32	SP/54	SP/586--432--	1999	new	south	0
Site 40	Long March Industrial Estate	32	SP/56	SP/582--615--	2005	new	south	1
Site 41	Queniborough	55	SK/61	SK/645--126--	2006	new	south	0
Site 42	Buckby Lion 9siteof former public house	32	SP/66	SP/653--685--	2004	new	south	0
Site 43	Brill Common	24	SP/61	SP/654--144--	1994-1996	new	south	5
Site 44	Daffodil Valley, Waddesdon Manor Park	24	SP/71	SP/732--163--	1998	new	south	0
Site 45	Brampton Valley Way, near Brixworth	32	SP/76	SP/737--620--	2004	new	south	0
Site 46	Brixworth Industrial Estate	32	SP/77	SP/750--712--	2005	new	south	0
Site 47	A508 Great Oxenden to Market harborough Road	32	SP/78	SP/736--847--	2004	new	south	0
Site 48	Laughton Forest - FC Comp. 2030	54	SK/89	SK/863--986--	2000-2001	new	south	0
Site 49	Verulamium Park: rough grass	20	TL/10	TL/134--067--	2000	new	south	5
Site 50	Dogsthorpe Star Pit SSSI	32	TF/20	TF/212--026--	2001	new	south	0
Site 51	No name	19	TL/81	TL/852--176--	2002	new	south	0
Site 52	Asheldham Pits	18	TL/90	TL/974--019--	1992	new	south	0
Site 53	VC19 North Essex	19	TM/02	TM/017--288-- TM/019--289--	1997-2004	new	south	0
Site 54	Alton Water	25	TM/13	TM/140--371--	2001	new	south	5
Site 55	No name	19	TM/22	TM/247--298--	1998	new	south	0
Site 56	Felixstowe	25	TM/33	TM/302--359--	2000-2004	new	south	0
Site 57	Shingle Street	25	TM/34	TM/372--437--	2001	new	south	0
Site 58	Bacton	27	TG/33	TG/3369-3460-	2007	new	south	0

Site 59	Aycliffe Quarry	66	NZ/22	NZ/282--218-- NZ/282--223--	1979	old	north	0
Site 60	Thrislington, Rough Furze Quarry, Thrislington	66	NZ/33	NZ/318--328-- NZ/318--324-- NZ/319--324--	1969-2006	old	north	0
Site 61	Trimdon Grange, Trimdon Grange Pit Heap CWS	66	NZ/33	NZ/361--352-- NZ/367--354-- NZ/368--353--	1976-2006	old	north	0
Site 62	Ludworth	66	NZ/34	NZ/363--416--	1969-1977	old	north	0
Site 63	Timber Beach : Salt Marsh Area	66	NZ/35	NZ/370--583--	1976	old	north	0
Site 64	Fulwell Quarry, Carley Hill Quarry SSSI, Fulwell Meadows	66	NZ/35	NZ/381--597-- NZ/383--597-- NZ/389--602-- NZ/388--601-- NZ/384--602-- NZ/383--596-- NZ/382--600-- NZ/384--602--	1958-2006	old	north	5
Site 65	Cleadon Hills And Park, Cleadon Pumping Station	66	NZ/36	NZ/387--638-- NZ/387--635--	1970-2010	old	north	0
Site 66	VC66 County Durham	66	NZ/36	NZ/383--666--	1957	old	north	0
Site 67	Marsden and Lizard Point	66	NZ/46	NZ/405--641-- NZ/408--642-- NZ/410--643-- NZ/410--645--	1975-1999	old	north	0

Site 68	Cold Hesledon Walkway, Hawthorn Tower, Hawthorn Dene, path at top of quarry, Hawthorn Hive	66	NZ/44	NZ/412--468-- NZ/436--459-- NZ/4375-4618- NZ/438--461-- NZ/4386-4632- NZ/4387-4639- NZ/4389-4641- NZ/439--460-- NZ/439--461-- NZ/441--460-- NZ/441--462--	1979*-2011	old	north	5
Site 69	Barony Colliery, New Cumnock	75	NS/52	NS/524--217-- NS/525--218-- NS/5250-2182-	2003-2007	new	north	0
Site 70	Kinmount NY16P (NY16P)	72	NY/16	NY/1485069012 NY/1513669123 NY/1484569133	2011	new	north	0
Site 71	Walltown Quarry, Nature Reserve	67	NY/66	NY/670--660-- NY/671--660--	2011	new	north	0
Site 72	Hexham, N bank of RiverTyne, E of Hexham Bridge, Egger Factory Hexham	67	NY/96	NY/947--644-- NY/945--644-- NY/943--645-- NY/945--645-- NY/944--645--	2003-2009	new	north	2
Site 73	A6072, north verge by New Shildon industrial estate.	66	NZ/23	NZ/257--331--	2005	new	north	0
Site 74	Low Barns, NR Witton le Wear	66	NZ/13	NZ/16---31---	2007	new	north	0
Site 75	Druridge Bay Country Park, along side of Ladyburn Lake	67	NZ/20	NZ/2721-0994-	2004-2006	new	north	0

Site 76	Horsegate Paddock	66	NZ/16	NZ/13---60--- NZ/132--600-- NZ/131--600--	2004-2010	new	north	5
Site 77	STARGATE POND	66	NZ/16	NZ/16---62---	2007	new	north	0
Site 78	Wallbottle Brick Works Local Nature Reserve	67	NZ/16	NZ/172--655--	2002	new	north	0
Site 79	Pegswood Pit, old spoil heap	67	NZ/28	NZ/230--879--	2011	new	north	3
Site 80	East Chevington	67	NZ/29	NZ/272--984--	2004	new	north	0
Site 81	Druridge Bay Country Park, along sdie of Ladyburn Lake	67	NZ/29	NZ/267--998-- NZ/268--998-- NZ/2678-9984- NZ/2686-9984- NZ/272--999-- NU/267--000-- NU/2679-0001-	2004-2006	new	north	5
Site 82	North Shields, dismantled railway line	67	NZ/37	NZ/317--701-- NZ/317--702-- NZ/317--703-- NZ/3163-7037- NZ/3161-7040- NZ/3160-7041-	1999-2009	new	north	5
Site 83	East Holywell, waste ground	67	NZ/37	NZ/3126-7284-	2011	new	north	0
Site 84	Holywell, Sewage Pumping Station	67	NZ/37	NZ/3239-7468-	2007	new	north	0
Site 85	Seaton Sluice, dunes, next to cycle-track, Hartley Links	67	NZ/37	NZ/3333-7695- NZ/3317-7714-	2008-2009	new	north	0
Site 86	BILLINGHAM BECK VALLEY COUNTRY PARK	66	NZ/42	NZ/454--228--	1996	new	north	0
Site 87	Hartlepool Docks	66	NZ/53	NZ/520--340--	1994	new	north	0

Site 88	E of Redcar Works, S. Gare	62	NZ/53	NZ/5745-3533-	2010	new	north	0
Site 89	Newton Links	68	NU/22	NU/230--268--	2004	new	north	0

sites shaded in pale gray were used to collect data used in analysis,

*the site name was the same but the 1979 record was only 1 x 1 km square grid reference. Due to low numbers of old sites in the northern area and the matching location it was decided to include this record.

Chapter 3: Appendix IV

Appendix IVi

Species scores from DCA analysis from data from 2011 field work

Variable	DCA1	DCA2	DCA3	DCA4
AgrostisCapillaris	-0.97691	2.36831	-0.36665	1.77906
AgrostisStolinifera	-0.95826	1.58646	-1.88592	-1.25954
ArrhenatherumElatius	-1.1127	-1.54953	0.2101	0.91392
AvenulaPratensis	0.45311	2.32069	-0.68246	0.39747
AvenulaPubescens	-1.4699	2.30594	-1.74717	0.42559
BrachypodiumSylvaticum	2.98639	0.02656	1.30341	1.96924
BromusCommutatus	-1.69888	-0.54964	0.8926	1.90433
BromusErectus	-0.42627	-1.76106	0.05413	-2.28917
BromusHordeaceus	-1.34773	0.67743	-1.3123	-1.26152
BromusSpOS4	-0.71122	0.23268	-1.74867	2.01691
CynosurusCristatus	-1.00891	0.85051	-1.35734	-1.48446
DactylisGlomerata	-1.2842	1.67159	2.13677	0.27345
DeschampsiaCespitosa	-1.72198	-0.78617	-0.80341	-1.17806
ElymusRepens	-1.19385	2.37342	0.09275	0.35578
FestucaRubra	1.01618	-1.17212	1.15203	1.82833
HolcusLanatus	-1.15643	-0.62494	0.34663	-0.99046
HolcusMollis	-1.20756	-2.29885	-0.36199	0.97162
LoliumPerenne	-1.38193	1.82207	-2.5331	0.02082
PoaAnnua	-0.30464	-1.53847	-0.54917	1.59854
PoaPratensis	0.10961	2.00508	-1.99961	1.06579
PoaSpNewSi3	-1.25836	-1.81915	-1.10565	0.97308
PoaTrivialis	-1.48392	2.03454	1.86151	2.49926
TrisetumFlavescens	-1.25549	0.3354	1.51378	1.13296
BareGround	0.21445	0.5166	0.09595	-0.03725
AchilleaMillefolium	2.08722	-1.26679	0.67255	-1.6529

AgrimoniaEupatoria	3.05632	-0.01987	0.22855	0.68102
AnagallisArvensis	-1.051	0.89759	-1.75983	-0.42414
ArenariaSerpyllifolia	2.95815	0.07473	0.44671	0.87705
AsteraceaeSpNewSi38	-1.2202	-0.08234	-1.51094	-2.20777
AsteraceaeSpNewSi39	-2.27474	1.53301	2.80959	-1.03022
AsteraceaeSpOldSi20	2.9144	0.10328	0.5111	1.23397
AsteraceaeSp2NewSi38	-1.90199	1.41532	-3.04062	-1.1488
BellisPerennis	-1.01712	1.00868	-1.51248	-1.23468
BlackstoniaPerfoliata	3.05473	-0.25099	-0.55219	-1.55325
CalystegiaSepium	-1.94453	-2.32264	0.05818	1.79417
CarexFlacca	2.9524	-0.0874	0.15304	0.58754
CarexSpOldSi4	-1.27189	2.21438	0.39238	2.43445
CentaureaNigra	2.47096	-0.81717	0.31234	-0.05429
CentaureaScabiosa	2.94391	-0.25309	-0.53388	-1.50229
CentauriumErythraea	2.23296	-0.63347	-0.8307	-1.9963
CerastiumFontanum	-0.82339	0.37042	-1.52399	-1.56596
ChamerionAngustifolium	1.74734	-1.34827	0.64162	-0.34071
CirsiumArvense	-0.37178	-0.59941	-0.41694	0.08557
CirsiumVulgare	-0.98365	1.49077	2.29504	2.32525
ClematisVitalba	0.60318	1.89972	2.89955	0.57826
ConvolvulusArvensis	-0.99677	-0.91878	-0.52601	-0.48163
CrataegusMonogyna	1.58357	0.12792	2.27343	-1.62623
CytisusScopariusSspScoparius	-0.8015	-2.61935	1.55097	-3.15206
DactylorhizaFuchsii	2.34064	0.68793	0.40904	-0.70325
DipsacusFullonum	-2.09458	0.74688	-2.24898	-1.38799
EpilobiumspNS3	-0.8015	-2.61935	1.55097	-3.15206
EpilobiumSpNewSi38	-1.86924	0.6667	2.05765	1.64812
EpilobiumSpOldSi4	-1.6922	2.22362	-2.68454	0.68165
EquisetumArvensis	-1.6687	1.77687	2.88534	-0.44985
ErigeronAcris	0.00742	0.48113	-0.30589	-1.4474

EuphrasiaOfficinalisAgg	2.71819	-0.51174	0.04983	-1.13516
FraxinusExcelsior	-1.08811	1.21662	-1.01116	-1.46018
GaliumAparine	-2.26357	1.94488	2.01237	-1.81067
GaliumMollugo	-1.73732	-0.18344	-1.34012	-1.46354
GaliumParisiense	-1.0729	-2.03011	1.13157	-2.1657
GaliumVerum	3.0612	-0.24087	-0.4402	-0.91439
GentianellaAmarella	3.06258	-0.15174	-0.50311	-1.44005
GeraniumDissectum	-0.03029	0.46175	-1.12751	0.34423
GeraniumPusillum	-1.57745	-2.50769	-1.52199	2.84531
GeraniumRobertianum	0.78311	-1.57106	1.11669	-0.20967
GeraniumSpNewSi3	-0.8015	-2.61935	1.55097	-3.15206
GeumUrbanum	-0.17933	-1.42688	-0.213	-1.96832
GlechomaHederacea	-0.6715	-1.84973	-1.44697	1.97859
HederaHelix	-0.95339	-1.96466	2.17218	-2.39511
HelminthothecaEchioides	-1.4764	0.68651	-1.44748	-1.25059
HeracleumSphondylium	-1.49944	-0.64835	1.33354	0.57314
HypericumHirsutum	1.94769	-1.44847	-0.0467	-0.79973
HypericumPerforatum	1.95703	0.01768	1.05907	0.30556
JuncusInflexus	-1.48738	2.28793	-1.59232	-1.38446
LamiaceaeSpNewSi38	-1.22206	1.0134	-1.59353	-1.81111
LatherusNisolia	-0.91271	2.417	-1.07885	-1.09978
LeontodonHispidus	2.78962	-0.108	-0.20606	-0.19846
LeucanthemumVulgare	-0.54884	-1.73151	-0.9789	1.66441
LinariaVulgaris	-0.98497	-1.9922	-0.48719	1.20357
LotusCorniculatus	2.37867	1.68073	-0.52483	1.12764
MedicagoLupulina	-0.15529	1.68791	-0.07547	0.57439
MelilotusAltissimus	-1.32451	1.55924	2.33188	2.2154
MelilotusOfficinalis	-0.56344	-1.51625	-1.04259	1.85533
Moss	-0.44739	-1.0121	1.07728	-0.12476
MyosotisRamosissima	-1.13215	-1.87944	-0.25753	-0.55395

OdontitesVernus	-1.54415	1.5132	2.36754	0.40609
OnonisRepens	2.96293	-0.07241	0.45319	1.29927
OriganumVulgare	2.65809	-0.25138	0.13062	-0.12925
PastinacaSativa	-1.66693	-1.37185	0.77626	2.34032
PilosellaOfficinarum	2.87721	-0.33813	-0.37093	-1.44557
PlantagoLanceolata	0.22913	-1.43847	0.76735	0.27857
PlantagoMajor	0.17981	1.5007	-1.32529	-2.03565
PolygalaVulgaris	2.91744	-0.16884	0.00477	-0.15367
PotentillaReptans	-0.28774	1.88458	-0.50419	2.14922
PrimulaVeris	1.32976	0.85638	-1.61574	-1.24467
PrunellaVulgaris	1.24424	1.59741	-1.46742	-1.10358
PrunusSp	-2.32745	0.26077	-2.25107	-0.94372
PrunusSpinosa	-0.92447	-1.83585	0.76648	-0.07565
QuercusRobur	-1.61196	-0.62191	1.84378	2.0172
RanunculusRepens	-0.43043	1.28237	-0.67735	-0.09706
RosaCaninaAgg	1.86909	0.64153	0.04307	-1.64419
RubusFruticosusAgg	-1.00268	-1.71156	0.50873	-1.63672
RumexSpNS3	-1.06233	-2.12136	-0.34395	1.25399
RumexSpNewSi38	-1.04936	-0.12654	-0.96759	-0.84732
RumexSpOldSi4	-1.23912	2.41599	1.44433	-0.01206
SalixSp	-0.69539	1.32239	2.29874	2.37514
SanguisorbaMinor	3.34672	-0.18259	0.01035	-0.38365
SenecioErucifolius	-0.2564	0.98493	-0.65025	-0.50854
SenecioJacobaea	-0.32732	-1.786	-0.36655	1.17583
SenecioSpOldSi4	-1.64264	2.3903	-1.60391	-1.58485
SileneDioica	-0.45806	-1.93821	-1.85283	1.85119
SileneLatifolia	-0.45806	-1.93821	-1.85283	1.85119
SonchusArvensis	-1.66606	-1.01915	1.29309	2.28263
SonchusAsper	-1.61749	-0.77606	1.02267	0.48836
StellariaGraminea	-2.48021	-1.14009	-0.24285	-0.37035

StellariaHolostea	-1.08682	-1.96025	2.18544	-2.35523
TanacetumVulgare	-1.94887	-2.69201	-1.62703	3.00626
TaraxacumOfficinaleAgg	-1.21528	0.92374	-1.58264	-1.52167
TorilisJaponica	-1.64519	0.16334	0.80175	-0.7623
TragopogonPratensis	-2.11674	-1.52902	0.50766	0.24754
TrifoliumCampestre	-1.94887	-2.69201	-1.62703	3.00626
TrifoliumDubium	-1.17806	1.49453	-1.34119	-1.05128
TrifoliumPratensis	2.89207	0.64887	1.42966	1.95774
TrifoliumRepens	-1.17929	1.90578	1.94187	1.61586
UrticaDioica	-1.51901	-2.12437	1.41027	-1.76352
VeronicaSerpyllifolia	1.25925	1.92318	-2.05118	1.41443
ViburnumSpNewSI38	-1.46543	1.20162	-1.64323	-1.48673
ViciaHirsuta	-1.58523	2.73809	1.24295	-2.16411
ViciaSativa	-0.06007	1.10736	-0.30462	1.38524
ViciaTetrasperma	-0.7652	-1.82444	0.39277	-0.20028
ViolaHirta	2.55071	-0.24205	0.42277	0.509
Elevation	1.01517	-0.24858	-0.07008	0.41325
Vegetationhight	0.25896	0.77522	0.61676	0.32141

Appendix IVii

Species scores from DCA analysis from data from 2011 field work with soil analysis

Variable	DCA1	DCA2	DCA3	DCA4
AgrostisCapillaris	-1.138701	2.265368	-0.051183	1.446608
AgrostisStolinifera	-1.290809	-1.216021	1.563438	-2.132783
ArrhenatherumElatius	-1.916239	-1.029333	0.329866	1.284744
AvenulaPratensis	-0.770962	2.007364	-1.545792	1.758068
AvenulaPubescens	-1.872523	3.344245	-0.205183	-0.634189
BrachypodiumSylvaticum	2.508074	0.95012	0.201345	1.762484
BromusCommutatus	-1.963416	-1.186742	-1.596421	-2.090538
BromusHordeaceus	-1.724376	-2.002423	-1.213064	-1.064505
BromusSpOS4	-1.038432	2.106529	-0.687021	1.591701
CynosurusCristatus	-1.724412	-1.703691	-1.326912	-1.88154
DactylisGlomerata	-1.089212	-1.267766	0.981574	-1.572443
ElymusRepens	-1.111034	2.140236	0.486978	0.382966
FestucaRubra	1.355551	1.549649	-1.727711	-0.049003
HolcusLanatus	-1.582856	-1.588777	-0.672887	0.013185
LoliumPerenne	-1.731527	2.063333	1.036247	-1.101816
PoaPratensis	-1.309351	1.827085	0.360505	-1.493667
PoaTrivialis	-1.095641	-0.909337	0.086724	-1.631364
TrisetumFlavescens	-1.610574	-1.939368	-0.124701	1.62751
BareGround	-0.48216	-1.127121	-0.823276	1.205555
AchilleaMillefolium	2.339294	0.588395	3.358572	1.020192
AgrimoniaEupatoria	2.469933	0.256933	-1.945516	-0.198895
AnagallisArvensis	-1.777174	-2.657428	-0.729146	-1.5352
ArenariaSerpyllifolia	2.31633	0.263639	-2.229122	0.570383
AsteraceaeSpNewSi38	-2.239991	-0.982463	-0.211529	0.126416
AsteraceaeSpNewSi39	-1.239281	-3.634412	1.78079	-1.899898
AsteraceaeSpOldSi20	2.168588	0.448131	-3.005831	0.746366

AsteraceaeSp2NewSi38	-1.967444	-1.634903	1.571607	-3.914985
BellisPerennis	-1.748566	-1.915212	-1.165993	-1.10325
BlackstoniaPerfoliata	2.534244	-0.501121	-1.136641	-0.906185
CarexFlacca	2.325329	0.202849	-2.131778	0.309482
CarexSpOldSi4	-0.995937	1.948585	-0.136458	1.992947
CentaureaNigra	2.374337	0.176004	2.214293	0.131485
CentaureaScabiosa	2.389493	-0.46974	-1.280243	-0.913
CentauriumErythraea	1.788613	-0.870152	1.017198	0.010835
CerastiumFontanum	-1.79725	1.233294	0.31327	-1.686521
ChamerionAngustifolium	2.08306	0.192052	-3.05589	0.660981
CirsiumArvense	-1.170655	1.417074	-1.328912	-0.141906
CirsiumVulgare	-0.695323	-1.959609	-1.599286	1.427737
ClematisVitalba	0.916646	-1.839798	2.065082	1.432916
ConvolvulusArvensis	-1.64574	-2.04455	-0.609693	1.187971
CrataegusMonogyna	1.827981	-0.086467	2.474671	-0.171072
DactylorhizaFuchsii	1.723649	-1.080575	-1.838174	1.441323
DipsacusFullonum	-1.967444	-1.634903	1.571607	-3.914985
EpilobiumSpNewSi38	-1.959825	-2.219986	1.248492	1.689114
EpilobiumSpOldSi4	-1.837299	2.791915	0.681298	-0.926933
EquisetumArvensis	-0.778296	-2.921611	2.072766	-1.249635
ErigeronAcris	-1.335064	-2.469976	-1.309678	2.022118
EuphrasiaOfficinalisAgg	2.346835	0.518464	2.471912	0.653427
FraxinusExcelsior	-1.666355	-1.615016	-0.873877	-1.795432
GaliumAparine	-1.576451	0.412977	1.969126	-3.005743
GaliumMollugo	-2.09844	-2.073648	-0.253745	-1.746755
GaliumVerum	2.546529	-0.276663	-1.279237	-1.240719
GentianellaAmarella	2.525842	-0.357039	-0.161524	-0.922731
GeraniumDissectum	-1.462037	1.544136	-0.775398	-1.528384
HelminthothecaEchioides	-1.820713	-1.80841	-0.12864	-1.380215
HeracleumSphondylium	-1.689567	-1.386423	0.652609	1.401299

HypericumHirsutum	2.135768	-0.222587	1.915781	-0.838663
HypericumPerforatum	2.182106	0.606827	3.136408	0.778509
JuncusInflexus	-1.459164	2.517971	0.349849	-1.457413
LamiaceaeSpNewSi38	-1.784004	-1.713605	-0.773497	0.025297
LatherusNisolia	-1.147528	2.378827	-0.218315	-0.845267
LeontodonHispidus	2.22861	-0.038101	1.153616	-0.76651
LotusCorniculatus	1.811761	1.28481	-1.915516	-0.251302
MedicagoLupulina	-0.922682	1.347605	-0.396457	-0.800549
MelilotusAltissimus	-0.892478	-2.103587	-1.204708	1.372062
Moss	-0.82139	-1.071152	-0.184987	1.225131
MyosotisRamosissima	-1.523013	-1.535822	-1.272128	2.02838
OdontitesVernus	-1.478479	-1.79758	1.766608	-0.727589
OnonisRepens	2.287891	0.643239	-2.3884	1.056692
OriganumVulgare	2.150004	0.346545	2.165547	-0.155838
PastinacaSativa	-2.111778	0.846803	1.970352	3.403154
PilosellaOfficinarum	2.400665	0.282455	2.213401	-1.156248
PlantagoLanceolata	1.032815	-2.28133	1.343185	-1.5894
PlantagoMajor	-1.215009	-2.098886	-1.048865	-0.885858
PolygalaVulgaris	2.3696	0.028958	-0.193945	-0.559247
PotentillaReptans	-0.982795	1.898308	-0.70869	1.625091
PrimulaVeris	0.368691	-1.935984	-0.404742	-1.420982
PrunellaVulgaris	0.378729	-0.646071	-0.963504	-1.214945
QuercusRobur	-1.793465	-1.629801	0.810731	2.173526
RanunculusRepens	-1.037846	1.631906	1.653908	-1.57948
RosaCaninaAgg	1.222379	-2.216791	-0.968943	1.634819
RubusFruticosusAgg	-1.995952	-0.903852	-0.051543	1.457609
RumexSpOldSi4	-0.591456	2.037148	2.038811	-2.814672
SalixSp	-0.444725	-0.72832	-2.029604	-1.789156
SanguisorbaMinor	2.927617	0.027498	1.127308	-0.764057
SenecioErucifolius	-0.867915	-1.47917	-1.319026	0.155227

SenecioJacobaea	-1.790502	-0.041941	-0.39025	-1.323951
SenecioSpOldSi4	-1.630617	2.804157	0.08881	-1.230364
SonchusArvensis	-2.111778	0.846803	1.970352	3.403154
StellariaGraminea	-2.876536	1.092969	0.358992	-0.963695
TaraxacumOfficinaleAgg	-1.85888	-1.399289	-0.294423	-1.473777
TorilisJaponica	-1.718208	-1.839225	-0.756316	-1.233997
TragopogonPratensis	-2.876536	1.092969	0.358992	-0.963695
TrifoliumDubium	-1.558578	-1.054609	-0.633665	1.064411
TrifoliumPratensis	2.296058	0.750727	-1.983643	1.504218
TrifoliumRepens	-1.191168	1.148353	1.731301	-0.757726
VeronicaSerpyllifolia	-1.281629	1.735555	-0.711129	-1.988098
ViburnumSpNewSI38	-1.448692	-1.962776	-0.695329	1.689838
ViciaHirsuta	-1.220649	2.263064	-0.091803	1.680668
ViciaSativa	-1.872523	3.344245	-0.205183	-0.634189
ViciaTetrasperma	-2.360128	-0.205332	1.627373	2.571882
ViolaHirta	2.149892	0.503068	2.735579	0.1578
Elevation	1.043993	0.143797	-0.162202	0.2284
Vegetationhight	-0.025212	0.952779	0.216163	1.195269
pH	0.644207	0.396947	-0.155342	-0.008795
OrganicMatter	0.521202	-0.225736	0.633424	0.316688
AvailablePhosphorus	-0.444793	-0.282253	-0.044945	-0.633765
AvailablePotassium	-0.571872	-0.467385	0.771836	0.420476
AvailableMagnesium	-0.784541	1.18267	0.480633	-0.069634
Sand	-0.36994	0.816465	0.29331	0.022746
Silt	0.512486	-0.027407	0.086696	0.110002
Clay	1.028515	0.040079	-0.595856	-0.024499
NitrateNitrogen	-1.231431	-0.569955	0.793005	-1.417892
AmmoniumNitrogen	1.103248	0.423864	0.159796	-0.331977
DryMatter	0.442609	0.307701	-0.000183	-0.004383
AvailableNAtDepthGiven	0.784617	0.193668	0.341831	-0.838903

Appendix IViii

Species scores from DCA analysis from data from 2012 field work

Variable	DCA1	DCA2	DCA3	DCA4
AgrostisCapillaris	1.68278	-1.57935	0.71701	0.90995
AgrostisStolonifera	0.02109	-1.85354	-0.9624	-1.3408
AnthoxanthumOdoratum	2.58168	-0.41682	1.43668	1.22537
ArrhenatherumElatius	-0.8391	1.84305	-0.1419	-1.27374
BrachypodiumSylvaticum	-1.63179	-0.73658	0.83211	-2.40489
BrizaMedia	-1.97711	0.03071	-0.94659	1.59226
BromusHordeaceus	-0.98527	2.11234	-0.35289	1.72507
CatapodiumRigidum	-2.15662	-0.11465	-0.7859	-0.94835
CynosurusCristatus	-1.15868	-1.67192	1.66472	0.87089
DactylisGlomerata	-0.58773	0.683	-0.31379	-1.11145
ElymusRepens	-0.89576	-1.00428	-1.14953	-2.68295
FestucaPratensis	-1.50207	-0.01404	1.14322	-1.47346
FestucaRubra	-0.71695	-0.65656	-0.00447	-0.03836
HolcusLanatus	-0.23306	-1.01007	-1.01669	-1.05473
HolcusMollis	0.84853	2.26442	1.35445	1.53802
LeymusArenarius	-1.37676	-1.19939	0.36145	-2.4655
LoliumPerenne	-0.28973	-0.88212	-1.29627	-1.58631
LuzulaMultiflora	2.80001	0.059	0.71987	1.32807
PoaAnnua	-1.10718	-1.25778	-2.57921	-1.5782
PoaPratensis	0.66462	-1.20481	-1.32661	-0.47661
PoaTrivialis	1.1972	-2.417	-1.29054	-0.28378
TrisetumFlavescens	-1.40231	0.02144	-0.81869	2.04773
VulpiaBromoides	2.99466	0.28772	-0.18621	0.3
AcerCampestre	-0.72351	3.02898	1.33056	0.55149
AiraCaryophyllea	3.03863	0.25004	0.5511	0.39371
AiraPraecox	3.12966	0.22465	0.06505	0.03004

AchilleaMillefolium	-0.78966	2.11844	0.94262	-0.53724
AegopodiumPodagraria	-1.69163	-0.44746	1.31329	-2.97184
AgrimoniaEupatoria	-1.71899	2.25609	-2.01787	0.23999
AlchemillaMollis	2.32129	-0.03981	-0.06504	-0.20559
AnthyllisVulneraria	-1.32369	-1.46296	0.07801	1.73459
AphanesArvensis	2.70225	0.4862	-0.22349	-0.85963
ArenariaSerpyllifolia	-2.58419	0.18749	-0.57272	0.86445
AsteraceaeSp	-1.43622	-1.83029	1.69762	-0.35512
BellisPerennis	-0.43782	-1.60542	-0.50554	-0.97348
BlackstoniaPerfoliata	-2.0788	-0.08819	-0.16766	-1.40461
BroadLeafTreeSeadling	-0.92836	-1.87421	-1.75849	0.99782
CalystegiaSepium	0.35858	2.38672	-1.22351	1.1249
CarexHirta	-0.68294	0.38625	-2.72798	-1.5245
CarexFlacca	-1.38884	-1.63066	2.44294	0.16339
CarexFlacaORPanacea	-2.08372	0.03953	0.88242	-1.63095
CarexOtrubae	0.09177	-2.91204	-1.49785	0.08272
CarexPanicea	-1.33516	-2.00264	1.43461	1.28233
CarlinaVulgaris	-2.20734	0.48592	-1.26817	1.49257
CentaureaErythraea	2.12941	-1.36234	1.33145	1.63141
CentaureaNigra	-1.36229	-0.206	-0.56164	-0.74487
CentaureaScabiosa	-1.75192	-0.30172	-0.83668	0.19258
CerastiumFontanum	1.54667	-1.28092	-0.78605	-0.14246
ChamerionAngustifolium	-0.6054	0.2733	2.75082	0.42396
CirsiumArvense	1.23018	0.87135	-1.04238	-0.08905
CirsiumVulgare	-1.38765	1.06541	-2.27751	0.00609
ConvolvulusArvensis	0.35674	2.44088	1.45648	1.36457
Cotoneaster.sp	-0.96453	-1.79578	1.24063	1.74345
CrataegusMonogyna	-0.79504	0.18915	-1.29085	1.43839
CrepisCapillaris	0.00732	1.09058	-1.9582	-1.18359
CytisusScoparius	3.18611	0.45273	-0.10746	-0.23381

DactylorhizaFuchsii	-1.81666	-0.56619	0.39439	-0.11679
DactylorhizaPurpurella	-1.46832	-1.84107	-1.99514	1.56316
DaucusCarota	-1.3692	-0.82463	0.20104	1.92142
EleocharisPalustris	0.09177	-2.91204	-1.49785	0.08272
EpilobiumAngustifolium	-1.46832	-1.84107	-1.99514	1.56316
EpilobiumHirsutum	3.05478	0.31766	-0.28832	-0.0561
EpilobiumSp	2.2459	1.27597	0.22653	-0.59706
EquisetumArvense	-1.50575	1.25095	1.4824	1.42255
EuphrasiaAgg	-1.38688	-1.12145	-0.71745	-1.41966
FagusSylvatica	-0.19424	-0.0366	3.13649	-0.42396
FragariaVesca	0.64653	-2.0724	-1.59472	1.4501
FraxinusExcelsior	0.04944	1.32321	2.49315	0.43304
GaliumAparine	-1.69163	-0.44746	1.31329	-2.97184
GaliumMollugo	2.38896	1.04003	-0.54549	-1.55639
GaliumVerum	-1.32084	-0.70199	-1.54101	2.5332
GeraniumDissectum	2.12062	-0.27587	-0.85878	-1.46832
GeraniumMolle	2.82308	0.08089	-0.59382	0.26963
GeraniumPyrenaicum	0.42918	2.37546	-1.6367	-1.62431
GeumUrbanum	2.20742	-0.26281	-0.91213	-0.21528
GlechomaHederacea	-0.97681	3.0941	0.03722	-0.49315
HederaHelix	-1.05732	1.76222	0.11599	-0.37376
HeracleumSphondylium	-0.71236	1.72094	-1.42342	1.99435
HieraciumSp	-1.6464	-0.69297	0.23382	1.75481
HippocrepisComosa	-1.96589	1.60657	0.53464	1.90372
HypericumHirsutum	2.37461	0.83684	-0.4455	-1.43131
HypericumPerforatum	-0.22484	-0.40196	-1.02785	1.08761
HypericumXDesetangsii	-2.01909	-1.15751	-1.61327	1.32304
HypochaerisRadicata	-0.32081	-1.68521	0.34141	1.24373
ImpatiensGlandulifera	2.38896	1.04003	-0.54549	-1.55639
JuncusArticulatus	-0.56736	-2.59765	-1.81224	-0.86409

JuncusEffusus	-1.43445	-1.94019	-2.4303	-1.63059
JuncusInflexus	-1.47868	-1.58021	-1.53341	-1.8507
KoeleriaMacrantha	-1.45461	1.61969	-1.94357	2.69679
LamiumAlbum	0.42918	2.37546	-1.6367	-1.62431
LathyrusPratensis	1.68973	-1.74604	-0.97206	-1.30749
LeontodonHispidus	-1.64813	-1.11025	-1.36373	-0.6865
LeontodonSaxatilis	2.83752	0.02587	1.00953	1.51973
LeucanthemumVulgare	-1.37878	-1.53221	-1.33934	-1.57983
LinariaVulgaris	-1.03341	3.0914	-0.88007	-0.57423
LinumCatharticum	-1.41903	-1.23631	1.54008	0.30541
LotusCorniculatus	-1.15594	-1.30434	-0.25511	0.28944
LotusPedunculatus	-1.53785	-1.77497	1.57615	1.45833
LuzulaCampestris	-1.484	-1.7845	2.54535	0.54314
MedicagoArabica	-0.91181	1.20647	1.95986	-1.96043
MedicagoLupulina	1.99044	1.91719	0.16678	1.36781
MyosotisArvensis	0.29257	2.45804	-1.60104	-1.30879
MyosotisDiscolor	3.08861	0.41305	0.14142	0.31003
MyosotisSp	2.32129	-0.03981	-0.06504	-0.20559
MyosotisSylvatica	0.71993	1.608	0.56825	1.84122
NeottiaOvataSynListeraOvata	-1.40694	-1.14989	2.59735	0.10301
OrnithopusPerpusillus	3.20511	0.70423	-0.06402	-0.34722
PastinacaSativa	-0.96709	-1.93381	-1.56521	-1.7565
PhleumBertolonii	-1.28146	-1.18371	-1.23037	2.69496
PicrisEchioides	-0.9909	2.35499	0.83588	1.73669
PilosellaOfficinarum	-2.03173	0.54432	-1.40272	1.9578
PineSeedling	-0.01679	-1.9074	-1.4838	-0.25625
PlantagoLanceolata	0.20592	1.72189	-1.18179	-0.4213
PlantagoMajor	-1.41196	-0.45961	-2.09132	-1.68171
PolygalaVulgaris	-1.88742	-0.20563	0.88729	-2.12552
PotentillaReptans	-0.78646	-1.27616	-1.64514	-1.73502

PrimulaVeris	-1.47967	-1.66983	2.57864	0.47803
PrunellaVulgaris	1.48175	-0.91954	-0.76414	-1.29522
PrunusSeedling	2.78235	-0.09683	1.30462	1.22124
PrunusSpinosa	0.25446	2.46369	-1.4192	0.46071
QuercusRobur	2.35698	-0.4601	2.01994	0.29935
RanunculusAcris	-0.99158	-0.91557	1.78355	0.90424
RanunculusAulbosus	-0.9909	2.35499	0.83588	1.73669
RanunculusRepens	1.15092	2.0834	-1.25445	-1.46813
RanunculusSp	-1.45836	-1.8183	2.50282	0.48566
RhinanthusMinor	-1.08606	-1.26412	0.13495	1.92818
RosaHollandica	-1.4067	-0.0291	1.15725	-1.44416
RosaSp	-1.17828	2.58856	1.91454	-0.38705
RubusFruticosus	-0.78449	2.51774	0.59689	0.38047
RumexAcetosa	-1.4562	-1.41028	-1.98705	0.06346
RumexAcetosellaSynAcetosellaVulgaris	0.80899	1.03818	-1.91384	-1.56757
RumexConglomeratus	-1.27348	3.26339	-0.37545	-0.61911
RumexSp	1.83119	1.63477	-1.27404	0.46824
SaginaSp	3.16881	0.21374	-0.14671	-0.12628
SenecioErucifolius	-1.17903	-0.35495	-0.5999	-3.20895
SenecioJacobaea	0.83998	1.30434	-0.45537	-0.72109
TaraxacumOfficinale	1.80695	-1.14022	1.02091	1.13744
TragopogonPratensis	-1.00622	-0.45505	-1.28576	2.31236
TrifoliumArvense	3.12611	0.25262	-0.19976	-0.1
TrifoliumCampestre	-1.32182	-1.29053	-1.03137	2.69673
TrifoliumDubium	-0.12777	-1.83049	-0.177	0.3915
TrifoliumMicranthumSynChrysaspisMicrantha	0.51067	-1.9253	-1.69285	-1.87096
TrifoliumPratense	-1.37648	-0.36567	2.10597	-0.1524
TrifoliumRepens	0.37067	-1.44911	-0.6748	-1.56844
TroilisJaponica	0.52601	2.42341	-0.31365	0.89024
TussilagoFarfara	-1.27783	-1.1754	2.25919	-1.01608

UmbalifferaeSp	-0.16696	2.86412	1.70912	1.19261
UrticaDioica	-0.93566	0.39748	2.15657	-2.16944
VeronicaArvensis	2.38896	1.04003	-0.54549	-1.55639
VeronicaChamaedrys	-0.36779	1.32584	-1.74826	-1.50416
VeronicaSerpyllifolia	2.45452	0.63774	-1.34931	-1.39534
ViciaCracca	-1.43379	-0.10431	-2.24487	-1.54363
ViciaHirsuta	2.25101	1.16318	0.92015	1.71863
ViciaSativa	0.03319	0.81185	0.94876	1.07282
ViciaSepium	-0.96709	-1.93381	-1.56521	-1.7565
ViciaTetrasperma	-0.44517	1.5076	-1.68932	-1.41678
ViolaSp	-0.16696	2.86412	1.70912	1.19261
Moss	0.98205	1.00287	1.71558	-0.82359
BareGround	-0.52257	0.19044	1.10704	-1.0778
Elevation	0.88188	-0.08425	-0.5056	1.19119
Shade	0.41007	-0.1335	2.41783	-1.29383
VegHight	-0.27625	0.88129	0.06832	-0.05287
pH	-0.00437	-0.02071	0.79384	-0.00591

Chapter 3: Appendix V

Appendix Vi

Site scores from DCA analysis from data from 2011 field work

Age	Site	Quadrat	Orchid present	DCA1	DCA2	DCA3	DCA4
New	3	3	Orchid	-0.48012	-1.623	0.55469	-1.21761
New	3	4	Orchid	-0.51089	-1.01005	0.07723	-0.04564
New	3	5	Orchid	-0.33121	-1.2844	0.2773	0.31575
New	3	6	Orchid	-0.30826	-0.84204	0.1949	-0.10576
New	3	7	Orchid	-0.85081	-1.6208	-0.57626	1.57766
New	3	8	Orchid	0.09376	-0.92235	0.03381	0.57907
New	3	9	Orchid	0.28928	-0.87168	0.10701	0.23522
New	3	10	Orchid	0.21003	-0.88014	0.09925	0.57713
New	3	11	Orchid	-0.035	-0.95981	0.01915	0.75579
New	3	13	Orchid	-0.30677	-0.81818	0.59631	-0.18729
New	3	14	Orchid	0.34432	-0.17101	-0.05028	0.00729
New	3	15	Orchid	0.65989	-0.82684	0.09334	-0.02838
New	3	16	Orchid	-0.11021	-0.97652	0.19102	-0.79051
New	3	17	Orchid	-0.09153	-0.48896	0.38973	0.10554
New	3	18	Orchid	-0.68236	-0.85496	0.62283	-0.07311
New	3	19	Orchid	-0.6141	-1.21217	0.95131	-0.95129
New	3	20	Orchid	-0.00108	-0.61658	1.04029	-0.76431
New	3	3	None	-0.22676	-1.14168	-0.64503	0.85451
New	3	4	None	-0.48101	-1.17209	0.39095	-0.16562
New	3	5	None	-0.11549	-0.98875	0.67008	0.01166
New	3	6	None	-0.42697	-1.25036	0.03891	0.6823
New	3	7	None	-0.8133	-1.39955	0.29663	0.35812
New	3	8	None	-0.01606	-0.71056	-0.11149	0.97294
New	3	9	None	-0.1398	-0.78852	-0.31217	0.89105

New	3	10	None	-0.34173	-0.93989	-0.22804	0.66037
New	3	11	None	0.62924	-0.51989	0.27947	0.32773
New	3	13	None	0.16352	-0.68295	0.24315	-0.16877
New	3	14	None	-0.0791	-1.13814	-0.18186	0.85078
New	3	15	None	0.08988	-0.83187	0.3057	0.48235
New	3	16	None	-0.61899	-1.25598	0.48725	-0.42063
New	3	17	None	0.22457	-0.75111	0.50912	0.31048
New	3	18	None	-0.3776	-0.95256	-0.13567	0.35709
New	3	19	None	0.15754	-0.26712	0.10512	0.2776
New	3	20	None	-0.13293	-0.62844	-0.30588	0.65829
Old	4	2	Orchid	-0.4825	1.5535	0.13676	1.27916
Old	4	3	Orchid	-0.11166	1.03416	0.04072	0.56162
Old	4	4	Orchid	-0.00271	1.19462	-0.11598	0.52634
Old	4	5	Orchid	0.05336	1.00049	-0.20786	0.19866
Old	4	6	Orchid	-0.30981	1.24179	-0.5518	-0.06151
Old	4	7	Orchid	-0.15692	1.40453	-0.07581	0.26099
Old	4	8	Orchid	-0.59958	1.453	-0.66962	-0.45701
Old	4	9	Orchid	-0.64321	1.43422	-0.7846	0.28144
Old	4	2	None	-0.30158	0.8887	0.01821	1.23216
Old	4	3	None	0.27364	1.4204	-0.41052	0.41099
Old	4	4	None	-0.53508	1.00365	0.85979	0.93598
Old	4	5	None	-0.65781	1.17195	-1.22259	0.05579
Old	4	6	None	-0.61474	1.64927	0.14893	-0.39125
Old	4	7	None	0.66567	1.21086	-1.08581	0.5177
Old	4	8	None	-0.41472	1.41919	0.16495	-0.0589
Old	4	9	None	-0.24668	1.09054	0.36898	0.29404
Old	5	1	Orchid	0.27672	0.08747	0.32363	0.3616
Old	5	1	None	0.28193	0.36383	0.099	0.40252
Old	20	1	Orchid	2.21441	0.06251	0.26511	0.70824
Old	20	2	Orchid	2.36993	-0.12141	-0.07577	-0.27768

Old	20	3	Orchid	2.2427	0.41871	0.32513	0.6441
Old	20	4	Orchid	2.39226	-0.07285	-0.04924	-0.10682
Old	20	5	Orchid	2.02434	-0.39206	0.29988	-0.58169
Old	20	6	Orchid	2.22555	-0.02359	-0.1868	-0.68339
Old	20	1	None	2.35798	0.01182	0.4766	0.64615
Old	20	2	None	2.29596	-0.08951	0.23408	0.56436
Old	20	3	None	1.67673	-0.2213	0.19931	-0.0904
Old	20	4	None	2.02379	-0.09621	-0.08353	-0.0093
Old	20	5	None	1.90279	-0.19537	0.36384	0.08697
Old	20	6	None	2.69877	-0.20512	-0.11718	-0.39521
New	38	1	Orchid	-0.69159	-0.1898	0.51492	0.67323
New	38	2	Orchid	-0.62228	-0.4782	0.54976	0.76345
New	38	3	Orchid	-0.47416	-0.27838	-0.18936	-0.20736
New	38	4	Orchid	-1.15534	-0.2929	0.24241	-0.01401
New	38	5	Orchid	-0.5008	0.48561	0.56342	0.54462
New	38	6	Orchid	-0.57497	-0.0642	0.74127	0.45548
New	38	7	Orchid	-0.42996	0.48825	-0.55425	-0.52686
New	38	8	Orchid	-0.43578	0.62322	-0.79857	-0.79764
New	38	9	Orchid	-0.58427	0.60199	-0.79902	-0.86424
New	38	10	Orchid	-0.08096	0.40165	-0.78255	-0.91565
New	38	11	Orchid	-0.43861	0.17098	-0.34212	-0.37784
New	38	12	Orchid	-0.4611	0.10278	-0.39708	-0.45245
New	38	13	Orchid	-0.38722	0.01161	-0.1873	-0.34058
New	38	14	Orchid	-0.41154	0.66637	-0.43724	-0.46837
New	38	15	Orchid	-0.83636	0.52501	-0.78188	-0.74992
New	38	16	Orchid	0.123	0.69451	-0.57008	-0.82888
New	38	17	Orchid	-0.62661	-0.04799	0.44741	0.18844
New	38	18	Orchid	-0.04303	0.21085	-0.03755	-0.40224
New	38	19	Orchid	-0.74733	0.15394	0.63632	0.276
New	38	20	Orchid	-0.08407	0.25475	-0.06047	-0.48071

New	38	1	None	-0.66535	-0.06674	-0.23452	-0.39419
New	38	2	None	-0.51268	0.18249	-0.27066	-0.18652
New	38	3	None	-0.59641	-0.17579	0.35981	0.11842
New	38	4	None	-0.64782	0.53176	0.95177	0.66748
New	38	5	None	-1.02713	0.04577	-0.0214	-0.24296
New	38	6	None	-0.39076	0.22827	0.24212	0.18521
New	38	7	None	-0.24107	0.53103	-0.5274	-0.39083
New	38	8	None	-0.35263	0.37531	-0.82698	-0.58483
New	38	9	None	-0.29222	-0.12528	-0.2535	-0.28919
New	38	10	None	-0.15288	0.47131	-0.5588	-0.4971
New	38	11	None	-0.57844	0.80514	-0.65933	-0.69577
New	38	12	None	-0.53741	0.77361	-0.70501	-0.74991
New	38	13	None	-0.53229	0.09598	-0.37771	-0.48428
New	38	14	None	-0.24979	0.54443	-0.34719	-0.38354
New	38	15	None	-0.56833	0.64823	-0.45131	-0.53191
New	38	16	None	-0.29893	0.97318	-0.99347	-0.69371
New	38	17	None	-1.06312	0.38583	-0.94021	-0.71749
New	38	18	None	-0.89553	0.25373	-0.19889	-0.51618
New	38	19	None	-0.87304	0.73291	-1.31682	-0.73245
New	38	20	None	-0.77161	-0.08183	-0.44857	-0.74875
New	39	1	Orchid	-0.34791	1.19262	1.92429	0.28419
New	39	2	Orchid	-0.04122	0.36982	1.00714	0.92837
New	39	3	Orchid	-0.2354	0.53323	1.06938	1.04294
New	39	1	None	-1.00445	0.71707	1.54384	-0.18314
New	39	2	None	-0.55271	0.71543	1.27787	0.89163
New	39	3	None	-1.0153	1.18154	1.12376	-0.17014

Appendix VIii

Site scores from DCA analysis from data from 2011 field work soil analysis

Age	Site	Quadrat	Orchid present	DCA1	DCA2	DCA3	DCA4
Old	4	2	Orchid	-0.224876	0.896841	0.130683	0.436999
Old	4	3	Orchid	-0.211489	0.564532	0.100513	0.168782
Old	4	4	Orchid	-0.175899	0.494293	-0.008437	0.070934
Old	4	5	Orchid	-0.136858	0.433749	0.06518	-0.227739
Old	4	6	Orchid	-0.263288	0.952968	-0.008827	-0.004208
Old	4	7	Orchid	-0.154067	0.770917	0.016452	-0.026333
Old	4	8	Orchid	-0.399436	1.03518	0.110489	-0.337765
Old	4	9	Orchid	-0.586404	1.398584	0.000822	-0.212291
Old	4	2	None	-0.114333	0.550011	0.020969	0.400863
Old	4	3	None	-0.094435	0.804974	-0.259889	0.223301
Old	4	4	None	-0.204643	0.146951	0.175252	-0.045949
Old	4	5	None	-0.520769	0.730707	0.313432	-0.378691
Old	4	6	None	-0.264834	0.862726	0.11188	0.241487
Old	4	7	None	-0.341674	0.597634	-0.12983	-0.58339
Old	4	8	None	-0.082948	0.789094	0.498948	-0.385777
Old	4	9	None	-0.084291	0.132858	0.290083	-0.07766
Old	20	1	Orchid	1.01911	0.30157	-0.716139	0.24837
Old	20	2	Orchid	1.275448	0.007778	-0.440409	-0.071376
Old	20	3	Orchid	1.136521	0.18421	-0.640413	0.224122
Old	20	4	Orchid	1.246432	0.138233	0.028377	-0.077335
Old	20	5	Orchid	1.25162	0.213797	1.193444	0.113847
Old	20	6	Orchid	1.162888	-0.182695	-0.128465	-0.098926
Old	20	1	None	1.334985	0.317717	-0.159102	0.358817
Old	20	2	None	1.164141	0.169014	-0.969623	0.24127

Old	20	3	None	0.834068	0.079142	0.070332	0.081182
Old	20	4	None	1.034196	0.007553	0.219954	-0.260038
Old	20	5	None	0.995874	0.197398	0.938446	0.122113
Old	20	6	None	1.55637	0.026577	-0.172556	-0.236686
New	38	0	Orchid	-0.662999	0.070624	0.468202	1.018174
New	38	0	Orchid	-1.000854	-0.059963	0.258932	0.065829
New	38	0	Orchid	-0.519593	-0.379722	0.166324	0.59441
New	38	0	Orchid	-0.583171	-0.537698	-0.28332	-0.306098
New	38	0	Orchid	-0.616204	-0.46421	-0.229508	-0.428576
New	38	1	Orchid	-0.418964	-0.394709	-0.070524	-0.023261
New	38	1	Orchid	-0.490804	-0.347665	-0.271515	0.129479
New	38	1	Orchid	-0.320891	-0.41405	-0.10059	0.238458
New	38	1	Orchid	-0.27743	-0.415718	-0.212086	-0.152724
New	38	1	Orchid	-0.420175	-0.667393	-0.346076	0.550365
New	38	1	Orchid	-0.604335	-0.548178	0.12603	0.362558
New	38	2	Orchid	-0.287203	-0.752102	-0.250729	0.468319
New	38	0	None	-0.612114	-0.37303	-0.468821	-0.136
New	38	0	None	-0.315046	-0.153052	0.313402	0.153065
New	38	0	None	-0.425345	-0.299744	0.052708	0.390948
New	38	0	None	-0.49995	-0.764753	-0.193389	-0.191191
New	38	0	None	-0.356084	-0.330458	-0.314126	0.430361
New	38	1	None	-0.39786	-0.310774	-0.086398	-0.22824
New	38	1	None	-0.572473	-0.526956	-0.038582	-0.148169
New	38	1	None	-0.345284	-0.431906	-0.211227	-0.083057
New	38	1	None	-0.239272	-0.304627	0.128101	-0.488365
New	38	1	None	-0.704265	-0.690018	-0.108238	-0.232219
New	38	1	None	-0.600268	-0.347865	0.344054	-0.925429
New	38	2	None	-0.878594	-0.572654	-0.024333	0.105824
New	39	0	Orchid	0.032256	-0.390974	0.852999	-0.07331
New	39	0	Orchid	0.02419	0.0679	-0.24199	-0.135189

New	39	0	Orchid	-0.078053	-0.12143	-0.221634	0.206778
New	39	0	None	-0.282169	-0.898707	0.495047	-0.343636
New	39	0	None	-0.183425	-0.271682	0.137056	0.029104
New	39	0	None	-0.430183	-0.039148	0.54963	-0.448479

Appendix Viii

Site scores from DCA analysis from data from 2012 field work

Age	North/South	Site	Quadrat	DCA1	DCA2	DCA3	DCA4
New	North	72	1	1.514	0.00211	-0.33307	-0.53808
New	North	72	2	1.72373	0.43431	-0.25751	-0.72463
New	North	76	1	0.24892	-0.51602	-0.05991	0.62738
New	North	76	2	0.03954	-0.73835	-0.28533	0.03143
New	North	76	3	0.12909	-0.71049	-0.05259	0.60739
New	North	76	4	0.03692	-0.70522	-0.34432	0.23713
New	North	76	5	0.07844	-0.54129	-0.22679	0.62733
New	North	79	1	0.16871	-0.68481	-0.46491	0.17721
New	North	79	2	0.45033	-0.95755	-0.11703	0.4591
New	North	79	3	0.41817	-0.64364	0.56321	0.44654
New	North	81	1	0.2918	-1.46118	-0.92144	-0.46174
New	North	81	2	-0.84065	-0.95628	0.94487	0.41536
New	North	81	3	-0.90328	-0.97427	1.61628	0.24354
New	North	81	4	-0.57126	-0.50804	1.21162	0.12533
New	North	81	5	-0.6818	-1.11876	1.31484	0.2188
New	North	82	1	-0.05424	-0.32284	0.45088	0.69604
New	North	82	2	-0.70387	-0.87191	-0.99919	0.65446
New	North	82	3	-0.30464	-0.65076	0.31475	0.60987

New	North	82	4	-0.66616	-0.98701	-0.90024	-0.31256
New	North	82	5	-0.74536	-0.88032	-0.46854	-0.43514
New	South	25	1	0.39108	0.10334	1.31517	-0.14064
New	South	25	2	0.0849	0.37162	1.84705	-0.30335
New	South	25	3	0.21524	0.33512	1.84408	-0.18639
New	South	25	4	-0.13195	0.52006	1.52237	0.27538
New	South	28	1	1.9545	-0.04199	0.1039	0.5155
New	South	28	2	2.39907	0.34074	0.09736	0.17333
New	South	28	3	1.7107	-0.02115	0.5211	0.86877
New	South	28	4	2.04097	-0.14397	0.61392	0.68889
New	South	28	5	2.39413	0.16099	0.04635	0.21242
New	South	40	1	0.52454	-0.50034	-0.85355	-0.78673
New	South	43	1	-0.56032	-0.42634	-0.46548	1.51286
New	South	43	2	-0.42907	-0.12179	-0.35772	1.15742
New	South	43	3	-0.50597	-0.34634	-0.63905	1.35347
New	South	43	4	-0.39033	0.35771	-0.17704	0.53275
New	South	43	5	-0.71697	0.47172	-0.92004	1.49616
New	South	49	1	0.28602	1.71534	-0.55994	0.19628
New	South	49	2	0.54871	1.45228	0.24267	0.35954
New	South	49	3	0.05083	0.68019	-0.10055	0.12536
New	South	49	4	0.39215	0.93356	-0.11073	0.71211
New	South	49	5	0.45778	1.44553	-0.81712	-0.61654
New	South	54	1	0.22502	0.92352	-1.01561	-0.89991
New	South	54	2	-0.29049	1.16041	0.07665	-0.39606
New	South	54	3	-0.1714	0.96952	-0.19188	-0.18219
New	South	54	4	0.10107	0.46771	-0.70544	-0.8226
New	South	54	5	-0.25814	0.47804	-1.23535	-1.06326
Old	North	64	1	-0.83507	-0.32218	-0.43742	-0.54736
Old	North	64	2	-1.45309	-0.16549	-0.68087	0.40757
Old	North	64	3	-0.30904	-0.77309	-0.5717	-0.57205

Old	North	64	4	-0.90949	0.01081	-0.40111	0.59804
Old	North	64	5	-0.85732	-0.48278	-0.00936	0.81182
Old	North	68	1	-0.65953	-0.08539	0.35679	-0.2999
Old	North	68	2	-1.20999	-0.25822	0.34987	-0.74027
Old	North	68	3	-0.95415	-0.38947	0.13988	-0.55528
Old	North	68	4	-0.30564	-0.60111	-0.2488	-0.81444
Old	North	68	5	-0.84694	-0.42902	0.46045	-1.23644
Old	South	11	1	-0.29537	-0.30292	-0.47227	-1.10407
Old	South	11	2	-0.52349	-0.00641	-0.21088	-1.14723
Old	South	11	3	0.1475	-0.40835	-0.3951	-0.90169
Old	South	11	4	0.3771	-0.39288	-0.25473	-0.64256
Old	South	11	5	0.24722	-0.30299	-0.48164	-0.30989
Old	South	12	1	0.14902	-0.03676	-0.20439	-0.38535
Old	South	12	2	-0.00319	-0.31331	-0.14717	-0.88965
Old	South	17	1	0.04706	1.84607	1.03252	0.49647
Old	South	17	2	-0.33872	0.41193	0.80783	-1.21333
Old	South	2	1	-0.58183	2.22161	0.01789	-0.26029
Old	South	5	1	-0.41534	1.27616	0.07187	0.78863
Old	South	5	2	-0.90705	0.27624	-1.02279	-0.40253
Old	South	5	3	-1.11112	0.3931	0.32253	0.68315
Old	South	5	4	-0.39144	0.72912	-0.28949	-0.46148
Old	South	5	5	-0.37325	0.9658	0.40578	-0.26518

Chapter 3: Appendix VI

Appendix VIi

Ellenburg values for all taxa identified down to species level in 2011 field work

Vairable	Light	Moisture	Reaction	Nitrogen	Salt
Geum urbanum	4	6	7	7	0
Hedera helix	4	5	7	6	0
Fraxinus excelsior	5	6	7	6	0
Geranium robertianum	5	6	6	6	0
Silene dioica	5	6	6	7	0
Stellaria holostea	5	5	6	6	0
Agrostis capillaris	6	5	4	4	0
Brachypodium sylvaticum	6	5	6	5	0
Chamerion angustifolium	6	5	6	5	0
Clematis vitalba	6	4	8	5	0
Crataegus monogyna	6	5	7	6	0
Deschampsia cespitosa	6	6	5	4	0
Galium aparine	6	6	7	8	0
Glechoma hederacea	6	6	7	7	0
Holcus mollis	6	6	3	3	0
Hypericum hirsutum	6	5	7	5	0
Origanum vulgare	6	4	7	4	0
Prunus spinosa	6	5	7	6	1
Ranunculus repens	6	7	6	7	0
Rosa canina agg	6	5	7	6	0
Rubus fruticosus agg	6	6	6	6	0
Urtica dioica	6	6	7	8	0
Achillea millefolium	7	5	6	4	1
Agrimonia eupatoria	7	4	7	4	0
Agrostis stolonifera	7	6	7	6	1
Anagallis arvensis	7	4	6	5	0
Arrhenatherum elatius	7	5	7	7	0
Avenula pratensis (Helictotrichon pratense)	7	4	7	2	0
Avenula pubescens (Helictotrichon pubescens)	7	4	7	3	0
Bromus commutatus	7	4	8	6	0
Bromus erectus	7	4	8	3	0
Calystegia sepium	7	8	7	7	1
Carex flacca	7	5	6	2	0
Centaurea nigra	7	5	6	5	0
Cerastium fontanum	7	5	5	4	0
Cirsium vulgare	7	5	6	6	0
Convolvulus arvensis	7	4	8	6	0
Cynosurus cristatus	7	5	6	4	0
Dactylis glomerata	7	5	7	6	0
Dactylorhiza fuchsii	7	8	7	3	0

Elymus repens (Elytrigia repens)	7	5	7	7	2
Equisetum arvensis	7	6	6	6	0
Galium mollugo	7	4	7	4	0
Galium verum	7	4	6	2	0
Geranium dissectum	7	5	7	6	0
Geranium pusillum	7	4	7	7	0
Helminthotheca echioides (Picris echioides)	7	5	7	6	0
Heracleum sphondylium	7	5	7	7	0
Holcus lanatus	7	6	6	5	0
Hypericum perforatum	7	4	7	5	0
Juncus inflexus	7	7	7	5	1
Linaria vulgaris	7	4	8	6	0
Lotus corniculatus	7	4	6	2	1
Medicago lupulina	7	4	8	4	0
Odontites vernus	7	5	6	5	0
Pastinaca sativa	7	4	7	5	0
Plantago lanceolata	7	5	6	4	0
Plantago major	7	5	6	7	0
Poa annua	7	5	6	7	1
Poa pratensis (sens. Str)	7	5	6	5	0
Poa trivialis	7	6	6	6	0
Potentilla reptans	7	5	7	5	0
Primula veris	7	4	7	3	0
Prunella vulgaris	7	5	6	4	0
Quercus robur	7	5	5	4	0
Sanguisorba minor	7	4	8	3	0
Senecio erucifolius	7	5	7	5	0
Senecio jacobaea	7	4	6	4	0
Silene latifolia	7	4	7	6	0
Sonchus asper	7	5	7	6	0
Stellaria graminea	7	6	5	4	0
Tanacetum vulgare	7	6	7	7	0
Taraxacum officinale agg	7	5	7	6	1
Torilis japonica	7	5	7	7	0
Trifolium dubium	7	4	6	5	0
Trifolium pratense	7	5	7	5	0
Trifolium repens	7	5	6	6	0
Trisetum flavescens	7	4	7	4	0
Veronica serpyllifolia	7	5	6	5	0
Vicia hirsuta	7	5	6	6	0
Vicia sativa	7	4	7	4	0
Vicia tetrasperma	7	5	7	6	0
Viola hirta	7	4	8	2	0
Arenaria serpyllifolia	8	3	7	5	0
Bellis perennis	8	5	6	4	0
Blackstonia perfoliata	8	5	8	2	0

Bromus hordeaceus	8	4	7	4	0
Centaurea scabiosa	8	3	8	3	0
Centaurium erythraea	8	5	6	3	0
Cirsium arvense	8	6	7	6	0
Cytisus scoparius ssp scoparius	8	5	4	4	0
Dipsacus fullonum	8	7	7	7	0
Erigeron acris (Erigeron acer)	8	5	7	6	0
Euphrasia officinalis agg	8	5	5	3	0
Festuca rubra	8	5	6	5	2
Galium parisiense	8	3	7	2	0
Gentianella amarella	8	4	8	2	0
Latherus nisolia	8	6	5	6	0
Leontodon hispidus	8	4	7	3	0
Leucanthemum vulgare	8	4	7	4	0
Lolium perenne	8	5	6	6	0
Melilotus altissimus	8	6	7	7	0
Melilotus officinalis	8	5	7	5	0
Myosotis ramosissima	8	3	6	3	0
Ononis repens	8	4	6	3	0
Pilosella officinarum	8	4	7	2	0
Polygala vulgaris	8	5	6	3	0
Sonchus arvensis	8	6	7	6	1
Tragopogon pratensis	8	4	7	5	0
Trifolium campestre	8	4	6	4	0

Appendix VIii

Ellenburg values for all taxa identified down to species level in 2011 field work subset which included soil sampels

Varable	Light	Moisture	Reaction	Nitrogen	Salt
Achillea millefolium	7	5	6	4	1
Agrimonia eupatoria	7	4	7	4	0
Agrostis Capillaris	6	5	4	4	0
Agrostis stolonifera	7	6	7	6	1
Anagallis arvensis	7	4	6	5	0
Arenaria serpyllifolia	8	3	7	5	0
Arrhenatherum elatius	7	5	7	7	0
Avenula pratensis (Helictotrichon pratense)	7	4	7	2	0
Avenula pubescens	7	4	7	3	0
Bellis perennis	8	5	6	4	0
Blackstonia perfoliata	8	5	8	2	0
Brachypodium sylvaticum	6	5	6	5	0
Bromus commutatus	7	4	8	6	0
Bromus hordeaceus	8	4	7	4	0
Carex flacca	7	5	6	2	0
Centaurea nigra	7	5	6	5	0

Centaurea scabiosa	8	3	8	3	0
Centaurium erythraea	8	5	6	3	0
Cerastium fontanum	7	5	5	4	0
Chamerion angustifolium (Epilobium angustifolium??)	6	5	6	5	0
Cirsium arvense	8	6	7	6	0
Cirsium vulgare	7	5	6	6	0
Clematis vitalba	6	4	8	5	0
Convolvulus arvensis	7	4	8	6	0
Crataegus monogyna	6	5	7	6	0
Cynosurus cristatus	7	5	6	4	0
Dactylis glomerata	7	5	7	6	0
Dactylorhiza fuchsii	7	8	7	3	0
Dipsacus fullonum	8	7	7	7	0
Elymus repens (Elytrigia repens?)	7	5	7	7	2
Equisetum arvense	7	6	6	6	0
Erigeron acer	8	5	7	6	0
Euphrasia officinalis agg	8	5	5	3	0
Festuca rubra	8	5	6	5	2
Fraxinus excelsior	5	6	7	6	0
Galium aparine	6	6	7	8	0
Galium mollugo (Galium album??)	7	4	7	4	0
Galium verum	7	4	6	2	0
Gentianella amarella (Gentiana amarella?)	8	4	8	2	0
Geranium dissectum	7	5	7	6	0
Helminthotheca echioides (Picris echioides)	7	5	7	6	0
Heracleum sphondylium	7	5	7	7	0
Holcus lanatus	7	6	6	5	0
Hypericum hirsutum	6	5	7	5	0
Hypericum perforatum	7	4	7	5	0
Juncus inflexus	7	7	7	5	1
Lathyrus nissolia	8	6	5	6	0
Leontodon hispidus	8	4	7	3	0
Lolium perenne	8	5	6	6	0
Lotus corniculatus	7	4	6	2	1
Medicago lupulina	7	4	8	4	0
Melilotus altissimus	8	6	7	7	0
Myosotis ramosissima	8	3	6	3	0
Odontites vernus	7	5	6	5	0
Ononis repens	8	4	6	3	0
Origanum vulgare	6	4	7	4	0
Pastinaca sativa	7	4	7	5	0
Pilosella officinarum	8	4	7	2	0
Plantago lanceolata	7	5	6	4	0
Plantago major	7	5	6	7	0
Poa pratensis	7	5	6	5	0

Poa trivialis	7	6	6	6	0
Polygala vulgaris	8	5	6	3	0
Potentilla reptans	7	5	7	5	0
Primula veris	7	4	7	3	0
Prunella vulgaris	7	5	6	4	0
Quercus robur	7	5	5	4	0
Ranunculus repens	6	7	6	7	0
Rosa canina agg	6	5	7	6	0
Rubus fruticosus agg	6	6	6	6	0
Sanguisorba minor	7	4	8	3	0
Senecio erucifolius	7	5	7	5	0
Senecio jacobaea	7	4	6	4	0
Sonchus arvensis	8	6	7	6	1
Stellaria graminea	7	6	5	4	0
Taraxacum officinale agg	7	5	7	6	1
Torilis japonica	7	5	7	7	0
Tragopogon pratensis	8	4	7	5	0
Trifolium dubium	7	4	6	5	0
Trifolium pratense	7	5	7	5	0
Trifolium repens	7	5	6	6	0
Trisetum flavescens	7	4	7	4	0
Veronica serpyllifolia	7	5	6	5	0
Vicia hirsuta	7	5	6	6	0
Vicia sativa	7	4	7	4	0
Vicia tetrasperma	7	5	7	6	0
Viola hirta	7	4	8	2	0

Appendix VIiii

Ellenburg values for all taxa identified down to species level in 2012 field work

Varable	Light	Moisture	Reaction	Nitrogen	Salt
Acer campestre	5	5	7	6	0
Achillea millefolium	7	5	6	4	1
Aegopodium podagraria	6	5	6	7	0
Agrimonia eupatoria	7	4	7	4	0
Agrostis capillaris	6	5	4	4	0
Agrostis stolonifera	7	6	7	6	1
Aira caryophyllea	8	2	5	2	0
Aira praecox	8	2	4	2	0
Alchemilla mollis	6	5	7	6	0
Anthoxanthum odoratum	7	6	4	3	0
Anthyllis vulneraria	8	4	7	2	0
Aphanes arvensis	8	4	6	4	0
Arenaria serpyllifolia	8	3	7	5	0
Arrhenatherum elatius	7	5	7	7	0

Bellis perennis	8	5	6	4	0
Blackstonia perfoliata	8	5	8	2	0
Brachypodium sylvaticum	6	5	6	5	0
Briza media	8	5	7	3	0
Bromus hordeaceus	8	4	7	4	0
Bromus mollis	8	4	7	4	0
Calystegia sepium	7	8	7	7	1
Carex flacca	7	5	6	2	0
Carex hirta	7	7	7	6	0
Carex otrubae	6	8	7	7	2
Carex panicea	8	8	4	2	0
Carlina vulgaris	8	4	7	2	0
Catapodium rigidum	8	3	7	2	0
Centaurium erythraea	8	5	6	3	0
Centaurea nigra	7	5	6	5	0
Centaurea scabiosa	8	3	8	3	0
Cerastium fontanum	7	5	5	4	0
Chamerion angustifolium	6	5	6	5	0
Cirsium arvense	8	6	7	6	0
Cirsium vulgare	7	5	6	6	0
Convolvulus arvensis	7	4	8	6	0
Crataegus monogyna	6	5	7	6	0
Crepis capillaris	7	4	7	4	0
Cynosurus cristatus	7	5	6	4	0
Cytisus scoparius	8	5	4	4	0
Dactylis glomerata	7	5	7	6	0
Dactylorhiza fuchsii	7	8	7	3	0
Dactylorhiza purpurella	8	8	7	2	1
Daucus carota	8	4	7	3	2
Eleocharis palustris	8	10	6	4	1
Elymus repens	7	5	7	7	2
Epilobium angustifolium	8	8	6	3	0
Epilobium hirsutum	7	8	7	7	0
Equisetum arvense	7	6	6	6	0
Euphrasia agg	8	5	5	3	0
Fagus sylvatica	3	5	5	5	0
Festuca pratensis	7	6	6	6	0
Festuca rubra	8	5	6	5	2
Fragaria vesca	6	5	6	4	0
Fraxinus excelsior	5	6	7	6	0
Galium aparine	6	6	7	8	0
Galium mollugo	7	4	7	4	0
Galium verum	7	7	6	2	0
Geranium dissectum	7	5	7	6	0
Geranium molle	7	5	6	5	0
Geranium pyrenaicum	8	4	7	6	0

Geum urbanum	4	6	7	7	0
Glechoma hederacea	6	6	7	7	0
Hedera helix	4	5	7	6	0
Heracleum sphondylium	7	5	7	7	0
Hippocrepis comosa	8	3	8	2	0
Holcus lanatus	7	6	6	5	0
Holcus mollis	6	6	3	3	0
Hypericum hirsutum	6	5	7	5	0
Hypericum perforatum	7	4	7	5	0
Hypochaeris radicata	8	4	5	3	0
Impatiens glandulifera	6	8	7	7	0
Juncus articulatus	8	9	6	3	0
Juncus effusus	7	7	4	4	0
Juncus inflexus	7	7	7	5	1
Koeleria macrantha	8	4	7	2	0
Lamium album	7	5	7	8	0
Lathyrus pratensis	7	6	6	5	0
Leontodon hispidus	8	4	7	3	0
Leontodon saxatilis	8	5	6	3	0
Leucanthemum vulgare	8	4	7	4	0
Leymus arenarius	9	5	7	6	3
Linaria vulgaris	7	4	8	6	0
Linum catharticum	8	5	7	2	0
Lolium perenne	8	5	6	6	0
Lotus corniculatus	7	4	6	2	1
Lotus pedunculatus	7	8	6	4	0
Luzula campestris	7	4	5	2	0
Luzula multiflora	7	6	3	3	0
Medicago arabica	7	5	6	5	0
Medicago lupulina	7	4	8	4	0
Myosotis arvensis	7	5	6	6	0
Myosotis discolor	7	5	5	3	0
Myosotis sylvatica	6	5	7	5	0
Neottia ovata	6	5	7	5	0
Ornithopus perpusillus	7	4	4	3	0
Pastinaca sativa	7	4	7	5	0
Phleum bertolonii	8	4	7	4	0
Picris echioides	7	5	7	6	0
Pilosella officinarum	8	4	7	2	0
Plantago lanceolata	7	5	6	4	0
Plantago major	7	5	6	7	0
Poa annua	7	5	6	7	1
Poa pratensis sens. lat.	7	5	6	5	1
Poa trivialis	7	6	6	6	0
Polygala vulgaris	8	5	6	3	0
Potentilla reptans	8	9	5	3	0

Primula veris	7	4	7	3	0
Prunella vulgaris	7	5	6	4	0
Prunus spinosa	6	5	7	6	1
Quercus robur	7	5	5	4	0
Ranunculus acris	7	6	6	4	0
Ranunculus bulbosus	7	4	7	4	0
Ranunculus repens	8	9	6	2	0
Rhinanthus minor	7	5	6	4	0
Rubus fruticosus agg.	6	6	6	6	0
Rumex acetosa	7	5	5	4	0
Rumex acetosella	7	5	4	3	0
Rumex conglomeratus	8	8	7	7	0
Senecio erucifolius	7	5	7	5	0
Senecio jacobaea	7	4	6	4	0
Taraxacum officinale	7	5	7	6	1
Tragopogon pratensis	8	4	7	5	0
Trifolium arvense	9	3	5	2	1
Trifolium campestre	8	4	6	4	0
Trifolium dubium	7	4	6	5	0
Trifolium micranthum	8	5	5	5	0
Trifolium pratense	7	5	7	5	0
Trifolium repens	7	5	6	6	0
Trisetum flavescens	7	4	7	4	0
Torilis japonica	7	5	7	7	0
Tussilago farfara	7	6	6	6	0
Urtica dioica	6	6	7	8	0
Veronica arvensis	8	4	6	5	0
Veronica chamaedrys	6	5	6	5	0
Veronica serpyllifolia	7	5	6	5	0
Vicia cracca	7	6	7	5	0
Vicia hirsuta	7	5	6	6	0
Vicia sativa	7	4	7	4	0
Vicia sepium	6	5	6	6	0
Vicia tetrasperma	7	5	7	6	0
Vulpia bromoides	8	4	5	3	0

Chapter 3: Appendix VII

List of bedrock types as used (British Geological Society) with chalk/non chalk classification

Chalk	Bedrock classification (RCS_D)
N	ANORTHOSITE
N	BRECCIA AND METABRECCIA
N	BRECCIA, CONGLOMERATE AND SANDSTONE
Y	CHALK
Y	CHALK AND SANDSTONE
N	CLAY AND LIGNITE
N	CLAY, SILT AND SAND
N	CLAY, SILT, SAND AND GRAVEL
N	CONGLOMERATE AND [SUBEQUAL/SUBORDINATE] SANDSTONE, INTERBEDDED
N	CONGLOMERATE, SANDSTONE, SILTSTONE AND MUDSTONE
N	DIAMICTITE
N	DOLERITE AND THOLEIITIC BASALT
Y	DOLOMITISED LIMESTONE AND DOLOMITE
N	DOLOSTONE
N	FELSIC LAVA
N	FELSIC LAVA AND FELSIC TUFF
N	FELSIC TUFF
N	FELSIC-ROCK
N	GNEISS
N	GNEISSOSE PSAMMITE AND GNEISSOSE SEMIPELITE
N	GNEISSOSE SEMIPELITE AND GNEISSOSE PSAMMITE
N	GRAPHITIC PELITE, CALCAREOUS PELITE, CALCSILICATE-ROCK AND PSAMMITE
N	GRAVEL, SAND, SILT AND CLAY
N	HORNBLENDE SCHIST
N	LAVA AND TUFF
N	LAVA, TUFF, VOLCANICLASTIC ROCK AND SEDIMENTARY ROCK
Y	LIMESTONE
Y	LIMESTONE AND CALCAREOUS SANDSTONE
Y	LIMESTONE AND MUDSTONE, INTERBEDDED
Y	LIMESTONE WITH SUBORDINATE SANDSTONE AND ARGILLACEOUS ROCKS
Y	LIMESTONE, ARGILLACEOUS ROCKS AND SUBORDINATE SANDSTONE, INTERBEDDED
Y	LIMESTONE, MUDSTONE AND CALCAREOUS MUDSTONE
Y	LIMESTONE, MUDSTONE, SANDSTONE AND SILTSTONE, WITH SUBORDINATE CHERT, COAL AND CONGLOMERATE
Y	LIMESTONE, SANDSTONE, SILTSTONE AND MUDSTONE
N	MAFIC GNEISS
N	MAFIC IGNEOUS-ROCK
N	MAFIC LAVA
N	MAFIC LAVA AND MAFIC TUFF
N	MAFIC TUFF
N	MAFITE

N	METALIMESTONE
N	METASEDIMENTARY ROCK
N	METAVOLCANICLASTIC IGNEOUS-ROCK AND METAVOLCANICLASTIC SEDIMENTARY-ROCK
N	MICA SCHIST
N	MIGMATITIC ROCK
N	MUDSTONE, CHERT AND SMECTITE-CLAYSTONE
N	MUDSTONE, SANDSTONE AND CONGLOMERATE
Y	MUDSTONE, SANDSTONE AND LIMESTONE
N	MUDSTONE, SILTSTONE AND SANDSTONE
Y	MUDSTONE, SILTSTONE, LIMESTONE AND SANDSTONE
N	MUDSTONE, SILTSTONE, SANDSTONE, COAL, IRONSTONE AND FERRICRETE
N	MYLONITIC-ROCK AND FAULT-BRECCIA
N	PELITE
N	PSAMMITE
N	PSAMMITE AND PELITE
N	PSAMMITE AND SEMIPELITE
N	PSAMMITE, PELITE, SEMIPELITE AND CALCSILICATE-ROCK
N	PSAMMITE, SEMIPELITE AND PELITE
N	PYROCLASTIC-ROCK
N	QUARTZ-ARENITE
N	QUARTZITE
N	SAND, SILT AND CLAY
N	SANDSTONE AND [SUBEQUAL/SUBORDINATE] ARGILLACEOUS ROCKS, INTERBEDDED
Y	SANDSTONE AND [SUBEQUAL/SUBORDINATE] LIMESTONE, INTERBEDDED
N	SANDSTONE AND CONGLOMERATE, INTERBEDDED
N	SANDSTONE AND MUDSTONE
N	SANDSTONE AND SILTSTONE, INTERBEDDED
N	SANDSTONE AND SUBORDINATE BRECCIA
Y	SANDSTONE WITH SUBORDINATE ARGILLACEOUS ROCKS AND LIMESTONE
N	SANDSTONE WITH SUBORDINATE CONGLOMERATE AND SILTSTONE
N	SANDSTONE WITH SUBORDINATE CONGLOMERATE, SILTSTONE AND MUDSTONE
N	SANDSTONE, BRECCIA AND CONGLOMERATE
N	SANDSTONE, CONGLOMERATE AND [SUBORDINATE] ARGILLACEOUS ROCKS
Y	SANDSTONE, LIMESTONE AND ARGILLACEOUS ROCKS
N	SANDSTONE, MUDSTONE, SILTSTONE AND CONGLOMERATE
N	SANDSTONE, SILTSTONE AND MUDSTONE
N	SCHIST
N	SEDIMENTARY ROCK CYCLES, CLACKMANNAN GROUP TYPE
N	SEDIMENTARY ROCK CYCLES, STRATHCLYDE GROUP TYPE
N	SEMIPELITE
N	SEMIPELITE AND PELITE
N	SERPENTINITE, METABASALT, METALIMESTONE AND PSAMMITE
N	SILTSTONE AND SANDSTONE WITH SUBORDINATE MUDSTONE
N	SYENITIC-ROCK
N	ULTRAMAFITITE
N	WACKE

Abbreviations used and terminology

Abbreviation and terminology	Definition
DC	Date Class
DC1	Date Class 1
DC2	Date Class 2
Ellenberg indicator value L	Ellenberg indicator value for Light
Ellenberg indicator value F	Ellenberg indicator value for Moisture
Ellenberg indicator value N	Ellenberg indicator value for Nitrogen
Ellenberg indicator value R	Ellenberg indicator value for Reaction
Ellenberg indicator value S	Ellenberg indicator value for Salt
Family 3	A plant family with ≥ 3 species used in this analysis
Family 5	A plant family with ≥ 5 species used in this analysis
Native	Using data considered native and excluding all records considered introduced(as defined by BSBI)
Including Introduced	Using records which are either native or introduced (as defined by BSBI)
BSBI	Botanical Society of Britain and Ireland

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