# The establishment of non-native plant species in relation to climate and land use in Britain

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# Abstract

Human transport of species around Earth has led to the intentional and accidental introduction of many species into new regions. Introduced species can have significant impacts outside their native ranges, with a range of positive and negative ecological effects on native biota, community productivity and nutrient cycling. Climate and land use are major determinants of non-native species distributions, with climate setting the broad limits to plant distribution and productivity, and with human activity associated with different land uses affecting the dispersal and success of introduced species. There is potential for future changes in land use and climate to have an impact on distributions of non-native species, due to possible changes to transport, establishment and spread. This thesis uses records of plant species in Britain to determine patterns of non-native species richness with climate and land use, predict possible changes with climate change, quantify establishment of non-native species and to examine levels of establishment for groups of non-native species with different traits (Plant Functional Types). Models were used to examine the relationship between species richness of non-natives and natives with climate variables and land cover types, and projected climate data was used to predict possible future changes. An establishment index was calculated to quantify establishment of non-native species; it was found that date of introduction and range size are not necessarily good predictors of level of establishment and that well established species are less likely to be associated with urban areas than poorly established species. Distributions and establishment of Plant Functional Types were examined, showing that some groups have distinct patterns with land cover related to where they are most likely to be introduced. The least established groups show greater associations with land cover than with climate. Climate and land use changes have the potential to allow new species to establish and to allow already established species to spread due to shifts or expansions in their potential climatic ranges. Future studies of non-native species should attempt to distinguish between time since arrival and the level of establishment because the two may not be associated.

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# Declaration

I declare that the work presented in this thesis is my own, and is written by me.

# Chapter 1: General introduction

## 1.1 Rationale

Human transport of species around Earth is homogenising Earth's biota, intentionally or accidentally introducing many species into new areas (Vitousek *et al*., 1997; Hulme, 2009a). Non-native plants are introduced into new regions for a variety of reasons, including intentionally for use as crops or as ornamentals, and accidentally as seed contaminants and with raw materials such as timber, ballast and wool (Clement and Foster, 1994). A proportion of introduced species will appear in the wild, but will not necessarily form self-perpetuating populations; some of these species will become established by reproducing and spreading successfully in the wild, and a smaller proportion will spread more widely (e.g. Kowarik, 1995; Williamson and Fitter, 1996; Aikio *et al*., 2010). A limited number of introduced species may be considered to be invasive, defined as those which have a detrimental impact in their area of introduction either ecologically, socially or economically (GB Non-native species secretariat, 2011a). Impacts of invasive non-native species can include effects on biodiversity, survival of resident biota, activity of animals, community productivity, fire frequency and nutrient cycling in their areas of introduction (e.g. Pysek *et al*., 2012).

Climate and land use are major determinants of non-native species distributions (Carboni *et al*., 2010; Pyšek *et al*., 2010; Albuquerque *et al*., 2011; Polce *et al*., 2011). Climate sets the broad limits to plant distribution and productivity (e.g. Box, 1995; Chapin *et al*., 1996), and can cause a newly introduced species to fail to survive or establish depending on climate similarity between the areas of origin and introduction (Sakai *et al*., 2001). Non-native species are more likely to be introduced into areas with high levels of human activity (Pyšek, 1998; Botham *et al*., 2009) and may be more likely to establish and spread in areas with a high anthropogenic influence (Burke and Grime, 1996; Williamson *et al*., 2003; Williamson *et al*., 2005; Pyšek and Hulme, 2005). Previous studies have shown that the general pattern for non-native species richness is greater species richness associated with urban areas and other habitats with high levels of human activity, with higher temperatures in cooler regions of the world, and with higher rainfall in warm regions (e.g.

Lambdon *et al*., 2008; Carboni *et al*.,2010; Pyšek *et al*., 2010; Albuquerque *et al*., 2011; Polce *et al*., 2011). Studies examining non-native species distributions in relation to climate and land use or level of anthropogenic influence have shown different variables to be of main importance, with some finding climatic variables to be the main determinant of non-native species richness (e.g. Albuquerque *et al*., 2011; Carboni *et al*., 2010) while others have shown anthropogenic influence to be more important (Pyšek *et al*., 2010; Polce *et al*., 2011).

There is potential for future changes in land use and climate to have an impact on distributions of non-native species. Climate change may favour invasions due to possible changes to transport, establishment and spread of non-native species (Theoharides and Dukes, 2007; Burgiel and Muir, 2010). Non-native species may be imported into new areas (Raghu *et al*., 2006; Barney and Ditomaso, 2008; Burgiel and Muir, 2010), have shifts in climatic range restrictions (e.g. Simberloff, 2000; Kriticos *et al*., 2003) and may be able to survive and/or spread where previously unable (Simberloff, 2000). They could also potentially show greater adaptability (Schweitzer and Larson, 1999) or dispersal ability (Rejmanek, 1996; Simberloff, 2000) than native species.

Non-native species are an important part of the British flora, with non-native species currently accounting for 44% of species in the flora (Preston *et al*., 2002; see Figure 1.1). Britain has a long history of botanical recording and is well-recorded (Perring and Walters, 1962; Preston *et al*., 2002). The Botanical Society of the British Isles (www.bsbi.org.uk) holds a large number of records of vascular plant species allowing study of distributions and establishment of species over time. This thesis uses data provided by the Botanical Society of the British Isles to determine patterns of non-native species richness with climate and land use, predict possible changes with climate change, quantify establishment of non-native species and to examine levels of establishment for different groups of non-native species in relation to environmental variables. The rest of this chapter provides a review of relevant background literature and an outline of remaining chapters.

## 1.2 Non-native plant species

Non-native species are species introduced into an area by human activity, either intentionally or accidentally (e.g. Richardson *et al*., 2000b; Rejmánek *et al*., 2005). Introduced plant species are often classified into archaeophytes and neophytes (Preston *et al*., 2002). An archaeophyte is defined as a species which has become naturalised in the wild, meaning spreading vegetatively or reproducing by seed, before 1500AD. A neophyte is a species which was first introduced after 1500AD, or which was only present as a casual prior to this date. There is some uncertainty in defining some species as a native or an archaeophyte, with separation of introduced from native species relying on a variety of historical evidence. Archaeophytes are defined as having been introduced from the Neolithic to 1500AD (Preston *et al*., 2004) and are expected to be absent from the fossil record in the last glacial, late glacial and early glacial periods (Preston *et al*., 2002). There are few botanical records before 1500AD, but most archaeophytes have been recorded before 1700AD. Non-native species make up a large proportion of the British flora (Figure 1.1): 1728 species which have been recorded in the wild are non-native (166 archaeophytes and 1562 neophytes) out of a total of 3948 species in the flora, including 2220 native species. The total species richness has increased over time, with additions greater than losses due to extinctions; however, this is likely to underestimate turnover further back in time as it is not possible to be certain of the number of 'failed' introductions of non-natives i.e. species which have been introduced and appeared in the wild, but have not been recorded prior to their subsequent extinction. The proportion of non-native species has increased over time, with non-native species currently accounting for 44% of species in the flora following a dramatic increase from 1500AD onwards due to large numbers of neophyte introductions.

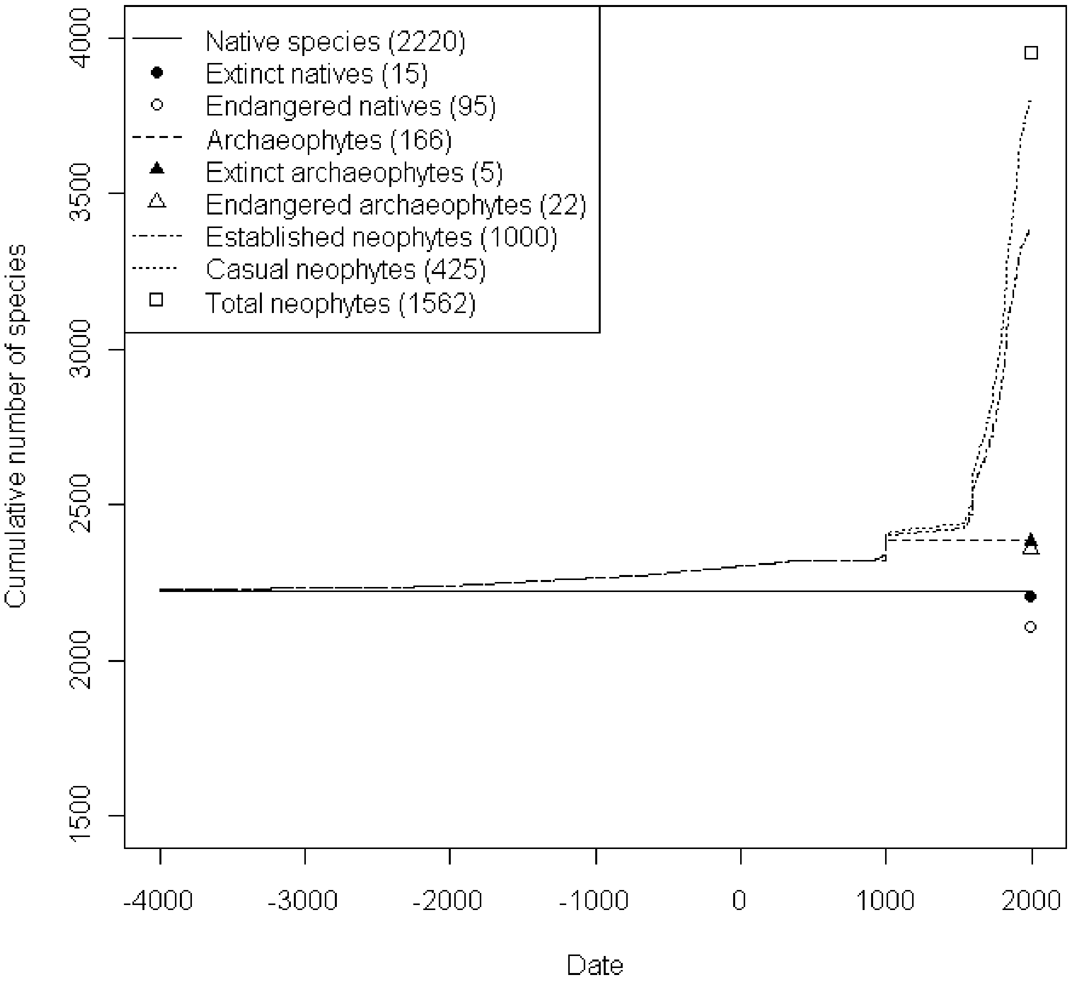

Figure 1.1. Cumulative plant species richness in Britain over time for natives, archaeophytes (non-native species established before 1500AD) and neophytes (non-native species introduced after 1500AD or not established before this date) included in the New Atlas of the British and Irish Flora (Preston *et al.*, 2002). Established neophytes are those which have been recorded as reproducing and spreading in the wild, while casual neophytes have been recorded in the wild but not as reproducing or spreading. Numbers of extinct and endangered species are taken from Cheffings and Farrell (2005). Non-native species make up a large proportion of the flora (44%), leading to an increase in total species richness over time. Refer to Chapter 2 for a description of the data used.

*Impact of non-native species*

Non-native species can have significant impacts outside their native ranges (e.g. Millenium Ecosystem Assessment, 2005; Defra, 2008; Pysek *et al*., 2012). 'Invasive' non-natives have been defined as those which have a detrimental impact in their area of introduction either ecologically, socially or economically (GB Non-native species secretariat, 2011a). Quantifying impacts of non-native species depends on their range, abundance and the per capita or unit of biomass effect of the invader in the region they have been introduced to (Parker *et al*., 1999). The impacts of individual non-native species are very variable (Pyšek and Richardson, 2010), depending on: the identity of the introduced species; the characteristics of the community they have been introduced into in terms of structure, composition and functioning; the environment they are introduced into (e.g. soil, climate); and the interactions between these three factors over space and time. Pysek *et al*. (2012) carried out a global overview of studies of ecological impacts of 167 non-native plant species considered to be invasive, and found that in the majority of cases reviewed the presence of an invasive plant species caused a significant change in a variety of observed outcomes including survival of resident biota, activity of animals, community productivity, fire frequency and nutrient cycling. However, both positive and negative impacts were found for different species.

Negative impacts of non-native plant species can include loss of native biodiversity, with invasive non-native species of flora and fauna considered to be the second biggest threat to global biodiversity after habitat loss and destruction (Millenium Ecosystem Assessment, 2005; Defra, 2008). Invasive plants have been shown to have negative effects on native plant species richness and diversity (e.g. Vilà *et al*., 2006; Hedja *et al*., 2009) and abundance (e.g. Standish *et al*., 2001; Vilà *et al*., 2011) in areas they have been introduced to. They have also been shown to have a negative impact on species richness and abundance of other taxonomic groups e.g. invertebrates (Gerber *et al*., 2008). Non-native plant species can cause disruption of plant reproductive mutualisms, such as pollination and seed-dispersal mutualistic interactions (Traveset and Richardson, 2006). For example, the introduction of *Lythrum salicaria*[1] in the U.S.A. has been shown to have altered the plant-pollinator mutualism between the native species *Lythrum alatum* and native insects

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[1] Nomenclature follows Stace (1997).

(Brown *et al*., 2002). The presence of the non-native species, with comparatively showy flowers, reduced pollinator visitation and seed set in the native species. Impacts on ecosystem functioning which could be considered negative include changes to nutrient cycling such as an increase in nitrogen fixation and availability (Vitousek and Walker, 1989; Ehrenfeld, 2003; Liao *et al*., 2007), potentially leading to feedbacks which can accelerate or stabilise the invasion of the non-native species (Liao *et al*., 2007). Changes in fire frequency can also occur due to increases in biomass accumulation by non-native grass species (D'Antonio and Vitousek, 1992), which can have detrimental effects on native communities by e.g. suppressing growth of woody species. Other negative impacts include economic costs associated with attempted control and eradication of species considered problematic; for example, the total annual cost of *Fallopia japonica* to the British economy has been estimated at over £165 million (Williams *et al*., 2010). This figure includes costs of survey and removal on development sites, road and railway networks, riparian habitats and research into biological control methods. *Fallopia japonica* has been shown to cause reductions in local biodiversity by out-competing native flora (Gerber *et al*., 2008), and can cause structural damage by pushing through tarmac, concrete and drains.

However, some non-native species can also be considered to have positive economic and ecological impacts in areas they are introduced into (e.g. Schlaepfer *et al*., 2010). Many non-native species are deliberately introduced as they are economically valuable for agriculture, horticulture or forestry (Gozlan and Newton, 2009; Pejchar and Mooney, 2009). Ecosystem effects which could be considered beneficial include increased net primary productivity, biomass accumulation and changes in nutrient cycling associated with the presence of invasive non-native species, which have been shown to increase carbon stocks in the vegetation, meaning some invaded communities can sequester more carbon than native communities (Liao *et al*., 2007). Changes to plant-pollinator interactions associated with the presence of non-native plant species can lead to positive impacts on insects, by providing increased food resources (Schweiger *et al*., 2010). Presence of non-native species may lead to the loss of species diversity on a local scale in some situations by out-competing native species, but can lead to an increase in total species richness, including non-native species, on a larger scale (as shown in Figure 1.1). There is also potential for increased species richness due to hybridisation between native and non-native species and the possibility of the appearance of new and endemic taxa (Schlaepfer *et al*., 2010; Thomas, 2013). One example is the new species *Senecio eboracensis*

(Lowe and Abbott, 2003, 2004), a self-pollinating hybrid between a native and non-native species which is reproductively isolated from its parents and was discovered in York, U.K., in 1979.

## 1.3 Pathways of introduction

Non-native plants are introduced into new regions intentionally or accidentally for a variety of reasons. Species have been introduced intentionally for use as crops or as ornamentals, and accidentally as seed contaminants and with raw materials such as timber, ballast and wool (Clement and Foster, 1994). Table 1.1 shows the main introduction pathways for 1376 non-native plant species considered established in Great Britain (Roy *et al.*, 2012). The majority of species have been introduced intentionally as ornamentals (70.6%), with smaller numbers introduced accidentally as contaminants (10.5%) or intentionally for agricultural uses (6.4%). However, reasons for introduction have changed over time, with earlier introductions more likely to be associated with agriculture and later introductions more associated with the horticultural trade. Out of 133 archaeophytes with known primary reasons for introduction, 20% of introductions were as crops, 44% were related to agriculture e.g. as seed contaminants, but only 7% were introduced as ornamentals (GB Non-native species secretariat, 2011b). More recently introduced non-native plant species in Britain have mainly been introduced for ornamental purposes, usually as garden plants and for landscape planting (Dehnen-Schmutz *et al.*, 2007; Roy *et al.*, 2012). Only 4% of neophytes were primarily introduced intentionally for agricultural purposes, with an additional 5% related to agriculture e.g. as agricultural seed contaminants, while 74% were introduced as ornamentals (GB Non-native species secretariat, 2011b).

Table 1.1. Number of non-native plant species arriving in Great Britain by different pathways (from Roy *et al.*, 2012).

| | Agricultural | Animal husbandry | Aquaculture | Contamination | Forestry | Hybridisation | Ornamental | Stowaway | Unknown | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| Terrestrial | 88 | 1 | | 145 | 11 | 29 | 955 | 54 | 67 | 1350 |
| Freshwater | | | 7 | | | | 14 | | 2 | 23 |
| Terrestrial - Marine | | | | | | 1 | 2 | | | 3 |
| Total | 88 | 1 | 7 | 145 | 11 | 30 | 971 | 54 | 69 | 1376 |
| % of total | 6.4 | 0.1 | 0.5 | 10.5 | 0.8 | 2.2 | 70.6 | 3.9 | 5.0 | 100 |

Numbers of established non-native plant species introduced to Britain from different areas are shown in Table 1.2 (Roy *et al.*, 2012). The largest proportion is of European origin (48.5%), followed by Asia (16.5%) and North and South America (16.2%). Region of origin has varied through time, with the majority of earlier introductions coming from Europe: 94% of archaeophytes have been introduced from Europe, while only 47% of neophytes are of European origin with 20% from Asia and 22% from North and South America (GB Non-native species secretariat, 2011b). This is related to patterns of human movement and trade through time (Hulme, 2009a), with movement mainly within Europe prior to 1500AD. From the late 15th century to the beginning of the 16th century was the start of major changes to patterns of global trade, with establishment of a sea route from Europe to India, increasing trade with Asia, and the European rediscovery of the Americas with the first British colonisation in North America early 1600s (Andrews, 1984). Associated with this increased travel was a dramatic increase in the number of species introduced after around 1500AD (as shown in Figure 1.1), with higher numbers from areas outside Europe through time (Roy *et al.*, 2012). From around 1800AD there was a progressive increase in the movement of species between continents, coinciding with the Industrial Revolution and subsequent increased international trade and continuing globalisation (Hulme, 2009a).

Table 1.2. Number of non-native plant species arriving in Great Britain from different areas (from Roy *et al.*, 2012).

| | Africa | Asia - Temperate | Asia - Tropical | Australasia | Europe | North America | Pacific | South America | No data | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| Terrestrial | 44 | 197 | 28 | 49 | 666 | 153 | | 52 | 161 | 1350 |
| Freshwater | 2 | 2 | | 1 | 2 | 13 | | 3 | | 23 |
| Terrestrial-Marine | | | | | | 2 | | | 1 | 3 |
| Total | 46 | 199 | 28 | 50 | 668 | 168 | | 55 | 162 | 1376 |
| % of total | 3.3 | 14.5 | 2.0 | 3.6 | 48.5 | 12.2 | 0 | 4.0 | 11.8 | 100 |

## 1.4 Establishment of non-native plant species

When a new species has been introduced into an area, three main phases can be identified: escape, establishment and spread (e.g. Williamson, 1993; Kowarik, 1995; Williamson and Fitter, 1996; Aikio *et al.*, 2010). A proportion of introduced species will appear in the wild, but will not necessarily become established; a 'casual' can be defined as a species which is present only as individuals which fail to persist as wild populations for periods of more than approximately five years, and such a species is therefore dependent on constant re-introduction (Macpherson *et al.*, 1996; Preston *et al.*, 2002). Some species will become established i.e. a species which has been present in the wild for at least five years and is spreading vegetatively or reproducing effectively by seed (Macpherson *et al.*, 1996; Preston *et al.*, 2002), but will not necessarily spread far from where they have been introduced. A smaller proportion of species will spread more widely, including into semi-natural or natural habitats, and some of these may be considered to be invasive. Studies which have tried to assess the number of species which become established and spread out of the total introduced have suggested that approximately 1 in 10 of those imported are likely to appear in the wild (Williamson, 1993), 1 in 10 are likely to become established and 1 in 10 are likely to become a pest (Williamson and Brown, 1986). Kowarik (1995) tested this 10:10:10 rule for non-native woody species in Brandenburg, Germany and found that less than 10% of species appeared in the wild, 2% become established and 1% may successfully invade the natural vegetation.

### *Factors influencing survival and establishment*

To become established in a new area, a non-native species must colonise a site and develop self-sustaining populations. Factors affecting whether a species can survive in the wild and become established in a new area include climate, soil type, resource availability, disturbance, biotic interactions and propagule pressure (e.g. D'Antonio *et al*., 2001; Theoharides and Dukes, 2007). Climate sets the broad limits to plant distribution and productivity (e.g. Box, 1995; Chapin *et al*., 1996), and can cause a newly introduced species to fail to survive or establish depending on climate similarity between the areas of origin and introduction (Sakai *et al*., 2001). For example, if an introduced species from the tropics is frost sensitive or unable to reproduce due to low temperatures it is unlikely to become established in the wild in a cool temperate region and will be reliant on repeated introductions. The aquatic species *Eichhornia crassipes*, native to South America, has been widely introduced as an ornamental plant and is now found in more than 50 countries (ISSG, 2006). It is a very fast growing plant, with populations known to double in as little as 12 days, and causes significant economic and ecological impacts in many regions it has been introduced into. However, although it has been introduced to Britain and found at several locations in the wild it does not appear to survive the winter and is therefore currently unlikely to become established (GB Non-native species secretariat, 2011b). Non-native species which are already adapted to a new area or are bred for adaptation are more likely to become established:  for example, crop plants are selected to be able to grow well in the area they are introduced to for cultivation and are therefore more likely to appear in the wild as casuals or become established (Williamson and Fitter, 1996).

Non-native species have been shown to be more likely to be successful in areas of high resource availability (light, moisture and soil nutrients) or under fluctuating resource conditions (e.g. Huenneke *et al*., 1990; Burke and Grime, 1996; Davis *et al*., 2000; Leishman and Thompson, 2005). For example, non-native species have show limited success in California grasslands on serpentine soils, while establishing successfully in adjacent areas with other soil types (McNaughton, 1968; D'Antonio *et al*., 2001). This is thought to be due to low levels of available nutrients and soil moisture, as addition of nitrogen and phosphorus fertilisers has been shown to allow invasion by non-native species with non-native species responding more strongly than native species (Huenneke *et al*., 1990), and invasions of these grasslands by non-native species have also been reported to increase following wet years (Hobbs and Mooney, 1991).

The importance of disturbance in facilitating establishment of non-native species has been widely recognised (Elton, 1958; Crawley, 1987; Lodge, 1993; Burke and Grime, 1996; Davis *et al*., 2000). Closed cover of native species has often been suggested as a major barrier to successful establishment (e.g. Crawley, 1987; Rejmánek, 1989). Disturbance can facilitate invasions by reducing competition and thereby increasing available resources: an experimental study on the effect of disturbance on the susceptibility of a native community to invasion (Burke and Grime, 1996) showed that invasion was strongly related to availability of bare ground. It was concluded that this was due to the related release of light and mineral nutrient resources for invading plants. Plant community diversity also has an influence on invasibility: communities with high species richness are thought to be less likely to be invaded as they are highly competitive and resist invasion (e.g. Kennedy *et al*., 2002) and experimental reductions in plant species richness have been shown to increase vulnerability to invasions (Knops *et al*., 1999). However, Hooper *et al*. (2005) argued that although susceptibility to invasion by non-native species generally decreases with increasing species richness, other factors such as disturbance regime and resource availability also have a strong influence and can often override the effects of species richness.

Other biotic factors influencing establishment include facilitation interactions between introduced species which can encourage invasion by other non-natives (Simberloff and Von Holle, 1999); for example, non-native species which change soil nutrients, such as an increase in nitrogen fixation and availability (Vitousek and Walker, 1989; Ehrenfeld, 2003; Liao *et al.*, 2007), can then facilitate invasion of other non-native species previously limited by nitrogen availability (Yelenik *et al*., 2004). Allelopathic agents produced by non-native species may also facilitate establishment by reducing competition (e.g. Callaway and Ridenour, 2004; Stinson *et al*., 2006). Callaway and Ridenour (2004) argued that root exudates, which may be relatively ineffective against plant species in native regions due to adaptation, may be highly inhibitory to newly encountered plants in invaded communities. Stinson *et al*. (2006) suggested that an introduced species in North American forests (*Alliaria petiolata*) successfully invades relatively undisturbed forest habitat by disrupting mutualistic associations between native species and mycorrhizal fungi, suppressing native plant growth.

The presence or absence of species which are pests or mutualists in a new region will have an effect on survival and establishment. It has been suggested that escape from herbivory or disease present in native ranges may increase growth rates or likelihood of establishment in new areas (Elton, 1958) and that, in the absence of predators, selection shifts resource allocation to growth rather than defence (Blossey and Notzold, 1995). There is evidence that some non-native species can grow larger and reproduce more successfully in new areas (e.g. Daehler, 2003; Leger and Rice, 2003); however, other factors such as reduction in competition (Leger and Rice, 2003) and increased resource availability (Blumenthal, 2006) in the introduced ranges compared to the native ranges are also likely to be having an influence. Species with mutualistic relationships with soil biota, pollinators or dispersers may be unlikely to establish if a necessary species is not present in a new region and no substitute is present; however, species which are e.g. pollinated by generalists, can reproduce vegetatively or are self-compatible may have advantages (Richardson *et al*., 2000a; Theoharides and Dukes, 2007).

Propagule pressure, the combined measure of the number of individuals reaching a new area in any one release event and the number of discrete release events, strongly influences whether a species will become established in a new area (Williamson, 1996; Lockwood *et al*., 2005; Theoharides and Dukes, 2007). In an environment with suitable abiotic conditions and reduced competition with native species due to e.g. disturbance, it is possible that low propagule pressure may lead to the establishment of a non-native species; however, high propagule pressure may be required with harsher climatic conditions or high levels of competition in the native vegetation (D'Antonio *et al*., 2001; Lockwood *et al*., 2005; Theoharides and Dukes, 2007). Non-native species which are widely introduced may have a higher chance of finding suitable locations (Lockwood *et al*., 2005) and repeated introductions may increase genetic variation, increasing the probability that the population will persist (Ellstrand and Elam, 1993; Newman and Pilson, 1997; Sakai *et al*., 2001) and potentially allowing increased adaptation to novel environmental conditions (Sakai *et al*., 2001; Lockwood *et al*., 2005).

### *Lag phases and rates of spread*

After a new species has been introduced into an area and has become established, initial establishment may remain at a low frequency or in a restricted area for some time before any change in occurrence or range size (Elton, 1958; Kowarik, 1995; Pyšek and Hulme, 2005; Aikio *et al*., 2010). A variety of reasons have been suggested for the presence of a 'lag phase' between initial establishment and exponential growth (Sakai *et al*., 2001; Pyšek and Hulme, 2005), including time taken for evolutionary change allowing adaptation to a new environment or evolution of life history characteristics allowing rapid spread (Hobbs and Humphries, 1995; Sakai *et al*., 2001). However, the possibility that it may be an artefact has also been suggested, due to difficulties distinguishing between a single exponential phase of increase and one that has both a lag and exponential phase (Williamson *et al*., 2005, Pyšek and Hulme, 2005) or that the pattern is due to changes in recorder effort over time or is dependent on scale of observation (Pyšek and Hulme, 2005).

Previous studies have shown wide variations in lag times between first establishment in the wild and spread for non-native species in different areas (Kowarik, 1995; Caley *et al*., 2008; Daehler, 2009; Aikio *et al*., 2010). Kowarik (1995), for example, found a wide range of lag times in the spread of woody plant species in Brandenburg, Germany, with 6% beginning to spread within 50 years of their first cultivation, three-quarters doing so within 200 years, and the remainder taking more than 200 years to spread. Kowarik also concluded that the most successful invaders were not necessarily the fastest to initiate their invasions. Aikio *et al*. (2010) looked at the time interval between first naturalisation to invasive spread for 105 introduced species in New Zealand and found that a lag phase of several decades was common for New Zealand weeds. Lags averaged 20-30 years, but were greater than 40 years for about 5% of species. About 9% of species had no detectable lag phase. This average lag phase is shorter than for similar studies for Germany (Kowarik, 1995) and Australia (Caley *et al*., 2008), but longer than for Hawai'i (Daehler, 2009).

Studies looking at rates of spread have also shown wide variations (Williamson *et al*., 2003; Williamson *et al*., 2005; Pyšek and Hulme, 2005). Williamson *et al*. (2003) examined rates of spread of non-native plants in Britain, comparing data from two time periods 30 years apart and calculating frequencies of increase, stasis and decrease for 118 species. A wide variation in rates of spread was found: some had spread up to 10km per year, many had not spread detectably, and a smaller number had retreated. A review by Pyšek and Hulme (2005) found average rates of local dispersal of invasive species ranging from 2 to 370 m per year reported in the literature, while average rates of long distance dispersal were found to be at least two orders of magnitude greater than estimates of local dispersal, with a maximum average rate of long distance dispersal of 167 km per year (Batianoff and Franks, 1997).

Reasons for these variations in rates of spread between species and in different areas are not certain. Traits which have been found to influence invasion success could be expected to be important in determining rate of spread, including length of juvenile period, frequency of reproduction, mode of dispersal and seed size (e.g. Hamilton *et al*., 2005; Lloret *et al*., 2005; Theoharides and Dukes, 2007). However, several studies have found few patterns between biological factors and rates of spread, and have concluded that factors relating to human dispersal (such as human population density and economic activity) may be more important (Williamson *et al*., 2003; Williamson *et al*., 2005; Pyšek and Hulme, 2005). Williamson *et al*. (2003) suggested that important factors in rates of spread of non-natives in Britain include methods of human transport, available habitat at different scales and details of biology at the generic level, and it was concluded that consistent characters relating to rate of spread are unlikely to be found for all species. Williamson *et al*. (2005) considered taxonomy, life form, strategy, breeding system and propagule size for non-native species in the Czech Republic and found that none appeared to influence the rate of spread significantly; it was concluded that non-biological factors, such as economic and landscape factors, may have more influence. Pyšek and Hulme (2005) concluded that although species traits may be important in determining species establishment, the available literature does not provide evidence of a close relationship between the rates of spread and traits of invading species.

### *Invasive species*

There has been much research on identifying traits of non-native species which have successfully established or which are considered invasive (e.g. Noble, 1989; Roy, 1990; Rejmánek and Richardson, 1996; Goodwin *et al*., 1999; Kolar and Lodge, 2001). Baker (1974) outlined characteristics which an 'ideal weed' could be expected to possess, including  tolerance to a wide range of environmental conditions, rapid growth, self-compatibility or pollination by wind or unspecialised pollinators, high seed output, vegetative reproduction and adaptations for short and long distance dispersal. Baker proposed that species with many of these characteristics were more likely to be highly weedy than those with none or very few. However, studies attempting to distinguish successful or invasive non-natives from unsuccessful non-native or native species have generally found no definitive set of traits describing successful non-native species (e.g. Pyšek *et al*., 1995; Kolar and Lodge, 2001; Tecco *et al*., 2010). It has been suggested that traits historically associated with invasive species (e.g. weeds) may be related to initial colonisation (Sakai *et al*., 2001), with traits required for successful establishment dependent on habitat (e.g. Grime, 1974, 2001; Thompson *et al*., 1995, Pyšek *et al*., 1995). Frequently disturbed communities would be expected to favour non-native species which produce seeds and have high dispersal ability, while closed communities would favour those with high competitive ability and which are capable of vegetative reproduction (Thompson *et al*., 1995).  Pyšek *et al*. (1995) found that successful invaders of man-made habitats are more likely to be annuals, using a competitor-ruderal strategy (with high reproduction with rapid seedling establishment and growth), while successful invaders of semi-natural habitats are more likely to be perennials with high vegetative growth rate.

The absence of a universal set of traits associated with species which are likely to be most successful in a new area creates difficulties with attempts to identify the small proportion of introduced species which may cause problems. Risk assessments can be used to identify potentially problematic species before they are introduced, or to select species which have already been introduced which need to be prioritised for management (GB Non-native species secretariat, 2011c). Factors which need to be considered on a case-by-case basis are the potential for escape, establishment, spread, hybridisation with natives, ecological consequences, and potential for control and risk management (e.g. Manchester and Bullock, 2000; Baker *et al*., 2008). Current frameworks for risk assessment in the U.K. include the GB Non-native Species Risk Analysis Mechanism (GB Non-native species secretariat, 2011c) and Pest Risk Analysis (EPPO, 2013) at the European scale. Current legislation relating to the prevention of spread of species known to cause problems includes some species already relatively widely established. The Wildlife and Countryside Act 1981 (available from legislation.gov.uk) is the principal legislation dealing with non-native species in Britain: it is illegal to plant or otherwise cause to grow in the wild, sell, offer for sale, or possess or transport for the purposes of sale any plant listed in Schedule 9 to the Act, which lists 54 plant species or groups for England and Wales and/or Scotland. There is also legislation relating to disposal of waste containing viable propagules of invasive non-native plant species as controlled waste under the Environmental Protection Act 1990 (available from legislation.gov.uk).

### 1.5 Climate and land use

Land use changes in Britain have had a major influence on the distributions of non-native plant species (Preston *et al*., 2002; Braithwaite *et al*., 2006). The development and expansion of arable farming has led to the introduction of some non-native species, either as crops or contaminants, which have subsequently become widely established (Preston *et al*., 2004). However, there have also been declines of some previously common species associated with changes in agricultural practices (Preston *et al*., 2002; Braithwaite *et al*., 2006). A number of previously frequent arable weed archaeophytes underwent declines between c. 1880 and 1970, due to changes in agricultural practices including intensification of arable farming, involving increased use of agrochemicals and increased density of modern crops, improved seed cleaning and shifts from spring to winter sown crops (Preston *et al*., 2002). Some of these species are now considered UK Biodiversity Action Plan priority species, identified as being the most threatened and requiring conservation action under the UK Biodiversity Action Plan (JNCC, 2007). Arable weed archaeophytes which are listed as UK BAP priority species are *Adonis annua, Arnoseris minima, Bupleurum rotundifolium, Centaurea cyanus, Filago pyramidata, Galeopsis angustifolia, Galium tricornutum, Ranunculus arvensis, Scandix pecten-veneris, Silene gallica, Torilis arvensis* and *Valerianella rimosa*.

Increasing human population densities and associated urbanisation have also had an impact on the introduction, establishment and spread on non-native species (Burke and Grime, 1996; Pyšek, 1998; Williamson *et al*., 2003; Pyšek and Hulme, 2005; Williamson *et al*., 2005; Botham *et al*., 2009). There was a rapid increase in population in Britain starting around the time of the Industrial Revolution in the late 18th century, with the population of England having more than doubled from 8.3 million in 1801 to 16.8 million in 1851. By 1901, it had nearly doubled again to 30.5 million and by 2001 the population was nearly six times higher than 200 years earlier (Jeffries, 2005). This was associated with increasing urbanisation and extension of transport networks, including building of railways, roads and canals. Non-native species are more likely to be introduced in areas with higher population densities, as accidental introductions are more likely in areas of high human activity and urban areas are associated with gardens and parks where many non-native species are grown and may escape (Pyšek, 1998; Botham *et al*., 2009). Non-native species may be more likely to establish in habitats with a high anthropogenic influence, as disturbance associated with human activities can facilitate invasions (e.g. Burke and Grime, 1996) and human activity disperses many non-native species allowing range expansion (Williamson *et al*., 2003; Williamson *et al*., 2005; Pyšek and Hulme, 2005).

Studies examining patterns of non-native species richness or individual species have generally found both land use and climate variables to be important factors in determining distributions (Carboni *et al*., 2010; Pyšek *et al*., 2010; Albuquerque *et al*., 2011; Polce *et al*., 2011). Climate sets the broad limits to plant distribution and productivity (e.g. Box, 1995; Chapin *et al*., 1996) and climatic conditions of a new area will influence survival and reproduction of an introduced species depending on similarity to conditions in its native range (Sakai *et al*., 2001). Previous studies have shown that the general pattern for non-native species richness is greater species richness associated with urban areas and other habitats with a large anthropogenic influence, with higher temperatures in cooler regions of the world, and with higher rainfall in warm regions (e.g. Lambdon *et al*., 2008; Carboni *et al*., 2010; Pyšek *et al*., 2010; Albuquerque *et al*., 2011; Polce *et al*., 2011). Some studies have suggested climate is most important in determining species richness of non-native species. For example, when examining the impact of climate and human factors such as population density on non-native species richness, Albuquerque *et al*. (2011) found a positive relationship with temperature and Carboni *et al*. (2010) showed a positive relationship with rainfall, with both studies suggesting climate variables were more important than anthropogenic influence on species richness. Other studies have suggested that anthropogenic influence is more important; Pyšek *et al*. (2010) and Polce *et al*. (2011) found that climate was less important in determining distributions of non-native species than factors such as human population density, wealth and human disturbance.

### *Climate change*

There has been an increase in global mean surface temperature of 0.74°C over the last century (IPCC, 2007) and eleven of the twelve years between 1995-2006 ranked among the twelve warmest years in the instrumental record of global surface temperature (since 1850). There is evidence that native species are already shifting their ranges in response to on-going changes in regional climates (e.g. Parmesan and Yohe, 2003; Kelly and Goulden, 2008), that species are altering their phenology (e.g. Fitter and Fitter, 2002; Parmesan and Yohe, 2003; Franks *et al*., 2007) and that some species are facing extinction or have become extinct (e.g. Thomas *et al*., 2004). Evidence that non-native species are responding to climate change is more limited. In northern Italy and southern Switzerland, a new type of warm temperate forest has established (Klötzli, 1988 and Klötzli *et al*., 1996; see Walther *et al*., 2003). Changes in climate have pushed an area from conditions suitable for deciduous broad-leaved vegetation towards conditions suitable for evergreen broad-leaved vegetation. As there are few evergreen broad-leaved species indigenous to the area, the newly opened ecological niche has been occupied preferentially by introduced species. There has also been establishment of non-native thermophilous species in the native flora in Spain, with the appearance of tropical and sub-tropical species from South Africa and South America (Sobrino *et al*., 2001; see Walther *et al*., 2003), and new species of bryophytes and vascular plants establishing in sub-Antarctic regions (Kennedy, 1995; Convey and Smith, 2006).

Climate change may favour invasions due to potential changes to transport, establishment and spread of non-native species (Theoharides and Dukes, 2007; Burgiel and Muir, 2010). Non-native species may be imported into new areas; for example, new crops and horticultural species which could be able to survive in new areas with climate change. It has been suggested that increasing interest in renewable energy sources and the possibility of growth in biomass derived energy will lead to new species being cultivated as biofuels (Raghu *et al*., 2006; Burgiel and Muir, 2010). Species used as biofuel crops are likely to be selected, bred, or engineered from non-native taxa to have few resident pests, to be able to tolerate poor growing conditions, and to have rapid growth to produce competitive monospecific stands (Raghu *et al*., 2006; Barney and Ditomaso, 2008); these are characteristics of some invasive non-natives and could potentially cause problems where they are introduced.  Some non-native species that have hitherto been unable to establish in climatically unsuitable areas may in future be able to survive and/or spread (Simberloff, 2000). Climatic range restrictions will shift with climate change causing increases or decreases in potential ranges of non-native species with changes in rainfall or temperature, and shifts in latitude or elevation in response to temperature increases (e.g. Simberloff, 2000; Kriticos *et al*., 2003). Some traits of non-natives could mean they may be more adaptable to change than natives: for example, invasive non-natives which have greater phenotypic plasticity than natives may be more adaptable to changing conditions (Schweitzer and Larson, 1999). There is also the possibility of increased dispersal of non-natives compared to natives, with some invasives possessing 'weedy' traits which have been associated with effective dispersal e.g. small seed mass, short juvenile period, and short interval between large seed crops (Rejmanek, 1996; Simberloff, 2000). It has been suggested that dispersal limitations will not impede the movement of many established non-natives, and some species may be able to migrate more rapidly than non-invasive non-natives or natives (Simberloff, 2000). However, there is uncertainty over how climate change may affect distribution changes due to variation in climate model projections and many possible direct and indirect effects of climate change on the dispersal process (e.g. Bullock *et al*., 2012; Travis *et al.*, 2013).

Climate projections for the UK for 2100, averaged over 21 climate models, predict temperature increases of up to around 3°C in the south and 2.5°C further north from a 1960-1990 baseline (Met Office, 2011). Precipitation is also generally predicted to increase, with projected increases of up to 10%, though some southern parts of the UK may experience decreases of up to 5% (Met Office, 2011). These changes in climate will have the potential to make some areas of Britain more (or less) suitable for non-native species already here, possibly changing the proportion of non-native species in the flora depending on impacts on native species. Species present as ornamentals in gardens which have not yet been recorded in the wild may be able to become established or spread with changes in climate. Non-native species which are currently casuals could become established, already established species could spread due to shifts or expansions in their potential climatic ranges and some species which currently do not cause problems could become invasive.

## 1.6 Plant Functional Types

Plant Functional Types (PFTs) can be defined as groups of plants that show similar responses to an environment (Diaz and Cabido, 1997*;* Duckworth *et al*., 2000; Lavorel and Garnier, 2002; Lavorel *et al*., 2007). A variety of classifications have been proposed based on differences in plant morphology, life history or method of regeneration (e.g. Grime *et al*., 1997; Lavorel and Garnier, 2002). Global vegetation is often grouped into broad PFTs (e.g. Box, 1981, 1996; Diaz and Cabido, 1997) which are used in Dynamic Global Vegetation Models (DGVMs) when simulating changes in vegetation composition and associated hydrological and biogeochemical processes in response to changes in climate (e.g. Smith *et al*., 2001; Malcolm *et al*., 2002). Smith *et al*. (2001) used a broad life form based classification consisting of five PFTs in their models of terrestrial ecosystems within European climate space. The PFTs used were boreal/temperate needle-leaved evergreen, temperate shade-tolerant broadleaved summergreen, boreal/temperate shade-intolerant broadleaved summergreen, temperate broadleaved evergreen and a grass type.

PFTs have also been used to study non-native species (e.g. Pyšek *et al*., 1995; Hulme, 2009b; Smith, 2010; Marini *et al*., 2012), as way of grouping species with similar traits which would be expected to show predictable patterns with climate and land use variables. PFT classifications based on life form (e.g. Raunkiaer, 1934) capture variation in several important functional traits, with life forms having been shown to have predictable responses to changes in climate (e.g. Chapin *et al*., 1996; Diaz and Cabido, 1997) and disturbance (e.g. McIntyre *et al*., 1995). Hulme (2009b) compared the distributions of different life forms of native species in Britain with distributions of a limited number of alien species, to examine patterns in relation to climate and land use categories. PFTs have also been used to study which groups of non-native species are most successful in man-made habitats compared to semi-natural vegetation (Pyšek *et al*., 1995) and to study the impacts of invasive alien plants on native biota by looking at differences in structural composition between invaded and uninvaded plots (Smith, 2010).

## 1.7 Theoretical framework

Community ecology theory can be used to understand biological invasions by applying niche concepts to non-native species and the communities that they invade (Shea and Chesson, 2002). Ecological niches are defined by the relationships between organisms and physical factors (e.g. climate, soil type, disturbance regime) and biological factors (e.g. resource availability, biotic interactions). These ideas lead to the concept of 'niche opportunity', which defines conditions that can promote invasions in terms of resources, natural enemies, the physical environment, interactions between these factors, and the way in which they vary in time and space. Factors which can increase the likelihood of non-native invasion of a native community by providing niche opportunities include high resource availability or greater competitive ability of non-natives compared to native species (e.g. Huenneke *et al*., 1990; Burke and Grime, 1996; Davis *et al*., 2000; Leishman and Thompson, 2005), natural enemy escape opportunities where an introduced species might not be affected by specialist natural enemies in an invaded community (e.g. Elton, 1958; Blossey and Notzold, 1995), and disturbance which can create niche opportunities by disrupting communities (e.g. Elton, 1958; Crawley, 1987; Lodge, 1993; Burke and Grime, 1996; Davis *et al*., 2000). The physical environment can promote or decrease invasions; favourable conditions can increase opportunities for invasion and unfavourable conditions can decrease opportunities, but as both non-natives and natives respond to this, it is the difference in response that influences success (Shea and Chesson, 2002). Species richness in a native community can modify opportunities for invasion, with low niche opportunities (invasion resistance) having been shown to result from high species diversity (e.g. Kennedy *et al*., 2002), although this effect is also modified by covarying external factors (Shea and Chesson, 2002; Hooper *et al*., 2005).

Other studies have made a distinction between level of invasion and invasibility: the number or proportion of non-native species in an area compared to habitat susceptibility to invasion (Perrings *et al*., 2010). Successful invasion of a habitat requires dispersal, establishment, and survival, with number of species determined by the balance between extinction and immigration (Williamson, 1996; Lonsdale, 1999). The number of non-native species existing in a habitat is given by the number of species introduced modified by their survival rate, which differs in individual habitats based on their properties. The survival rate depends on constraints to invasion, due to competition with species already present, the effects of herbivores and pathogens, chance events, and maladaption. To invade, a species must survive all these factors. A habitat is more prone to invasions if the survival rate of non-native species, introduced by means of propagule pressure, is higher than in another habitat.

Therefore, it would be expected that level of invasion by non-native species would be higher in areas with higher propagule pressure, with a resident community with low species richness, higher levels of disturbance, and high resource availability. Lower levels of invasion would be expected in areas with low propagule pressure, with a resident community with high species richness, low levels of disturbance, and low resource availability. Habitats with high human influence would be expected to have a higher propagule pressure, due to increased introduction and transport of non-native species, higher disturbance, and potentially higher resource availability due to fertilisation etc. Higher species richness of non-natives would be expected to be present in areas with favourable climate (warmer, wetter), and habitats with high levels of human activity such as urban and arable, as they are more likely to be introduced and potentially more likely to be able to survive, compete and reproduce.

## 1.8 Thesis overview

This thesis examines the establishment of non-native plant species in relation to climate and land use in Britain. The primary aims of this thesis are:
1) to determine patterns of non-native species richness with climate and land use;
2) to quantify the level of establishment of non-native species; and
3) to examine the distributions and establishment of Plant Functional Types.
Therefore, this thesis will provide information on climate and land use variables which influence distributions and establishment of non-native plant species and which factors are most important for different groups. Determining current patterns will allow prediction of possible future changes, helping to identify groups of species which may increase with climate or land use change. Further detail on Chapters 3-5 is given below.

### *1) Non-native species richness with climate and land use*

Climate and land use are both important factors in determining the distributions of non-native species (e.g. Pyšek *et al*., 2010; Albuquerque *et al*., 2011). Given that some published studies emphasise the importance of level of anthropogenic influence and land use (e.g. Pyšek *et al*., 2010; Polce *et al*., 2011) and others climate (e.g. Albuquerque *et al*., 2011; Carboni *et al*., 2010) on the distributions of non-native species, examination of the importance of climate and land use variables for non-native plant species richness is needed.

Chapter 3, therefore, examines non-native plant species richness in relation to climate and land use. Models were used to examine the relationship between species richness of non-natives, natives, neophytes and archaeophytes with climate variables and land cover types. Variation in recorder effort was examined by comparing modelled and recorded species richness for different groups. Projected climate data was used to look at possible changes in native and non-native species richness and proportion of non-natives in the flora with climate change. This tested the hypotheses that: 1) different groups (natives, non-natives, neophytes and archaeophytes) show distinct patterns with climate and land use variables; and 2) current species richness can be modelled from climate and land use variables.

### *2) Establishment of non-native species*

There is support for the observation that the distribution sizes of well-established species tend to increase following introduction (e.g. Wilson *et al*., 2007; Williamson *et al*., 2009; Gassó *et al*., 2010); however, the link between time and the level of establishment is not guaranteed due to variations in lag times between date of introduction and establishment or spread (e.g. Kowarik, 1995; Caley *et al*., 2008; Daehler, 2009; Aikio *et al*., 2010) and in rates of spread (e.g. Williamson *et al*., 2003; Williamson *et al*., 2005; Pyšek and Hulme, 2005). Therefore, the relationships between time since introduction, range size and establishment are not certain and require investigation.

Chapter 4 develops a measure for the extent to which each species has established in the wild, and examines the relationship between establishment of non-native species with time since introduction. An establishment index was calculated for each species, based on the population performance of each introduced species, ranging from planted non-reproducing individuals through to fully self-sustaining wild populations (using records assigned a status by each recorder). This was used to test the hypotheses that: 1) level of establishment increases with greater time since introduction; and 2) range size increases with level of establishment. Current distributions were modelled to determine the importance of different climate and land cover variables for non-native species with different levels of establishment. It was predicted that the well-established flora would show richness patterns more closely related to climate, while poorly established species might be expected to show patterns of higher species richness in areas with high human activity, such as urban areas. Models were used to test the hypotheses that: 1) species richness of poorly established species is more associated with urban land use than for well-established species; and 2) well-established species richness is more associated with climate than land-use.

### *3) Distribution and establishment of Plant Functional Types*

Analyses using traits show that Plant Functional Type classifications are useful as they can capture variation in several important functional traits, with life forms having been shown to have predictable responses to changes in environmental variables such as water availability and temperature (e.g. Chapin *et al*., 1996; Diaz and Cabido, 1997) and disturbance (e.g. McIntyre *et al*., 1995). Previous studies attempting to distinguish successful or invasive non-natives from unsuccessful non-native or native species using traits have generally found no definitive set of traits describing successful non-native species (e.g. Noble, 1989; Roy, 1990; Pyšek *et al*., 1995; Tecco *et al*., 2010). Therefore, patterns in the distribution and establishment of life forms of non-native species in relation to climate and land use require examination.

Chapter 5 uses the establishment index from Chapter 3 to examine the distribution and establishment of Plant Functional Types (PFTs) based on life form. Non-native plant species were classified into two PFTs: Raunkiaer life forms, using position of over-wintering buds, and a second life form classification similar to those used in vegetation modelling, dividing groups based on leaf-type and evergreen/deciduous. These two classifications were chosen as they have been shown to be useful when using PFTs in climate modelling, and different groups would be expected to show distinct responses to projected climate changes. Species richness of PFTs was modelled in relation to climate and land cover variables, as successfully modelling current species richness from environmental variables would allow prediction of future changes with climate and land use change, showing which groups may be most likely to increase in future. Levels of establishment for each group were compared using the calculated establishment index, to examine which groups are most successful in relation to climate and land use variables. Analyses were used to test the hypotheses that: 1) non-native PFTs are forming distinct patterns with climate and land use variables; and 2) PFTs with more well-established species are forming patterns associated with climate, while PFTs with more poorly established species are more associated with land use due to methods of introduction.

# Chapter 2: Materials and methods

This chapter provides descriptions of the data and analyses used in Chapters 3-5. Reasoning behind the selection of methods of analysis and limitations and possible biases related to the data and methods used are discussed. Further detail on methods relating to a specific data chapter are given in those chapters (e.g. calculation of level of establishment in Chapter 4 and classification of species into Plant Functional Types in Chapter 5).

## 2.1 Data

### *2.1.1 Botanical data*

*Plant records*

Britain has a long history of botanical recording and is well-recorded (Perring and Walters, 1962; Preston *et al*., 2002). The Botanical Society of the British Isles (www.bsbi.org.uk) holds a large number of records of vascular plant species allowing study of distributions and establishment of species over time. Records are from a variety of sources, including recording by members of the BSBI, and more targeted recording for vice-county floras and the New Atlas of the British and Irish Flora (Preston *et al*., 2002). Interest in recording non-native species has increased over time as the importance of documenting new arrivals and their spread has become more apparent. Non-native species were not covered systematically during recording for the first Atlas of the British Flora (Perring and Walters, 1962): all generally accepted native British species and most well-established introductions were mapped, but less common non-native species or those which had been recently introduced at the time were not included. The New Flora of the British Isles (Stace, 1991) was the first flora to try to deal systematically with non-natives, including all vascular plants and with coverage of intoduced taxa as thorough and consistent as possible. The revised second edition published in 1997 provided the list of taxa recorded for and mapped in the New Atlas of the British and Irish Flora (Preston *et al*., 2002). The New Atlas covered vascular plants including all native species (except microspecies in the genera *Hieracium*, *Rubus* and *Taraxacum*), all naturalised introductions or frequently recurrent casuals, all field crops, forestry crops and ornamental trees planted on a large scale, the more distinctive native and introduced subspecies, and all hybrids listed in Stace (1997). The third edition of Stace (2010) has more detail on many more recently introduced species, making it possible to identify more non-native species easily in the field. It includes more non-native species than previous floras, but some traditionally included in others are omitted. For inclusion, a non-native must either be naturalised (i.e. permanent and competing with other vegetation, or self-perpetuating) or, if casual, frequently recurrent so that it can be found in most years. Cultivated species are included if they are field or forestry crops, or tree ornamentals planted on a large scale. Exclusively garden plants are not covered, but most of the commoner taxa are included anyway because of their occurrence as escapes or throw-outs. This new edition aimed to include all the taxa that a recorder might reasonably be able to find 'in the wild' in any one year.

The plant data used were records on a hectad (10 x 10 km grid square) scale, provided by the Botanical Society of the British Isles. There are some limitations relating to the data set of plant records held by the BSBI, including variation in recorder effort in different areas of Britain (Preston *et al*., 2002). Recorder effort in Britain will have been influenced by recording for the two Atlases (Perring and Walters, 1962; Preston *et al*., 2002) and will also have varied by vice-county depending on which areas have had additional recording for local floras. It has been shown that recorder effort can bias the species richness cited in plant distribution atlases (e.g. Petřík *et al*., 2010). Factors which can affect variation in species richness include: duration of mapping projects, with longer projects recording higher species richness (Petřík *et al*., 2010); spatial scale, with larger biases in smaller mapping projects (Petřík *et al*., 2010); and resolution (size of grid cells) of the studies, with more accurate results for smaller grid cells (Graham and Hijmans, 2006). Other factors influencing reported species richness include the use of different taxonomic concepts, including splitting or joining of taxa and subtaxa (Gaston, 1996) and areas of high sampling activity ("botanical hotspots") which can mean that some species are more likely to be recorded than others (e.g. Moerman and Estabrook, 2006).

Methods of correcting for recorder effort when analysing data include calculating recorder effort by analysing species richness in neighbouring grid cells and taking this into account with analysis (e.g. Hill, 2012) or using methods of analysis which are likely to give accurate results for presence-only data and less likely to be affected by pseudo-absences (e.g. Phillips *et al*., 2009). However, there are specific problems relating to recorder effort of non-native species which do not necessarily apply to native species (Preston *et al*., 2002). Vice-counties which have had additional recording for flora will have varied in which non-native species have been included (e.g. excluding species which are considered casual or planted), with some vice-county recorders identifying and recording more non-natives species than others. Some groups are also more likely to be recorded than others; for example, urban non-native species are known to be better recorded than forestry conifers due to recorder bias. There has also been an increase in recording of non-natives over time e.g. records of species like *Acer pseudoplatanus* have increased, but the distribution on a hectad scale has remained relatively stable for a long time.

This study used a subsample of well-recorded 10 x 10 km grid squares for statistical model building, with a systematic recording system, to minimise differences in recorder effort. These are the BSBI Monitoring Scheme (or Local Change) grid squares (Braithwaite *et al*., 2006): 291 squares regularly arranged in a systematic grid of 1 in 9 which have had additional recording in 1987/1988 and 2003/2004, and thereby have a higher number of non-native species recorded than surrounding squares (Figure 2.1). These high intensity repeat-survey squares minimise recording variation associated with unsystematic botanical surveying across the remainder of Britain (Preston *et al*., 2002).

Details of the BSBI Monitoring Scheme and Local Change recording methods are given in Braithwaite *et al*. (2006). In 1987-88 members of the BSBI recorded the vascular plants in a series of tetrads (2 x 2 km squares) throughout Britain and Ireland. The British tetrads were re-surveyed in 2003-2004. The original survey was the ‘BSBI Monitoring Scheme’ and the resurvey in 2003-2004 was the ‘BSBI Local Change’ project, to look at changes between the two time periods. Local Change project instructions to BSBI recorders were to record three tetrads (A, J and W) within one-in-nine hectads. Non-native taxa to be recorded were those recorded for the New Atlas plus planted field-crops, with species that were planted or casuals to be recorded as such. There was a target of ten hours per tetrad (except in uplands), typically divided into three or four visits at different times of the year of two or three hours each. For upland tetrads, one comprehensive visit in summer may have been all that was appropriate. Recorders were aiming to visit a representative selection of habitats and produce a list of species present.

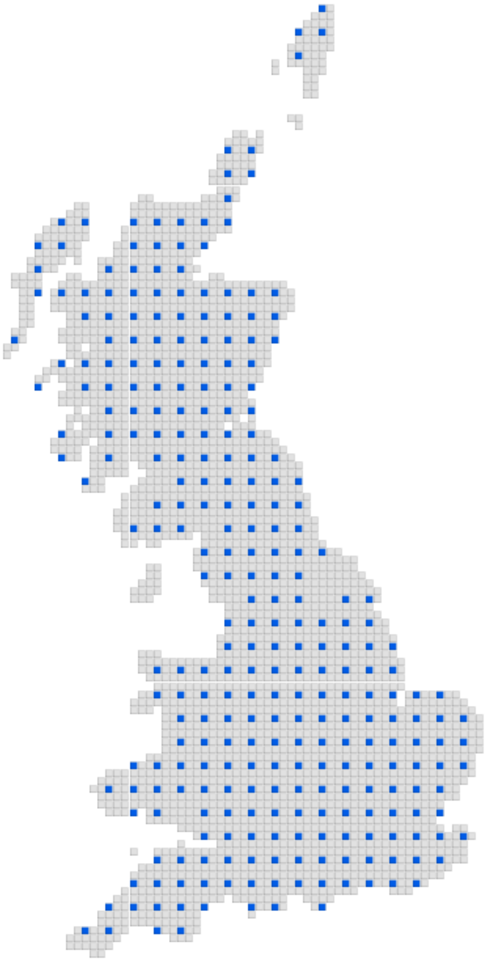


Figure 2.1. Blue squares are BSBI Monitoring Scheme grid squares which have had additional recording in 1987/1988 and 2003/2004. Missing squares are those which were inadequately sampled according to the method in Braithwaite *et al*. (2006) or were not recorded in both time periods.

*Record statuses*

Non-native species have been classified into different groups based on whether or not they are considered to be established or naturalised in the wild, generally defined as successfully reproducing and forming self-perpetuating populations. Stace (1997, 2010) separated introduced (non-native) species into three sub-categories: naturalised, casual or survivor, where naturalised is a non-native plant that has become established and self-perpetuating, casual is a non-native plant not naturalised, persisting only for a short time, and a survivor is a non-native plant which is not naturalised, but can be long-persistent and is usually a relic of planting. The recording for the New Atlas (Preston *et al*., 2002) also sought to classify records of non-natives as to whether they were established/naturalised, surviving, casual or planted, as defined by Macpherson *et al*. (1996) and Macpherson (1997) (Table 2.1).

Table 2.1. Definitions of the status of non-native species used by the Botanical Society of the British Isles plant recorders (Macpherson *et al*., 1996; Macpherson, 1997).

| **Record status** | **Definition** |
|---|---|
| **Established** | Established in the wild (i.e. outside areas of habitation) for at least five years and spreading vegetatively or reproducing effectively by seed |
| **Casual** | Present briefly i.e. for less than five years, often for just one season, or intermittently |
| **Surviving** | Present in the wild for at least five years but neither spreading vegetatively nor reproducing effectively from seed |
| **Planted** | Deliberately planted in a wild situation but not established |

Recorders assigning a status to a record follow the status definitions and make an informed decision based on a number of factors including population size, evidence of regeneration, available habitat, and how a species was likely to have been introduced into the area. In some cases, assigning plants to a particular status in the field may be difficult as not all cases are clear-cut. In guidance for recorders provided in Macpherson (1997), an example is given relating to problems of interpretation with trees and shrubs whose presence is due to their having been planted initially. A taxon which has been planted remains in that category for the whole of its life, even when it has grown into a mature tree or shrub. If it produces progeny, this is initially labelled as ‘casual’, but if persistent for more than 5 years then comes into the ‘surviving’ category. If this progeny then spreads either vegetatively or effectively by seed, then the record for the site is ‘established’. If more than one of these categories applies to the same taxon in the same site, only the status of the highest priority applies (in the order ‘established’, ‘surviving’, ‘casual’, down to ‘planted’). Where a recorder experiences difficulty assigning a taxon to a status, it can be recorded simply as ‘alien’.

Records with information regarding whether or not a species is reproducing in the wild were used to estimate the extent of establishment of each species. An 'establishment index' was calculated for each species for Britain using BSBI records with status, showing the proportion of records considered to be established for each species (see Chapter 4 for more detail).

*Date of introduction and first record in the wild*

Date of introduction and date of first record in the wild were used for species in some of the analyses (see Chapter 1: Figure 1.1 and Chapter 4). These dates are taken from information collated for the GB Non-native Species Information Portal project (GB Non-native species secretariat, 2011b). For most recently introduced neophyte species, reasonably accurate dates are known from information on when species were first imported to be sold or grown and from botanical records in the wild. For archaeophytes and neophytes introduced further back in time, dates have been estimated from a variety of sources including fossil evidence, pollen records, records of plants grown in medieval gardens and herbarium specimens. Some detail relating to problems in estimating historical dates of introduction are discussed below; however, for a more complete discussion of difficulties see Preston *et al*. (2004).

The study of fossil plant remains has provided much evidence relating to the history of the probable archaeophytes in Britain before 1500 AD (Godwin, 1975; West, 2000; Preston *et al*., 2004). Pollen records are often used in studies of past vegetation communities; however, macrofossils (include fruits, seeds, wood, charcoal and leaves) are more useful for identification and dating of individual species, as pollen is rarely identifiable to species level (Birks and Birks, 2000). If a species was present in previous interglacial periods, this cannot be taken as evidence that they are natives in the current interglacial: it means that they were capable of spreading to Britain without the assistance of modern man under the specific conditions of earlier periods, but does not necessarily mean they are natives in the current interglacial. For example, *Azolla filiculoides* and *Rhododendrum ponticum* are considered to be neophytes as they have been introduced by humans after 1500 AD (Preston *et al*., 2002), but are known to have been present as natives during previous interglacials (Preston *et al*., 2004). Medieval documents containing references to garden plants predate the taxonomic treatment of plants which developed from the 16th century onwards, resulting in difficulties equating medieval names to their modern equivalents (Harvey, 1981); however, in most cases the species are also known as fossils from the medieval period. There are some difficulties with determining if a species was established in the wild; with remains of edible fruits or medicinal plants, it is more likely that they have been cultivated or imported. In these cases archaeological records simply establish presence of material of a species in Britain, and the possibility that it might have become naturalised. Species introduced later can be dated form early botanical records, and in some cases based on herbarium specimens. There are few botanical records before 1500AD, but most archaeophytes have been recorded before 1700AD. Where there is uncertainty relating to the exact date of introduction and ranges have been given, the latest estimated date of introduction has been used for all species as this gives the length of time a species has definitely been present in the area.

### *2.1.2 Climate data*

Environmental variables which have previously been shown to be useful when analysing vegetation distributions were chosen (e.g. Box 1981, 1995, 1996; Sykes and Prentice 1995). Climate variables used were annual averages over the time period 1960-1990 for mean summer (June to August) precipitation in mm (SPRE), mean winter (December to February) precipitation in mm (WPRE), growing degree days over 5°C (GDD5), mean temperature warmest month in °C (MTWA) and mean temperature of the coldest month in °C (MTCO). Details relating to the recording and calculation of these long-term climate averages are available from the UK Met Office (www.metoffice.gov.uk/climate/uk/averages). The ratio of actual to potential evapotranspiration (APET) was also used, which is estimated using soil moisture accounting models and gives an index of effective drought (Prentice *et al*., 1992; Huntley *et al*., 1995).

### *2.1.3 Land use data*

Proportions of each 10 x 10 km grid square associated with different land cover classifications were estimated from the Land Cover Map 2000 (Fuller *et al*., 2002): arable, urban, improved grassland, neutral grassland, acid grassland, calcareous grassland, broadleaved woodland, coniferous woodland, heath, inland rock and standing water. Some description of the methods used to produce the Land Cover Map 2000 (LCM2000) data set and associated problems are given here; for a more complete description see Fuller *et al*. (2002). The LCM2000 used summer and winter satellite images and the pixels which make up the image were grouped into areas or segments broadly equivalent to land parcels (e.g. individual fields), with small segments excluded. Ground reference data from field surveys were used to identify image segments of known land cover ('training areas'). Segments were classified into land categories using a maximum likelihood algorithm; for segments classified with low confidence, knowledge based corrections were used to allocate an alternative class label.

The LCM2000 project compared classifications assigned to the satellite images with the Countryside Survey 2000 field data survey (www.countrysidesurvey.org.uk) to check the accuracy of designated categories. The largest differences were found to be in upland areas where field and satellite-based mapping were most problematic. Differences in resolution, the data-model and timing of surveys contributed to the differences between LCM2000 and the field survey. Comparison as a whole suggests that LCM2000 may record classes with around 85% success; however, individual classes differ in their level of agreement between the field survey and LCM2000, with some problems with specific classes. For example, for 'broadleaved woodland' there were problems with mapping small areas, as many woodlands and clearings are at or below the minimum mappable unit of LCM2000. For arable land, apparent confusions with improved grassland related mainly to rotation farming in squares where field and satellite survey years differed. Improved grassland was the most extensive single cover class, and distinction between improved from semi-natural types could be difficult and controversial. Assigning semi-natural grasslands to neutral, calcareous and acid grasslands was difficult as there was no consistent spectral characteristic by which to determine soil acidity, and external data was found to be of limited value. The LCM2000 does not attempt to distinguish inland standing water from flowing water, therefore the category standing water used in this study is an aggregate of standing open water and canals and rivers and streams. For the urban category, the field survey treated urban land as continuous without recording open spaces in the urban zone while LCM2000 recorded open spaces greater than 0.5 ha.

The LCM2000 data shows that more than half of the UK is used for intensive agriculture or is developed, with the remainder largely semi-natural. Woodland occupies a quarter of the semi-natural land, with most of the rest consisting of heath and semi-natural grasslands.

The 291 BSBI Monitoring Scheme grid squares used for analyses in this study include a range of land covers with both rural and highly urban squares sampled, from a proportion of 0 to 0.628 urban land cover, mean 0.072 (compared with a range from 0 to 0.875, mean 0.067, for the 2499 grid squares not belonging to the BSBI Monitoring Scheme).

### *2.1.4 Projected data*

Projected climate data were used to predict possible future changes in natives and non-native species richness (using the 'predict' function in the 'stats' package in R), and change in proportion of non-natives in the flora was calculated. Mean projections for 2071-2100 from three emission scenarios and three climate models were used to look at variation in predictions. Projections from three different emissions scenarios (IPCC, 2000; IPCC, 2007) were used for one climate model (Hadley Centre: HadCM3; IPCC, 2012), a high emission scenario (A1, see Jiang *et al*., 2000), a moderate emission scenario (A2, see Sankovski *et al*., 2000) and a low emission scenario (B1, see de Vries *et al*., 2000). Two additional climate models were also used for the moderate emission scenario, NCAR: CSM and NCAR: PCM (IPCC, 2012).

There are also projected land use change data available (Rounsevell *et al*., 2006) based on interpretation of the global storylines presented in the IPCC report on emissions scenarios (IPCC, 2000). However, obtaining data with corresponding time periods and at a similar scale to the projected climate data used was difficult at the time of this study, therefore only climate data were used to assess possible future changes (see Chapter 3). Possible implications of future land use change are discussed in Chapter 6.

## 2.2 Analyses

### *2.2.1 Species' distribution modelling*

There is evidence that native species are shifting their distributions in response to climate change (e.g. Parmesan and Yohe, 2003; Kelly and Goulden, 2008). Evidence that non-native species are responding to climate change is more limited (Kennedy, 1995; Walther *et al*., 2003; Convey and Smith, 2006), although it has been suggested that climate change may favour invasions due to potential changes to transport, establishment and spread of non-native species (Theoharides and Dukes, 2007; Burgiel and Muir, 2010; see Introduction for more detail). It has become increasingly popular in recent studies to relate presences or absences of species, species richness or species abundances to current climatic conditions, then predict these models onto predicted future climate surfaces to look at possible future changes in distributions (e.g. Berry *et al*., 2002; Bradley *et al*., 2009; Bradley *et al*., 2010): this is known as ‘climate envelope modelling’. This technique has been used with native species, to help determine which species are most at risk and focus conservation efforts (e.g. Berry *et al*., 2002), and also with non-native species in order to predict which areas might be more or less affected by invasions under climate change (e.g. Bradley *et al*., 2009; Bradley *et al*., 2010).

General steps in species distribution modelling include: gathering relevant data (predictor and response data), assessing the completeness and comprehensiveness of the data, selecting an appropriate modelling algorithm, fitting the model to a training data set, and evaluating the model performance including fit to data, characteristics of residuals and predictive performance on test data (Elith and Leathwick, 2009). Many different statistical modelling techniques have been developed and used depending on the type of data and the question being addressed. Early numerical distribution models used envelope models to describe species’ ranges in relation to a set of environmental predictors (e.g. Box, 1981). Regression based models extend envelope approaches by modelling variation in species occurrence or abundance within occupied environmental space, and selecting predictors according to their observed importance. Generalised Linear Models (GLMs) can be used with presence-absence or count data and simple additive combinations of linear terms; however, as nonlinear species’ responses to the environment were recognised (Austin *et al*., 1990), more studies included quadratic, cubic or other parametric transforms. General

Additive Models (GAMs) are similar to GLMs, although use data-defined, scatter plot smoothers to describe nonlinear responses (Guisan *et al*., 2002; Elith and Leathwick, 2009). Many alternative methods are regression-like, assuming that species' occurrence or abundance can be modelled using additive combination of predictors. Bayesian alternatives can incorporate process-based information (such as rates of spread), but require more specialized mathematics and programming than simpler techniques such as GLMs and GAMs (Latimer *et al*., 2006; Hooten *et al*., 2007). Many complex methods have been developed more specifically for prediction e.g. multivariate adaptive regression splines (e.g. Moisen and Frescino, 2002), regression trees (e.g. Elith *et al*., 2008) and maximum entropy models (e.g. Philips *et al*., 2006). Data sets consisting of presence-only data, where occurrences are known but information about known absences is lacking, has led to the development of methods for comparison of presence records with background or pseudoabsence points: examples include regression methods, GARP and MaxEnt (Elith *et al*., 2006; Franklin, 2009; Phillips *et al*., 2009). There are also a wide variety of model selection and evaluation techniques available. Commonly used model selection methods include statistical techniques based on p-values for model selection, AIC (Akaike's Information Criterion) or multimodel inference (Burnham and Anderson, 2002; Elith and Leathwick, 2009). Methods of model evaluation include summaries of performance based on kappa, area under the receiver operating curve (AUC) and correlation coefficients (Elith and Leathwick, 2009).

The use of climate envelope methods for modelling and prediction of species' distributions with climate change has been criticised as ecologically and statistically naïve (e.g. Pearson and Dawson, 2003; Beale *et al*., 2008). Key assumptions include species being at equilibrium with their environments and that relevant gradients have been adequately sampled (Elith and Leathwick, 2009). Use in non-equilibrium conditions, such as with invasions and under climate change, usually involves species records unrepresentative of new conditions and prediction in novel environments. Predictions to new geographic areas or past/future climates (extrapolation or forecasting) are inherently risky as there are no observations of occurrence to directly support predictions. Problems with extrapolation to new areas or environmental conditions include the possibility that different environmental factors may limit distributions, biotic interactions may change, outcomes may be influenced by factors not included such as genetic variability, phenotypic plasticity and evolutionary changes and that dispersal pathways are difficult to predict (Brooker *et al*., 2007; Dormann, 2007; De Marco *et al*., 2008; Elith and Leathwick, 2009). Beale *et al*. (2008) investigated the effectiveness of climate envelope methods for European bird species and found that associations were no better than chance for 68 out of 100 species, concluding that many published climate associations for different species and groups may be unreliable. It was suggested that other factors may be more important than climate (such as land use or historical factors) and should also be considered, and that caution should be used when interpreting results from climate envelope modelling to inform policy. However, climate envelope models have been shown to successfully 'retrodict' population trends (Green *et al*., 2008) and can predict responses of far-dispersing species fairly well (Zurell *et al*., 2009), suggesting some use in predicting future responses. Models for prediction need to balance specific fit to the model building data set against generality that allows reliable prediction to new cases; information criteria such as AIC help to address this balance by trading off explained variation against model complexity (Elith and Leathwick, 2009). Model performance can also be tested by using a subset of data to build models and assessing model performance on held out data, both within the model–fitting process, and for model evaluation.

### *2.2.2 Selection of statistical techniques*

All analysis was carried out using R (version 2.13.1). Mainly non-parametric tests were used due to limitations of the data sets used and difficulties transforming data to conform to a normal distribution. Spearman’s rank correlations (function 'cor.test', method = ’spearman’, in the package 'stats'), Wilcoxon signed rank tests (function 'wilcox.test', paired = ‘true’, in the package 'stats'), Wilcoxon rank sum tests (function 'wilcox.test', paired = ‘false’, in the package 'stats') and Kruskal-Wallis rank sum test (function 'kruskal.test', in the package 'stats') and multiple comparison test after Kruskal-Wallis (function 'kruskalmc', in the package 'pgirmess') were used. Generalised Linear Models, Hierarchical Partitioning and Moran's I were also used; further detail on these methods is given in the sections below.

#### *Generalised Linear Models*

There has been much debate surrounding the ‘best’ modelling technique when relating climate variables to records of species’ occurrence (Tsoar *et al*., 2007; Elith and Graham, 2009). Regression-based methods are widely used by ecologists and can be extended to model complex data types, including abundance data with many zeros and records with imperfect detection of presence (Elith and Leathwick, 2009). Generalised linear models (GLMs) are used extensively in species’ distribution modelling because of their strong statistical foundation and ability to realistically model ecological relationships (Austin 2002; Elith *et al*., 2006). GLMs are relatively well understood by the majority of ecologists and are useful in a variety of situations: dependent variables can include presence/absence, proportion or abundance, and additive combinations of linear terms can be used or they can include quadratic, cubic or other parametric transforms to represent non-linear responses. GLMs have been found to perform less well than other techniques when discriminating between areas of likely presence and absence of a species; however, they are more appropriate for generalisation to other geographical areas than non-parametric techniques such as GAMs as they do not tend to over-fit to the sample dataset (Randin *et al*., 2006).

Generalised Linear Models (GLMs) were used to determine the relationships between species richness, climate variables and land use. GLMs were carried out using the 'glm' function in the 'stats' package in R. Distribution of the count data (species richness) used as the response variable was tested using the function ‘goodfit’ in the package ‘vcd’ to determine family (Poisson, binomial or negative binomial) specified in the GLMs. Climate variables and proportions of land cover were used as the predictor variables. The climate and land use predictor variables were standardised (using function ‘std.data’ in the package ‘smoothSurv’) to give a mean of 0 and a standard deviation of 1, allowing comparison of the slope estimates from the models. Where non-linear responses gave a better fit to the data, second order polynomials were used. Predictor variables were removed using the Akaike information criterion (AIC). Assumptions of GLMs include normality and homoscedasticity of residuals: model residuals were tested for normality (using ‘ad.test’ in the package ‘nortest’ and ‘shapiro.test’ in the package ‘stats’) and dispersion parameters were used to correct for overdispersion of residuals. Spatial autocorrelation in residuals was checked using Moran’s I; see section on spatial autocorrelation below for more detail.

The BSBI Monitoring Squares (Figure 2.1) were used to create the models, which were then used to predict species richness for the rest of the grid squares from their climate and land use data (using the 'predict' function in the 'stats' package). These predictions were compared with numbers of species actually recorded for these grid squares (using Spearman’s rank correlations and Wilcoxon signed rank tests) to test the model accuracy and look for patterns in recorder effort.

### *Hierarchical Partitioning*

Hierarchical Partitioning (HP) analyses were used to calculate the independent contribution of each predictor to the species richness for different groups of non-native species. This method was used in addition to GLMs as it shows the importance of different environmental variables used in the models and confirms the patterns shown by the GLMs. HP was carried out using the 'hier.part' package in R (MacNally and Walsh, 2004). HP involves measuring the increase of goodness-of-fit of all models with a particular variable compared with the equivalent model without that variable. The improvement in fit is then averaged across all possible models in which that variable occurs to produce a measure of its independent effects. A Poisson distribution with the default goodness-of-fit measure (RMSPE, Root-mean-square ‘prediction’ error) was specified.

### *Spatial autocorrelation*

Spatial autocorrelation is an important part of the relationship between environmental and geographic space. The response of species to spatially autocorrelated environmental factors can result in geographic clustering of species; however, this can also be due to the effects of factors operating primarily in geographic space (Legendre, 1993; Elith and Leathwick, 2009). Where the distribution of a species is largely determined by environmental factors, a properly specified model fitted using an adequate set of predictors will display minimal spatial autocorrelation in its residuals. Methods for testing for spatial patterns in both data used to build models and in model residuals include Moran’s I or Geary’s c to measure the amount of spatial autocorrelation. This study used a subset of data in model building (Figure 2.1) which meant model building data was less positively spatially autocorrelated than if all squares used. Residuals of all models were checked for positive spatial autocorrelation: if this was not found to be significant, it was assumed not to be a major issue. Significance of spatial autocorrelation was tested for using Moran’s I using function 'Moran.I' in the 'ape' package in R (Paradis, 2009). A significant positive value indicates a distribution is more clustered than expected and a significant negative value indicates a distribution is more dispersed than expected.

# Chapter 3: Non-native plant species richness in relation to climate and land use

## 3.1 Abstract

Analyses of the spatial distributions of non-native species richness or individual species have generally found both land use and climate variables to be important factors in determining distributions. However, the relative importance of climate and land use variables for non-native species distributions is less clear. The main aims of this study were to determine how general patterns of non-native species richness vary with climate and land use; to test whether current distributions could be modelled using climate and land use variables, so that future distributions can be predicted from projected changes in climate; and to determine the importance of different environmental variables for native, non-native, archaeophyte (non-native species introduced before 1500AD) and neophyte (non-native species introduced after 1500AD) species richness. 10 x 10 km grid square records of 1728 non-native plant taxa recorded in Britain between 1987 and 2009 were used for analyses. Generalised Linear Models (GLMs) were used to model species richness and the importance of different climate and land use variables for different groups were examined using results from GLMs and Hierarchical Partitioning. Projected climate data was used to predict possible changes in native and non-native species richness, and the proportion of non-native species in the flora. Higher non-native species richness is found in warmer, drier, more urban areas of Britain. Current species richness of different groups can be predicted well. Urban land cover shows the clearest pattern when comparing species richness for different groups. Non-natives, natives, neophytes and archaeophytes all show positive relationships with proportion of urban land cover; however, non-native species are more often associated with urban areas than natives and neophytes are more urban than archaeophytes. Comparisons between predicted and recorded species richness suggests variation in recorder effort on a vice-county level, with higher recorder effort in vice-counties with recent recording for floras. Using projected climate data suggests future increases in the proportion of non-native species in the flora in upland areas in the north and west of Britain.

## 3.2 Introduction

Analyses of the spatial distribution of non-native species richness or individual species have generally found both land use and climate variables to be important factors in determining distributions (e.g. Pyšek *et al*., 2010; Albuquerque *et al*., 2011). Previous studies have shown that non-native species richness generally increases with higher temperatures in cool regions of the world, with higher rainfall in warm regions, and with the area of urban land and other anthropogenic habitats, such as arable land (e.g. Polce *et al*., 2011; Lambdon *et al*., 2008). Successful colonisations by non-native species are likely to be greater in mesic environments, with moderate temperate or moisture levels, as these conditions provide greater suitability for establishment and survival of a larger pool of species (Rejmánek, 1989). It has been shown that non-native species are more likely to be found in locally warm sites in cool regions and in cool microclimates in hot regions (Polce *et al*., 2011), and higher non-native species richness is found with high rainfall in warm regions (Carboni *et al*., 2010).

Higher non-native species richness in habitats with a large anthropogenic influence is caused by increased likelihood of introduction in these habitats with human activities aiding dispersal and levels of disturbance creating suitable habitats for colonisation. Non-native species are more likely to be introduced in urban areas due to gardens and amenity planting where many non-native species are grown and may escape (Pysek, 1998; Dehnen-Schmutz *et al*., 2007; Botham *et al*., 2009; Roy *et al*., 2012), and sources of non-native species in farmland include as escapes from crops and as grain contaminants (Preston *et al*., 2002; Clement and Foster, 1994). Disturbance associated with anthropogenic activities provides suitable habitats for non-native species, with urban habitats favouring species that can tolerate irregularly disturbed sites (e.g. *Buddleja davidii*, *Conyza canadensis* and *Oenothera glazioviana)*, while habitats such as arable farmland have species with more annual associates, either crops or arable weeds, as disturbance is more regular (Hill *et al*., 2002). The spread of non-native species is also facilitated by railways and roads, as associated disturbance and habitat fragmentation makes colonisation easier and vehicle traffic can aid dispersal (e.g. Hansen and Clevenger, 2005; von der Lippe *et al*., 2013).

However, the relative importance of climate and land use variables for non-native species distributions is less clear, with previous studies reaching different conclusions on the main variables influencing species richness. Studies indicating that climatic variables are most important in determining non-native species richness include Albuquerque *et al*. (2011), who found that human alteration of ecosystems is far less important for variation in richness than climate, with richness primarily and positively associated with temperature and showing a much weaker positive relationship with the human footprint. Carboni *et al*. (2010) looked at the relative effects of environmental and human factors on the abundance of native and non-native plant species on the Italian coast. Non-native species richness was also found to be strongly related to climatic factors, with more non-natives found in areas with high rainfall. Secondarily, non-native introductions appear to be related to recent urban sprawl and associated gardening. Studies concluding land use to be the most important factor with climate secondary include Pyšek *et al*. (2010), when examining the role of environmental and human pressures on biological invasions across Europe. Human population density and wealth were found to be most important when analysed jointly with environmental factors such as climate, geography and land cover. Polce *et al*. (2011) also tested whether the distribution and cover of non-native plant species in Europe was related to human disturbance and microclimate. The role of temperature was found to be weaker overall than land use in explaining the pattern of non-native species in Europe.

It would therefore be expected that in Britain, higher non-native species richness would occur in warmer, more urban areas. Previous studies examining the relationships between non-native plant species richness and climate and land use in Britain have found higher species richness in warmer, drier areas of Britain when compared to native species richness (Maskell *et al*., 2006; Hulme, 2009b; Albuquerque *et al*., 2011). The majority of studies have also found positive associations between non-native species richness and habitats with a large anthropogenic influence such as urban areas (Maskell *et al*., 2006; Hulme, 2009; Pearman and Walker, 2009; Albuquerque *et al*., 2011). However, negative associations with urban areas have also been found for non-native species when looking at individual species, with analysis showing that a large percentage of non-native plant species were not strongly associated with urban land cover or were negatively associated with such habitats (Botham *et al*., 2009). Studies of non-native species richness in Britain have also reached different conclusions relating to the relative importance of different factors, with Albuquerque *et al*. (2011) concluding that climate is a more important determinant of non-native species richness than human factors and others finding a strong association of non-native species with anthropogenic habitats, suggesting that land-use change is a major factor determining the change in relative distribution of these species (Maskell *et al*., 2006; Hulme, 2009b). These studies have used different numbers of non-native species; Hulme (2009b) used the limited number of non-native species included in PLANATT (Hill *et al*., 2004), while Albuquerque *et al.* (2011) used all non-native species in Britain included in the New Atlas of the British and Irish Flora (Preston *et al*., 2002) excluding those considered casual. Different climate and land use variables were also studied, either considering associations with a large number of land cover variables (Hulme, 2009b) or only including a measure of anthropogenic influence on habitats (Albuquerque *et al*., 2011).

Non-native species are frequently separated into archaeophytes, non-native species which have been introduced before 1500AD, and neophytes, non-native species introduced after 1500AD, for analysis (e.g. Hulme, 2009b; Botham *et al*., 2009). In Britain, archaeophyte species have mainly been introduced intentionally as crops, for medicinal reasons, or unintentionally as seed contaminants or with raw materials (Clement and Foster, 1994; Preston *et al*., 2002). The majority of more recent introductions have been intentionally brought to Britain as ornamentals for planting in gardens and parks (Roy *et al*., 2012). As archaeophytes have been introduced further back in time and have therefore had more time to become established and to colonise a range of semi-natural habitats, it could be expected that they are more likely to have formed distributions related to climate than neophytes. Archaeophytes have also historically been introduced into habitats away from urban areas as many species are arable crop species or weeds. Neophytes have been more recently introduced and have had less time to establish, and it would therefore be expected that patterns of neophyte species richness are more related to where they are most likely to be introduced. Urban areas are associated with gardens and amenity planting where many non-native species are grown and may escape (Pysek, 1998; Dehnen-Schmutz *et al*., 2007; Botham *et al*., 2009; Roy *et al*., 2012). Therefore, a higher neophyte than archaeophyte species richness would be expected in urban areas, with archaeophyte distribution more likely to be related to climate.

Previous studies contrasting neophyte and archaeophyte distributions in Britain have not shown consistent patterns with climate and land use. Hulme (2009b) found that non-native species in general are strongly associated with habitats with more human influence (boundary, built-up and arable habitats) and that numbers of neophytes and archaeophytes found in different broad habitats were significantly correlated. This does not suggest that neophytes are more likely to be found in anthropogenic habitats than archaeophytes. Botham *et al*. (2009) showed that archaeophytes were less associated with urban habitats than neophytes, with analysis at the individual species level showing that a large percentage of archaeophytes were not strongly associated or were negatively associated with urban land cover, indicating neophytes are more likely to be associated with urban areas than archaeophytes. Albuquerque *et al*. (2011) found that archaeophyte species richness had a larger proportion of variation explained by climate than for neophytes, however, archaeophytes and neophytes had a similar proportion of variation explained by human factors. These studies varied in the number of non-native species included and in the climate and land use variables considered. To resolve these discrepancies, this study uses all non-native species in Britain included in the New Atlas of the British and Irish Flora (Preston *et al*., 2002) and a subset of grid squares that are well-recorded are used to build models, which are then tested against the remaining grid squares to minimise differences in recorder effort.

The main aims of this chapter were to determine how general patterns of non-native species richness vary with climate and land use; to determine the importance of different variables for native, non-native, archaeophyte and neophyte species richness; and to test whether current distributions could be modelled using climate and land use variables so that future distributions could be predicted from projected changes in climate. This tested the hypotheses that: 1) different groups (natives, non-natives, neophytes and archaeophytes) show distinct patterns with climate and land use variables; and 2) current species richness can be modelled from climate and land use variables.

## 3.3 Methods

### *3.3.1. Data*

#### *Plant species data*

Records of plant species in 10 x 10 km grid squares were provided by the Botanical Society of the British Isles (BSBI). Analyses of non-native plants used all 1728 non-native plant species, included in the New Atlas of the British and Irish Flora (Preston *et al*., 2002), that had been recorded in Britain between 1987 and 2009. This includes both neophytes (non-native species introduced after 1500) and archaeophytes (non-native species introduced before 1500). Comparative analyses using native species richness used records of all native taxa from the same time period.

All statistical model building was based on a subset of 10 x 10 km grid squares which are known to have been consistently recorded for non-native species. These are the BSBI Monitoring Scheme (or Local Change) grid squares (Braithwaite *et al*., 2006): 291 squares regularly arranged in a systematic grid of 1 in 9 which have had additional recording in 1987/1988 and 2003/2004, and thereby have a higher number of non-native species recorded than surrounding squares (Figure 2.1). These high intensity repeat-survey squares minimise recording variation associated with unsystematic botanical surveying across the remainder of Britain (Preston *et al*., 2002).

*Climate and land use data*

Environmental variables which have previously been shown to be useful when analysing vegetation distributions were chosen (e.g. Box 1981, 1995, 1996; Sykes and Prentice 1995). Climate variables used were annual averages over the time period 1960-1990 for mean summer (June to August) precipitation in mm (SPRE), mean winter (December to February) precipitation in mm (WPRE), growing degree days over 5°C (GDD5), mean temperature warmest month in °C (MTWA) and mean temperature of the coldest month in °C (MTCO). The ratio of actual to potential evapotranspiration (APET) was also used, which is estimated using soil moisture accounting models and gives an index of effective drought (Prentice *et al*., 1992; Huntley *et al*., 1995). Proportions of each 10 x 10 km grid square associated with different land cover classifications were estimated from the Land Cover Map 2000 (Fuller *et al*., 2002): arable, urban, improved grassland, neutral grassland, acid grassland, calcareous grassland, broadleaved woodland, coniferous woodland, heath, inland rock and standing water.

### ***3.3.2 Analyses***

Spearman’s rank correlations, Wilcoxon signed rank tests, Wilcoxon rank sum tests, Moran's I, Generalised Linear Models and Hierarchical Partitioning were used to examine relationships between different variables. All analysis was carried out using R (version 2.13.1).

### *Generalised Linear Models*

Generalised Linear Models (GLMs) were used to determine the relationships between species richness, climate variables and land use. GLMs were carried out using the 'glm' function in the 'stats' package in R, specifying the family 'Poisson' as the response variable was count data (species richness). Climate variables and proportions of land cover were used as the predictor variables. Dispersion parameters were used to correct for overdispersion of residuals and predictor variables were removed using the Akaike information criterion (AIC). The climate and land use predictor variables were standardised to give a mean of 0 and a standard deviation of 1, allowing comparison of the slope estimates from the models. Second order polynomials were used for climate variables. The BSBI Monitoring Squares (Figure 2.1) were used to create the models, which were then used to predict species richness for the rest of the grid squares from their climate and land use data (using the 'predict' function in the 'stats' package in R). These predictions were compared with numbers of species actually recorded for these grid squares (using Spearman’s rank correlations and Wilcoxon signed rank tests) and also to test the model accuracy and look for patterns in recorder effort. If recorded number of species minus predicted number of species is a negative value, this indicates over-prediction by the model or lower recorder effort. If it is a positive value, this indicates under-prediction by the model or higher recorder effort. To determine if differences are due to variation in recording of non-native species in different vice-counties, spatial autocorrelation in recorded minus predicted species richness was calculated for natives, non-natives, neophytes and archaeophytes and correlations between mean values for each vice county were examined. Figure 3.1 gives a map of the vice-counties of Britain, with vice-county names in Table 3.1.

Projected climate data were used to predict possible future changes in natives and non-native species richness (using the 'predict' function in the 'stats' package in R), and change in proportion of non-natives in the flora was calculated. Mean projections for 2071-2100 from three emission scenarios and three climate models were used to look at variation in predictions. Projections from three different emissions scenarios (IPCC, 2000; IPCC, 2007) were used for one climate model (Hadley Centre: HadCM3; IPCC, 2012), a high emission scenario (A1), a moderate emission scenario (A2) and a low emission scenario (B1). Two additional climate models were also used for the moderate emission scenario, NCAR: CSM and NCAR: PCM (IPCC, 2012).

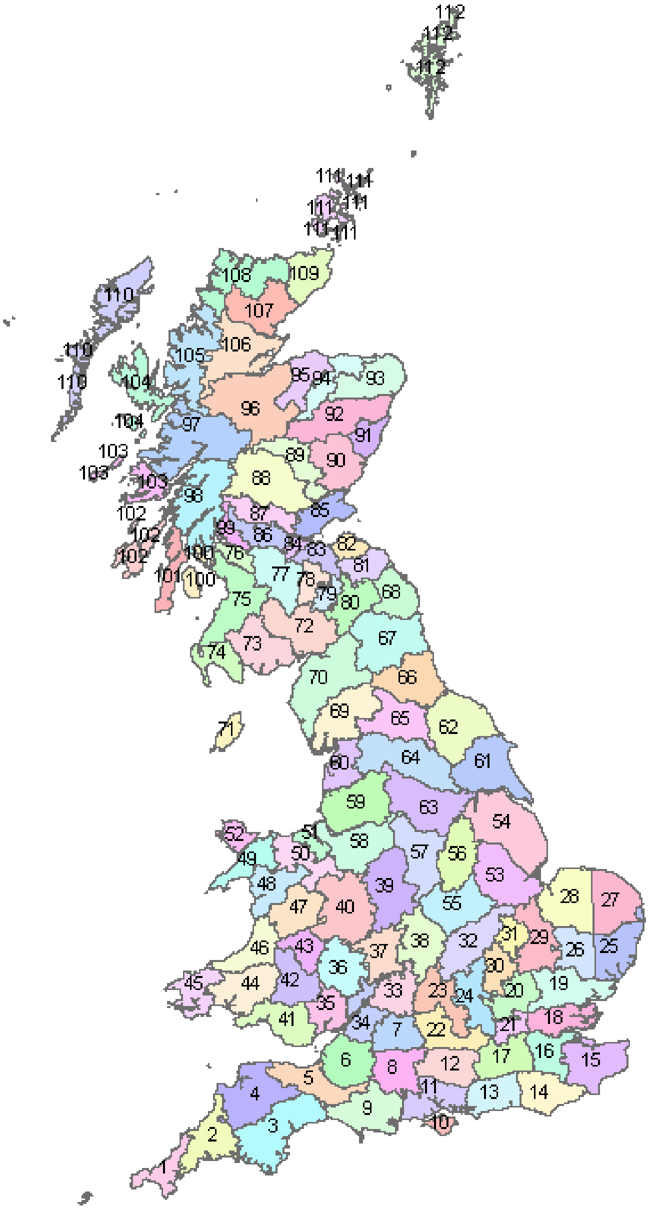


Figure 3.1. Map of vice-counties in England, Wales, Scotland and Isle of Man. Names of vice-counties are given in Table 5.

Table 3.1. Vice-counties in England, Wales, Scotland and Isle of Man.

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 1 | West Cornwall with Scilly | 29 | Cambridgeshire | 57 | Derbyshire | 85 | Fife |
| 2 | East Cornwall | 30 | Bedfordshire | 58 | Cheshire | 86 | Stirlingshire |
| 3 | South Devon | 31 | Huntingdonshire | 59 | South Lancashire | 87 | West Perthshire |
| 4 | North Devon | 32 | Northamptonshire | 60 | West Lancashire | 88 | Mid Perthshire |
| 5 | South Somerset | 33 | East Gloucestershire | 61 | South-east Yorkshire | 89 | East Perthshire |
| 6 | North Somerset | 34 | West Gloucestershire | 62 | North-east Yorkshire | 90 | Angus |
| 7 | North Wiltshire | 35 | Monmouthshire | 63 | South-west Yorkshire | 91 | Kincardineshire |
| 8 | South Wiltshire | 36 | Herefordshire | 64 | Mid-west Yorkshire | 92 | South Aberdeenshire |
| 9 | Dorset | 37 | Worcestershire | 65 | North-west Yorkshire | 93 | North Aberdeenshire |
| 10 | Isle of Wight | 38 | Warwickshire | 66 | Durham | 94 | Banffshire |
| 11 | South Hampshire | 39 | Staffordshire | 67 | South Northumberland | 95 | Moray |
| 12 | North Hampshire | 40 | Shropshire | 68 | North Northumberland | 96 | Easterness |
| 13 | West Sussex | 41 | Glamorgan | 69 | Westmoreland with Furness | 97 | Westerness |
| 14 | East Sussex | 42 | Breconshire | 70 | Cumberland | 98 | Main Argyll |
| 15 | East Kent | 43 | Radnorshire | 71 | Isle of Man | 99 | Dunbartonshire |
| 16 | West Kent | 44 | Carmarthenshire | 72 | Dumfriesshire | 100 | Clyde Isles |
| 17 | Surrey | 45 | Pembrokeshire | 73 | Kircudbrightshire | 101 | Kintyre |
| 18 | South Essex | 46 | Cardiganshire | 74 | Wigtownshire | 102 | South Ebudes |
| 19 | North Essex | 47 | Montgomeryshire | 75 | Ayrshire | 103 | Mid Ebudes |
| 20 | Hertfordshire | 48 | Merioneth | 76 | Renfrewshire | 104 | North Ebudes |
| 21 | Middlesex | 49 | Caernarvonshire | 77 | Lanarkshire | 105 | West Ross |
| 22 | Berkshire | 50 | Denbighshire | 78 | Peebleshire | 106 | East Ross |
| 23 | Oxfordshire | 51 | Flintshire | 79 | Selkirkshire | 107 | East Sutherland |
| 24 | Buckinghamshire | 52 | Anglesey | 80 | Roxburghshire | 108 | West Sutherland |
| 25 | East Suffolk | 53 | South Lincolnshire | 81 | Berwickshire | 109 | Caithness |
| 26 | West Suffolk | 54 | North Lincolnshire | 82 | East Lothian | 110 | Outer Hebrides |
| 27 | East Norfolk | 55 | Leicestershire with Rutland | 83 | Midlothian | 111 | Orkney |
| 28 | West Norfolk | 56 | Nottinghamshire | 84 | West Lothian | 112 | Shetland |

### *Hierarchical Partitioning*

Hierarchical Partitioning (HP) analyses were used to calculate the independent contribution of each predictor to the species richness for different groups of non-native species. HP was carried out using the 'hier.part' package in R (MacNally and Walsh, 2004). HP involves measuring the increase of goodness-of-fit of all models with a particular variable compared with the equivalent model without that variable. The improvement in fit is then averaged across all possible models in which that variable occurs to produce a measure of its independent effects. A Poisson distribution with the default goodness-of-fit measure (RMSPE, Root-mean-square 'prediction' error) was specified.

*Spatial autocorrelation*

Significance of spatial autocorrelation was tested for using Moran's I (using function 'Moran.I' in the 'ape' package in R). A significant positive value indicates a distribution is more clustered than expected and a significant negative value indicates a distribution is more dispersed than expected.

## 3.4 Results

### *3.4.1. Patterns of species richness with climate variables and land use*

Non-native plant species richness shows a positive correlation with temperature (Spearman's rank correlation coefficients for GDD5, MTCO and MTWA are 0.77, 0.38 and 0.83 respectively, all N = 291, all *P* <0.001; all correlations are shown in Appendix 1, Table A1.1). Figure 3.2 shows maps of mean temperature of the warmest month and non-native species richness. Non-native plant species richness is negatively correlated with rainfall (Spearman's rank correlation coefficients for APET, SPRE and WPRE are -0.78, -0.63 and -0.61 respectively, all N = 291, all *P* <0.001). Figure 3.3 shows maps of the ratio of actual to potential evapotranspiration and non-native species richness. The strongest correlation with a land cover variable is with proportion of urban land cover (Spearman's rank correlation coefficient 0.82, N = 291, *P* <0.001). Figure 3.4 shows maps of the relationship between the proportion of urban land cover and non-native species richness.

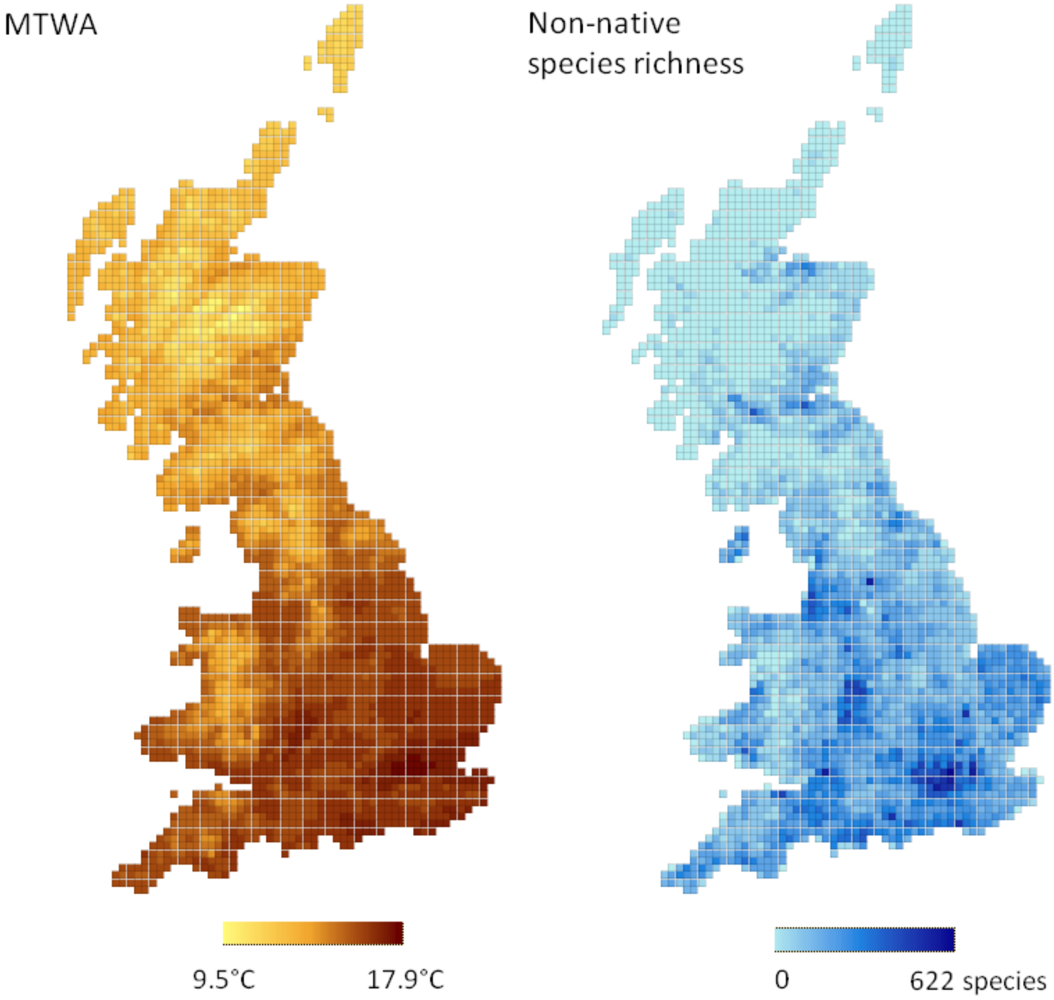


Figure 3.2. Mean temperature of the warmest month in °C (MTWA) and non-native plant species richness using records from 1987 to 2009. Significant positive correlation (Spearman's rank correlation coefficient 0.83, N = 291, $P < 0.001$).

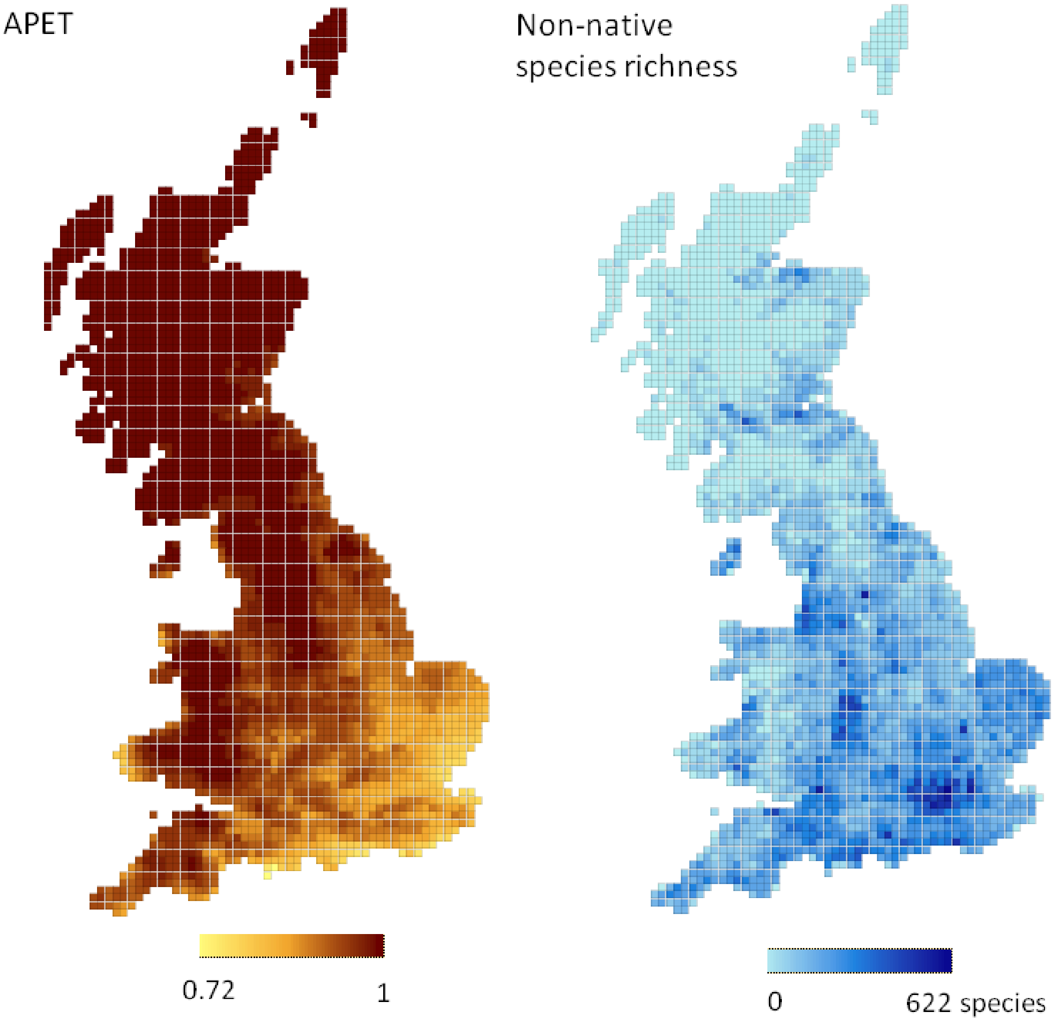


Figure 3.3. Ratio of actual to potential evapotranspiration (APET) and non-native plant species richness using records from 1987 to 2009. Significant negative correlation (Spearman's rank correlation coefficient -0.78, N = 291, *P* < 0.001).

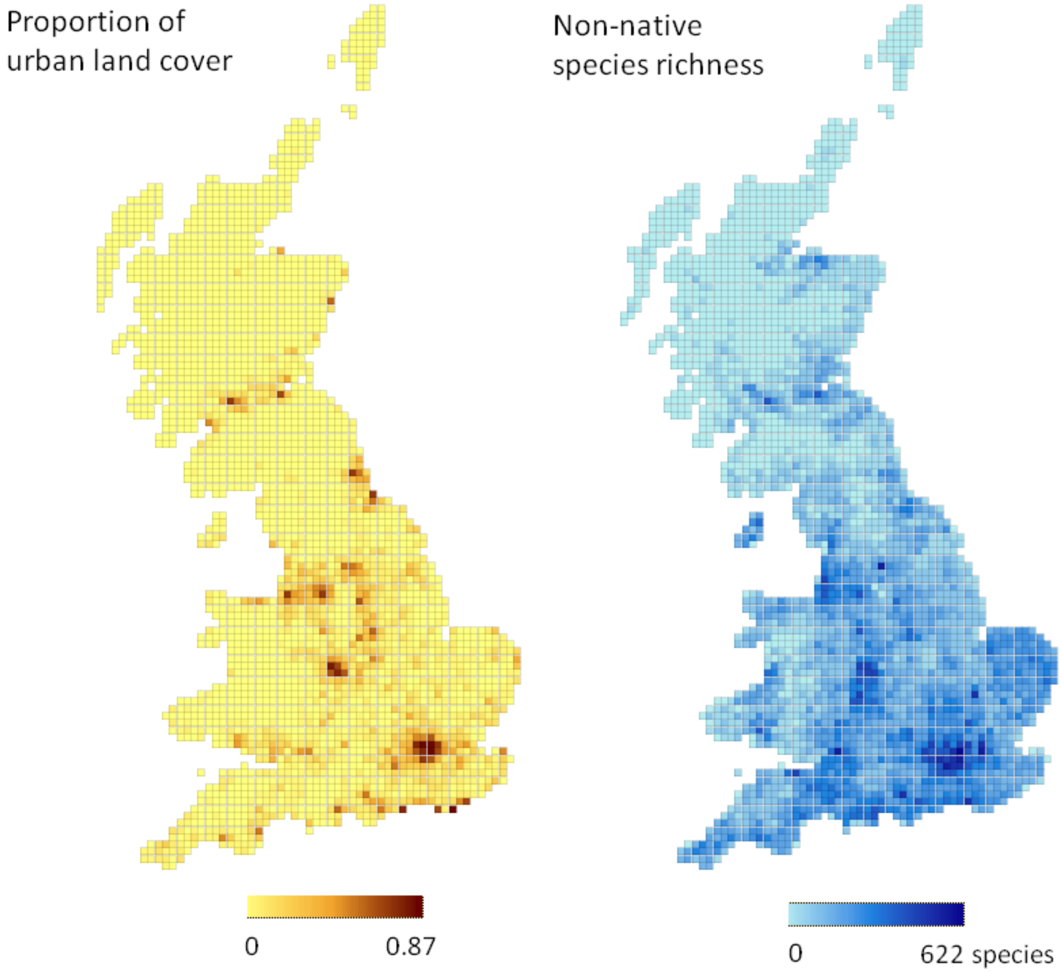


Figure 3.4. Proportion of urban land cover and non-native plant species richness using records from 1987 to 2009. Significant positive correlation (Spearman’s rank correlation coefficient 0.82, N = 291, *P* < 0.001).

### *3.4.2.Modelling species richness*

#### *Comparison of predicted and recorded species richness for non-natives and natives*

<u>Non-native species</u>. Using the models based on the BSBI Monitoring Scheme grid squares (Table 3.2), non-native species richness was predicted for all other squares using values for climate and land use variables (Figure 3.5). This predicted species richness was then compared to actual recorded species richness, showing a significant positive correlation between predicted and recorded species richness (Figure 3.6). However, predicted species richness is significantly higher than recorded (Figure 3.6), indicating that the model is over-predicting species richness, which suggests that recorder effort may be lower in other grid squares.

Table 3.2. GLMs for native and non-native species richness. Slope estimate, standard error, Z value and significance are shown for each climate and land cover variable included (after elimination using AIC). Predictor variables were standardised to allow comparison of relative importance.

| | Native | | | | | Non-native | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. |
| poly(GDD5, 2)1 | 8.42 | 6.26 | 1.35 | 0.1788 | | 2.84 | 12.94 | 0.22 | 0.8265 | |
| poly(GDD5, 2)2 | 0.72 | 0.86 | 0.84 | 0.4007 | | 5.37 | 2.30 | 2.34 | 0.0195 | * |
| poly(MTCO, 2)1 | -3.37 | 1.75 | -1.93 | 0.0541 | . | -2.50 | 3.64 | -0.69 | 0.4925 | |
| poly(MTCO, 2)2 | -0.74 | 0.63 | -1.17 | 0.2437 | | -2.82 | 1.56 | -1.80 | 0.0713 | . |
| poly(MTWA, 2)1 | -3.68 | 5.06 | -0.73 | 0.4672 | | 7.19 | 10.56 | 0.68 | 0.4956 | |
| poly(MTWA, 2)2 | -1.49 | 0.64 | -2.35 | 0.0191 | * | -6.65 | 1.73 | -3.85 | 0.0001 | *** |
| poly(APET, 2)1 | -1.51 | 0.76 | -2.00 | 0.0451 | * | -2.69 | 1.47 | -1.82 | 0.0683 | . |
| poly(APET, 2)2 | -0.54 | 0.30 | -1.78 | 0.0754 | . | -0.70 | 0.56 | -1.25 | 0.2132 | |
| poly(SPRE, 2)1 | 1.00 | 1.22 | 0.81 | 0.4155 | | 0.33 | 3.18 | 0.10 | 0.9173 | |
| poly(SPRE, 2)2 | -1.23 | 0.63 | -1.96 | 0.0495 | * | -4.18 | 1.91 | -2.19 | 0.0285 | * |
| poly(WPRE, 2)1 | 0.08 | 1.13 | 0.07 | 0.9431 | | 0.30 | 2.91 | 0.10 | 0.9181 | |
| poly(WPRE, 2)2 | 0.71 | 0.63 | 1.13 | 0.2600 | | 3.09 | 1.75 | 1.76 | 0.0777 | . |
| acid | 0.05 | 0.02 | 2.35 | 0.0186 | * | 0.05 | 0.04 | 1.23 | 0.2179 | |
| arable | 0.05 | 0.03 | 1.58 | 0.1136 | | 0.24 | 0.05 | 4.70 | 0.0000 | *** |
| bwood | 0.06 | 0.01 | 4.60 | 0.0000 | *** | 0.09 | 0.02 | 4.04 | 0.0001 | *** |
| calc | 0.01 | 0.01 | 0.73 | 0.4664 | | | | | | |
| cwood | 0.05 | 0.02 | 3.41 | 0.0007 | *** | 0.16 | 0.03 | 4.93 | 0.0000 | *** |
| heath | 0.05 | 0.03 | 1.70 | 0.0893 | . | | | | | |
| improved | 0.10 | 0.02 | 4.46 | 0.0000 | *** | 0.22 | 0.04 | 5.68 | 0.0000 | *** |
| inrock | 0.03 | 0.01 | 2.20 | 0.0277 | * | 0.05 | 0.04 | 1.42 | 0.1565 | |
| neutral | 0.04 | 0.02 | 2.56 | 0.0104 | * | 0.10 | 0.03 | 3.08 | 0.0021 | ** |
| swater | | | | | | | | | | |
| urban | 0.08 | 0.02 | 4.63 | 0.0000 | *** | 0.25 | 0.03 | 9.18 | < 2e-16 | *** |

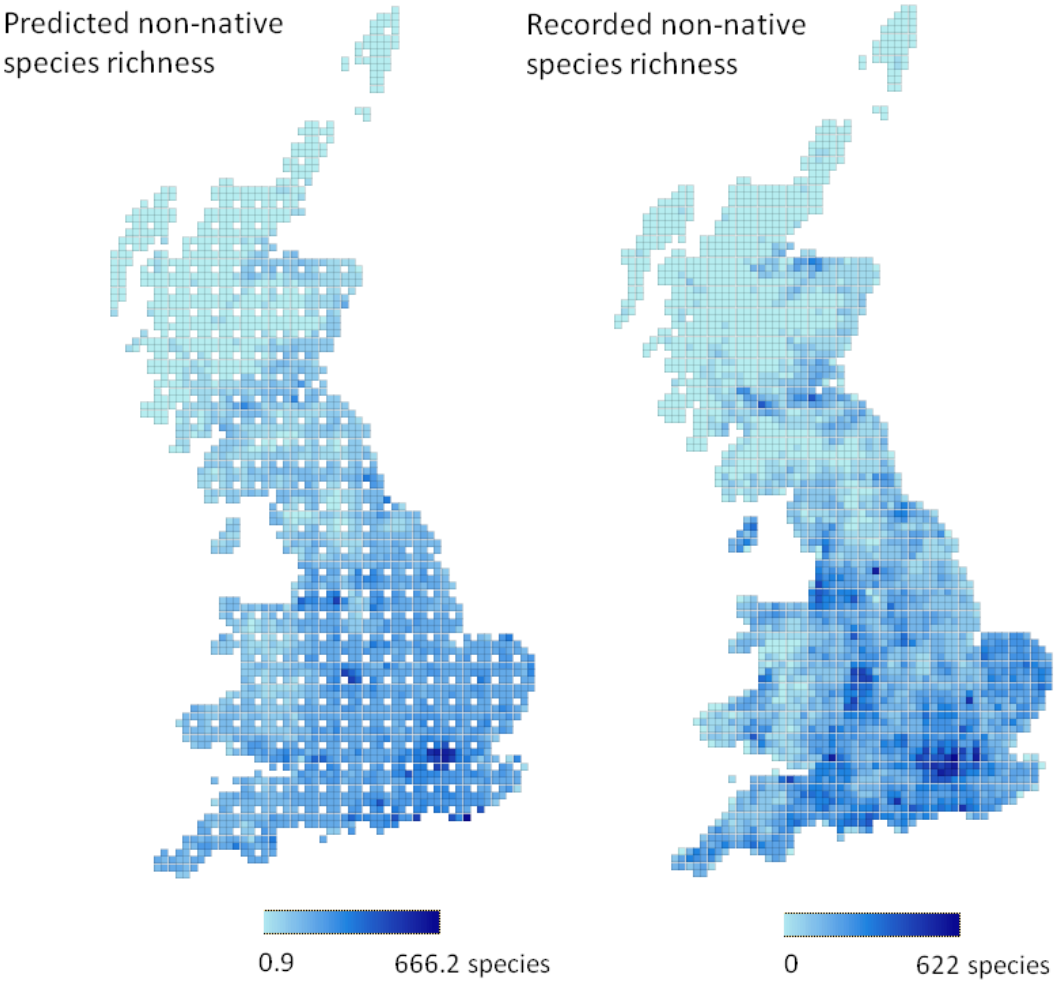


Figure 3.5. The map on the left shows non-native species richness predicted by the GLM from climate and land use variables. White squares are BSBI Monitoring Scheme squares used to make the model. The map on the right shows recorded species richness of non-native species.

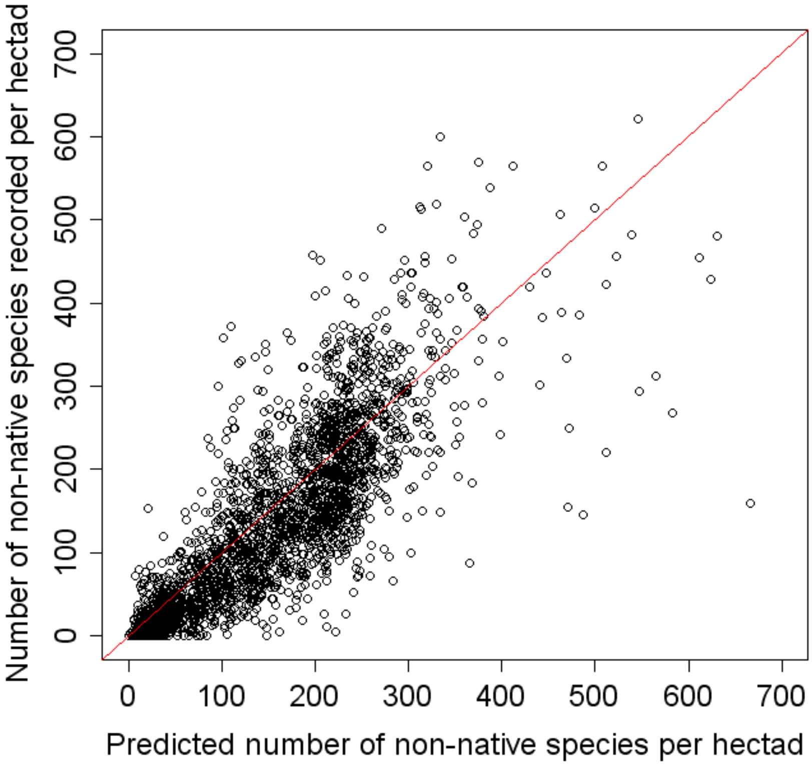


Figure 3.6. Relationship between the predicted number of non-native species per 10 x 10 km square and the recorded number of non-native species. Significant positive correlation (Spearman's rank correlation coefficient 0.863, N = 2499, *P* < 0.0001). Wilcoxon signed rank test V=1026069, N = 2499, *P* < 0.0001 (mean of predicted = 151.5, mean of recorded = 137.0).

<u>Native species.</u> Using the models based on the BSBI Monitoring Scheme grid squares (Table 3.2), native species richness was predicted for all other squares using values for climate and land use variables (Figure 3.7). This predicted species richness was then compared to actual recorded species richness, giving a significant positive correlation between predicted and recorded species richness (Figure 3.8). However, predicted species richness is significantly higher than recorded, with means of 495.6 and 460.1 respectively (Figure 3.8). This indicates that the model is over-predicting species richness and that recorder effort may be lower in other grid squares.

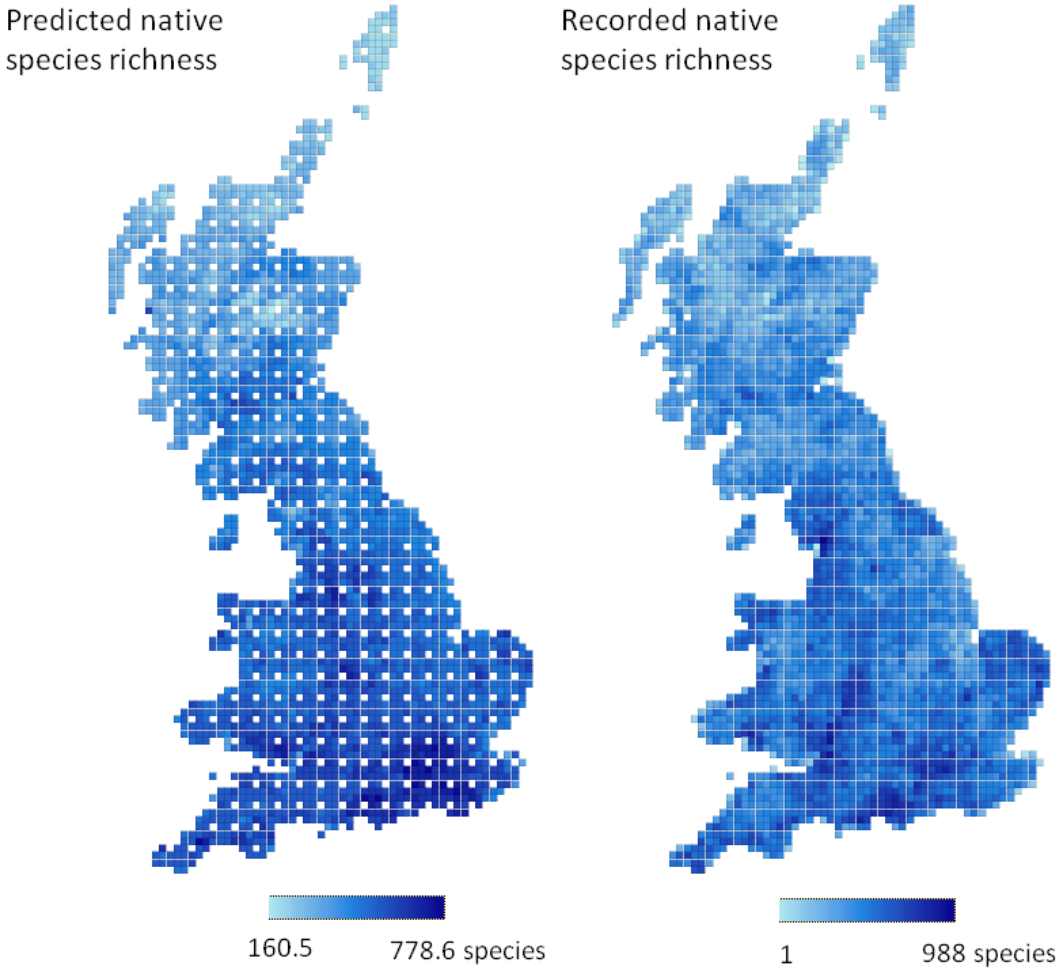


Figure 3.7. The map on the left shows native species richness predicted by the GLM from climate and land use variables. White squares are BSBI monitoring scheme squares used to make the model. The map on the right shows recorded species richness of native species.

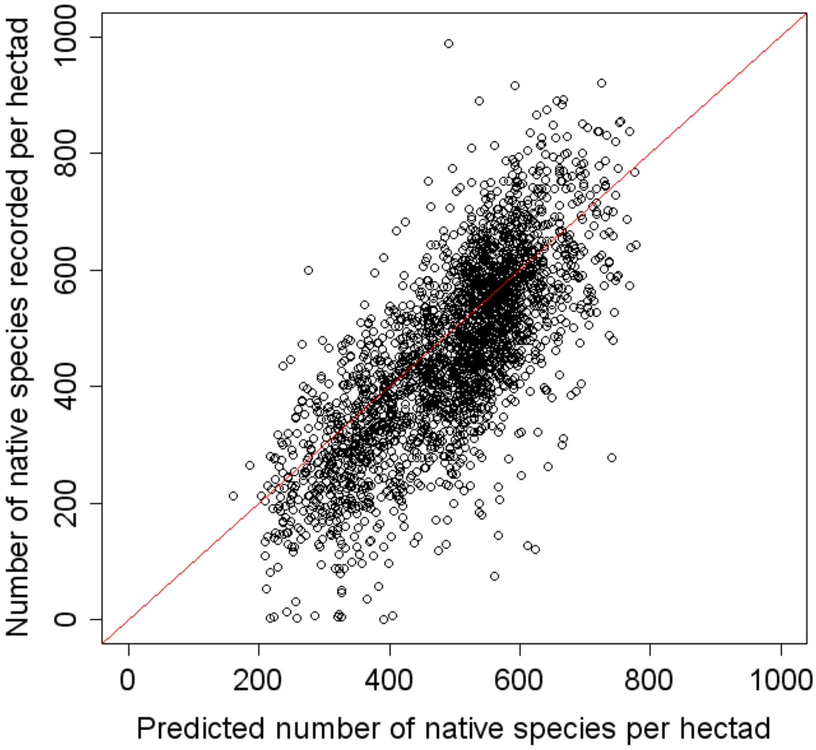


Figure 3.8. Relationship between the predicted number of native species per 10 x 10 km square and the recorded number of native species. Significant positive correlation (Spearman's rank correlation coefficient 0.755, N = 2499, *P* < 0.0001). Wilcoxon signed rank test V=975466, N = 2499, *P* < 0.0001 (mean of predicted = 495.6, mean of recorded = 460.1).

### *Comparison of predicted and recorded species richness for neophytes and archaeophytes*

Neophytes. Using the models based on the BSBI Monitoring Scheme grid squares (Table 3.3), neophyte species richness was predicted for all other squares using values for climate and land use variables (Figure 3.9). This predicted species richness was then compared to actual recorded species richness, giving a significant positive correlation between predicted and recorded species richness (Figure 3.10). However, predicted species richness is significantly higher than recorded, with means of 99.8 and 89.9 respectively (Figure 3.10). This indicates that the model is over-predicting species richness and that recorder effort may be lower in other grid squares.

Table 3.3. GLMs for neophyte and archaeophyte species richness. Slope estimate, standard error, Z value and significance are shown for each climate and land cover variable included (after elimination using AIC). Predictor variables were standardised to allow comparison of relative importance.

| | Neophyte | | | | | Archaeophyte | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. |
| poly(GDD5, 2)1 | 3.64 | 15.56 | 0.23 | 0.8152 | | -7.78 | 2.25 | -3.47 | 0.0005 | *** |
| poly(GDD5, 2)2 | 7.34 | 2.85 | 2.57 | 0.0101 | * | 2.46 | 0.89 | 2.78 | 0.0054 | ** |
| poly(MTCO, 2)1 | -2.49 | 4.37 | -0.57 | 0.5689 | | | | | | |
| poly(MTCO, 2)2 | -4.05 | 1.91 | -2.12 | 0.0337 | * | | | | | |
| poly(MTWA, 2)1 | 6.01 | 12.74 | 0.47 | 0.6368 | | 16.74 | 2.61 | 6.43 | 0.0000 | *** |
| poly(MTWA, 2)2 | -7.93 | 2.20 | -3.61 | 0.0003 | *** | -4.73 | 0.94 | -5.01 | 0.0000 | *** |
| poly(APET, 2)1 | -2.88 | 1.76 | -1.63 | 0.1029 | | -2.59 | 1.11 | -2.34 | 0.0193 | * |
| poly(APET, 2)2 | -0.80 | 0.69 | -1.16 | 0.2470 | | -0.54 | 0.41 | -1.33 | 0.1833 | |
| poly(SPRE, 2)1 | 1.35 | 3.77 | 0.36 | 0.7202 | | -0.83 | 2.37 | -0.35 | 0.7265 | |
| poly(SPRE, 2)2 | -4.90 | 2.24 | -2.19 | 0.0288 | * | -3.02 | 1.57 | -1.93 | 0.0535 | . |
| poly(WPRE, 2)1 | -0.07 | 3.44 | -0.02 | 0.9832 | | 0.34 | 2.24 | 0.15 | 0.8807 | |
| poly(WPRE, 2)2 | 3.74 | 2.08 | 1.80 | 0.0718 | . | 1.95 | 1.43 | 1.36 | 0.1734 | |
| acid | 0.08 | 0.06 | 1.43 | 0.1542 | | | | | | |
| arable | 0.31 | 0.08 | 4.13 | 0.0000 | *** | 0.15 | 0.04 | 3.89 | 0.0001 | *** |
| bwood | 0.12 | 0.03 | 4.40 | 0.0000 | *** | 0.04 | 0.02 | 2.28 | 0.0225 | * |
| calc | | | | | | | | | | |
| cwood | 0.21 | 0.04 | 5.33 | 0.0000 | *** | 0.06 | 0.03 | 2.09 | 0.0366 | * |
| heath | 0.08 | 0.09 | 0.87 | 0.3832 | | -0.11 | 0.05 | -2.07 | 0.0384 | * |
| improved | 0.29 | 0.06 | 4.87 | 0.0000 | *** | 0.12 | 0.03 | 3.98 | 0.0001 | *** |
| inrock | 0.05 | 0.04 | 1.19 | 0.2348 | | 0.06 | 0.03 | 1.96 | 0.0503 | . |
| neutral | 0.13 | 0.04 | 2.89 | 0.0039 | ** | 0.07 | 0.03 | 2.69 | 0.0071 | ** |
| swater | | | | | | | | | | |
| urban | 0.33 | 0.04 | 8.72 | < 2e-16 | *** | 0.11 | 0.02 | 4.93 | 0.0000 | *** |

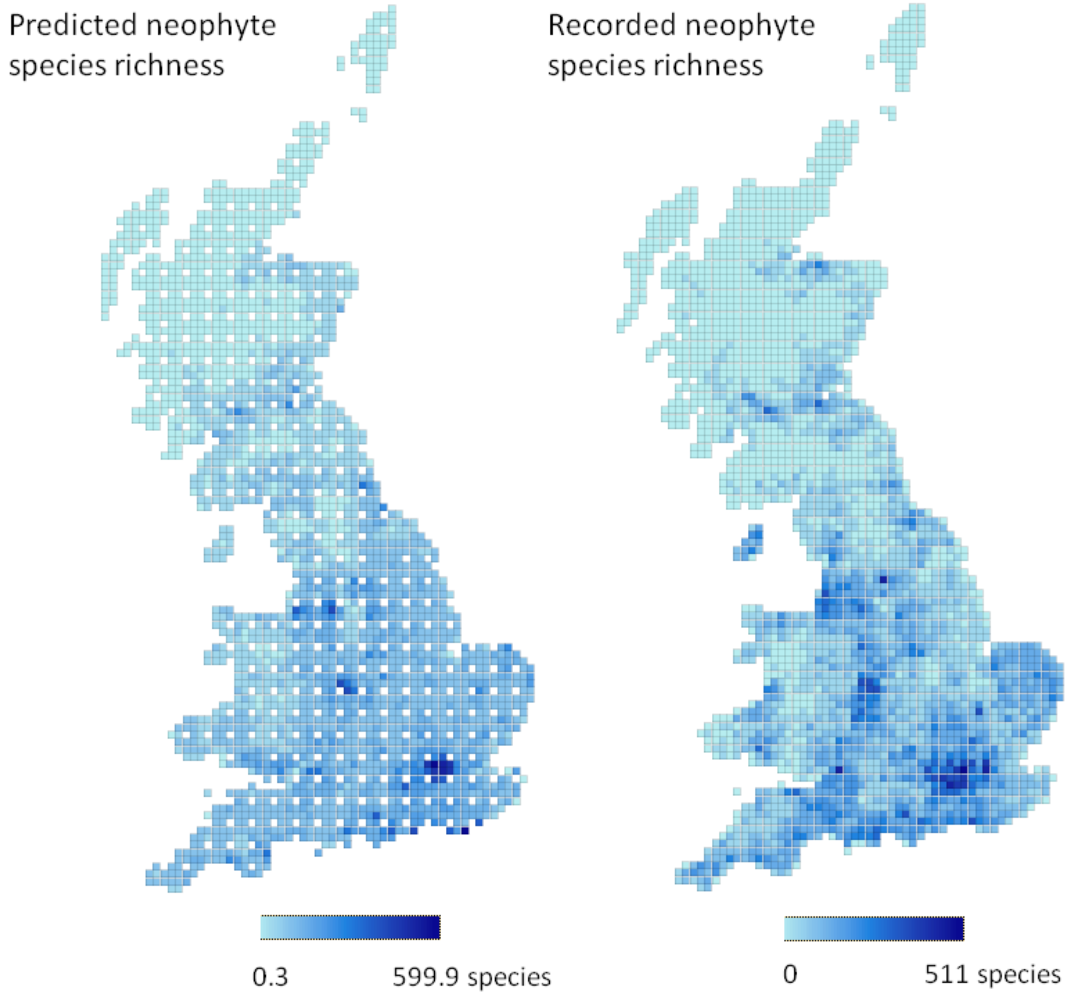


Figure 3.9. The map on the left shows neophyte species richness predicted by the GLM from climate and land use variables. White squares are BSBI Monitoring Scheme squares used to make the model. The map on the right shows recorded species richness of neophyte species.

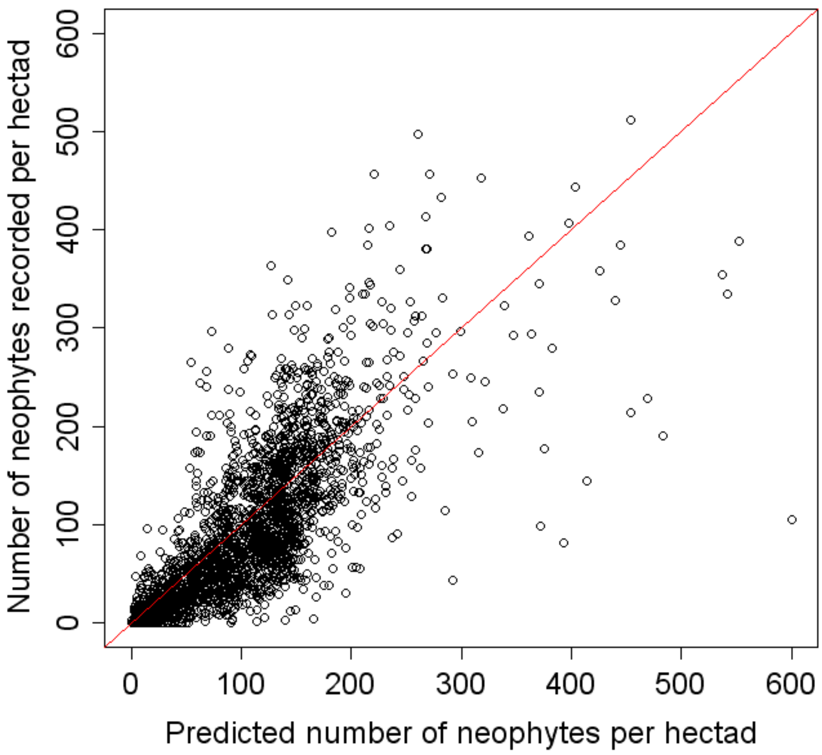


Figure 3.10. Relationship between the predicted number of neophytes per 10 x 10 km square and the recorded number of neophytes. Significant positive correlation (Spearman's rank correlation coefficient 0.832, N = 2499, *P* < 0.0001). Wilcoxon signed rank test V=1051477, N = 2499, *P* < 0.0001 (mean of predicted = 99.8, mean of recorded = 89.9).

Archaeophytes. Using the models based on the BSBI Monitoring Scheme grid squares (Table 3.3), archaeophyte species richness was predicted for all other squares using values for climate and land use variables (Figure 3.11). This predicted species richness was then compared to actual recorded species richness, showing a significant positive correlation between predicted and recorded species richness (Figure 3.12). However, predicted species richness is significantly higher than recorded, with means of 51.8 and 47.1 respectively (Figure 3.12). This indicates that the model is over-predicting species richness and that recorder effort may be lower in other grid squares.

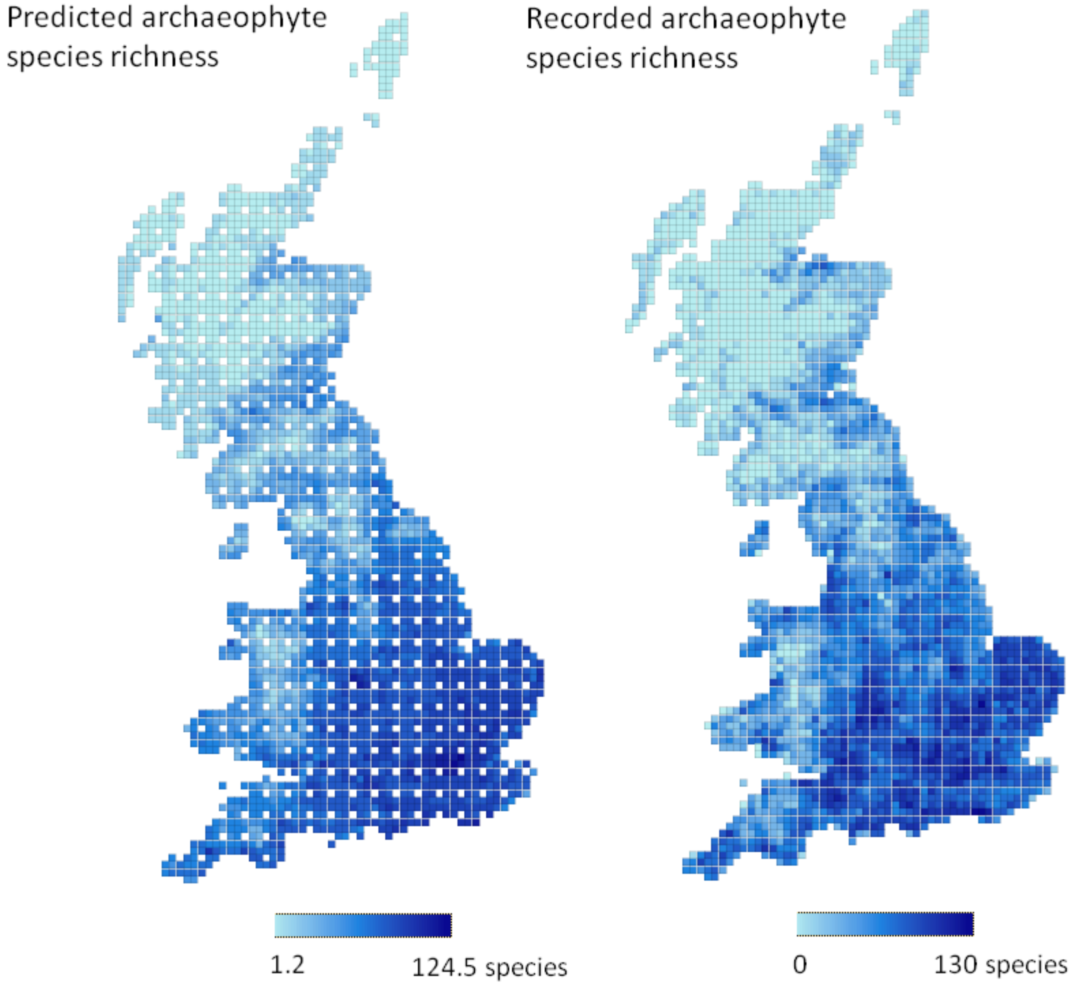


Figure 3.11. The map on the left shows archaeophyte species richness predicted by the GLM from climate and land use variables. White squares are BSBI Monitoring Scheme squares used to make the model. The map on the right shows recorded species richness of archaeophyte species.

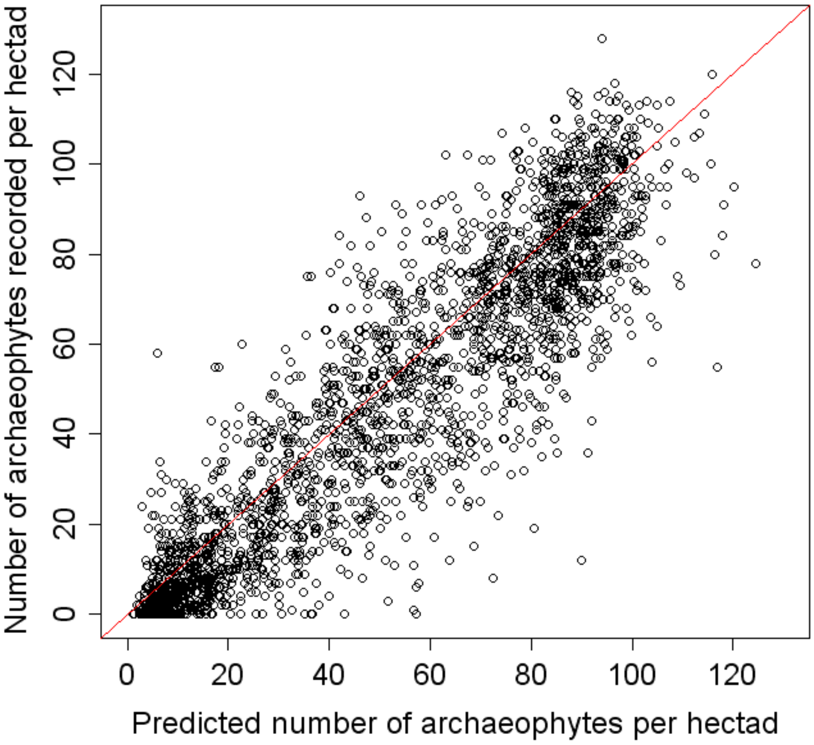


Figure 3.12. Relationship between the predicted number of archaeophytes per 10 x 10 km square and the recorded number of archaeophytes. Significant positive correlation (Spearman's rank correlation coefficient 0.905, N = 2499, $P < 0.0001$). Wilcoxon signed rank test V=960486, N = 2499, $P < 0.0001$ (mean of predicted = 51.8, mean of recorded = 47.1).

### *3.4.3 Recorder effort*

*Variations in recording effort between native and non-native species*

Comparing recorded number of species minus predicted number of species for natives and non-natives, the same grid squares are over- or under-predicted by the model with a significant positive correlation (Figure 3.13). This suggests that the same grid squares are well-recorded and under-recorded for native and non-native species.

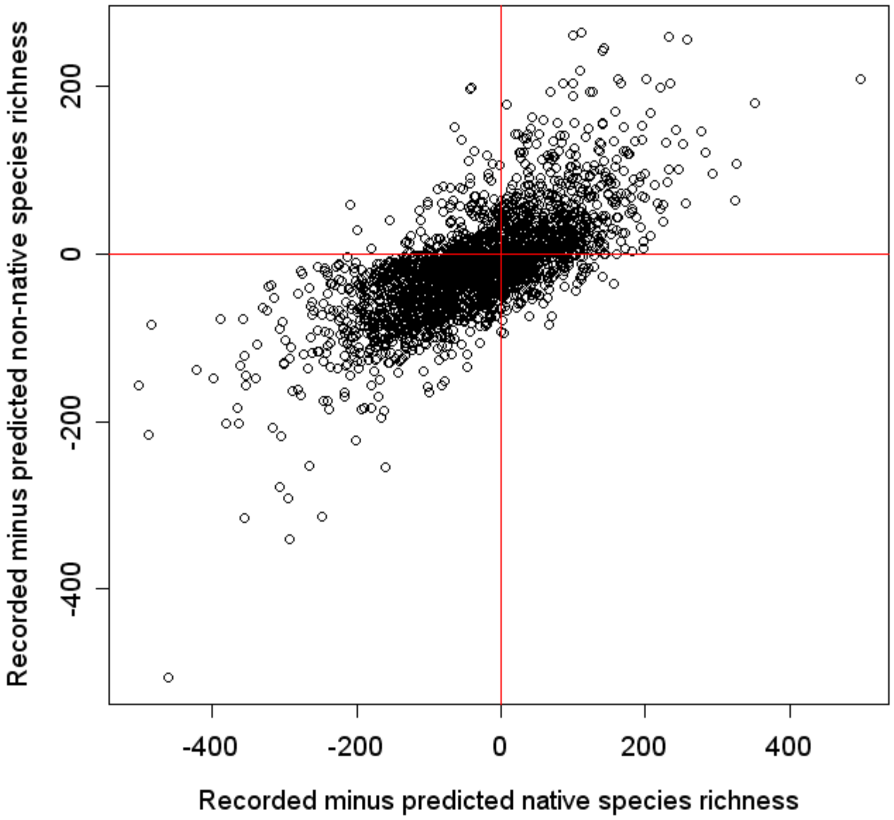


Figure 3.13. Relationship between native and non-native recorded minus predicted species richness. Significant positive correlation (Spearman’s rank correlation coefficient 0.710, N = 2499, $P < 0.0001$).

*Variations in recording effort between neophytes and archaeophytes*

Comparing recorded number of species minus predicted number of species for neophytes and archaeophytes, the same grid squares are over- or under-predicted by the model, with a significant positive correlation (Figure 3.14). This suggests that the same grid squares are well-recorded and under-recorded for neophyte and archaeophyte species.

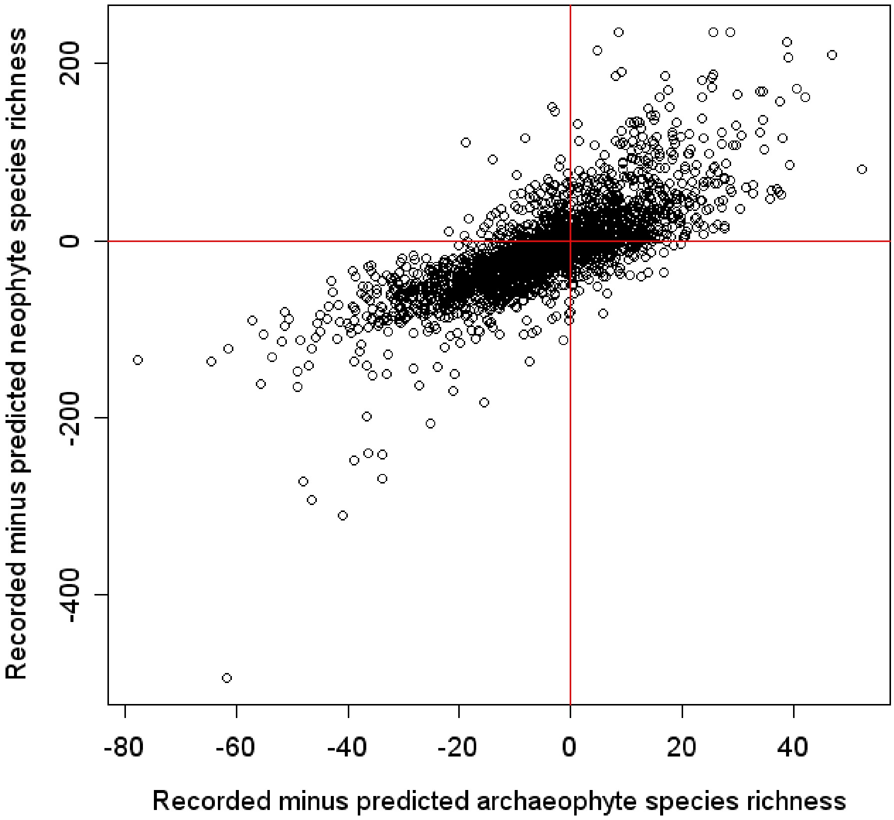


Figure 3.14. Relationship between archaeophyte and neophyte recorded minus predicted species richness.  Significant positive correlation (Spearman's rank correlation coefficient 0.788, N = 2499, *P* < 0.0001).

### *Variation of recorder effort between vice-counties*

There is significant positive spatial autocorrelation in recorded minus predicted for natives and non-natives (Figure 3.15), meaning values are more clustered than would be expected. There is a significant positive correlation (Figure 3.16) between mean native and mean non-native recorded minus predicted species richness for each vice-county. This suggests that for native and non-native species, the same areas are over- and under-predicted by the models and that this may be related to variations in vice-county recorder effort.

Vice-counties with recent floras (published after 2000), which means they have had additional recording during the period 1987-2009, were identified. The mean recorded minus predicted species richness for vice-counties with floras and without floras were compared, and found to be higher for vice-counties with floras for natives (Wilcoxon rank sum test W=902, N with flora = 32, N without flora = 80, $P < 0.02$; mean with flora = -6.0, mean without flora = -37.9) and for non-natives (Wilcoxon rank sum test W=865, N with flora = 32, N without flora = 80, $P < 0.01$; mean with flora = 5.9, mean without flora = -17.7).

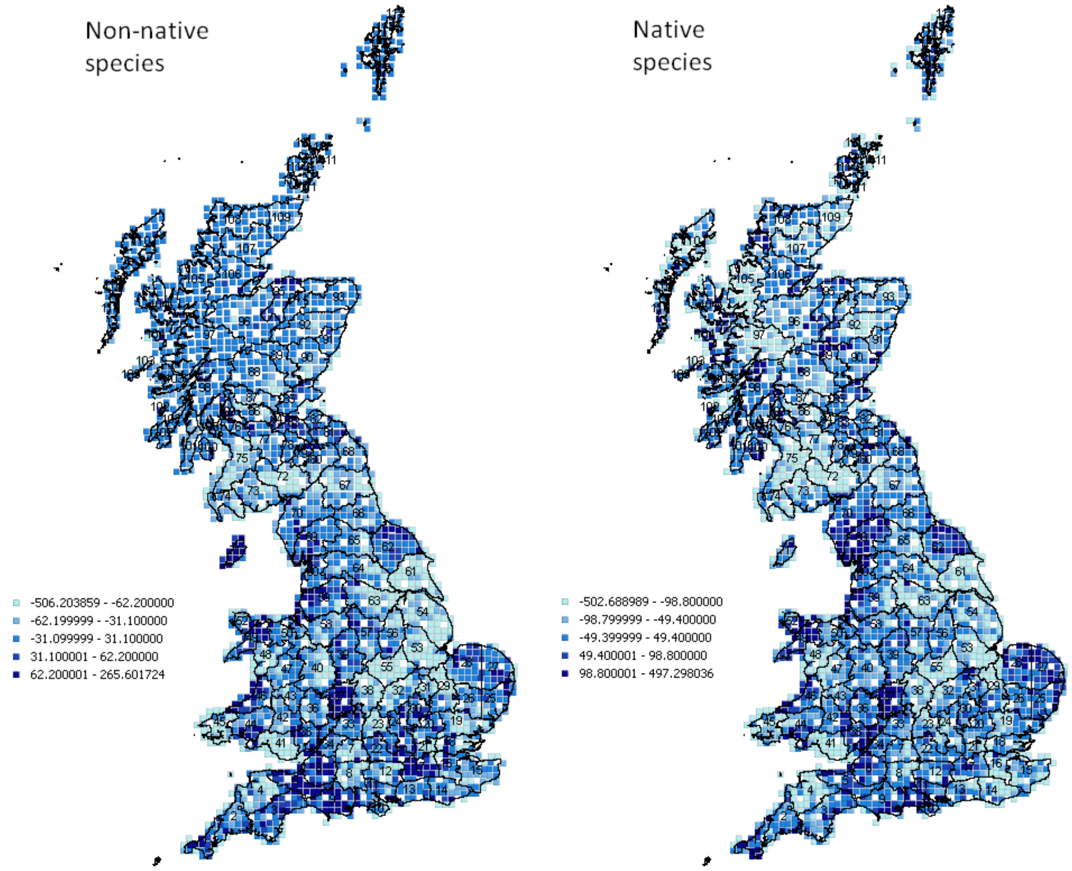


Figure 3.15. Maps showing recorded minus predicted number of species for non-native species and native species. Light blue indicates high negative values and dark blue high positive values. Significant positive spatial autocorrelation in recorded minus predicted for non-natives: Moran's I observed = 0.03634, expected -0.00040, N = 2499, *P* < 0.0001; and for natives: Moran's I observed = 0.03863, expected = -0.00040, N = 2499, *P* < 0.0001.

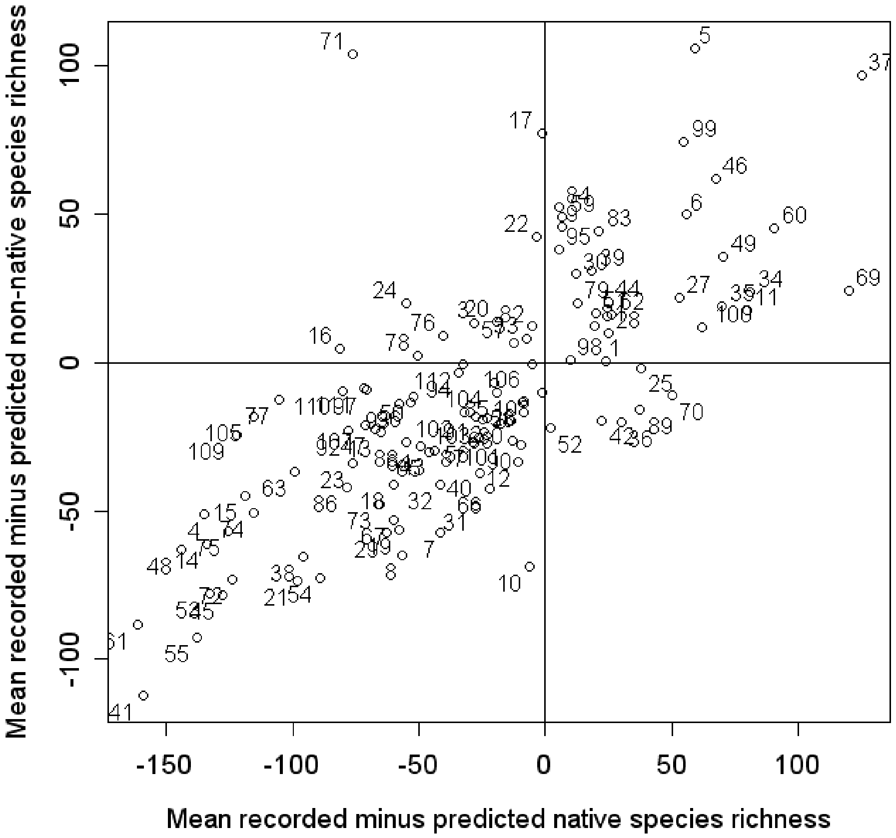


Figure 3.16. Relationship between mean native and mean non-native recorded minus predicted species richness for each vice-county. Significant positive correlation (Spearman’s rank correlation coefficient 0.734, N = 112, $P < 0.0001$). Table 3.1 gives vice-county names.

There is significant positive spatial autocorrelation in recorded minus predicted for neophytes and archaeophytes (Figure 3.17), meaning values are more clustered than would be expected. There is a significant positive correlation between mean neophyte and mean archaeophyte recorded minus predicted species richness for each vice-county (Figure 3.18). This suggests that for neophytes and archaeophytes, the same areas are over- and under-predicted by the models and that this may be related to variations in vice-county recorder effort.

Vice-counties with recent floras (published after 2000), which means they have had additional recording during the period 1987-2009, were identified. The mean recorded minus predicted species richness for vice-counties with floras and without floras were compared, and found to be higher for vice-counties with floras for neophytes (Wilcoxon rank sum test W=836, N with flora = 32, N without flora = 80, $P < 0.005$; mean with flora = 7.5, mean without flora = -13.0), although this was not significant for archaeophytes (Wilcoxon rank sum test W=1023, N with flora = 32, N without flora = 80, $P < 0.1$; mean with flora = -1.5, mean without flora = -4.9).

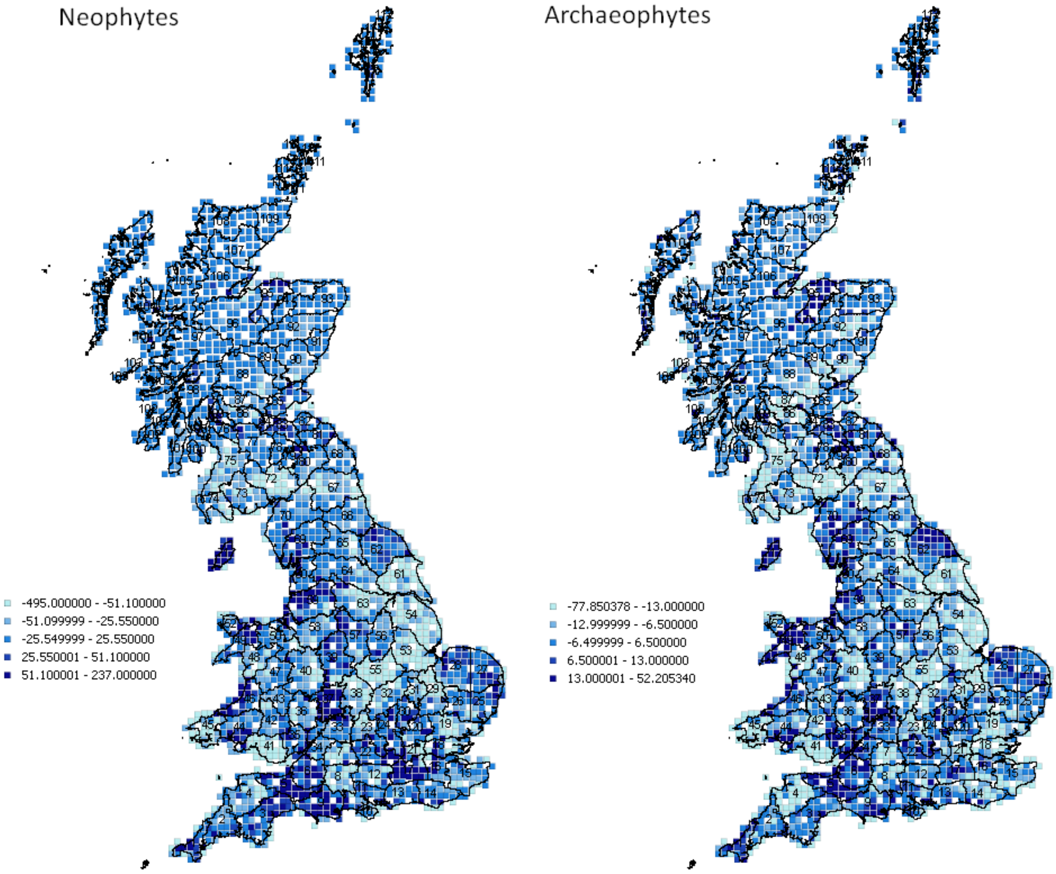


Figure 3.17. Maps showing recorded minus predicted number of species for neophytes and archaeophytes. Light blue indicates high negative values and dark blue high positive values. Significant positive spatial autocorrelation in recorded minus predicted for neophytes: Moran's I observed = 0.03399, expected = -0.00040, N = 2499, $P < 0.0001$; and for archaeophytes: Moran's I observed = 0.03498, expected = -0.00040, N = 2499, $P < 0.0001$.

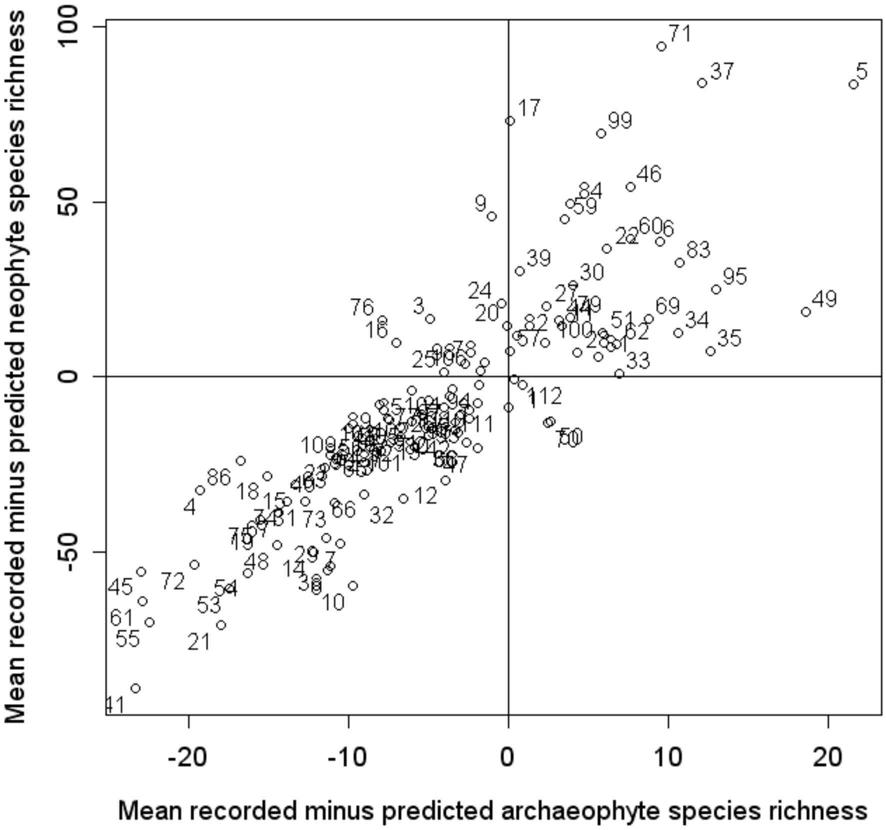


Figure 3.18. Relationship between mean archaeophyte and mean neophyte recorded minus predicted species richness for each vice-county. Significant positive correlation (Spearman's rank correlation coefficient 0.885, N = 112, *P* < 0.0001). Table 2.1 gives vice-county names.

### *3.4.4 Importance of climate and land use variables*

Figure 3.19 shows the urban slope estimates from GLMs for natives, non-natives, neophytes and archaeophytes (Table 3.2 and Table 3.3). All urban slope estimates are positive, indicating species richness for all groups is positively associated with urban land cover. However, non-native species have a higher slope value than for native species, showing that non-natives are more associated with urban land cover than natives. Within non-native species, neophytes are more associated with urban land cover than archaeophytes.

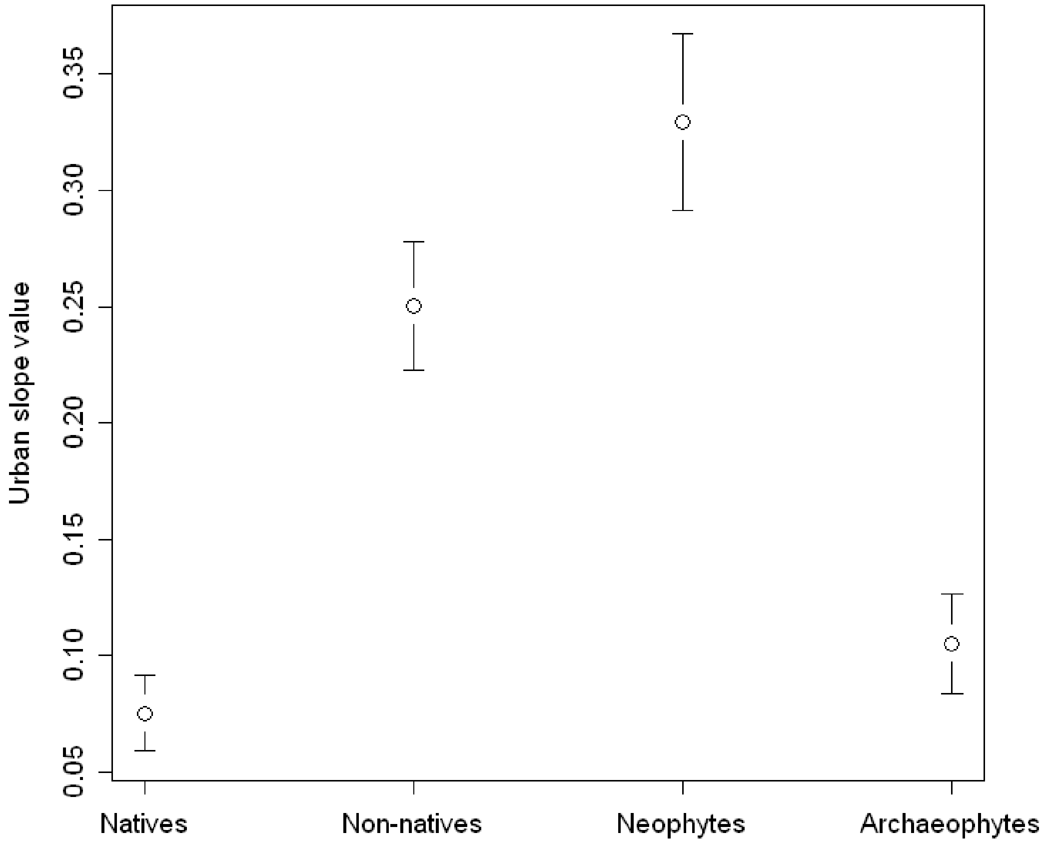


Figure 3.19. Urban slope estimates from GLMs for natives, non-natives, neophytes and archaeophytes (all N=291, $p<0.0001$). Error bars give ± standard error.

Figure 3.20 shows the percentage of variance explained by climate and land use variables for native, non-native, neophyte and archaeophyte species from Hierarchical Partitioning (see Appendix 1, Table A1.2 for full table of results). These results show a similar pattern to the results for urban land cover from the GLMs, with neophytes more associated with urban land cover than archaeophytes. For non-natives and neophytes, urban land cover explains the largest proportion of variation explained by land use (with 11.7% for non-natives and 12.6% for neophytes), and other variables including arable, broadleaved woodland and coniferous woodland explaining smaller proportions. For native species, broadleaved woodland is the most important land use variable at 18.5%, with urban second at 10.5%. Heathland (16.7%) and arable (8.1%) are the most important land use variables for archaeophytes, with urban third at 4.9%.

No clear pattern was found when comparing percentage of variance explained by all climate variables and percentage of variance explained by all land use variables, with non-natives and natives having similar results for climate and land use (47.8% and 41.2% for climate and 52.2% and 58.8% for land use respectively). Archaeophytes had a slightly higher percentage variance explained by climate (54.5%) than for land use (45.5%) when compared to neophytes, with 47.8% explained by climate and 52.2% explained by land use. Archaeophytes also had the highest percentage explained by temperature (MTCO, MTWA, GDD5) at 44.0% compared to other groups (all <21%) and the lowest proportion explained by rainfall (SPRE, WPRE, APET) at 10.5% compared to other groups (all >20%).

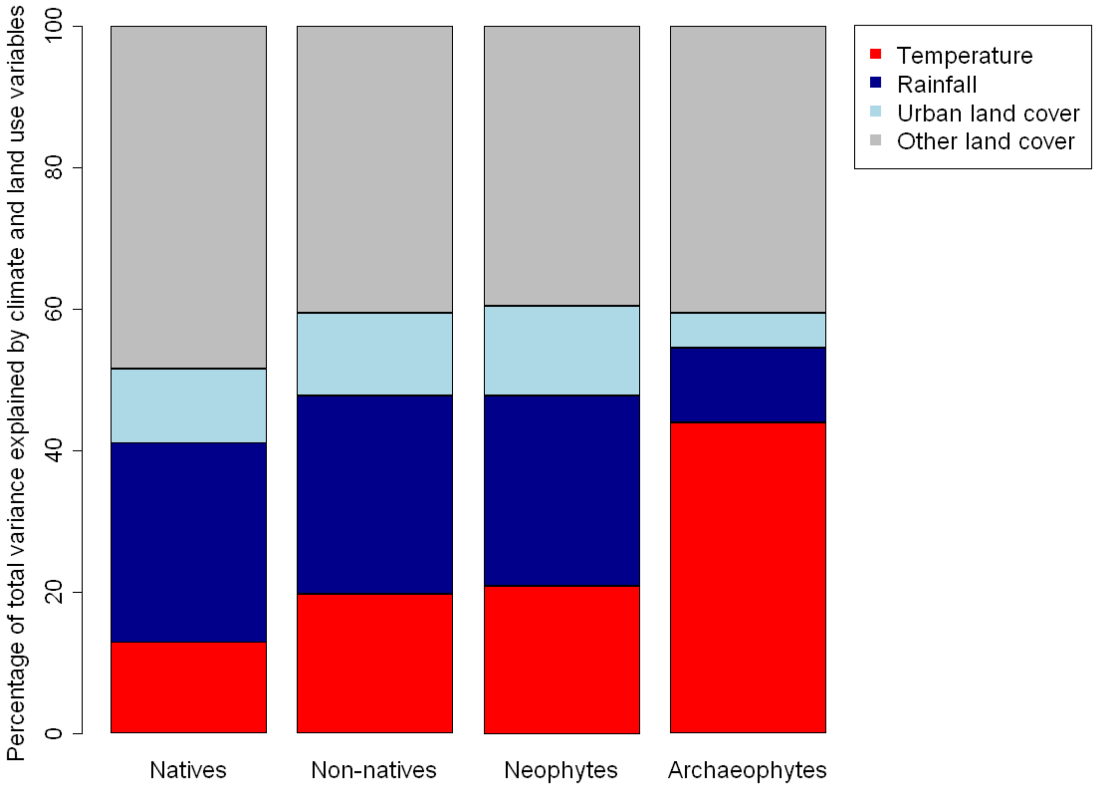


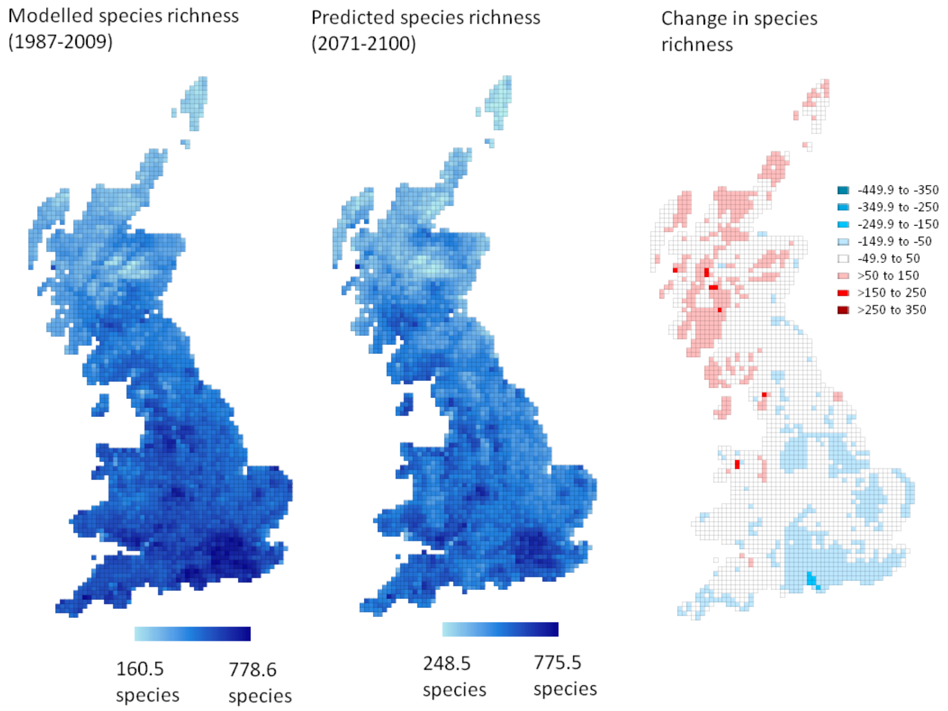
Figure 3.20. Results from hierarchical partitioning showing percentage of variance explained by temperature (MTCO, MTWA, GDD5), rainfall (SPRE, WPRE, APET), urban land cover and other land uses for natives, non-natives, neophytes and archaeophytes.

### *3.4.5 Predicted changes using projected climate data*

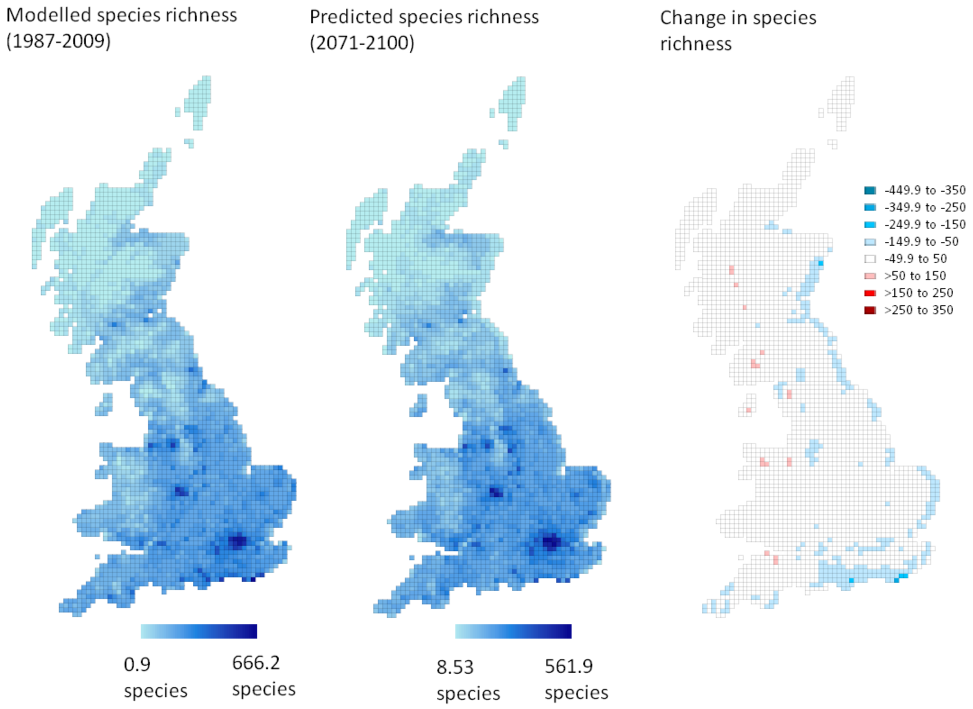
*Projected change in species richness*

Figures 3.21 to 3.25 show modelled current (1987-2009) species richness for natives and non-natives, predicted future (2071-2100) species richness and change in species richness (predicted minus modelled) for five SRES and climate model combinations.

All show similar patterns, with a predicted increase in species richness of natives and non-natives in the west and north and the greatest decrease in the south and east. Native species show a predicted increase in a slightly higher percentage of grid squares for all sets of climate data used (mean number of grid squares showing increase for natives = 45.4%, mean number showing increase for non-natives = 42.1%).



Native species



Non-native species

Figure 3.21. Modelled current species richness and predicted future species richness using B1 Hadley climate data. Change in species richness (predicted minus modelled): 40.3% of grid cells show an increase in species richness for natives and 39.6% show an increase for non-natives.

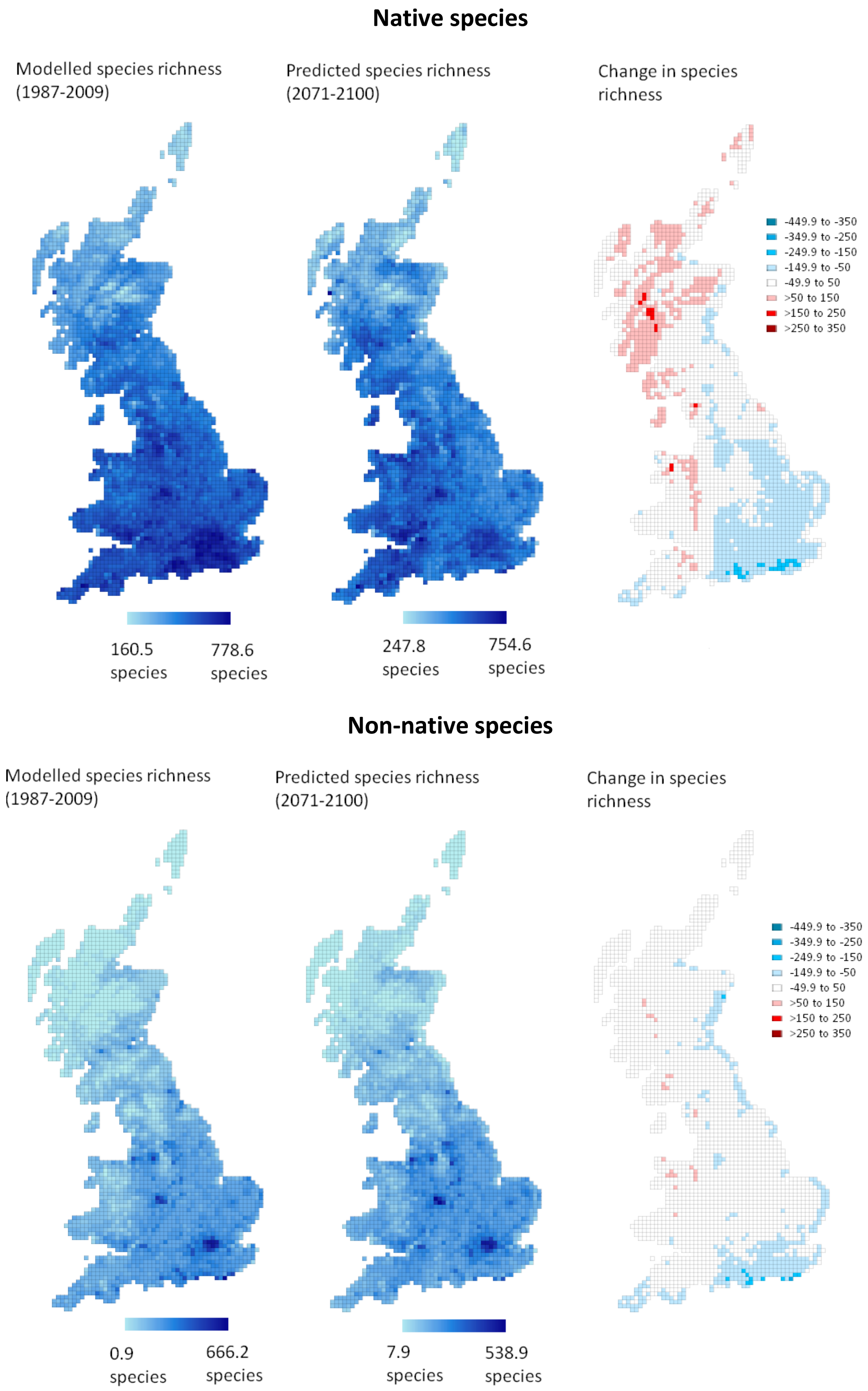
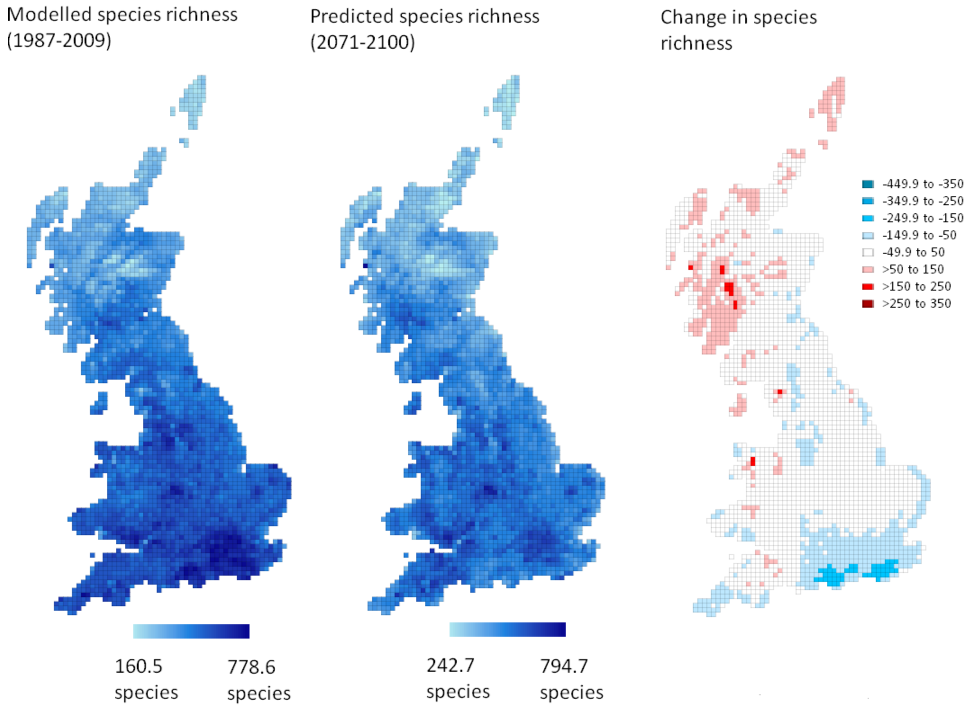


Figure 3.22. Modelled current species richness and predicted future species richness using A1 Hadley climate data. Change in species richness (predicted minus modelled): 46.9% of grid cells show an increase in species richness for natives and 41.5% show an increase for non-natives.

**Native species**



**Non-native species**

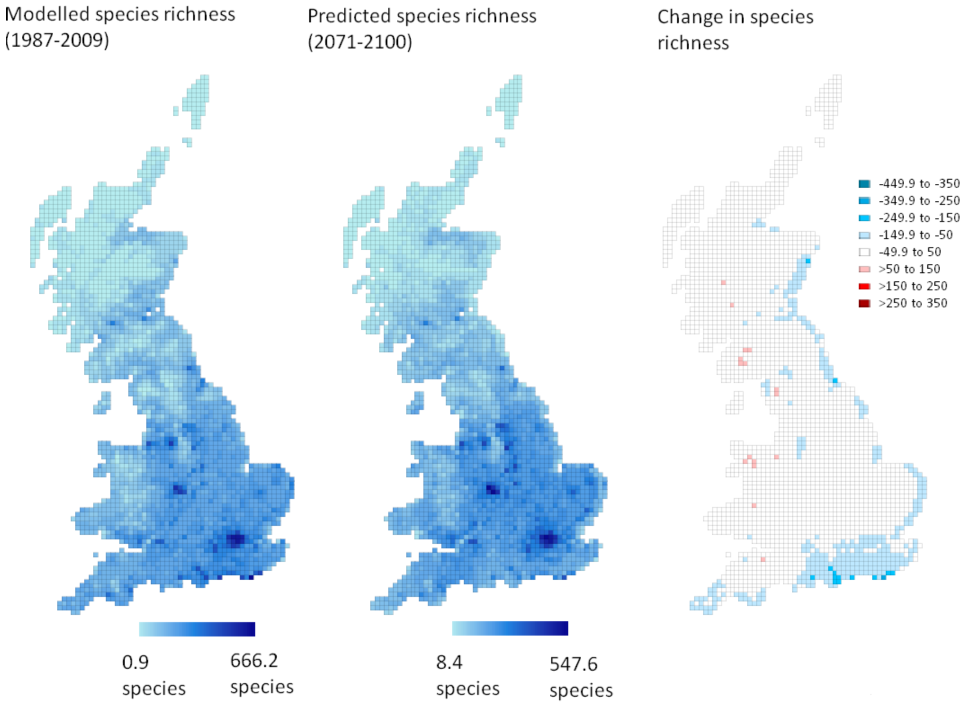
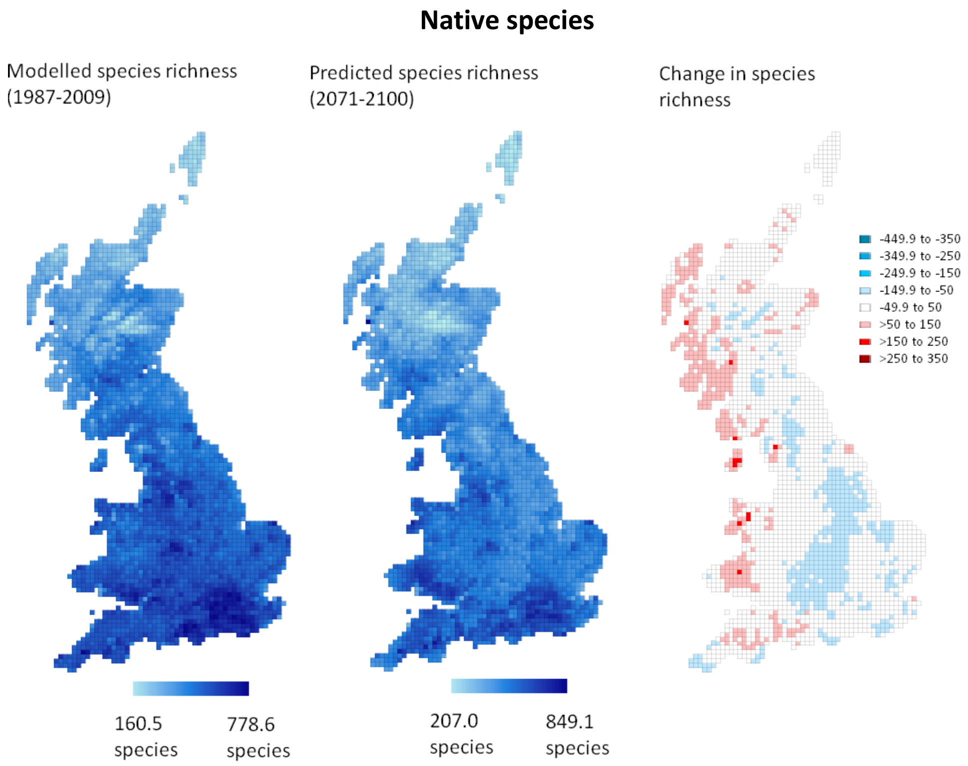
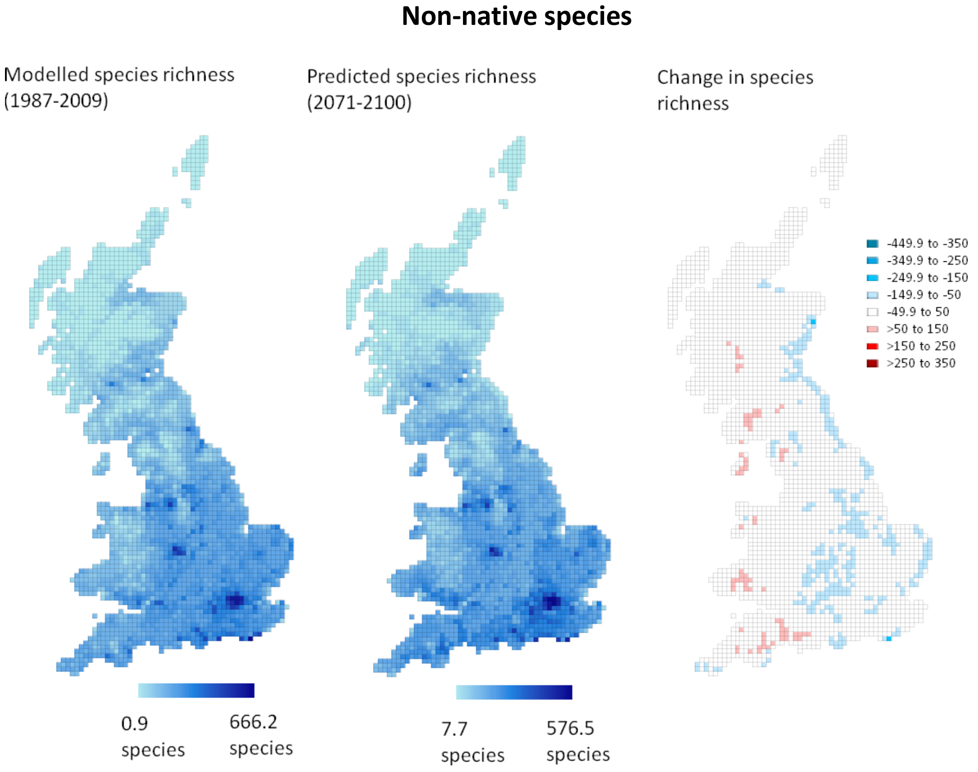


Figure 3.23. Modelled current species richness and predicted future species richness using A2 Hadley climate data. Change in species richness (predicted minus modelled): 45.9% of grid cells show an increase in species richness for natives and 43.6% show an increase for non-natives.



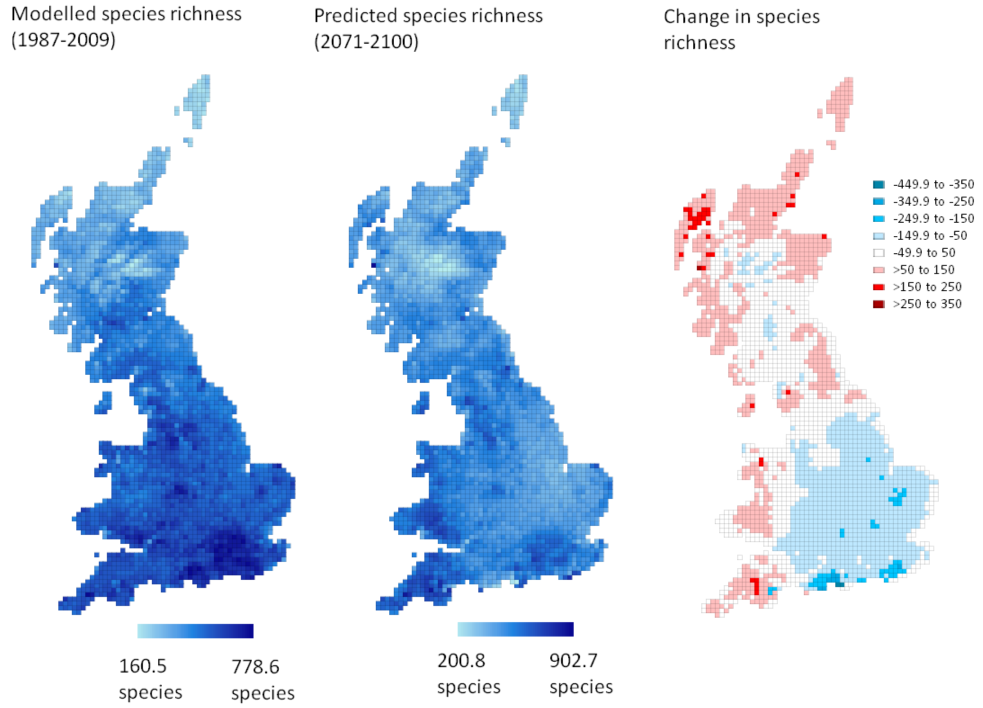
Native species



Non-native species

Figure 3.24. Modelled current species richness and predicted future species richness using A2 PCM climate data. Change in species richness (predicted minus modelled): 44.6% of grid cells show an increase in species richness for natives and 42.3 % show an increase for non-natives.

**Native species**



**Non-native species**

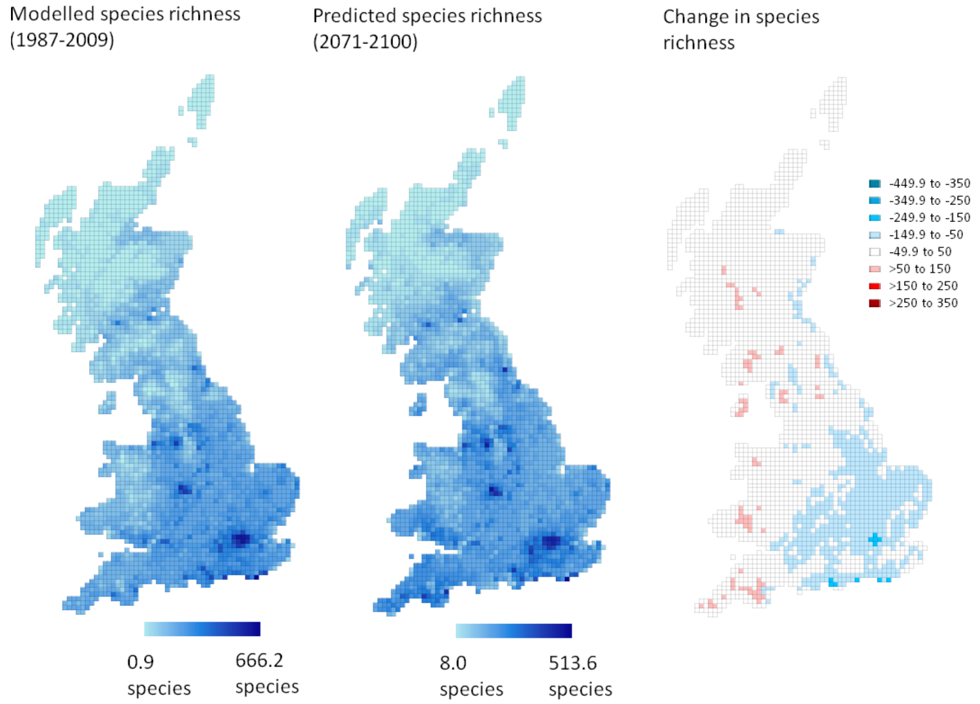


Figure 3.25. Modelled current species richness and predicted future species richness using A2 CSM climate data. Change in species richness (predicted minus modelled): 49.5% of grid cells show an increase in species richness for natives and 43.5% show an increase for non-natives.

### *Projected change in proportion of non-natives*

Figures 3.26 to 3.30 show modelled current (1987-2009) proportion of non-natives in the flora, predicted future (2071-2100) proportion of non-natives and change in proportion of non-natives (predicted minus modelled) for five SRES and climate model combinations.

All show similar patterns, with a predicted increase in proportion of non-natives in upland areas in the north and west and a decrease in the east and south. The mean number of grid squares showing an increase in the proportion of non-natives is 42.7%.

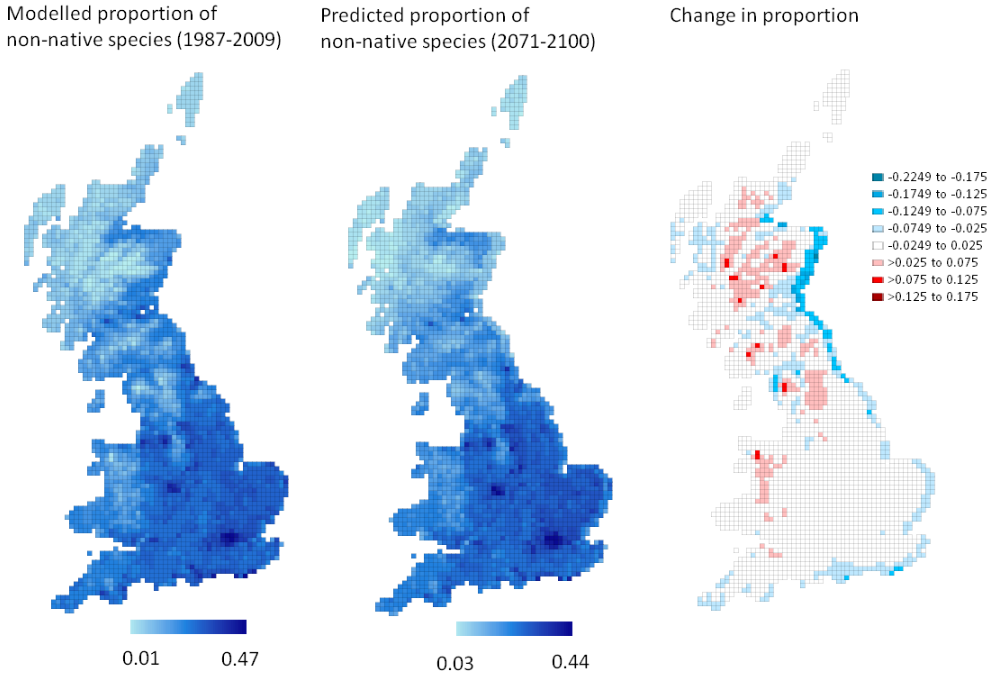


Figure 3.26. Modelled current proportion non-natives, predicted future proportion using B1 Hadley climate data and change in proportion (predicted minus modelled). 43.8% of grid cells show an increase in the proportion of non-native species.

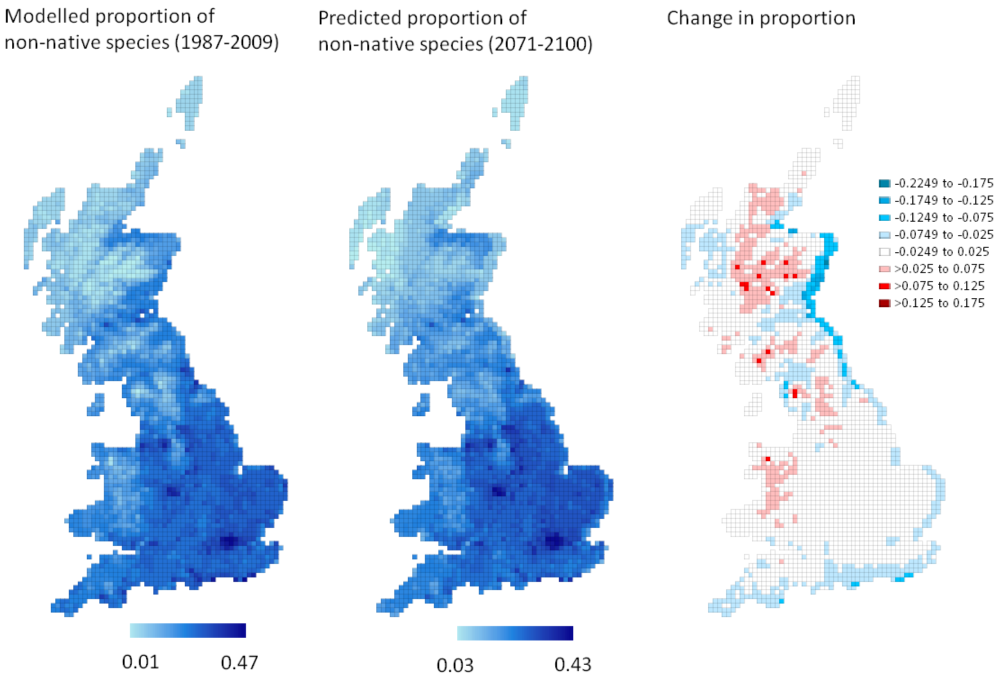


Figure 3.27. Modelled current proportion non-natives, predicted future proportion using A1 Hadley climate data and change in proportion (predicted minus modelled). 42.6% of grid cells show an increase in the proportion of non-native species.

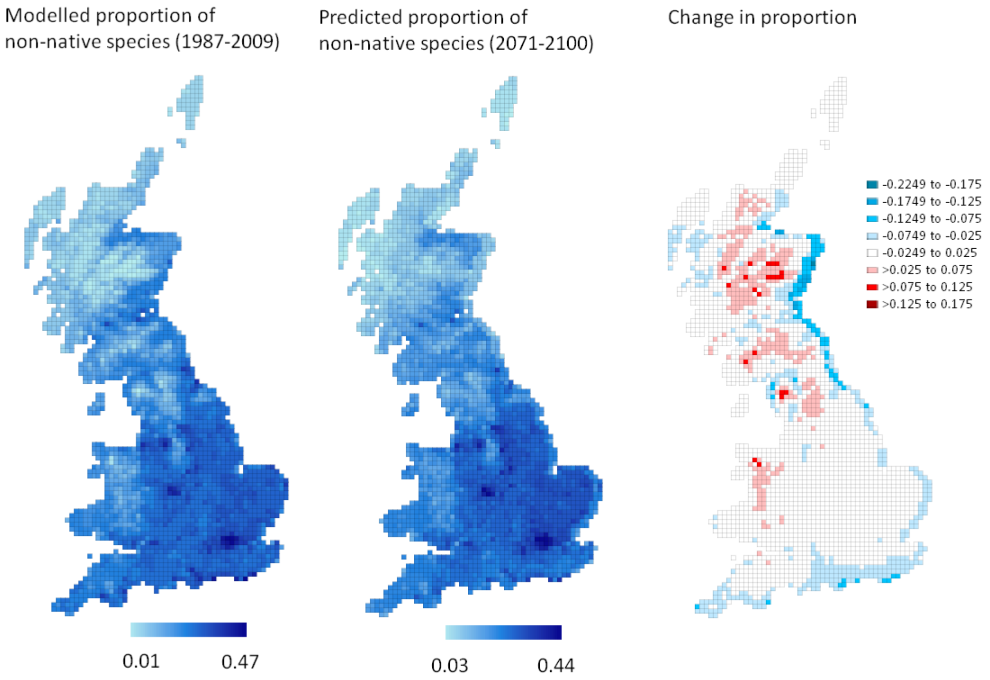


Figure 3.28. Modelled current proportion non-natives, predicted future proportion using A2 Hadley climate data and change in proportion (predicted minus modelled). 44.8% of grid cells show an increase in the proportion of non-native species.

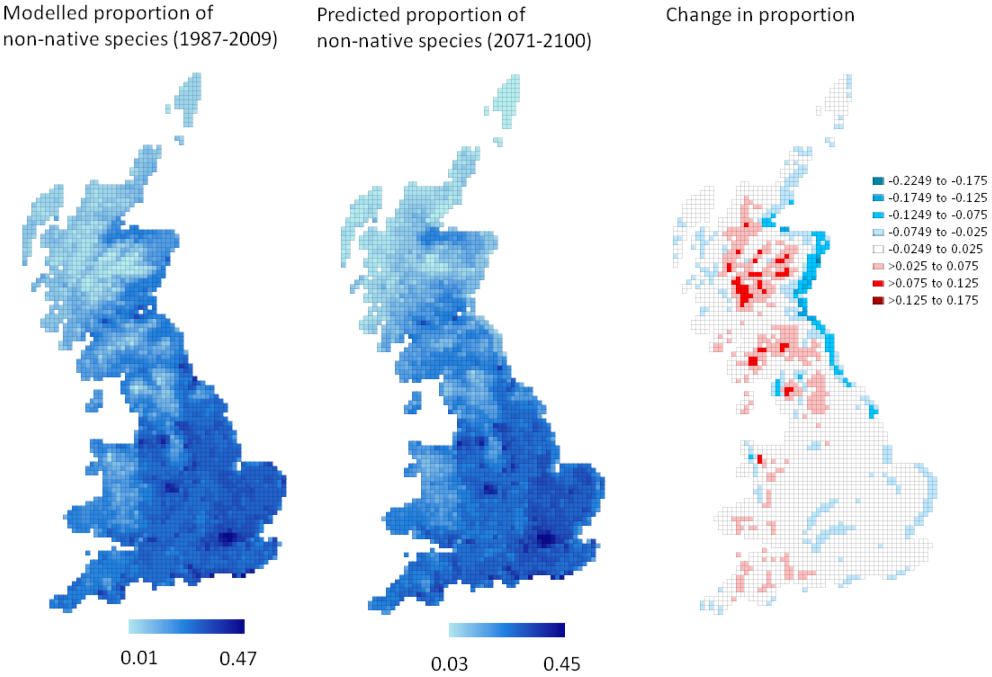


Figure 3.29. Modelled current proportion non-natives, predicted future proportion using A2 PCM climate data and change in proportion (predicted minus modelled). 44.6% of grid cells show an increase in the proportion of non-native species.

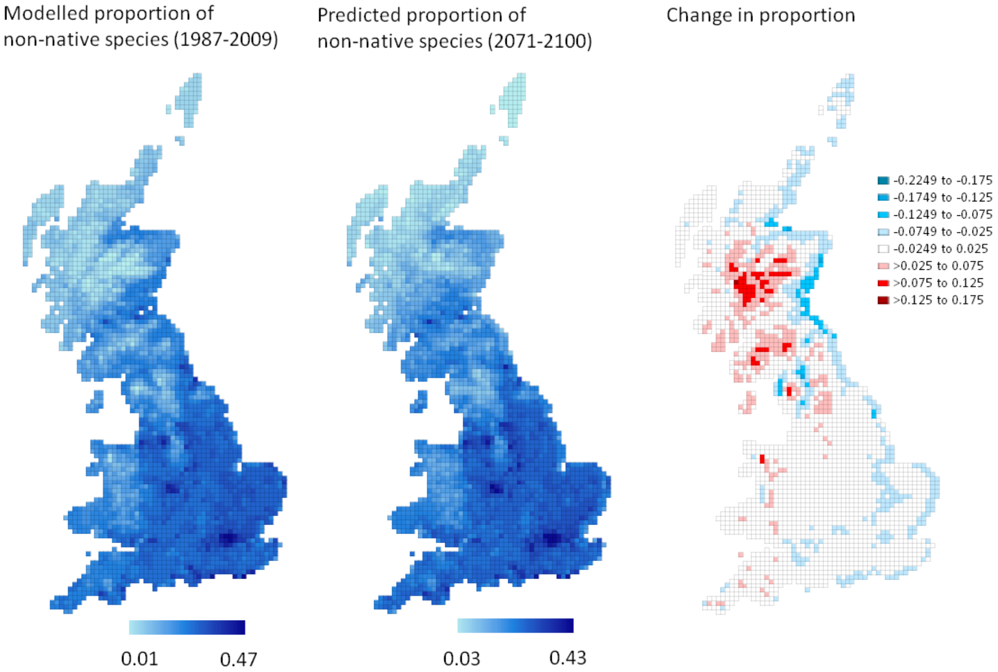


Figure 3.30. Modelled current proportion non-natives, predicted future proportion using A2 CSM climate data and change in proportion (predicted minus modelled). 37.7% of grid cells show an increase in the proportion of non-native species.

## 3.5 Discussion

### *3.5.1 Patterns of non-native species richness with climate and land use*

Non-native species richness and neophyte species richness show the strongest relationships with urban land cover (Table 3.2 and 3.3; highest Z value, positive slope). Natives and archaeophytes are also positive with urban land cover, but show weaker relationships. Native species richness and archaeophyte species richness show the strongest relationship with temperature, with greater species richness in warmer areas of Britain (Table 3.2 and 3.3; for natives, the highest Z value is for a positive first order polynomial slope with GDD5, and for archaeophytes, the highest Z value is for a positive first order slope with MTWA). GDD5 and MTWA are also positive for all non-native species and neophytes (first order polynomial slopes), but these groups show weaker relationships with temperature. Significant relationships with rainfall variables (APET, SPRE and WPRE) are negative for all groups. Thus, non-native species richness is higher in warmer and drier, more urban areas of Britain, with neophytes more associated with urban land cover and archaeophytes more associated with temperature. These results are consistent with the general patterns in previous studies, which showed positive associations with temperature (Hulme, 2009b; Albuquerque *et al*., 2011) and anthropogenic habitats (Maskell *et al.,* 2006; Hulme, 2009b; Albuquerque *et al*., 2011) and negative associations with rainfall (Hulme, 2009b; Albuquerque *et al*., 2011).

The results from Hierarchical Partitioning (HP) showed no clear pattern when proportion of total variance explained by climate variables was compared to land use variables (Figure 3.20, Table A1.2), with a similar proportion of variance explained by climate and land use for native and non-native species. Natives have a slightly higher proportion of variance explained by land use than non-natives; climate could be expected to be more important for non-natives than natives as many species have been introduced from warmer regions of the world, some of which may not be frost tolerant or will have less time to complete their life cycles and reproduce with lower growing degree days than in their native regions. There is a large proportion of non-native plant species in Britain from Europe (48.5%) and Asia (16.5%) (Table 1.2; GB Non-native species secretariat, 2011b), which may come from native climates which are warmer and drier than in Britain. For natives, variation in soil type and habitat heterogeneity may be more important than climate, with squares with more variation being more species rich (e.g. Tscharntke *et al*., 2012). Within non-native species, archaeophytes had a slightly higher percentage variance explained by climate (54.5%) than for land use (45.5%) when compared to neophytes, with 47.8% explained by climate and 52.2% explained by land use. Archaeophytes also had the highest percentage explained by temperature (MTCO, MTWA, GDD5) at 44.0% compared to other groups (all <21%) and the lowest proportion explained by rainfall (SPRE, WPRE, APET) at 10.5% compared to other groups (all >20%). As archaeophytes have been introduced further back in time and have therefore had more time to become established and to colonise a range of semi-natural habitats, it could be expected that they are more likely to have formed distributions related to climate than neophytes.

### *3.5.2 Importance of urban land cover*

Consistent results for the importance of urban land cover for different groups were found using both GLMs (Figure 3.19, Tables 3.2 and 3.3) and HP (Figure 3.20, Table A1.2). All urban slope estimates from GLMs are positive, indicating species richness for all groups is positively associated with urban land cover. However, non-native species have a higher slope and Z value than for native species showing non-natives are more associated with urban land cover than natives. For non-natives, the results from HP show that urban land cover explains the largest proportion of variation explained by land use (with 11.7% for non-natives), with other variables including arable, broadleaved woodland and coniferous woodland explaining smaller proportions. This is as expected, with higher non-native species richness in habitats with a large anthropogenic influence due to increased likelihood of introduction in these habitats, levels of disturbance creating suitable habitats for colonisation and human activities aiding dispersal (e.g. Pyšek, 1998; Hill *et al*., 2002; Hansen and Clevenger, 2005). For native species, broadleaved woodland is the most important land cover variable at 18.5%, with urban second at 10.5%. Heterogeneity of habitats in squares with land cover types such as broadleaved woodland and urban may be important for native species richness, compared to squares where the majority of land cover consists of homogeneous species poor habitats such as arable or heathland (e.g. Tscharntke *et al*., 2012). It is also possible that the same factors leading to increases in non-native species richness with higher proportions of urban land cover could cause increased native species richness; for example, introductions of non-native species due to deliberate planting and escape from habitats such as gardens and parks (e.g. Dehnen-Schmutz *et al.*, 2007) could also provide a source for native species.

Within non-native species, neophytes are more associated with urban land cover than archaeophytes. The results from HP (Figure 3.20, Table A1.2) show a similar pattern to the results from the GLMs (Table 3.3), with neophytes more associated with urban land cover than archaeophytes. Heathland (16.7%) and arable (8.1%) are the most important land use variables for archaeophytes, with urban third at 4.9%. Heathland has a negative relationship with archaeophytes species richness in the GLM; grid squares with the highest proportion of heathland are in the north-west of Britain, while archaeophytes show the highest species richness in the south-east. Arable land use is expected to be important in determining the distributions of archaeophytes, as many species are arable crop species or weeds, and has a positive relationship in the GLM. The positive association of archaeophytes with urban land use in this study can be explained due to the decline of many arable weed species due to changes in farming practices (Preston *et al.*, 2002; Braithwaite *et al.*, 2006); some arable weeds species now occur only as casuals and many are seeded or deliberately planted, for example *Agrostemma githago* and *Centaurea cyanus* (for more detail relating to establishment see Chapter 4).

For neophytes, urban land cover explains the largest proportion of variation explained by land use (12.6% for neophytes), with positive relationships with other variables including arable, broadleaved woodland and coniferous woodland explaining smaller proportions. Urban land cover was expected to be the most important land use variable for neophytes, as the majority of more recent introductions have been intentionally brought to Britain as ornamentals for planting in gardens and parks (Roy *et al.*, 2012). Urban areas are associated with gardens and amenity planting where many non-native species are grown, providing foci from which they may escape (Pyšek, 1998; Dehnen-Schmutz *et al.*, 2007; Botham *et al.*, 2009; Roy *et al.*, 2012). Therefore, a higher neophyte than archaeophyte species richness would be expected in urban areas.

Previous studies have shown variable results related to the importance of urban land use for non-native species introduced at different times. Albuquerque *et al.* (2011) showed weak relationships with human influences compared to climate for non-native species introduced at different times, whereas other studies have shown both neophytes and archaeophytes to be strongly associated with anthropogenic influences (e.g. Hill *et al*., 2002; Hulme, 2009b). Botham *et al*. (2009) found that archaeophytes had a mainly negative association with urban land cover over time, with only 19 out of 140 species positively associated with urban land cover, while neophytes were more likely to be positively associated with urban. The results from this study, using high quality distributional data, indicate that both neophytes and archaeophytes have positive relationships with urban land cover; however, there is a stronger relationship for neophytes and a weaker relationship for archaeophytes.

### ***3.5.3 Predicting distributions using models***

Non-native species recently introduced to an area would be expected to be expanding their ranges to colonise all suitable habitats within their climatic range. Therefore, it would be expected that modelling distributions from climate and land use variables would be more difficult than for recently introduced species than for those which have had longer to establish. The time taken for neophytes to reach their maximum range has been calculated in several studies. Kowarik (1995) looked at time lags of non-native species in Germany over the past 400 years. Time lags were found to have a broad range: 6% began to spread within 50 years after their first cultivation, 25% lagged up to 100 years, 51% up to 200 years, 14% up to 300 years and 4% invaded only after more than three centuries. On average, there was a delay in range expansion of 147 years after a species was first recorded in the wild. It was established that successful invaders are not necessarily quicker in starting invasions than less successful species and that less than 10% of introduced species escape and appear in the wild, 2% become established and 1% may successfully invade the natural vegetation. Other studies have calculated the average time taken for neophytes to achieve the same average range sizes as natives, using the relationship between residence time and the geographical range of non-native species in European countries (Williamson *et al*., 2009; Gassó *et al*., 2010). Times of 151, 177, 145, 141 and 143 years were found for Ireland, Britain, Germany, the Czech Republic and Spain respectively, suggesting that it takes about 150 years on average for neophytes to reach their maximum range in European countries. Albuquerque *et al*. (2011) suggests a threshold mean residence time of greater than 200 years for a non-native species to reach its maximum distribution in Great Britain, and that equilibrium of richness with climate may take longer than 500 years.

Current species richness of different groups can be predicted well using climate and land use variables (Figures 3.5 to 3.12), indicating non-native species have formed patterns with these variables either through where they are able to establish or where they have been introduced. The correlation between predicted and recorded species richness for all non-natives is 0.863 (Figure3.6), while for natives it is 0.755 (Figure 3.8). The correlation between predicted and recorded species richness for archaeophytes is better than for neophytes (0.905 and 0.832 respectively; Figures 3.10 and 3.12). As expected, it is easier to predict species richness for archaeophytes, as they have had longer to form patterns related to climate and land use rather than only occurring where they happen to be introduced.

### *3.5.4 Changes in species richness with projected climate data*

Modelled current (1987-2009) species richness for natives and non-natives, predicted future (2071-2100) species richness and change in species richness (predicted minus modelled) for five SRES and climate model combinations all showed similar patterns, with a predicted increase in species richness of natives and non-natives in the west and north and the greatest decrease in the south and east (Figures 3.21 to 3.25). Native species show a predicted increase in a slightly higher percentage of grid squares for all sets of climate data used (mean number of grid squares showing increase for natives is 45.4%, while mean number showing increase for non-natives is 42.1%). Modelled current (1987-2009) proportion of non-natives in the flora, predicted future (2071-2100) proportion of non-natives and change in proportion of non-natives (predicted minus modelled) for five SRES scenario and climate model combinations also showed similar patterns, with a predicted increase in proportion of non-natives in upland areas in the north and west and a decrease in the east and south (Figures 3.21 to 3.25). The mean number of grid squares showing an increase in the proportion of non-natives is 42.7%.

This does not indicate a predicted increase in the proportion of non-native species in the flora for much of Britain, as native species richness is also predicted to increase. Northern and upland areas are predicted to become more like the relatively species-rich south, with increases in temperature leading to an increase in species richness of both natives and non-natives. However, the climate in the south, which was not included in the original models, is shown to lead to a decline in native species richness but could potentially lead to a greater increase in non-native species than shown. The species richness of natives in southern areas will depend on adaptability to new climatic conditions, while new introductions from regions of the world with warmer climates and spread of species already present which have not become established or expanded their ranges due to constraints such as frost intolerance may lead to an increase in non-native species richness (e.g. Simberloff, 2000; Theoharides and Dukes, 2007). All changes in species richness are dependent on dispersal and habitat availability which have not been considered here; the predictions of species richness are based only on projected changes in climate. Potential future increases in urbanisation are also likely to favour higher non-native species richness due to the positive association between non-native species and urban land cover (Figure 3.19, Table 3.2).

### *3.5.5 Recorder effort*

The models based on the BSBI monitoring squares over-predict species richness in the rest of the grid squares; this suggests that recorder effort may be lower in other grid squares. When comparing differences between predicted and recorded species richness for native and non-native species and for neophytes and archaeophytes, the same grid squares appear to be over- or under-predicted (Figures 3.13 and 3.14). Comparing means of recorded minus predicted species richness for each vice-county, the same areas are over- and under-predicted by the models for non-native and native species (Figure 3.16) and for neophytes and archaeophytes (Figure 3.18). This appears to be related to variations in vice-county recorder effort rather than any environmental variables not included in the models. Vice-counties which have had recording for floras in the time period used have higher than predicted species richness relative to those without additional recording for floras; examples with recent floras include Dunbartonshire, Cardiganshire, Somerset, Dorset, Bedfordshire and Berkshire.

### *3.5.6 Implications and conclusions*

Non-native species richness was found to be higher in warmer, drier, and more urban areas of Britain. Current species richness of different groups can be predicted well using climate and land cover variables. Differences between predicted and recorded species richness appear to be related to recorder effort at the vice-county level, with similar patterns for all groups. Urban land cover shows the clearest pattern when comparing species richness for different groups. Non-natives, natives, neophytes and archaeophytes all show positive relationships with proportion of urban land cover; however, non-native species are more associated with urban areas than natives and recently introduced non-natives are more urban than those introduced further back in time. Results from using projected climate data do not indicate a predicted increase in the proportion of non-native species in the flora for much of Britain, as native species richness is also predicted to increase. However, the species richness of natives in areas predicted to have the greatest climatic changes will depend on adaptability to a new environment, while non-native species which are not well suited to current climatic conditions may be able to establish and spread potentially leading to greater non-native species richness than shown in some areas.

# Chapter 4: Establishment of non-native plant species

## 4.1 Abstract

Studies of the arrival of non-native species commonly use residence time as proxies for the extent to which they have become established in new regions, given that the longer a species is present, the greater the opportunity for it to spread from the point of introduction to all parts of the region that are climatically suitable for it, and to colonise all available habitats. Whilst there is support for the observation that the distribution sizes of well-established species tend to increase in the decades and centuries following introduction, the link between time and the level of establishment is not guaranteed. The aim of this study was to examine whether non-native plant species that have been present in Britain for the longest time show the strongest tendencies to have established self-perpetuating wild populations, and to determine whether species with different levels of establishment are associated with particular climatic conditions and land uses. Records of 1728 non-native plant species in Britain were analysed at 10 x 10 km grid resolution, from 1987 to 2009. An establishment index was calculated for each species, based on the population performance of each introduced species, ranging from planted non-reproducing individuals through to fully self-sustaining wild populations (using records assigned a status by each recorder). Current distributions were modelled using Generalised Linear Models, constructed using a subsample of well-recorded grid squares and then used to predict species richness of different groups for the rest of Britain. Hierarchical partitioning was used to determine the importance of different climate and land use variables for different groups of non-native species. The establishment of self-sustaining populations of non-native plant species in Britain showed no relationship with length of time since introduction. Species with all levels of establishment were present in archaeophytes (introduced before 1500), older neophytes (introduced between 1500 and 1800), intermediate neophytes (introduced between 1800 and 1900) and recent neophytes (introduced since 1900). Statistical models showed a good capacity to explain the current species richness of well-established non-native plants using climatic and land use predictor variables. The least established species were poorly predicted, and typically associated with urban areas. Non-native plant species in Britain have become integrated into the flora,

responding to climatic and land use variables, but their establishment is not predictable on the basis of their time since introduction. The less well-established species are likely to continue to be directly reliant on human activities to persist, whereas the best-established species are limited by climate and habitat. Future studies of non-native species should attempt to distinguish between time since arrival and the level of establishment because the two may not be associated.

## 4.2 Introduction

Studies of the arrival of non-native species throughout the world commonly use “time since introduction” or “time since first observation in the wild” as proxies for the extent to which they have become established in new regions, given that the longer a species is present, the greater the opportunity for it to spread from the point of introduction to all parts of the region that are climatically suitable for it, and to colonise all available habitats. Previous studies have shown that longer residence times of introduced species leads to greater range sizes in the area they have been introduced into. Wilson *et al*. (2007) investigated the range sizes of invasive plant species in relation to residence time in South Africa and found that species introduced earlier and those with larger potential climatic ranges have current larger range sizes. Williamson *et al*. (2009) and Gassó *et al*. (2010) looked at residence time and range sizes in neophytes (non-native species introduced after 1500AD) in five European countries: Ireland, Britain, Germany, Czech Republic and Spain. Longer residence time led to larger range size, neophytes taking an average of around 150 years to reach their maximum range in these European countries. Haider *et al*. (2010) used residence time when studying species richness along altitudinal gradients in Spain and found that the altitudinal range of species tended to increase with time since introduction, and that the species reaching the highest altitudes were mostly old introductions. Huang *et al*. (2010) used time since introduction when studying invasiveness of non-native species in China, showing that the number of provinces occupied by an invader is significantly related to the time since introduction. Albuquerque *et al*. (2011) studied the extent to which arrival times of non-native species in Britain are associated with range sizes and found that mean range size increased with residence time.

Whilst there is support for the observation that the distribution sizes of well-established species tend to increase in the decades and centuries following introduction, the link between time and the level of establishment is not guaranteed. Previous studies have shown wide variations in lag times and rates of spread for non-native species in different areas. Kowarik (1995), for example, found a wide range of lag times in the spread of woody plant species in Brandenburg, Germany, with 6% beginning to spread within 50 years of their first cultivation, three-quarters doing so within 200 years, and the remainder taking more than 200 years to spread. Kowarik also concluded that the most successful invaders were not necessarily the fastest to initiate their invasions. Aikio *et al*. (2010) looked at the time interval between first naturalisation to invasive spread for 105 introduced species in New Zealand and found that a lag phase of several decades was common for New Zealand weeds. Lags averaged 20-30 years, but were greater than 40 years for about 5%. About 9% of species had no detectable lag phase. This average lag phase is shorter than for similar studies for Germany (Kowarik, 1995) and Australia (Caley *et al*., 2008), but longer than for Hawai'i (Daehler, 2009). Williamson *et al*. (2003) examined rates of spread of alien plants in Britain, comparing data from two time periods 30 years apart and calculating frequencies of increase, stasis and decrease for 118 species. A wide variation in rates of spread was found: some had spread up to 10km per yr, many had not spread detectably, and a smaller number had retreated. None of the factors tested to explain variation in rate was significant, and it was concluded that species-and location-specific factors may need to be considered to explain rates of spread. Therefore, the relationship between time since arrival and the level of establishment requires formal examination, and should not be assumed. Indeed, many fully-established native plant species also have small ranges, so range size may also not be a sensible metric of establishment, although range size may still be a useful proxy for the likely impact (invasiveness) of a non-native species.

Analyses of the spatial distribution of non-native species richness or individual species have generally found both land use and climate variables to be important factors in determining distributions. Previous studies have shown that the general pattern for non-native species richness is greater species richness in urban areas and other habitats with a large anthropogenic influence, greater species richness associated with higher temperatures in cooler regions of the world, and greater species richness in areas of higher rainfall in warm regions (e.g. Lambdon *et al*. 2008; Polce *et al*., 2011). However, there is disagreement on the relative importance of major factors determining species richness such as climate and land use. Some studies have indicated that climatic variables are most important. For example, Albuquerque *et al*. (2011) concluded that human alteration of ecosystems is far less important for variation in non-native richness than climate in Britain, with richness primarily and positively associated with temperature. Carboni *et al*. (2010) found that non-native plant species richness was strongly related to climatic factors on the Italian coast, with more non-natives found in areas with high rainfall. Secondarily, non-native introductions appear to be related to recent urbanisation and associated gardening. In contrast, other studies have concluded that land use and other human factors are most important with climate secondary. Pyšek *et al*. (2010), for example, found that human population density and wealth were the most important determinants of biological invasions across Europe when analysed jointly with environmental factors such as climate, geography and land cover. Polce *et al*. (2011) also tested whether the distribution and cover of non-native plant species in Europe was related to human disturbance and microclimate. The role of temperature was found to be weaker overall than land use in explaining the pattern of non-native species in Europe. However, in none of these cases was the level of establishment of the different species considered, other than by using residence time or range size as a proxy. Hence, the extent to which the importance of climate and land use varies amongst species that show different levels of establishment in a region is largely unknown.

Exact dates of introduction are not always known, so non-native species have often been separated into groups for analysis based on date of introduction. In Europe, they are often divided into archaeophytes (species introduced before 1500) and neophytes (species introduced after 1500) for analysis (e.g. Hulme, 2009b), although Albuquerque *et al*. (2011) also distinguished older neophytes (minimum residence time 200 to 500 years), intermediate neophytes (minimum residence time 100 to 200 years) and recent neophytes (minimum residence time less than 100 years). Interpretation of the effects of introduction date on range size or establishment are complicated by the fact that the biogeographical regions of origin of non-native species are correlated with their dates of arrival e.g. the majority of species introduced pre 1500AD are of Mediterranean origin, while species of Asian and American origin make up a larger proportion of introductions post 1500AD (GB Non-native species secretariat, 2011b). However, although Albuquerque *et al*. (2011) found that mean range sizes increased with residence time, no strong effect of region of origin on range size was detected. The “time since arrival” hypothesis for establishment would predict that archaeophyte species would be well established, with their distributions related to climate and broad patterns of land use, whereas neophyte species would still be spreading, such that their distributions would be related to human activity and urban land use.

Examination of whether time since arrival is, in reality, a good predictor of population establishment is still needed. The first aim of this study was, therefore, to develop an index of establishment for each species that is independent of date of introduction and to examine whether it is related to the date of introduction. The establishment index was developed by examination of the proportion of records of each species directly associated with human activities (deliberately planted in the wild or reliant on repeated introductions) compared to proportion of records indicating a species is reproducing and spreading on its own. This was used to test the hypotheses that: 1) level of establishment increases with greater time since introduction; and 2) range size increases with level of establishment. The second aim was to determine whether the species richness of non-native plant species with different levels of establishment showed different levels of association with geographic variation in the climate and land use in Britain. It was predicted that well-established flora would show richness patterns more closely related to climate, while poorly established species might be expected to show patterns of higher species richness in areas with high human activity, such as urban areas. Models were used to test the hypotheses that: 1) species richness of poorly established species is more associated with urban land use than for well-established species; and 2) well-established species richness is more associated with climate than land-use.

## 4.3 Methods

### ***4.3.1 Data***

#### *Plant species data*

Records of plant species in 10 x 10 km grid squares were provided by the Botanical Society of the British Isles (BSBI). Analyses of non-native plants used all 1728 non-native plant species, included in the New Atlas of the British and Irish Flora (Preston *et al*., 2002), that had been recorded in Britain between 1987 and 2009. Date of introduction and date of first record in the wild were used (collated for the GB Non-native Species Information Portal project: GB Non-native species secretariat, 2011b).

All statistical model building was based on a subset of 10 x 10 km grid squares which are known to have been consistently recorded for non-native species. These are the BSBI Monitoring Scheme (or Local Change) grid squares (Braithwaite *et al*., 2006): 291 squares regularly arranged in a systematic grid of 1 in 9 which have had additional recording in 1987/1988 and 2003/2004, and have a higher number of non-native species recorded than surrounding squares (Figure 2.1). These high intensity repeat-survey squares minimise recording variation associated with unsystematic botanical surveying across the remainder of Britain (Preston *et al*., 2002).

*Climate and land use data*

Environmental variables which have previously been shown to be useful when analysing vegetation distributions were chosen (e.g. Box 1981, 1995, 1996; Sykes and Prentice 1995). Climate variables used were annual averages over the time period 1960-1990 for mean summer (June to August) precipitation in mm (SPRE), mean winter (December to February) precipitation in mm (WPRE), growing degree days over 5°C (GDD5), mean temperature warmest month in °C (MTWA)  and mean temperature of the coldest month in °C (MTCO). The ratio of actual to potential evapotranspiration (APET) was also used, which is estimated using soil moisture accounting models and gives an index of effective drought (Prentice *et al*., 1992; Huntley *et al*., 1995). Proportions of each 10 x 10 km grid square associated with different land cover classifications were estimated from the Land Cover Map 2000 (Fuller *et al*., 2002): arable, urban, improved grassland, neutral grassland, acid grassland, calcareous grassland, broadleaved woodland, coniferous woodland, heath, inland rock and standing water.

### *4.3.2 Calculation of an establishment index*

An establishment index was calculated for each species for Britain using BSBI records. A subset of records for each species is assigned a status, which gives additional information related to whether a plant is reproducing in the wild. Recorders placed records of introduced plants into the categories shown in Table 4.1, as defined by Macpherson *et al*. (1996) and Macpherson (1997). The percentage of all records with an assigned status considered to be established (out of those recorded as casual, surviving, established and planted) was calculated.

*Establishment value for a species =*
*100 x No. of records established ÷ Total no. of records (casual + planted + surviving + established)*

Table 4.1. Definitions of the status of non-native species used by the Botanical Society of the British Isles plant recorders (Macpherson *et al*., 1996; Macpherson, 1997), used for calculating the establishment index.

| **Record status** | **Definition** |
|---|---|
| **Established** | Established in the wild (i.e. outside areas of habitation) for at least five years and spreading vegetatively or reproducing effectively by seed |
| **Casual** | Present briefly i.e. for less than five years, often for just one season, or intermittently |
| **Surviving** | Present in the wild for at least five years but neither spreading vegetatively nor reproducing effectively from seed |
| **Planted** | Deliberately planted in a wild situation but not established |

An establishment index was calculated for 1109 species out of 1728, as not all species had sufficient records with status; species with fewer than 10 records were excluded. Example species were chosen to show the range of establishment with time since introduction. Four different time periods were used (following Albuquerque *et al*., 2011): archaeophytes (introduced before 1500AD), older neophytes (introduced between 1500 and 1800), intermediate neophytes (introduced between 1800 and 1900) and recent neophytes (introduced after 1900). A poorly established species (with an establishment index value of less than 15%) and a well established species (with an establishment index greater than 85%) were chosen for each time period. Classification of species into archaeophyte and neophyte follows the New Atlas of the British and Irish Flora (Preston *et al*., 2002) and nomenclature follows Stace (1997).

### ***4.3.3 Analyses***

Species were classified into 21 percentile groups based for analyses: 0% establishment, >0 and ≤5% establishment, >5% and ≤10%, etc. up to >95%.  Species shown as having 0% establishment using the calculated establishment index (160 species) were excluded from further analyses as these species are not reproducing in the wild, having solely been planted or are casuals entirely dependent on reintroductions, and would not be expected to provide information on where species are likely to persist or spread in relation to climate or land use. Spearman's rank correlations, Moran's I, Generalised Linear Models and Hierarchical Partitioning were used to examine relationships between different variables.

#### *Generalised Linear Models*

Generalised Linear Models (GLMs) were used to determine the relationships between species richness, climate variables and land use.  GLMs were carried out using R version 2.13.1 (using the 'glm' function in the 'stats' package in R), specifying the family 'Poisson' as the response variable was count data (species richness). Climate variables and proportions of land cover were used as the predictor variables. Dispersion parameters were used to correct for overdispersion of residuals and predictor variables were removed using the Akaike information criterion (AIC). The climate and land use predictor variables were standardised to give a mean of 0 and a standard deviation of 1, allowing comparison of the slope estimates from the models. Second order polynomials were used for climate variables.  The BSBI Monitoring Scheme grid squares (Figure 2.1) were used to create the models, which were then used to predict species richness for the rest of the grid squares from their climate and land use data (using the 'predict' function in the 'stats' package in R). These predictions were compared with numbers of species actually recorded for these grid squares (using Spearman's rank correlations and Wilcoxon signed rank tests) to test the model accuracy and to examine patterns in recorder effort.

### *Hierarchical Partitioning*

Hierarchical Partitioning (HP) analyses were used to calculate the independent contribution of each predictor to the species richness for different groups of non-native species.  HP was carried out using the 'hier.part' package in R (Mac Nally and Walsh, 2004). HP involves measuring the increase of goodness-of-fit of all models with a particular variable compared with the equivalent model without that variable. The improvement in fit is then averaged across all possible models in which that variable occurs to produce a measure of its independent effects. A Poisson distribution with the default goodness-of-fit measure (RMSPE, Root-mean-square ‘prediction’ error) was specified.

## 4.4 Results

### *4.4.1 Relationship between time since introduction and establishment*

There was no relationship between the establishment index values of introduced plants and their dates of introduction to Britain, and a weak relationship with the dates they were first recorded in the wild (Figure 4.1): date of introduction and first observation in the wild are not good predictors of the level of establishment of wild populations.

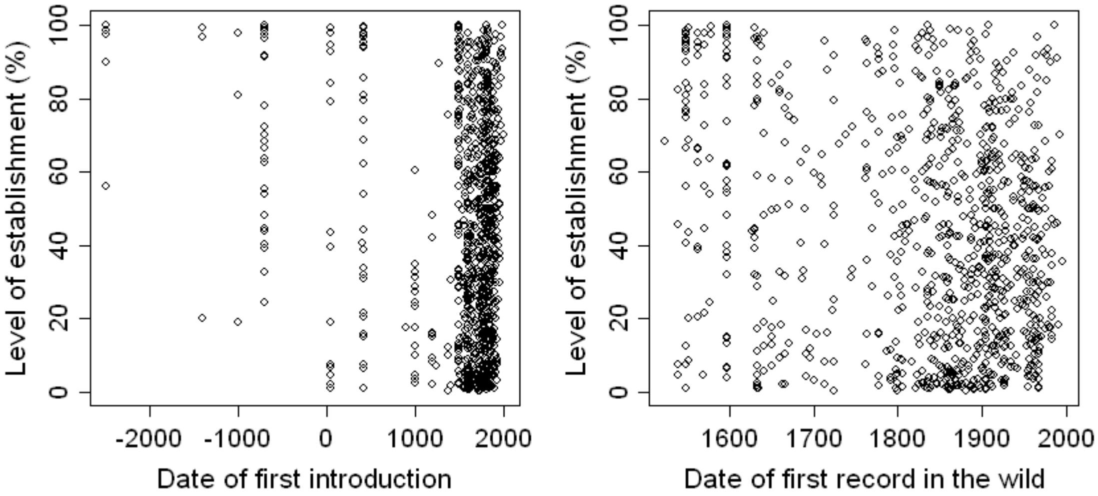
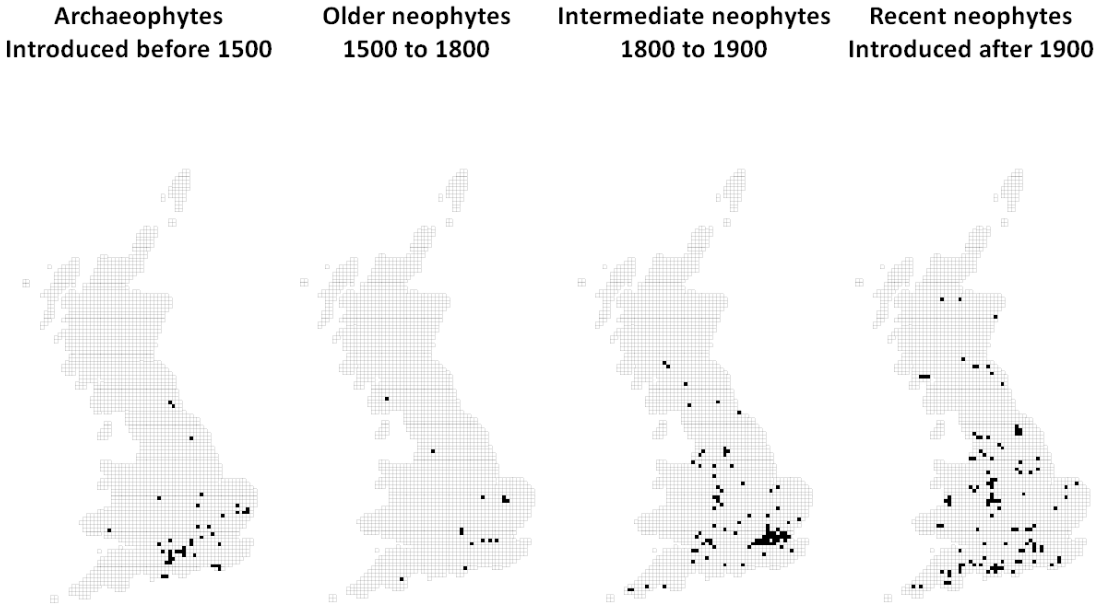


Figure 4.1. Relationships between the level of establishment of non-native species against their date of first introduction (Spearman's rank correlation coefficient -0.031, N = 949, p = 0.3478) and date they were first recorded in the wild (Spearman's rank correlation coefficient -0.167, N = 949, p < 0.0001).



*a. Adonis annua* (1.0%) *c. Berteroa incana* (4.8%) *e. Vicia villosa* (14.8%) *g. Nothofagus obliqua* (4.8%)

Poorly established species (<15% establishment)

*b. Geranium dissectum* (99.3%) *d. Pentaglottis sempervirens* (91.8%) *f. Calystegia silvatica* (98.8%) *h. Soleirolia soleirolii* (89.5%)

Well established species (>85% establishment)

Figure 4.2. Exemplar species chosen to illustrate the range of establishment of species introduced in four different time periods. Black squares indicate 10 x 10 km presence recorded between 1987 and 2009. Maps a, c, e and g show poorly established species, with a calculated establishment index <15%, and maps b, d, f and h show well established species, with a calculated establishment index >85%.

The lack of association between establishment and time since introduction is illustrated in Figure 4.2, which shows the current distributions in Britain of four poorly established species (with an establishment index value of less than 15%) and four well established species (with an establishment index greater than 85%), one each from four different periods of introduction.

The two archaeophyte examples given are *Adonis annua* and *Geranium dissectum* (Figure 4.2a and b). The date of introduction for *Adonis annua* was between 700BC and 0043AD, with the date of first record in the wild 1548AD. *Geranium dissectum* was introduced between 0043 and 0410AD, with date of first record in the wild 1629AD. Both species are annual weeds; however, *Adonis annua* has an establishment index of 1.0% (calculated from 207 records) while *Geranium dissectum* has an establishment index of 99.3% (calculated from 1532 records). *Adonis annua* is a cornfield weed with has low seed production and is thought to have declined in distribution due to changes in farming, with many recent records being deliberate introductions (Preston *et al*., 2002).

The two older neophyte examples (introduced between 1500 and 1800) are *Berteroa incana* and *Pentaglottis sempervirens* (Figure 4.2c and d). *Berteroa incana* was introduced in 1640, with date of first record in the wild in 1798, and *Pentaglottis sempervirens* was introduced in 1597, with date of first record in the wild in 1724. The poorly established *Berteroa incana* (establishment index 4.8%, calculated from 207 records) is a mainly casual biennial (occasionally annual/perennial) herb with a few naturalised populations (Stace, 2010). *Pentaglottis sempervirens* is a well established perennial herb (establishment index 91.8%, calculated from 2090 records) that has spread from gardens via seed and root fragments.

The intermediate neophyte examples (introduced between 1800 and 1900) are *Vicia villosa* and *Calystegia silvatica* (Figure 4.2e and f). *Vicia villosa* was introduced in 1815, with date of first record in the wild 1857. *Calystegia silvatica* was also introduced in 1815, with date of first record in the wild 1863. *Vicia villosa* is mainly a casual annual, introduced from grain, bird-seed and wool (Clement and Foster, 1994) and has an establishment index of 14.8% (calculated from 115 records). *Calystegia silvatica* is a well-established perennial climber of hedgerows and disturbed habitats, with an establishment index of 98.8%.

The two recent neophytes (introduced after 1900) are *Nothofagus obliqua* and *Soleirolia soleirolii* (Figure 4.2g and h). *Nothofagus obliqua* was introduced in 1902 with date of first record in the wild in 1956. *Soleirolia soleirolii* was introduced in 1905, with date of first record in the wild in 1917. *Nothofagus obliqua* is a deciduous tree, which sets seed and regenerates (Preston *et al*., 2002; Stace, 1997) but is currently poorly established as wild populations, with most recorded individuals having been planted (establishment index 4.8%, calculated from 62 records). *Soleirolia soleirolii* is a perennial herb which, although it can be frost sensitive, is well established where it occurs (Preston *et al*., 2002) with an establishment index 89.5%, calculated from 831 records.

### *4.4.2 Relationship between range size and establishment*

Figure 4.3 shows the relationship between level of establishment of non-native species against current range size, measured as the number of 10 x 10 km grid squares a species has been recorded in between 1987 and 2009. Range size has a weak positive correlation with establishment (Spearman's rank correlation coefficient 0.423, N = 1158, p<0.0001).

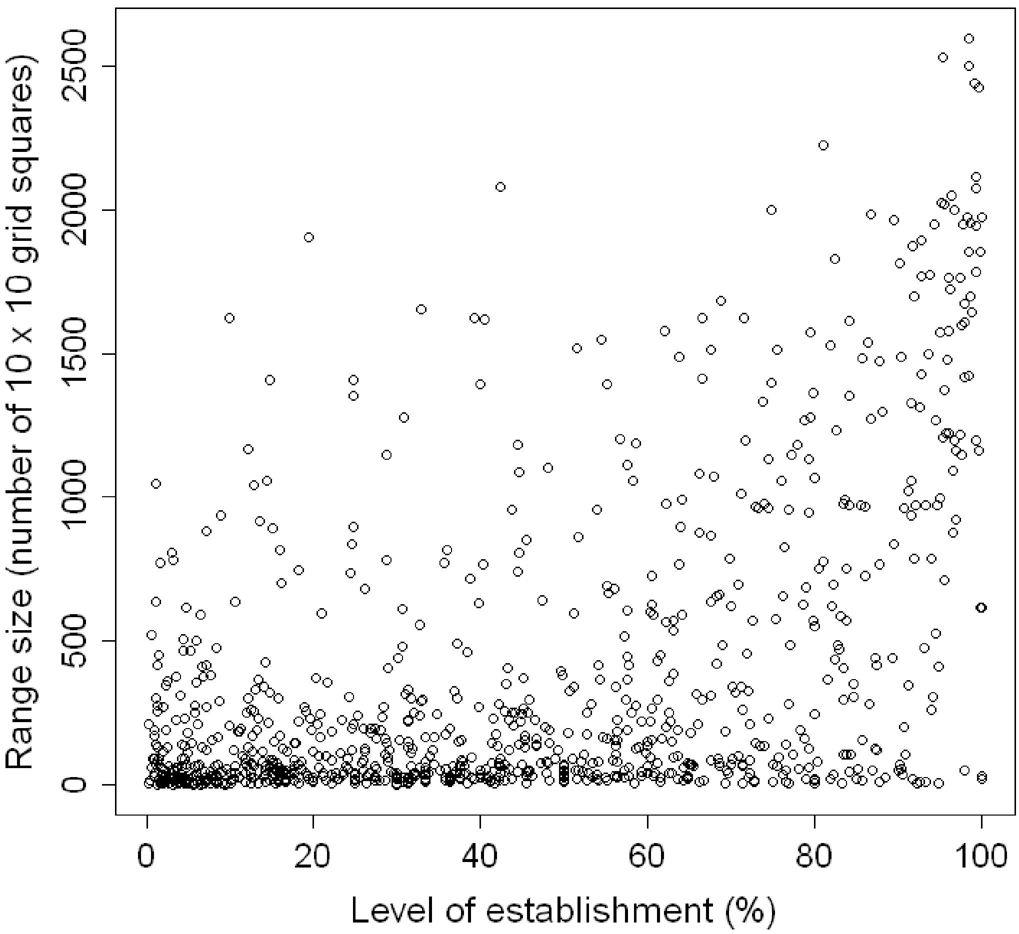


Figure 4.3. Relationship between level of establishment of non-native species and their current range size, using the number of 10 x 10 km grid squares a species has been recorded in between 1987 and 2009 (Spearman's rank correlation coefficient 0.423 (N = 949, p<0.0001).

Species with high establishment (>90%) and a large range (>2000 grid squares) are very common species which occur in a variety of habitats such as the neophytes *Matricaria discoidea* and *Acer pseudoplatanus* and the archaeophytes *Aegopodium podagraria* and *Capsella bursa-pastoris*.

Species with low establishment (<10%) and a small range (<50 grid squares) include species formerly cultivated which are now rarely grown and occur mainly as garden escapes and as bird seed aliens, such as the neophytes *Anchusa azurea* and *Dipsacus sativus* and the archaeophyte *Isatis tinctoria* (Clement and Foster, 1994; Preston *et al*., 2002). This group also includes trees occasionally planted as ornamentals or in plantations which regenerate in some areas, such as *Abies nordmanniana* and *Alnus rubra* (Stace, 1997).

Species with high establishment (>90%) and a small range (<50 grid squares) are mainly neophytes introduced for ornamental reasons, which are found occasionally as garden escapes or relics of cultivation and are well established where they occur. Examples include *Geum macrophyllum*, *Senecio smithii*, *Scilla liliohyacinthus*, *Narcissus minor* and *Genista aetnensis* (Preston *et al*., 2002).

Species with low establishment (<10%) and a large range (>800 grid squares) include tree species widely planted as ornamentals or in plantations which are occasionally self-sown, such as *Picea abies* and *Larix kaempferi* (Stace, 1997), and species widely grown as crops which frequently occur as crop relics or escapes from cultivation such as *Solanum tuberosum* and *Linum usitatissimum* (Preston *et al*., 2002).

### *4.4.3 Modelling species with different levels of establishment*

*Comparison of predicted and recorded species richness for different levels of establishment*

The results of the GLMs (Appendix 2, Table A2.1) indicate that the species richness of fully (>95%) established species is predicted better than that of poorly (≤5%) established species (Figure 4.4); Figure 4.5 shows that there is a significant positive correlation between predicted and recorded species richness, but that predictions are somewhat stronger (Spearman's rank correlation = 0.892) for established species (>95%) than for poorly established species (Spearman's rank correlation = 0.778). The correlation coefficients (as in Figure 4.5) for all 20 percentile groupings of establishment show that the predictive capacity of species richness GLMs increases with the level of establishment of the species considered (Figure 4.6). Graphs and correlations between predicted and recorded species richness for all establishment groups are shown in Appendix 2, Figure A2.1.

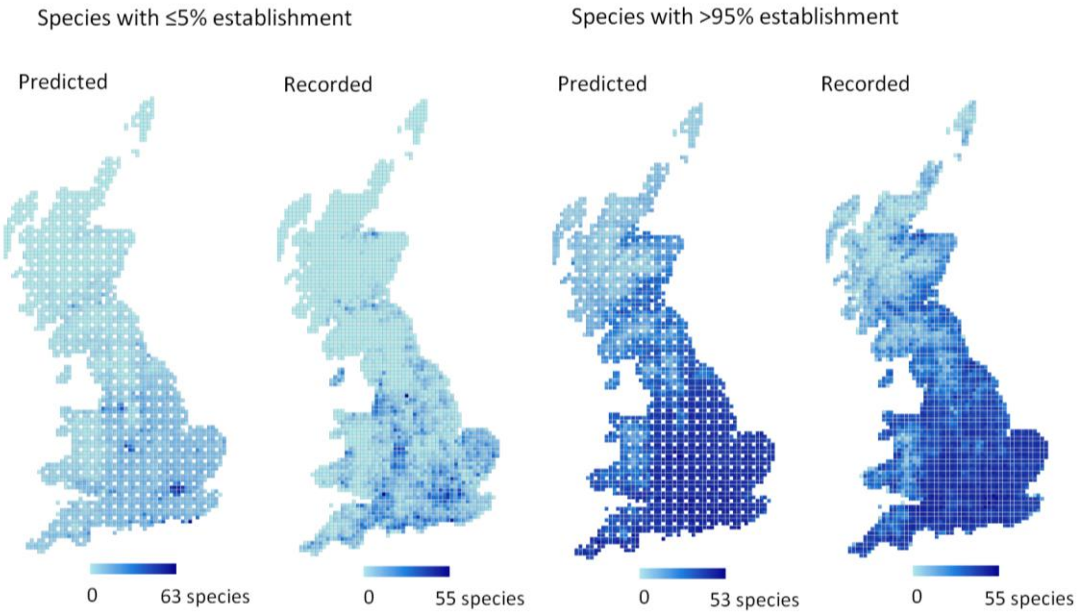


Figure 4.4. Modelled and recorded species richness for the least (≤5% establishment index) and most established species (>95% establishment index). White squares in a grid pattern on the predicted maps are BSBI monitoring scheme squares used to construct the model. Recorded species richness maps use all records from 1987 to 2009.

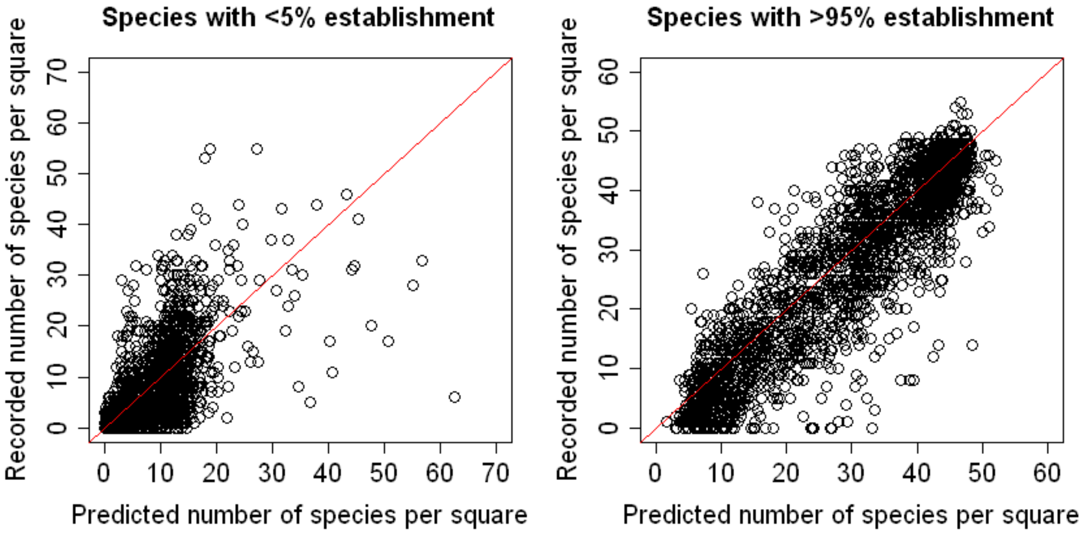


Figure 4.5. Relationships between modelled species richness and recorded species richness for each 10 x 10 km grid square (excluding model-building squares), for species with ≤5% establishment (Spearman’s rank correlation 0.778, N = 2499, p<0.0001) and for those with >95% establishment (Spearman’s rank correlation 0.892, N = 2499, p<0.0001).

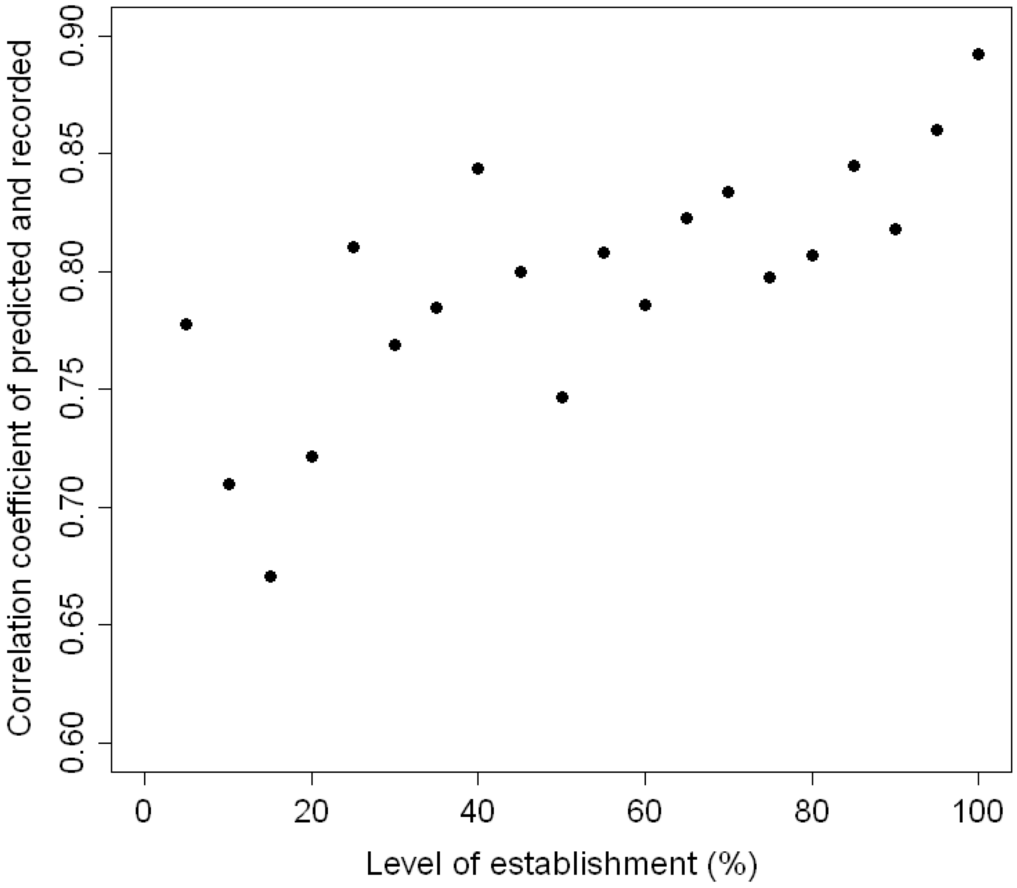


Figure 4.6. Correlation coefficients between species richness predicted from GLMs and recorded species richness, using species grouped by level of establishment (excluding model-building squares). The relationship between the two (Spearman's rank correlation coefficient 0.762, N = 20, p<0.001) indicates that GLMs are better at predicting the species richness of more established species.

### 4.4.4 Establishment with climate and land use

The proportion of urban land cover showed the clearest relationship with the level of establishment out of all climate and land cover variables used in the models. The urban slope estimate is always positive, indicating that non-native species richness is positively associated with urban land cover for all levels of establishment; but this relationship is far stronger for poorly established species than for those that are well established (Figure 4.7). This pattern can also be seen in the clustering of observed and predicted richness of poorly established (≤5%) species around London and other major urban areas, but not in the well established (>95%) species (Figure 4.4). The full results of the GLMs are shown in Appendix Table A2.1 (Appendix 2).

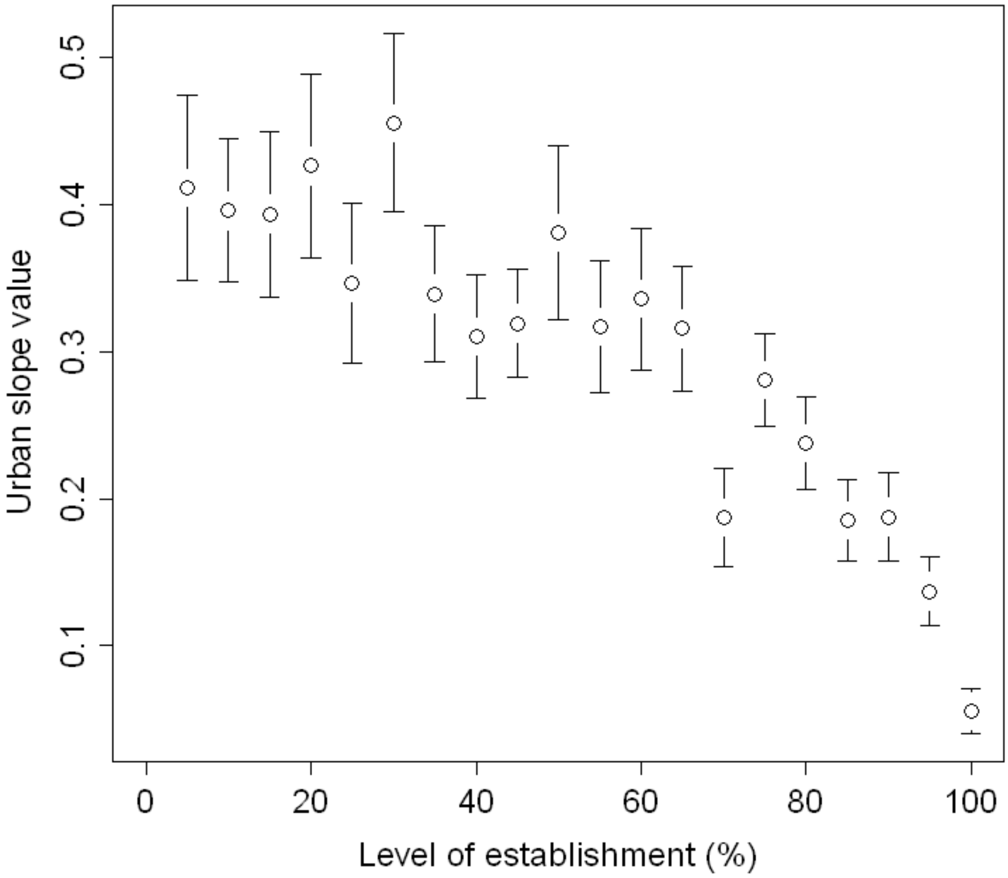


Figure 4.7. Urban slope estimates (± standard error) from GLMs of species richness, grouped by level of establishment. The urban slope estimate declines significantly with the level of establishment (Spearman's rank correlation -0. 914, N = 20, p<0.0001), showing that more established species are less associated with urban land cover.

Hierarchical Partitioning shows a similar pattern for the importance of urban land cover. Species richness for the most established species has a lower percentage of total variance explained by urban land cover than for the least established species, with a significant negative correlation between level of establishment and percentage of variance explained by urban land cover (Figure 4.8); more established species are less associated with urban land cover. Figure 4.9 shows the proportion of variance explained by climate variables for different levels of establishment. As predicted, there is a positive correlation between level of establishment and percentage of variance explained by climate, suggesting that more established species are more associated with climate; however, this relationship is not significant. Percentages for climate and all land cover variables are given in Appendix 2, Table A2.2.

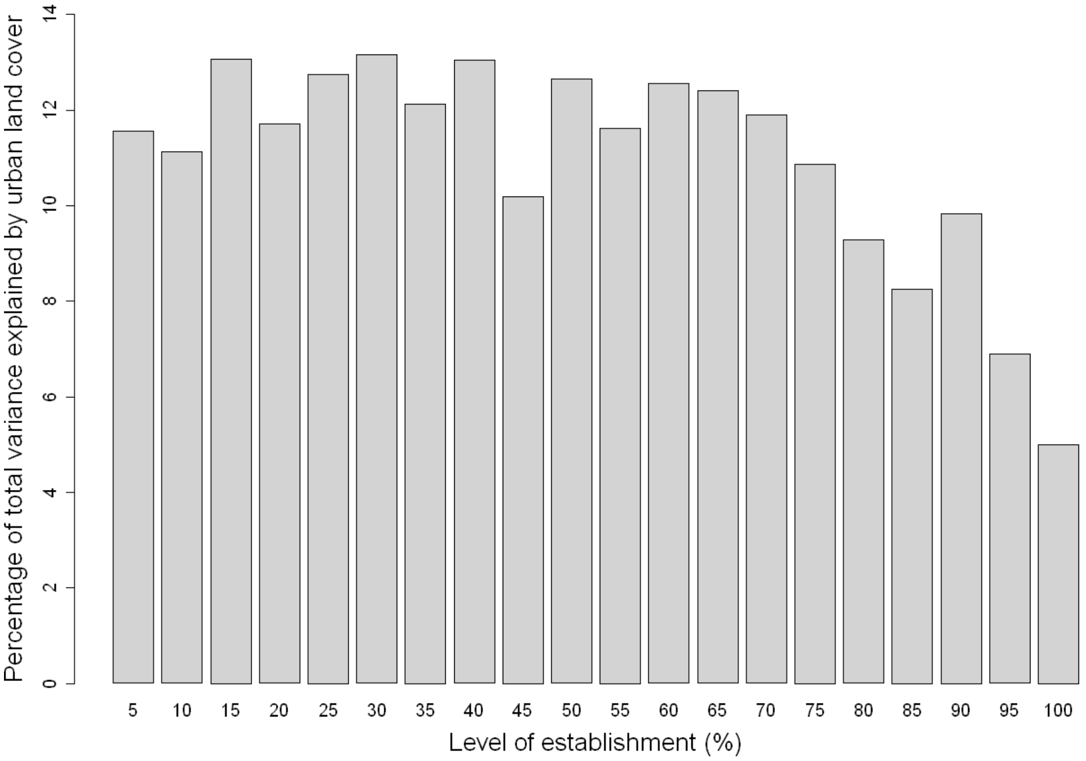


Figure 4.8. Percentage of variance from Hierarchical Partitioning explained by urban land cover for groups of species with different levels of establishment. The variance declines significantly with the level of establishment (Spearman's rank correlation coefficient -0.627, N = 20, $p<0.005$), showing that more established species are less associated with urban land cover.

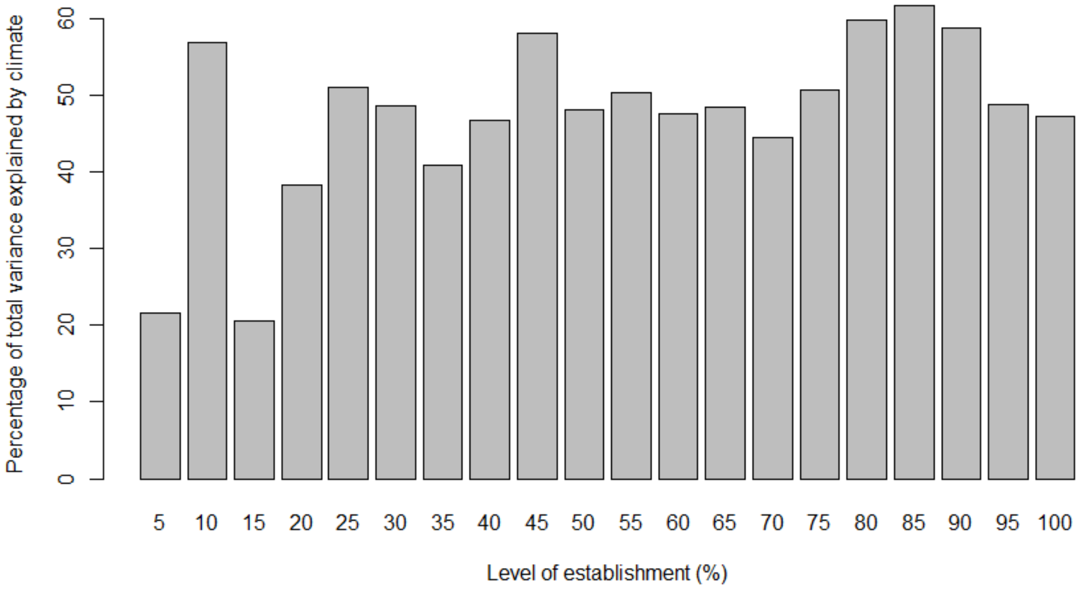


Figure 4.9. Percentage of variance from Hierarchical Partitioning explained by climate variables for groups of species with different levels of establishment. The variance shows a positive correlation with the level of establishment; however, this relationship is not significant (Spearman's rank correlation coefficient 0.435, N = 20, p=0.05692).

## 4.5 Discussion

### *4.5.1 Time since introduction, range size and establishment*

The residence time of non-native species has been used to group species when examining their distributions in relation to climate and land use (e.g. Albuquerque *et al*., 2011), either implicitly or explicitly assuming that time is related to the extent to which a species is established as self-sustaining wild populations in the region of introduction. However, the relationships between time since introduction and time first recorded in the wild with the calculated establishment index reported here (Figure 4.1) suggest that residence time is not necessarily a good predictor of level of establishment. This is consistent with previous studies which have shown that there is a wide variation in lag phases between introduction and the establishment of species (e.g. Kowarik, 1995; Aikio *et al*., 2010) and in rates of spread (Williamson *et al*., 2003), meaning that some species take much longer to become established and spread after introduction. It is also possible for the level of establishment to reverse, after an initial period of establishment and range expansion. Some archaeophyte species and older neophytes were once well established, but have since declined due to changes in land use and farming methods (Preston *et al*., 2002). Arable weed species such as *Adonis annua*, *Agrostemma githago* and *Centaurea cyanus* suffered major declines from c. 1880 to 1950 due to improved seed cleaning methods, increased use of agrochemicals and the density of modern crops, with their current distributions reliant on deliberate introductions.

Range size is also not necessarily a good predictor of level of establishment of non-native species (Figure 4.3). Studies which show a relationship between residence times and range size often only consider invasive species, the most established introductions; which may show a different relationship to those with less vigorous naturalised populations. Wilson *et al*. (2007) found that invasive plant species that were introduced early into South Africa (and those with large potential climatic ranges) have the largest current range sizes. Wilson *et al*. (2007) only included the successful alien species that have invaded natural and semi-natural habitats, the subset of species that could be expected to have short lag times and fast rates of spread, until they have expanded to fill all available habitats within their maximum suitable range. Huang *et al*. (2010) used time since introduction when studying invasiveness of non-native species in China and found that time since introduction is significantly related to the number of provinces occupied by an invader; this study also used only non-native species considered to be invasive. The inclusion of this subset of species with strong relationships between time and range size may drive all-species correlations found in some studies on all non-native species (cf. Albuquerque *et al*., 2011).

Some species may have a relatively large range and not be well established, reliant on repeated introductions, while others may have a small range due to climatic or habitat requirements but are relatively well-established within that area. Species with a large range and low establishment includes tree species frequently planted for forestry (e.g. *Picea abies* and *Larix kaempferi*) and commonly grown crop species (e.g. *Solanum tuberosum* and *Linum usitatissimum).* Species with a small range and high establishment includes many ornamental garden plants (e.g. *Senecio smithii, Narcissus minor* and *Geum macrophyllum*) which are not widely introduced, but can be persistent where they occur. Recently introduced species which are well-established with a small range could be considered most at risk of spreading in the future. These species may be recent arrivals which have not yet had time to expand their ranges, or may currently be restricted by poor natural dispersal or by climate and habitat requirements, such as low frost tolerance or poor ability to compete; increases in human dispersal or changes to climate or land use could allow these species to spread in the future.

### ***4.5.2 Predicting distributions using models***

The relationship between model prediction and level of establishment (Figure 4.6) indicates that models are better at predicting distributions of more established species than for less established species. This is likely to reflect the capacity of well established species to achieve distributions in the wild that are set by their climatic and land use limits (niches), while occurrence of poorly established species is related to where they are introduced. This is consistent with the strong association between urban areas and the species richness of established species in the GLM and Hierarchical Partitioning analyses (Figures 4.7 and 4.8); accidental introductions are more likely to occur in areas with high levels of human activity, especially in urban areas that contain gardens and parks, from which many non-native species may escape (Pysek, 1998; Dehnen-Schmutz *et al*., 2007; Botham *et al*., 2009; Roy *et al*., 2012).

### *4.5.3 Establishment with climate and land use*

It was found that species richness of poorly established species is more associated with urban land use than for well-established species, with a stronger positive relationship (Figure 4.7) and a larger proportion of variance explained by urban land cover (Figure 4.8) for poorly established species compared to well-established species. However, relationships with other land cover and climate variables were less clear (Tables A2.1 and A2.2). It was predicted that well-established species would be more associated would climate than with land use; a positive relationship between level of establishment and proportion of variance explained by climate was found, although this was not significant (Figure 4.9).

Previous studies separating species into archaeophytes and neophytes have found that archaeophytes are less associated with urban land use than neophytes (e.g. Hulme, 2009b; Botham *et al*., 2009). One explanation is that species may be introduced and establish wild populations in urban areas, and subsequently spread into the surrounding countryside, but it is equally plausible that there has been a shift in the modes of introduction. Archaeophytes may be more likely to grow away from urban areas due to the routes of introduction in the past. For example, arable weeds that were introduced over 500 years ago would predominantly have arrived as grain contaminants and with wool shoddy, or intentionally as crop species. In contrast, neophytes introduced in the last 200 years are more likely to have been introduced as garden plants, as amenity planting, from food waste etc., all activities that are more frequent in urban areas. It appears that both processes - shifts in modes of arrival, and expansions away from the points of arrival - are at play. For example, there are well-established neophyte species which have spread into semi-natural habitats despite their initial introduction through horticulture; *Impatiens capensis*, a neophyte originally introduced as an ornamental, has shown a steady expansion into semi-natural habitats since it was first recorded outside of cultivation in 1822 (Preston *et al*., 2002; GB Non-native species secretariat, 2011b). However, some of the poorly established archaeophytes have become restricted to habitats with greater human influence where they rely on the ongoing release of propagules; *Agrostemma githago* and *Adonis annua* are both previously well established species which now mainly occur as deliberate introductions (Preston *et al*., 2002).

### *4.5.4 Implications and conclusions*

The establishment index used has been calculated from records given a status (established, casual, planted and surviving) by recorders. Botanical recorders are asked to score records of non-native species according to the definitions of establishment listed in Table 4.1, but there is a degree of subjectivity in assigning records to these categories. Recorders assigning a status make an informed decision based on a number of factors including population size, evidence of regeneration, available habitat, and how a species was likely to have been introduced into the area. However, there will always be examples where it is very difficult to tell. There may be a more objective way of classifying records in the future: The Botanical Society of the British Isles is currently developing a new method to classify records by status, by classifying species in relation to the degree of regeneration and the extent to which they are invading semi-natural habitats (with suggested categories being survivor, casual, ruderal, established and transforming). However, using the status of records to quantify the level of establishment of non-native species does give clear patterns, and provides an alternative to using date of introduction when examining patterns with climate and land use.

The relationships of time since introduction and time first recorded in the wild with the calculated establishment index used in this study suggests that residence time is not a good predictor of level of establishment (Figure 4.1). Range size is also not necessarily a reliable indicator of level of establishment (Figure 4.3), except for the most established species with long residence times. As expected, models are better at predicting distributions of well established species than for poorly established species and poorly established species are more associated with urban land cover than well established species. Level of establishment is not necessarily related to residence time, meaning that newly arrived species can be as invasive as long established species; this warns against complacency in dealing with newly arrived species, especially if they have been shown to be a problem elsewhere. Recently introduced species which are well-established within a small area could be expected to be more likely to expand their ranges and become more abundant, potentially changing the composition of native communities, than poorly-established species with larger ranges. More informative ways of quantifying establishment of non-native species in the future could involve a classification which takes into account whether a species is producing seed or seedlings, population size, distance from point of origin and method of introduction; better recording of habitats would also give information on where non-native species are most likely to become frequent. Future studies of non-native species should attempt to distinguish between time since arrival and the level of establishment because the two may not be associated.

# Chapter 5: Distribution and establishment of Plant Functional Types

## 5.1 Abstract

Plant Functional Types (PFTs) can be defined as groups of plants exhibiting similar responses to an environment. Analyses using traits show that classifications based on life form capture variation in several important functional traits, with life forms having been shown to have predictable responses to changes in environmental variables such as water availability, temperature and disturbance. PFTs of non-native species were used to examine species richness in relation to climate and land use, as successfully modelling current species richness from environmental variables would allow prediction of future changes with climate and land use change, showing which groups may be most likely to increase in future. The level of establishment of different groups was also examined to determine which groups are most successful in relation to climate and land use variables. 1728 non-native plant species were classified into two PFTs: Raunkiaer life forms, using position of over-wintering buds, and a second life form classification similar to those used in vegetation modelling, dividing groups based on leaf-type and evergreen/deciduous. Generalised Linear Models (GLMs) were used to model species richness of PFTs in relation to climate and land use variables. The importance of different climate and land use variables were examined using results from GLMs and Hierarchical Partitioning. Levels of establishment for each group were compared using a calculated establishment index. General patterns with climate and land use show that species richness of all PFTs appears to have similar results with climate, with positive relationships with temperature variables and negative relationships with rainfall. Species richness of all groups is also positively associated with urban land cover; however, some PFTs are less associated with urban areas than with other land cover types. The least established groups (annuals and needle-leaved evergreens) show greater associations with land cover than with climate, with patterns related to where they are likely to be introduced. More established groups (chamaephytes, geophytes and hemicryptophytes) show a greater association with climate. Positive relationships with temperature and urban suggests all groups have potential to increase with future urbanisation and climate change.

## 5.2 Introduction

Plant Functional Types (PFTs) can be defined as groups of plants exhibiting similar responses to an environment (Diaz and Cabido, 1997; Duckworth *et al*., 2000; Lavorel and Garnier, 2002; Wang and Ni, 2005; Lavorel *et al*., 2007). Functional classifications of plant species include classifications according to plant morphology, life history and regeneration traits (Grime *et al*., 1997; Lavorel and Garnier, 2002). Many different classifications have been proposed based on the study area: previous work ranges from classifications of global vegetation into broad functional types for models (Box, 1981, 1996; Diaz and Cabido, 1997; Malcolm *et al*., 2002) to much more detailed classifications for specific communities of an area such as semi-arid woodland (Westoby and Leishman, 1997) or arctic tundra (Chapin *et al*., 1996).

PFT classifications based on life form (e.g. Raunkiaer, 1934) have been used to study distributions of non-native species in relation to climate and land use (Pyšek *et al*., 1995; Hulme, 2009b; Smith, 2010; Marini *et al*., 2012). Analyses using traits show that classifications based on life form are useful, as they capture variation in several important functional traits, with life forms having been shown to have predictable responses to changes in environmental variables such as water availability and temperature (e.g. Chapin *et al*., 1996; Diaz and Cabido, 1997) and disturbance (e.g. McIntyre *et al*., 1995). Raunkiaer's life form classification (Raunkiaer, 1934) groups plants according the position of dormant meristems over the unfavourable season. Raunkiaer argued that height of the renewal bud allowed prediction of a plant's tolerance for the likelihood, duration and severity of an unfavourable season, typically low temperature or drought or both. Species are divided into seven main categories (Figure 5.1): trees (phanerophytes), shrubs (nanophanerophytes) and sub-shrubs (chamaephytes), which survive the unfavourable season with buds at various heights above ground; rosette plants (hemicryptophytes), which survive with buds at or near soil surface; plants with bulbs, rhizomes, corms or tubers (geophytes), which survive below the ground; aquatic plants (hydrophytes) which survive under water; and annuals (therophytes) that survive as seeds. Later classifications used in models for studying response of vegetation to global climate are mostly based on subdivisions of life forms (e.g. Box, 1981, 1995; Chapin *et al*., 1996), including traits such as leaf type (e.g. broad, narrow/needle, absent) and seasonal photosynthetic habit (e.g. summer-green).

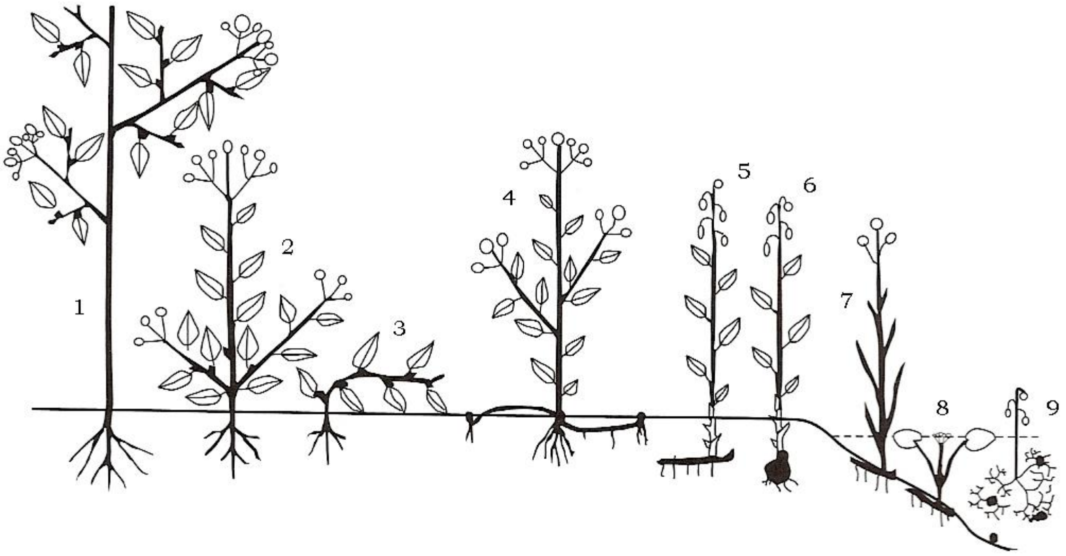


Figure 5.1. Raunkiaer life forms (Raunkiaer, 1934): 1 = phanerophyte (tree), 2 = nanophanerophyte (shrub), 3 = chamaephyte (sub-shrub), 4 = hemicryptophyte (rosette plant), 5 and 6 = geophytes (plants with rhizomes, corms, tubers or bulbs), 7, 8 and 9 = hydrophytes (aquatic plants), and therophyte (annual plant) (not shown).

If climate is having a greater effect than land use on the distributions of non-native plant species in Britain, species richness of PFTs would be expected to vary in a predictable way based on climatic variables. A previous study examining the distributions of life forms in a small sample of non-native species in Britain (Hulme, 2009b) found some relationships between life form and climatic variables, with chamaephytes more associated with cooler, wetter areas and geophytes and therophytes more associated with warmer, drier areas. Recurring drought or low temperatures would be expected to favour species with their renewal buds protected by the seed coat, as in all annual species, or by their position progressively near, at or below the soil surface (Raunkiaer, 1934). Therophytes have been found to be dominant in dry regions, with areas with Mediterranean climates or deserts being characterised by a high proportion of annuals that survive the dry season as seeds (e.g. Danin and Orshan, 1990). Growth forms with buds below or near the soil surface (geophytes, hemicryptophytes and chamaephytes) are replaced by nanophanerophytes and phanerophytes with increasing temperatures in cold regions (Chapin *et al*., 1996; Kaplan *et al*., 2003) or increasing rainfall in dry regions (Danin and Orshan, 1990). Within phanerophytes, tolerance to drought and cold are dependent on leaf type and phenology, with broad-leaved evergreen species most susceptible to drought and cold temperatures, and deciduous and needle-leaved species better adapted to adverse conditions. For example, Box (1995) described dominant plant forms in biome types. In warm, wet regions, evergreen broad-leaved trees with a continuous growing season are the dominant plant form. In temperate regions, broad-leaved deciduous and winter-dormant trees are dominant, and in cool temperate or boreal regions they are more likely to be needle-leaved evergreen or needle-leaved deciduous and winter-dormant.

However, PFTs are also likely to be forming patterns based on land use. Marini *et al*. (2012) found an absence of life form dependent responses among non-native species along an elevation gradient in Italy, with non-native species richness showing a consistent positive relationship with temperature across all life forms, and concluded distribution of non-native plant species richness was more related to propagule pressure and availability of habitats created by human activities than to climatic filtering. If climate is not creating distinct patterns of different non-native life forms, it is also likely that traits associated with different life forms are likely to mean some are over-represented in certain habitats. Studies looking at the distribution of life forms in man-made habitats have found some life forms are over-represented. Knapp *et al*. (2008) compared plant traits in urbanised with rural areas and found clear differences in the proportion of trait states. Therophytes were found to be over-represented in more urban areas, as cities have a high proportion of unstable habitats (e.g. urban brownfields) that favour annuals and biennials and reproduction by seeds. Well-drained habitats and the urban heat island effect (e.g. Oke, 1982) also favour plants either able to cope with drier, warmer conditions (e.g. plants with succulent or scleromorphic leaves), or that avoid drought e.g. annuals that complete their life cycle in a temporal niche like springtime, when temperatures and drought stress are low.

Previous studies attempting to distinguish successful or invasive non-natives from unsuccessful non-native or native species using traits have generally found no definitive set of traits describing successful non-native species (e.g. Noble, 1989; Roy, 1990; Pyšek *et al*., 1995; Tecco *et al*., 2010). Characteristics of successful non-native species appears to be dependent on habitat, as different traits are more important in different habitats (e.g. Grime, 1974, 2001; Thompson *et al*., 1995). It would be expected that frequently disturbed communities would favour seed production and high dispersal ability, while closed communities would favour competitive ability and vegetative reproduction. Pyšek *et al*. (1995) found that successful invaders of man-made habitats are more likely to be therophytes or geophytes, using a competitor or competitor-ruderal strategy (with high vegetative growth rate or high reproduction with rapid seedling establishment and growth), while successful invaders of semi-natural habitats are more likely to be hemicryptophyte or geophyte with high vegetative growth rate.

This study used Raunkiaer life forms and a classification incorporating phenology/leaf type similar to global models to examine the species richness of non-native plant species in relation to climate and land use variables. These two classifications were chosen as they have been shown to be useful when using PFTs in climate modelling, and different groups would be expected to show distinct responses to projected climate changes. The main aims were to determine if non-native species with different Plant Functional Types are assuming distributions related to climate and land use, to allow prediction of future distributions, and to evaluate the level of establishment (using the establishment index calculated in Chapter 4) of different Plant Functional Types to determine which groups are most successful in relation to climate and land use variables. Analyses were used to test the hypotheses that: 1) non-native PFTs are forming distinct patterns with climate and land use variables; and 2) PFTs with more well-established species are forming patterns associated with climate, while PFTs with more poorly established species are more associated with land use due to methods of introduction.

## 5.3 Methods

### ***5.3.1. Data***

#### *Plant species data*

Records of plant species in 10 x 10 km grid squares were provided by the Botanical Society of the British Isles (BSBI). Analyses of non-native plants used all 1728 non-native plant species, included in the New Atlas of the British and Irish Flora (Preston *et al*., 2002), that had been recorded in Britain between 1987 and 2009. This includes both neophytes (non-native species introduced after 1500) and archaeophytes (non-native species introduced before 1500).

All statistical model building was based on a subset of 10 x 10 km grid squares which are known to have been consistently recorded for non-native species. These are the BSBI Monitoring Scheme (or Local Change) grid squares (Braithwaite *et al*., 2006): 291 squares regularly arranged in a systematic grid of 1 in 9 which have had additional recording in 1987/1988 and 2003/2004, and thereby have a higher number of non-native species recorded than surrounding squares (Figure 2.1). These high intensity repeat-survey squares minimise recording variation associated with unsystematic botanical surveying across the remainder of Britain (Preston *et al*., 2002).

### *Climate and land use data*

Environmental variables which have previously been shown to be useful when analysing vegetation distributions were chosen (e.g. Box 1981, 1995, 1996; Sykes and Prentice 1995). Climate variables used were annual averages over the time period 1960-1990 for mean summer (June to August) precipitation in mm (SPRE), mean winter (December to February) precipitation in mm (WPRE), growing degree days over 5°C (GDD5), mean temperature warmest month in °C (MTWA) and mean temperature of the coldest month in °C (MTCO). The ratio of actual to potential evapotranspiration (APET) was also used, which is estimated using soil moisture accounting models and gives an index of effective drought (Prentice *et al*., 1992; Huntley *et al*., 1995). Proportions of each 10 x 10 km grid square associated with different land cover classifications were estimated from the Land Cover Map 2000 (Fuller *et al*., 2002): arable, urban, improved grassland, neutral grassland, acid grassland, calcareous grassland, broadleaved woodland, coniferous woodland, heath, inland rock and standing water.

### *Classification of species into functional types*

1728 non-native plant species were classified into two plant functional type classifications, a broad PFT classification and a modified Raunkiaer classification (Table 5.1). These two classifications were chosen as they have been shown to be useful when using PFTs in climate modelling (e.g. Box, 1981, 1995; Chapin *et al*., 1996; Diaz and Cabido, 1997), and different groups would be expected to show distinct responses to projected climate changes. The broad PFT classification, based on life form and phenology, is similar to those used in many vegetation models (e.g. Smith *et al*., 2001). Species were classified into Raunkiaer life forms using the classification given in PLANTATT (Hill *et al.,* 2004). This system is based on the Raunkiaer system of life forms set out by Clapham *et al*., (1962), and looks at the position of overwintering buds.

Table 5.1. Plant functional types

| | **Broad PFT** | **Raunkiaer PFT** |
|---|---|---|
| **Herbaceous** | **Herbaceous annual (HA)**<br>**Herbaceous perennial (HP)**, including biennials | **Therophyte (Th)**, passing unfavourable season as seeds<br>**Bulbous geophyte (Gb)**, with wintering buds below ground (bulb)<br>**Non-bulbous geophyte (Gn)**, with buds below ground (rhizome, corm or tuber)<br>**Hemicryptophyte (hc)**, with buds at soil surface |
| **Herbaceous or woody** | | **Chamaephyte(Ch)**, with wintering buds at 3-39 cm above ground |
| **Woody** | **Succulent evergreen (SE)**<br>**Broad-leaved deciduous (BLD)**<br>**Broad-leaved evergreen (BLE)**<br>**Needle-leaved deciduous (NLD)**<br>**Needle-leaved evergreen (NLE)** | **Nanophanerophyte (Pn)**, with wintering buds 40-399 cm above ground<br>**Phanerophyte (Ph)**, with wintering buds 400 cm above ground |
| **Aquatic** | **Aquatic (AQ)** | **Hydrophyte (Hy)**, perennial with buds under water |

### *5.3.1. Analyses*

Spearman's rank correlations, Moran's I, Generalised Linear Models, Hierarchical Partitioning , Kruskal-Wallis rank sum test and multiple comparison test after Kruskal-Wallis (function 'kruskalmc', in the package 'pgirmess') were used to examine relationships between different variables. All analysis was carried out using R (version 2.13.1).

*Generalised Linear Models*

Generalised Linear Models (GLMs) were used to determine the relationships between species richness, climate variables and land use. GLMs were carried out using the 'glm' function in the 'stats' package in R, specifying the family 'Poisson' as the response variable was count data (species richness). Climate variables and proportions of land cover were used as the predictor variables. Dispersion parameters were used to correct for overdispersion of residuals and predictor variables were removed using the Akaike information criterion (AIC). The climate and land use predictor variables were standardised to give a mean of 0 and a standard deviation of 1, allowing comparison of the slope estimates from the models. Second order polynomials were used for climate variables. The BSBI Monitoring Squares (Figure 2.1) were used to create the models, which were then used to predict species richness for the rest of the grid squares from their climate and land use data (using the 'predict' function in the 'stats' package in R). These predictions were compared with numbers of species actually recorded for these grid squares (using Spearman's rank correlations) to test the model accuracy.

*Hierarchical Partitioning*

Hierarchical Partitioning (HP) analyses were used to calculate the independent contribution of each predictor to the species richness for different groups of non-native species. HP was carried out using the 'hier.part' package (MacNally and Walsh, 2004). HP involves measuring the increase of goodness-of-fit of all models with a particular variable compared with the equivalent model without that variable. The improvement in fit is then averaged across all possible models in which that variable occurs to produce a measure of its independent effects. A Poisson distribution with the default goodness-of-fit measure (RMSPE, Root-mean-square 'prediction' error) was specified.

## 5.4 Results

### *5.4.1 Patterns of PFTs with climate and land use*

Figures 5.2 and 5.3 show maps of species richness for Raunkiaer life forms and for broad PFT species richness. Correlations with climate and urban land cover and number of species within each group are given in Appendix 3 (Tables A3.1 and A3.2).

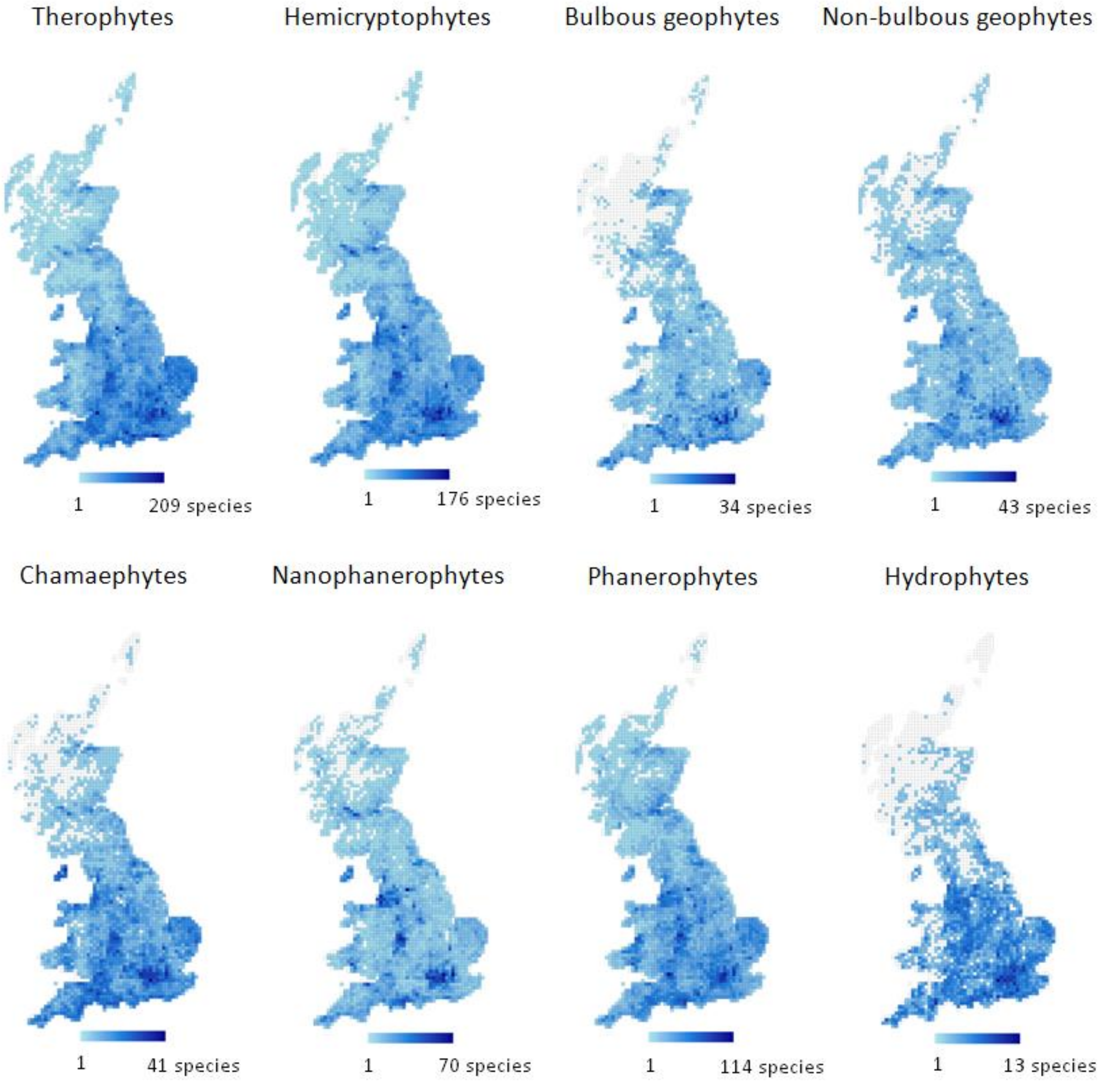


Figure 5.2. Species richness for Raunkiaer life forms using records from 1987 to 2009.

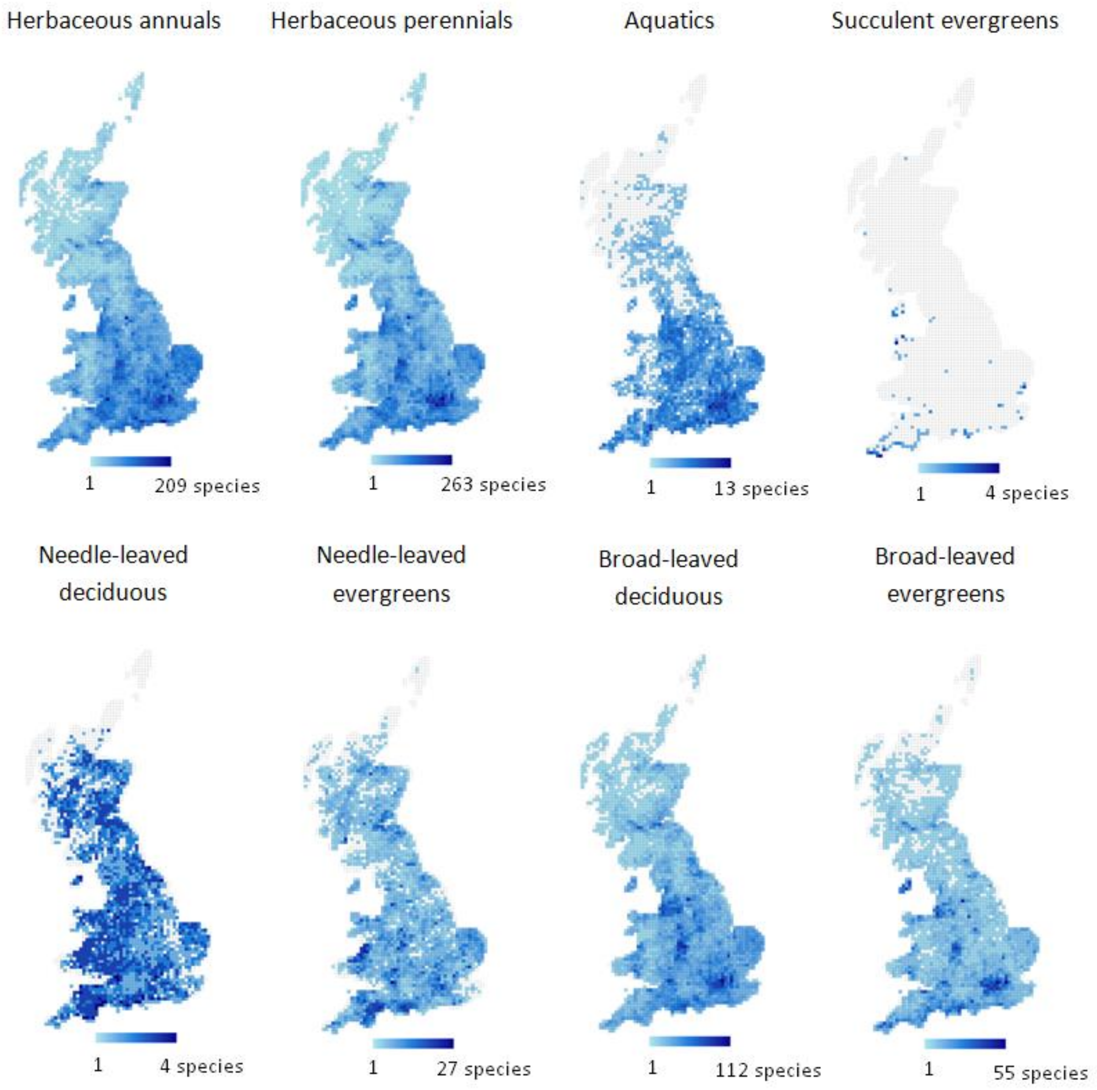


Figure 5.3. Species richness for broad PFTs using records from 1987 to 2009.

### *5.4.2 Modelling PFT species richness*

The models of the GLMs built on the BSBI Monitoring Squares (Table 5.2) were used to predict richness in all other 10 km grid squares. The species richness of each Raunkiaer life form can be predicted well using these models (Figure 5.4); all Spearman's rank correlations between modelled and recorded species richness are over 0.741 (N = 2499, p<0.0001). Nanophanerophytes have the weakest correlation between modelled and recorded species richness (Spearman's rank correlation coefficient 0.741, N = 2499, p<0.0001), while therophytes have the strongest correlation (Spearman's rank correlation coefficient 0.890, N = 2499, p<0.0001). Results for all life forms are shown in Figure 5.4; hydrophytes were not modelled due to too few species in this category.

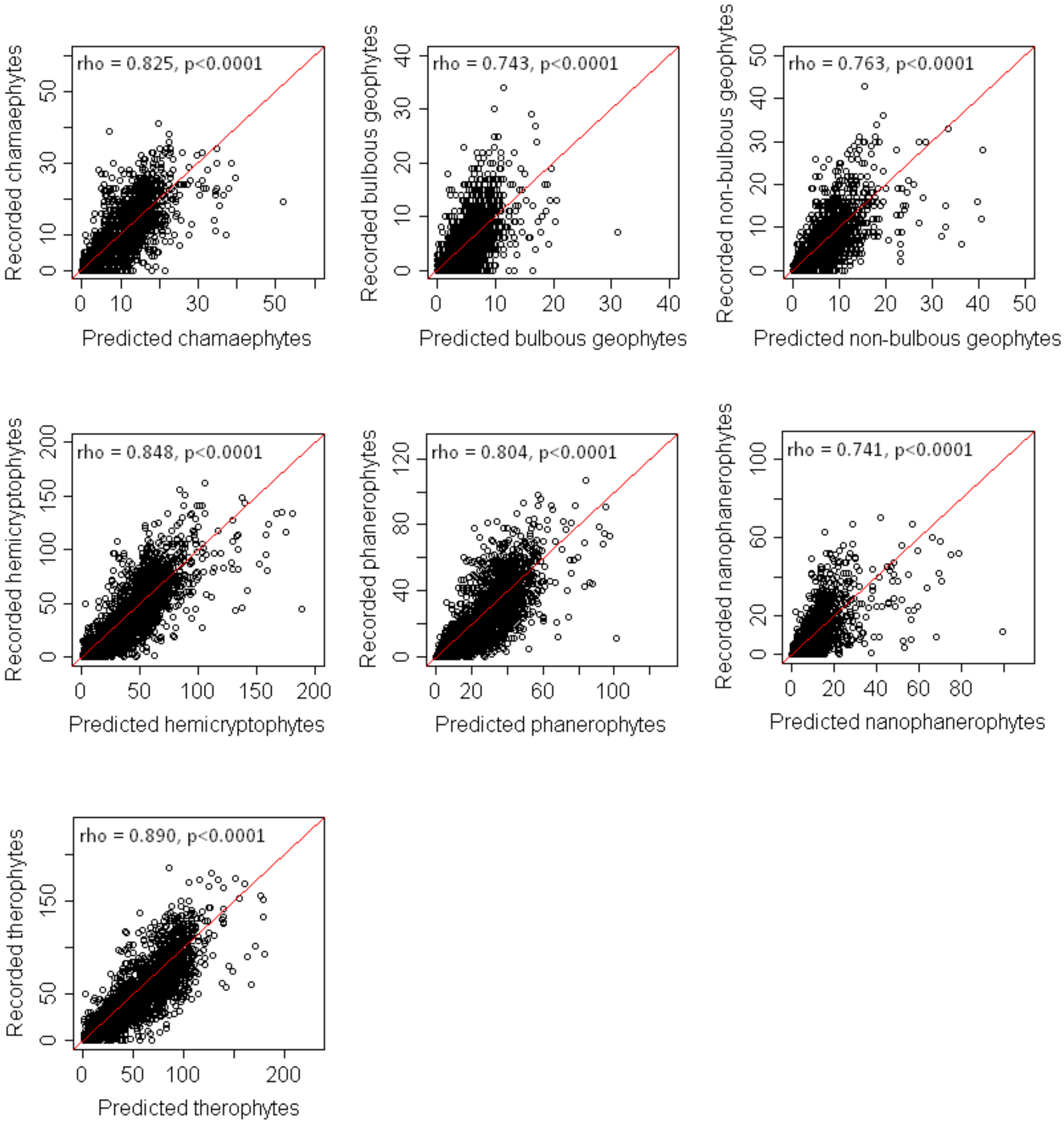


Figure 5.4. Relationships between modelled (predicted) species richness and recorded species richness for each 10 x 10 km grid square (excluding model-building squares) for Raunkiaer life forms. Results from Spearman's rank correlation shown on graphs (N=2499 for all groups).

The results of the GLMs for broad PFTs (Table 5.3) give a range of correlations between modelled and recorded species richness (Figure 5.5) from 0.545 to 0.890 (N = 2499, p<0.0001). Needle-leaved evergreen have the weakest correlation between modelled and recorded species richness (Spearman's rank correlation coefficient 0.545, N = 2499, p<0.0001), while herbaceous annuals have the strongest correlation (Spearman's rank correlation coefficient 0.890, N = 2499, p<0.0001). Results for all broad PFTs are shown in Figure 5.5; needle-leaved deciduous species, succulent evergreens and aquatics were not modelled due to small numbers of species in these categories.

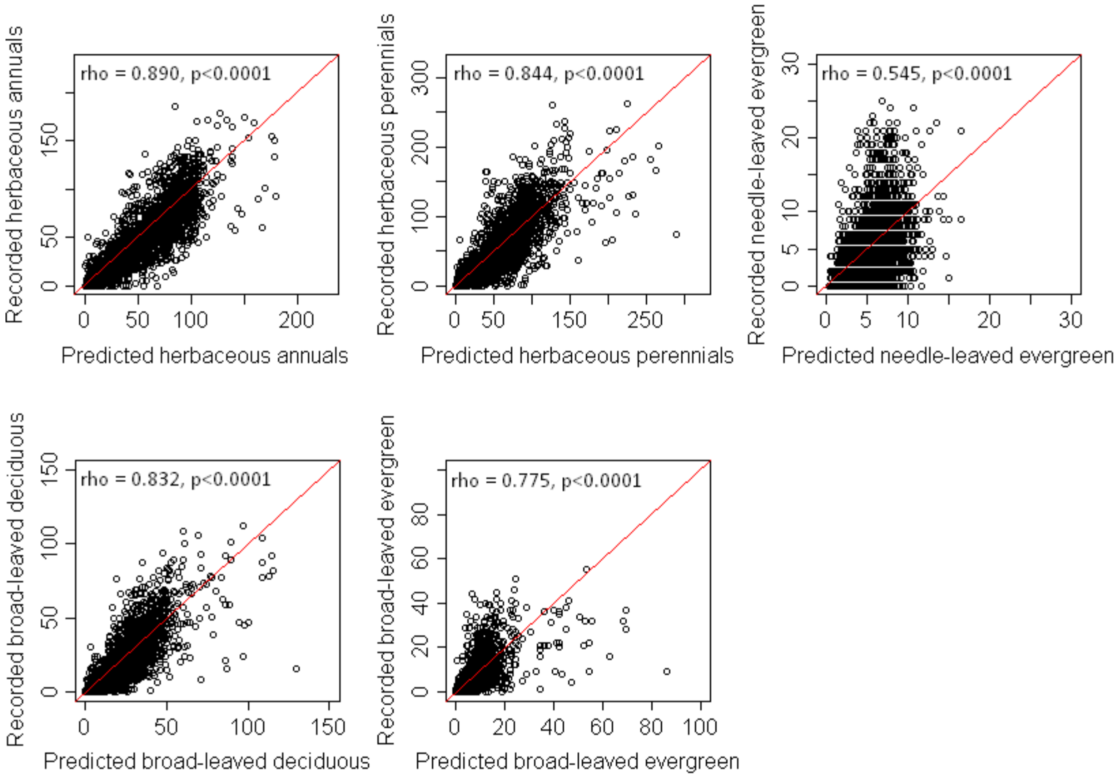


Figure 5.5. Relationships between modelled (predicted) species richness and recorded species richness for each 10 x 10 km grid square (excluding model-building squares) for broad PFTs. Results from Spearman's rank correlation shown on graphs (N=2499 for all groups).

Table 5.2. GLMs for Raunkiaer life form species richness. Slope estimate, standard error, Z value and significance are shown for each climate and land cover variable included (after elimination using AIC). Predictor variables were standardised to allow comparison of relative importance.

| | Ch | | | | | Gb | | | | | Gn | | | | | hc | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. |
| poly(GDD5, 2)1 | -31.04 | 18.25 | -1.70 | 0.0890 | . | -27.36 | 27.85 | -0.98 | 0.3259 | | -7.04 | 20.52 | -0.34 | 0.7316 | | 5.60 | 14.64 | 0.38 | 0.7019 | |
| poly(GDD5, 2)2 | 10.62 | 3.50 | 3.04 | 0.0024 | ** | 14.30 | 5.25 | 2.73 | 0.0064 | ** | 9.20 | 3.74 | 2.46 | 0.0140 | * | 7.72 | 2.66 | 2.90 | 0.0037 | ** |
| poly(MTCO, 2)1 | 5.68 | 5.22 | 1.09 | 0.2767 | | 8.14 | 7.93 | 1.03 | 0.3042 | | 3.79 | 5.80 | 0.65 | 0.5136 | | -4.61 | 4.11 | -1.12 | 0.2625 | |
| poly(MTCO, 2)2 | -1.82 | 2.31 | -0.79 | 0.4303 | | -5.01 | 3.51 | -1.43 | 0.1531 | | -5.76 | 2.59 | -2.22 | 0.0262 | * | -4.13 | 1.77 | -2.33 | 0.0199 | * |
| poly(MTWA, 2)1 | 40.76 | 14.92 | 2.73 | 0.0063 | ** | 24.73 | 22.93 | 1.08 | 0.2808 | | 9.30 | 16.77 | 0.55 | 0.5793 | | 5.69 | 11.94 | 0.48 | 0.6341 | |
| poly(MTWA, 2)2 | -13.04 | 2.70 | -4.84 | 0.0000 | *** | -14.50 | 4.05 | -3.58 | 0.0003 | *** | -8.07 | 2.79 | -2.90 | 0.0038 | ** | -8.74 | 1.99 | -4.40 | 0.0000 | *** |
| poly(APET, 2)1 | -4.41 | 2.07 | -2.13 | 0.0331 | * | -11.13 | 3.22 | -3.45 | 0.0006 | *** | -4.91 | 2.34 | -2.09 | 0.0362 | * | -2.74 | 1.67 | -1.64 | 0.1013 | |
| poly(APET, 2)2 | -0.95 | 0.78 | -1.22 | 0.2240 | | -2.41 | 1.22 | -1.98 | 0.0480 | * | -1.96 | 0.95 | -2.06 | 0.0390 | * | -0.90 | 0.65 | -1.39 | 0.1634 | |
| poly(SPRE, 2)1 | -0.32 | 4.64 | -0.07 | 0.9457 | | -1.41 | 7.60 | -0.19 | 0.8527 | | 9.29 | 4.92 | 1.89 | 0.0587 | . | -1.27 | 3.58 | -0.35 | 0.7232 | |
| poly(SPRE, 2)2 | -5.35 | 2.80 | -1.91 | 0.0560 | . | -15.30 | 5.12 | -2.99 | 0.0028 | ** | -2.84 | 2.70 | -1.05 | 0.2919 | | -5.66 | 2.23 | -2.54 | 0.0112 | * |
| poly(WPRE, 2)1 | 2.99 | 4.20 | 0.71 | 0.4770 | | 0.03 | 6.72 | 0.00 | 0.9965 | | -6.22 | 4.58 | -1.36 | 0.1749 | | 1.64 | 3.24 | 0.51 | 0.6127 | |
| poly(WPRE, 2)2 | 4.15 | 2.54 | 1.64 | 0.1016 | | 8.68 | 4.17 | 2.08 | 0.0371 | * | 2.04 | 2.65 | 0.77 | 0.4417 | | 3.91 | 2.01 | 1.94 | 0.0521 | . |
| acid | 0.07 | 0.06 | 1.12 | 0.2644 | | | | | | | | | | | | 0.03 | 0.05 | 0.64 | 0.5207 | |
| arable | 0.23 | 0.07 | 3.23 | 0.0013 | ** | 0.42 | 0.11 | 3.85 | 0.0001 | *** | 0.22 | 0.08 | 2.67 | 0.0077 | ** | 0.18 | 0.06 | 3.13 | 0.0018 | ** |
| bwood | 0.07 | 0.03 | 2.40 | 0.0164 | * | 0.15 | 0.05 | 3.32 | 0.0009 | *** | 0.14 | 0.03 | 3.89 | 0.0001 | *** | 0.09 | 0.03 | 3.71 | 0.0002 | *** |
| calc | | | | | | | | | | | | | | | | | | | | |
| cwood | 0.20 | 0.05 | 4.26 | 0.0000 | *** | 0.31 | 0.06 | 4.87 | 0.0000 | *** | 0.21 | 0.05 | 4.31 | 0.0000 | *** | 0.11 | 0.04 | 3.09 | 0.0020 | ** |
| heath | | | | | | | | | | | | | | | | | | | | |
| improved | 0.31 | 0.06 | 5.48 | 0.0000 | *** | 0.41 | 0.08 | 4.81 | 0.0000 | *** | 0.29 | 0.06 | 4.86 | 0.0000 | *** | 0.19 | 0.04 | 4.37 | 0.0000 | *** |
| inrock | | | | | | | | | | | | | | | | 0.05 | 0.04 | 1.13 | 0.2585 | |
| neutral | 0.13 | 0.05 | 2.53 | 0.0113 | * | 0.13 | 0.08 | 1.62 | 0.1053 | | 0.06 | 0.06 | 1.04 | 0.2964 | | 0.10 | 0.04 | 2.66 | 0.0078 | ** |
| swater | | | | | | | | | | | | | | | | | | | | |
| urban | 0.27 | 0.04 | 7.05 | 0.0000 | *** | 0.37 | 0.06 | 6.22 | 0.0000 | *** | 0.31 | 0.04 | 7.17 | 0.0000 | *** | 0.25 | 0.03 | 8.25 | < 2e-16 | *** |

Table 5.2. (continued) GLMs for Raunkiaer life form species richness.

| | Ph | | | | | Pn | | | | | Th | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. |
| poly(GDD5, 2)1 | -1.28 | 13.95 | -0.09 | 0.9269 | | 16.31 | 21.04 | 0.78 | 0.4382 | | 14.32 | 12.30 | 1.16 | 0.2444 | |
| poly(GDD5, 2)2 | 4.79 | 2.40 | 2.00 | 0.0460 | * | 4.22 | 3.64 | 1.16 | 0.2462 | | 1.51 | 2.14 | 0.71 | 0.4795 | |
| poly(MTCO, 2)1 | -3.22 | 3.86 | -0.84 | 0.4040 | | -2.50 | 5.94 | -0.42 | 0.6743 | | -4.96 | 3.47 | -1.43 | 0.1535 | |
| poly(MTCO, 2)2 | -2.06 | 1.53 | -1.34 | 0.1805 | | -3.86 | 2.59 | -1.49 | 0.1357 | | -1.88 | 1.46 | -1.29 | 0.1979 | |
| poly(MTWA, 2)1 | 11.80 | 11.66 | 1.01 | 0.3113 | | -8.04 | 17.24 | -0.47 | 0.6412 | | -1.96 | 10.05 | -0.20 | 0.8453 | |
| poly(MTWA, 2)2 | -5.52 | 1.82 | -3.03 | 0.0024 | ** | -6.80 | 2.73 | -2.49 | 0.0129 | * | -3.43 | 1.66 | -2.07 | 0.0382 | * |
| poly(APET, 2)1 | | | | | | -2.79 | 2.38 | -1.18 | 0.2398 | | -2.88 | 1.42 | -2.03 | 0.0428 | * |
| poly(APET, 2)2 | | | | | | -0.43 | 0.92 | -0.46 | 0.6455 | | -0.73 | 0.52 | -1.39 | 0.1637 | |
| poly(SPRE, 2)1 | 2.15 | 0.98 | 2.20 | 0.0281 | * | 5.58 | 4.95 | 1.13 | 0.2592 | | -2.18 | 3.25 | -0.67 | 0.5023 | |
| poly(SPRE, 2)2 | -0.24 | 0.74 | -0.33 | 0.7433 | | -3.92 | 2.86 | -1.37 | 0.1696 | | -5.04 | 2.04 | -2.47 | 0.0137 | * |
| poly(WPRE, 2)1 | | | | | | -3.42 | 4.55 | -0.75 | 0.4525 | | 0.53 | 2.97 | 0.18 | 0.8573 | |
| poly(WPRE, 2)2 | | | | | | 3.02 | 2.72 | 1.11 | 0.2681 | | 3.56 | 1.82 | 1.96 | 0.0500 | . |
| acid | 0.10 | 0.05 | 2.02 | 0.0429 | * | 0.08 | 0.07 | 1.24 | 0.2158 | | 0.06 | 0.05 | 1.28 | 0.1995 | |
| arable | 0.37 | 0.07 | 5.01 | 0.0000 | *** | 0.24 | 0.09 | 2.65 | 0.0080 | ** | 0.20 | 0.05 | 3.99 | 0.0001 | *** |
| bwood | 0.12 | 0.03 | 4.75 | 0.0000 | *** | 0.15 | 0.04 | 4.12 | 0.0000 | *** | 0.05 | 0.02 | 2.07 | 0.0383 | * |
| calc | | | | | | | | | | | | | | | |
| cwood | 0.19 | 0.04 | 5.12 | 0.0000 | *** | 0.20 | 0.05 | 4.10 | 0.0000 | *** | 0.09 | 0.03 | 2.75 | 0.0060 | ** |
| heath | 0.10 | 0.08 | 1.23 | 0.2206 | | | | | | | -0.05 | 0.07 | -0.72 | 0.4699 | |
| improved | 0.28 | 0.06 | 4.86 | 0.0000 | *** | 0.23 | 0.07 | 3.50 | 0.0005 | *** | 0.18 | 0.04 | 4.19 | 0.0000 | *** |
| inrock | 0.06 | 0.04 | 1.57 | 0.1167 | | 0.06 | 0.05 | 1.13 | 0.2572 | | 0.06 | 0.03 | 1.64 | 0.1016 | |
| neutral | 0.10 | 0.04 | 2.28 | 0.0225 | * | 0.13 | 0.05 | 2.46 | 0.0139 | * | 0.10 | 0.03 | 3.10 | 0.0020 | ** |
| swater | | | | | | | | | | | | | | | |
| urban | 0.28 | 0.04 | 7.60 | 0.0000 | *** | 0.40 | 0.05 | 8.77 | < 2e-16 | *** | 0.18 | 0.03 | 6.47 | 0.0000 | *** |

Table 5.3. GLMs for broad PFT species richness. Slope estimate, standard error, Z value and significance are shown for each climate and land cover variable included (after elimination using AIC). Predictor variables were standardised to allow comparison of relative importance.

| | BLD | | | | | BLE | | | | | HA | | | | | HP | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. |
| poly(GDD5, 2)1 | 7.25 | 14.97 | 0.48 | 0.6281 | | -6.46 | 23.55 | -0.27 | 0.7838 | | 14.32 | 12.30 | 1.16 | 0.2444 | | -3.30 | 15.26 | -0.22 | 0.8289 | |
| poly(GDD5, 2)2 | 5.30 | 2.72 | 1.95 | 0.0513 | . | 8.15 | 4.41 | 1.85 | 0.0643 | . | 1.51 | 2.14 | 0.71 | 0.4795 | | 8.41 | 2.79 | 3.01 | 0.0026 | ** |
| poly(MTCO, 2)1 | -3.85 | 4.21 | -0.91 | 0.3610 | | 4.71 | 6.83 | 0.69 | 0.4904 | | -4.96 | 3.47 | -1.43 | 0.1535 | | -1.42 | 4.29 | -0.33 | 0.7412 | |
| poly(MTCO, 2)2 | -3.93 | 1.84 | -2.14 | 0.0328 | * | -4.33 | 3.00 | -1.44 | 0.1487 | | -1.88 | 1.46 | -1.29 | 0.1979 | | -3.75 | 1.87 | -2.01 | 0.0445 | * |
| poly(MTWA, 2)1 | 3.64 | 12.25 | 0.30 | 0.7662 | | 15.22 | 19.17 | 0.79 | 0.4272 | | -1.96 | 10.05 | -0.20 | 0.8453 | | 12.04 | 12.46 | 0.97 | 0.3341 | |
| poly(MTWA, 2)2 | -6.81 | 2.04 | -3.34 | 0.0008 | *** | -9.62 | 3.34 | -2.88 | 0.0040 | ** | -3.43 | 1.66 | -2.07 | 0.0382 | * | -9.32 | 2.10 | -4.45 | 0.0000 | *** |
| poly(APET, 2)1 | -1.56 | 1.68 | -0.93 | 0.3508 | | -4.41 | 2.65 | -1.66 | 0.0964 | . | -2.88 | 1.42 | -2.03 | 0.0428 | * | -3.79 | 1.74 | -2.18 | 0.0295 | * |
| poly(APET, 2)2 | -0.18 | 0.66 | -0.27 | 0.7856 | | -1.19 | 0.99 | -1.19 | 0.2327 | | -0.73 | 0.52 | -1.39 | 0.1637 | | -1.14 | 0.67 | -1.70 | 0.0893 | . |
| poly(SPRE, 2)1 | 5.27 | 3.62 | 1.46 | 0.1455 | | 4.23 | 5.80 | 0.73 | 0.4661 | | -2.18 | 3.25 | -0.67 | 0.5023 | | 0.62 | 3.75 | 0.17 | 0.8680 | |
| poly(SPRE, 2)2 | -2.54 | 2.10 | -1.21 | 0.2265 | | -5.53 | 3.39 | -1.63 | 0.1026 | | -5.04 | 2.04 | -2.47 | 0.0137 | * | -5.50 | 2.31 | -2.38 | 0.0174 | * |
| poly(WPRE, 2)1 | -4.24 | 3.35 | -1.27 | 0.2051 | | 1.22 | 5.25 | 0.23 | 0.8162 | | 0.53 | 2.97 | 0.18 | 0.8573 | | 0.46 | 3.41 | 0.14 | 0.8922 | |
| poly(WPRE, 2)2 | 1.34 | 2.01 | 0.67 | 0.5044 | | 4.34 | 3.09 | 1.40 | 0.1603 | | 3.56 | 1.82 | 1.96 | 0.0500 | . | 3.76 | 2.10 | 1.79 | 0.0733 | . |
| acid | 0.06 | 0.05 | 1.19 | 0.2359 | | | | | | | 0.06 | 0.05 | 1.28 | 0.1995 | | 0.03 | 0.05 | 0.63 | 0.5260 | |
| arable | 0.27 | 0.06 | 4.39 | 0.0000 | *** | 0.26 | 0.10 | 2.63 | 0.0087 | ** | 0.20 | 0.05 | 3.99 | 0.0001 | *** | 0.21 | 0.06 | 3.50 | 0.0005 | *** |
| bwood | 0.10 | 0.03 | 3.78 | 0.0002 | *** | 0.14 | 0.04 | 3.59 | 0.0003 | *** | 0.05 | 0.02 | 2.07 | 0.0383 | * | 0.10 | 0.03 | 3.88 | 0.0001 | *** |
| calc | | | | | | -0.07 | 0.05 | -1.29 | 0.1984 | | | | | | | | | | | |
| cwood | 0.15 | 0.04 | 4.28 | 0.0000 | *** | 0.24 | 0.06 | 3.93 | 0.0001 | *** | 0.09 | 0.03 | 2.75 | 0.0060 | ** | 0.15 | 0.04 | 3.89 | 0.0001 | *** |
| heath | | | | | | | | | | | -0.05 | 0.07 | -0.72 | 0.4699 | | | | | | |
| improved | 0.22 | 0.05 | 4.87 | 0.0000 | *** | 0.26 | 0.07 | 3.59 | 0.0003 | *** | 0.18 | 0.04 | 4.19 | 0.0000 | *** | 0.24 | 0.05 | 5.09 | 0.0000 | *** |
| inrock | 0.04 | 0.04 | 0.90 | 0.3691 | | 0.11 | 0.06 | 1.98 | 0.0479 | * | 0.06 | 0.03 | 1.64 | 0.1016 | | 0.04 | 0.04 | 1.01 | 0.3110 | |
| neutral | 0.09 | 0.04 | 2.30 | 0.0216 | * | 0.15 | 0.06 | 2.43 | 0.0153 | * | 0.10 | 0.03 | 3.10 | 0.0020 | ** | 0.10 | 0.04 | 2.51 | 0.0122 | * |
| swater | | | | | | | | | | | | | | | | | | | | |
| urban | 0.29 | 0.03 | 9.31 | < 2e-16 | *** | 0.41 | 0.05 | 8.15 | 0.0000 | *** | 0.18 | 0.03 | 6.47 | 0.0000 | *** | 0.27 | 0.03 | 8.33 | < 2e-16 | *** |

Table 5.3. (continued) GLMs for broad PFT species richness.

| | NLE | | | | |
|---|---|---|---|---|---|
| | Slope | S.E. | Z | P | Signif. |
| poly(GDD5, 2)1 | -28.62 | 23.26 | -1.23 | 0.2186 | |
| poly(GDD5, 2)2 | 1.43 | 3.64 | 0.39 | 0.6945 | |
| poly(MTCO, 2)1 | 4.48 | 6.42 | 0.70 | 0.4850 | |
| poly(MTCO, 2)2 | 3.07 | 2.44 | 1.26 | 0.2082 | |
| poly(MTWA, 2)1 | 29.67 | 19.29 | 1.54 | 0.1241 | |
| poly(MTWA, 2)2 | -1.96 | 2.70 | -0.73 | 0.4661 | |
| poly(APET, 2)1 | | | | | |
| poly(APET, 2)2 | | | | | |
| poly(SPRE, 2)1 | | | | | |
| poly(SPRE, 2)2 | | | | | |
| poly(WPRE, 2)1 | 3.03 | 1.46 | 2.08 | 0.0380 | * |
| poly(WPRE, 2)2 | 0.51 | 1.11 | 0.46 | 0.6433 | |
| acid | 0.26 | 0.08 | 3.19 | 0.0014 | ** |
| arable | 0.63 | 0.15 | 4.30 | 0.0000 | *** |
| bwood | 0.25 | 0.05 | 5.36 | 0.0000 | *** |
| calc | | | | | |
| cwood | 0.32 | 0.06 | 5.25 | 0.0000 | *** |
| heath | 0.33 | 0.13 | 2.47 | 0.0134 | * |
| improved | 0.48 | 0.11 | 4.22 | 0.0000 | *** |
| inrock | 0.10 | 0.06 | 1.79 | 0.0738 | . |
| neutral | 0.16 | 0.08 | 2.07 | 0.0389 | * |
| swater | | | | | |
| urban | 0.29 | 0.08 | 3.70 | 0.0002 | *** |

### ***5.4.3 Importance of climate and land use variables***

The results from GLMs (Tables 5.2 and 5.3) show that all groups have positive relationships with urban land cover and the majority of groups have the highest z value with urban land cover out of all climate and land cover variables used. Needle-leaved evergreens are the only exception, with broadleaved woodland and coniferous woodland the most important land cover types. All groups have similar significant results with climate variables, showing positive first order effects with MTWA and negative with APET.

#### *Results with urban land cover from GLMs*

The GLM urban slope estimate is positive for all Raunkiaer life forms and all broad PFTs, indicating that non-native species richness is positively associated with urban land cover for all modelled groups (Figures 5.6 and 5.7). The Raunkiaer life form with the weakest association between species richness and urban land cover is therophytes (slope estimate 0.18, N=291, p<0.001) and with the strongest associations are nanophanerophytes (slope estimate 0.40, N=291, p<0.001) and bulbous geophytes (slope estimate 0.37, N=291, p<0.001). The broad PFT with the weakest association between species richness and urban land cover is herbaceous annuals (slope estimate 0.18, N=291, p<0.001) and with the strongest association is broad-leaved evergreens (slope estimate 0.41, N=291, p<0.001).

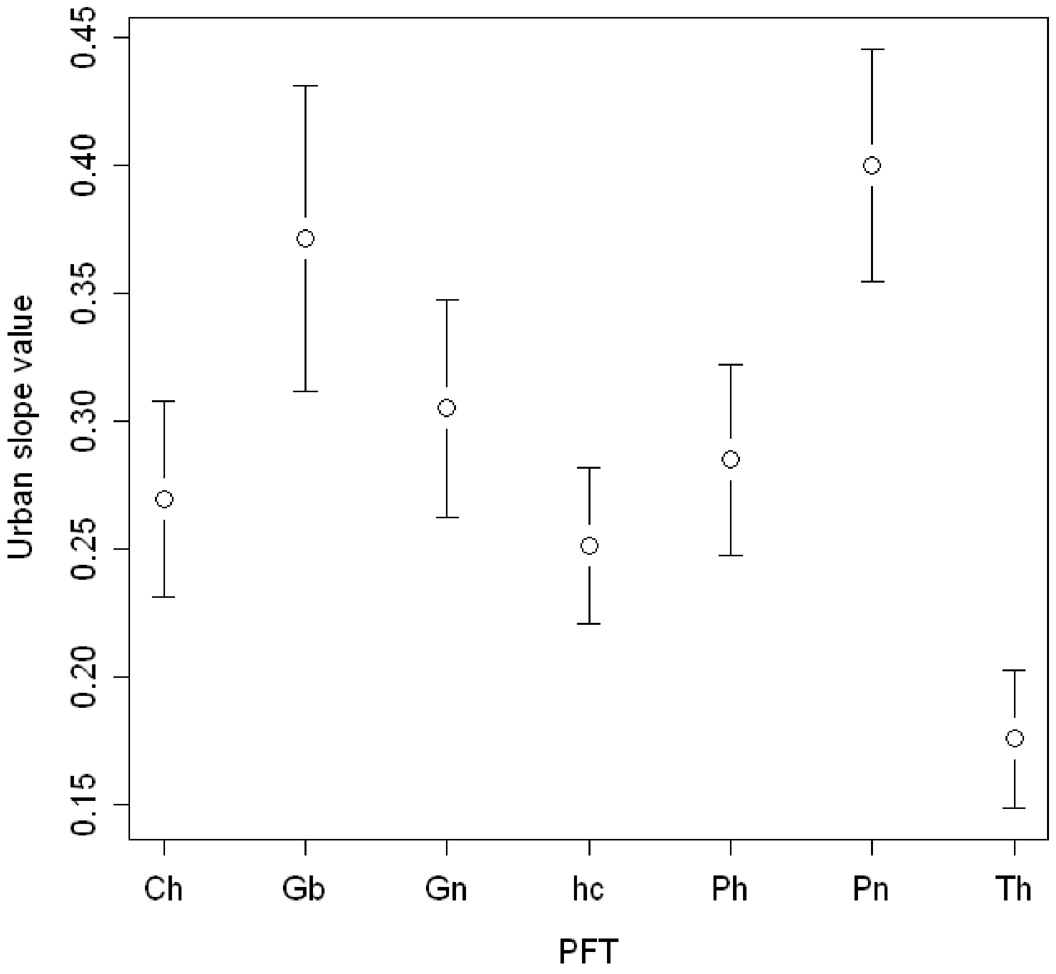


Figure 5.6. Urban slope values (± S.E., all N=291, $p<0.001$) from GLMs for Raunkiaer PFTs (Ch = Chamaephyte, Gb = Bulbous geophyte, Gn = Non-bulbous geophyte, hc = Hemicryptophyte, Hy = Hydrophyte, Ph = Phanerophyte, Pn = Nanophanerophyte, Th = Therophyte).

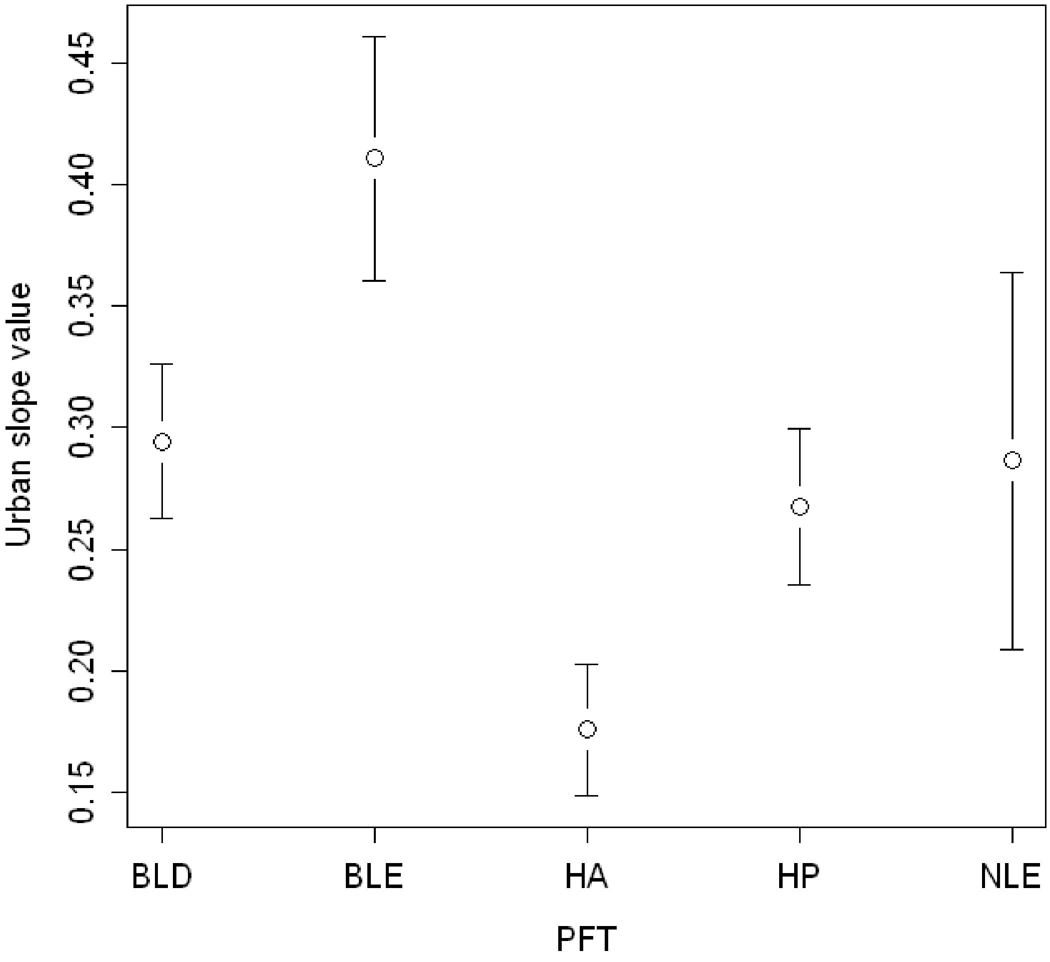


Figure 5.7. Urban slope values (± S.E., all N=291, p<0.001) from GLMs for broad PFTs (AQ = Aquatic, BLD = Broad-leaved deciduous, BLE = Broad-leaved evergreen, HA = Herbaceous annual, HP = Herbaceous perennial, NLE = Needle-leaved evergreen).

*Results with climate and land cover from Hierarchical Partitioning*

Results from hierarchical partitioning showing percentage of variance explained by temperature (MTCO, MTWA, GDD5), rainfall (SPRE, WPRE, APET), urban land cover and other land types of land cover for Raunkiaer life forms are shown in Figure 5.8. Percentages for all climate and land cover variables are shown in Appendix 3, Tables A3.3 and A3.4. Species richness of phanerophytes and nanophanerophytes has a higher proportion of variance explained by land cover than climate, while chamaephyte species richness has a higher proportion explained by climate. Urban land cover is the most important land cover variable for the majority of the Raunkiaer life forms; the exception is therophytes. Details for each life form are given below.

A larger proportion of total variance is explained by climate variables than land cover variables (61.1% compared to 38.9%) for chamaephytes. Climatic variables relating to temperature are more important than variables relating to rainfall, with 45.9% compared to 15.1%. The most important land cover variable is urban land cover (8.7%). Nanophanerophytes have a larger proportion of variance explained by land cover compared to climate (61.2% compared to 38.8%). Temperature and rainfall explain similar proportions (21.8% and 17.0%), and urban land cover is the most important land cover variable (13.9%). A larger proportion of total variance for species richness of phanerophytes is explained by land cover (67.1%) compared to climate (32.9%). Temperature is slightly more important than rainfall (19.8% for temperature and 13.1% for rainfall), and the most important land cover variable is urban land cover at 11.8%, with a similar proportion explained by broad-leaved woodland at 11.4%.

Climate and land cover explain similar proportions of variation for bulbous geophytes, at 49.7% for climate and 50.3% for land cover. Rainfall is more important than temperature (37.4% compared to 12.4%) and urban land cover is the most important land cover variable (at 10.7%). For non-bulbous geophytes, climate explains a slightly larger proportion of variation than land cover (at 58.8% for climate variables and 41.2% for land cover variables). Within climate, rainfall explains more variation than temperature (40.0% compared to 18.8%), and within land cover, urban explains the most variation at 11.9%. Hemicryptophytes have a similar amount of variation explained by climate and land cover variables (with 47.3% for climate and 52.7% for land cover). Rainfall explains slightly more variation than temperature (at 26.8% compared to 20.5%) and urban land cover is the most important land cover classification at 12.3%. Land cover explains a larger proportion of variance than climate for therophytes, with 55.9% for land cover and 44.1% for climate. Rainfall explains a larger proportion of variance than temperature (30.0% compared to 14.1%), and the most important land cover variables are arable (12.3%) and urban (10.0%).

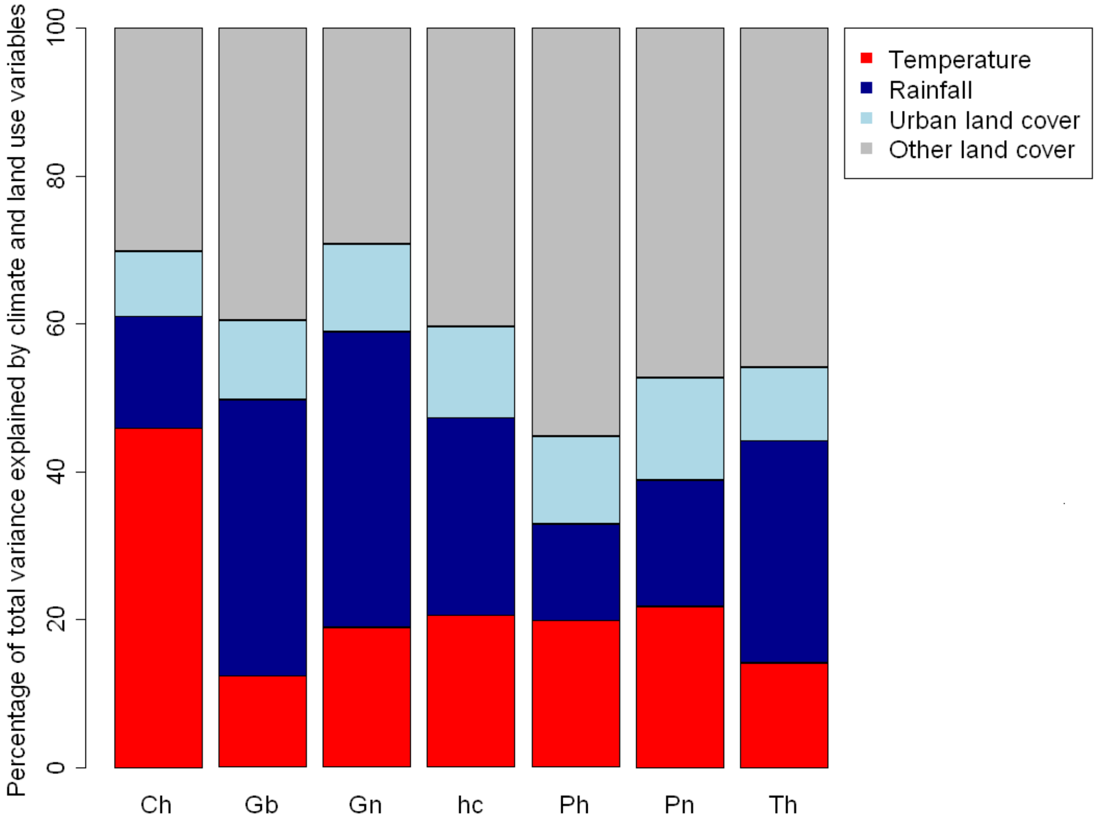


Figure 5.8. Results from hierarchical partitioning showing percentage of variance explained by temperature (MTCO, MTWA, GDD5), rainfall (SPRE, WPRE, APET), urban land cover and other land uses for Raunkiaer life forms (Ch = Chamaephyte, Gb = Bulbous geophyte, Gn = Non-bulbous geophyte, hc = Hemicryptophyte, Ph = Phanerophyte, Pn = Nanophanerophyte, Th = Therophyte).

Results from hierarchical partitioning showing percentage of variance explained by temperature (MTCO, MTWA, GDD5), rainfall (SPRE, WPRE, APET), urban land cover and other land types of land cover for broad functional types are shown in Figure 5.9. Species richness of needle-leaved evergreens has a higher proportion of variance explained by land cover than climate, while the other types have similar proportions explained by climate and land cover. Urban land cover is the most important land cover variable for half of the broad functional type categories, with other land cover variables explaining more variation than urban for needle-leaved evergreens and herbaceous annuals.  Details for each broad functional type are given below.

Land cover and climate variables explain similar proportions of variance for broad-leaved deciduous species richness (51.6% for climate and 48.4% for land cover). Within climate, variables related to rainfall explain a larger proportion than temperature (31.8% compared to 19.8%). The most important land cover variables are urban (12.0%) and broad-leaved woodland (9.6%). Slightly more variance is explained by land cover variables than climate variables for broad-leaved evergreen species richness (59.3% compared to 40.7%). Temperature and rainfall give similar results (21.5% and 19.1%), and the most important land cover variables are urban (14.0%) and broad-leaved woodland (10.1%). Land cover explains more variance than climate for needle-leaved evergreens (72.2% compared to 27.8%). Within climate, temperature is more important than rainfall variables (22.3% compared to 5.6%) and within land cover the most important variables are broad-leaved woodland (24.6%) and heath (16.0%), with urban land cover only explaining 5.0%.

Land cover and climate explain similar proportions of variance for species richness of herbaceous perennials (52.8% and 47.2%). Rainfall explains a slightly higher percentage than temperature (27.1% compared to 20.2%), and urban land cover is the most important land cover variable at 12.1%. Land cover explains a larger proportion of variance than climate for herbaceous annuals, with 55.9% for land cover and 44.1% for climate. Rainfall explains a larger proportion of variance than temperature (30.0% compared to 14.1%), and the most important land cover variables are arable (12.3%) and urban (10.0%).

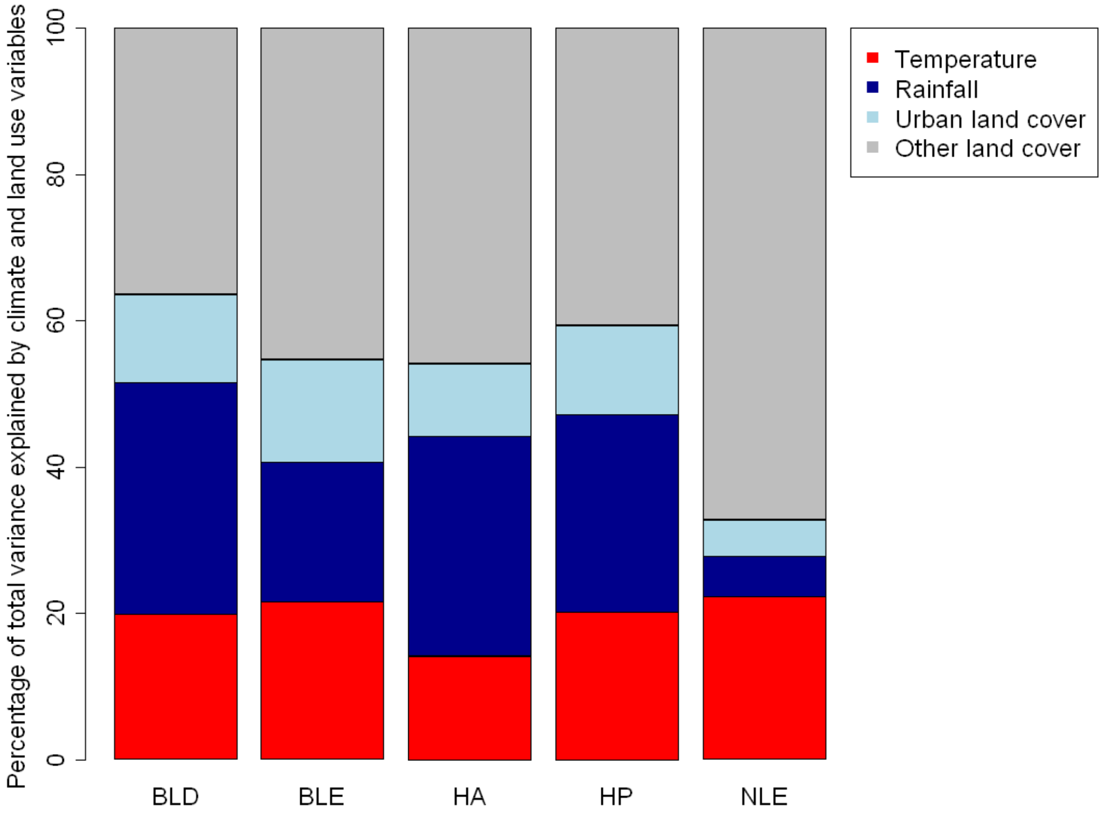


Figure 5.9. Results from hierarchical partitioning showing percentage of variance explained by temperature (MTCO, MTWA, GDD5), rainfall (SPRE, WPRE, APET), urban land cover and other land uses for broad PFTs (AQ = Aquatic, BLD = Broad-leaved deciduous, BLE = Broad-leaved evergreen, HA = Herbaceous annual, HP = Herbaceous perennial, NLE = Needle-leaved evergreen).

### *5.4.4 Establishment of PFTs*

The Raunkiaer life forms with species with the highest establishment indices (Figure 5.10) are hydrophytes (mean establishment index = 72.1%) and bulbous geophytes (mean establishment index = 54.8%). Hydrophytes and bulbous geophytes are significantly different from the two least established groups, therophytes and phanerophytes (multiple comparison test after Kruskal-Wallis, Table 5.4). The least established groups, therophytes (mean establishment index = 21.8%) and phanerophytes (mean establishment index = 24.4%), are significantly different from all six other groups, chamaephytes, bulbous geophytes, non-bulbous geophytes, hemicryptophytes, hydrophytes and nanophanerophytes (multiple comparison test after Kruskal-Wallis, Table 5.4).

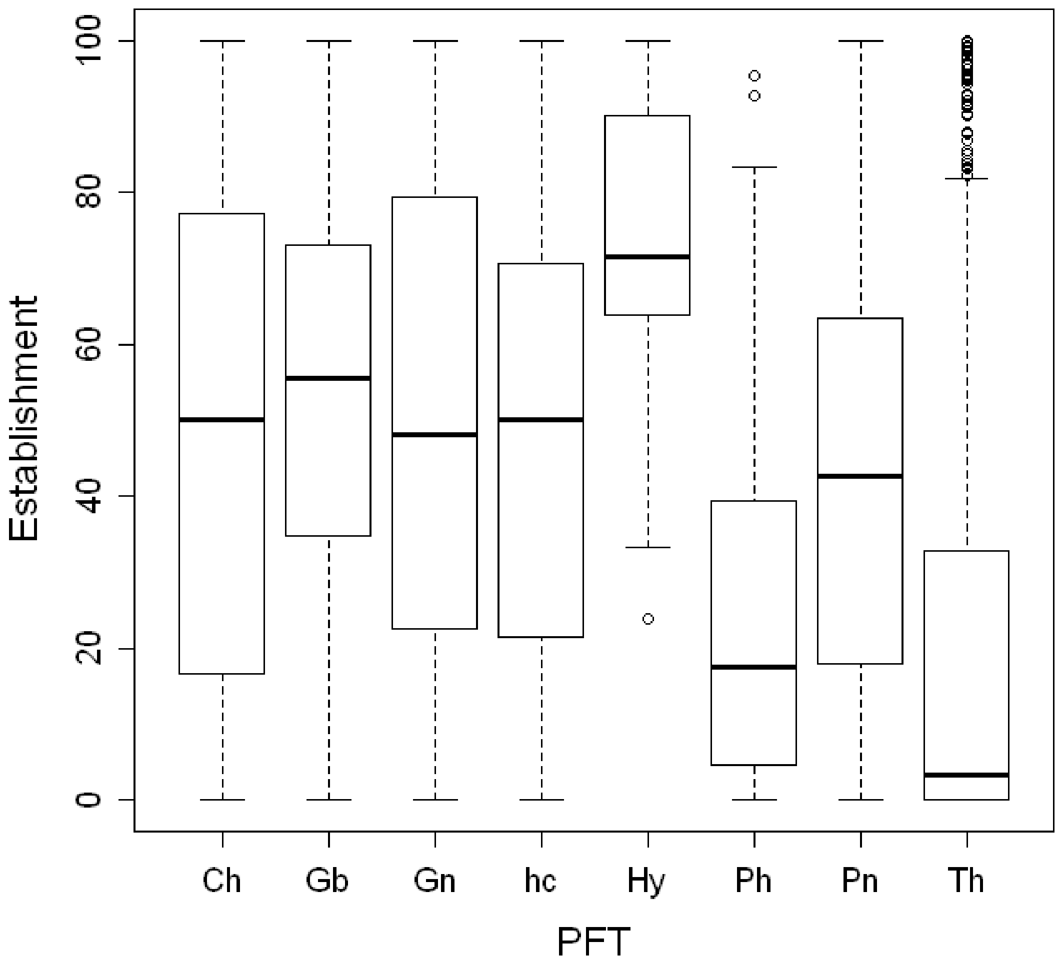


Figure 5.10. Establishment index of species within each Raunkiaer PFT (Ch = Chamaephyte, Gb = Bulbous geophyte, Gn = Non-bulbous geophyte, hc = Hemicryptophyte, Hy = Hydrophyte, Ph = Phanerophyte, Pn = Nanophanerophyte, Th = Therophyte). Significant differences between groups (Kruskal-Wallis chi-squared = 260.1, N=8, $p < 0.0001$).

Table 5.4. Comparisons of establishment index values for Raunkiaer life form with significant differences from multiple comparison test after Kruskal-Wallis (Kruskal-Wallis chi-squared = 260.1, N=8, $p < 0.0001$). Raunkiaer life form abbreviations are: Ch = Chamaephyte, Gb = Bulbous geophyte, Gn = Non-bulbous geophyte, hc = Hemicryptophyte, Hy = Hydrophyte, Ph = Phanerophyte, Pn = Nanophanerophyte, Th = Therophyte.

| Comparison | N | Observed difference | Critical difference | Significance |
|---|---|---|---|---|
| Ch-Ph | Ch=113, Ph=188 | 278.8 | 166.5 | p<0.05 |
| Ch-Th | Ch=113, Th=484 | 367.2 | 146.2 | p<0.05 |
| Gb-Ph | Gb=72, Ph=188 | 391.6 | 193.9 | p<0.05 |
| Gb-Th | Gb=72, Th=484 | 480.0 | 176.7 | p<0.05 |
| Gn-Ph | Gn=76, Ph=188 | 315.7 | 190.2 | p<0.05 |
| Gn-Th | Gn=76, Th=484 | 404.1 | 172.6 | p<0.05 |
| hc-Ph | hc=431, Ph=188 | 280.9 | 122.3 | p<0.05 |
| hc-Th | hc=431, Th=484 | 369.2 | 92.7 | p<0.05 |
| Hy-Ph | Hy=19, Ph=188 | 597.5 | 336.8 | p<0.05 |
| Hy-Pn | Hy=19, Pn=168 | 374.6 | 338.6 | p<0.05 |
| Hy-Th | Hy=19, Th=484 | 685.9 | 327.2 | p<0.05 |
| Ph-Pn | Ph=188, Pn=168 | 222.9 | 148.5 | p<0.05 |
| Pn-Th | Pn=168, Th=484 | 311.3 | 125.3 | p<0.05 |

The broad plant functional types with species with the highest establishment indices (Figure 5.11) are aquatics (mean establishment index = 72.1%), succulent evergreens (mean establishment index = 56.4%) and herbaceous perennials (mean establishment index = 48.3%). Aquatics and herbaceous perennials are both significantly different from three other groups, herbaceous annuals, broad-leaved deciduous and needle-leaved evergreens, while succulent evergreens are significantly different from herbaceous annuals and needle-leaved evergreens (multiple comparison test after Kruskal-Wallis, Table 5.5). The least established groups are needle-leaved evergreens (mean establishment index = 12.3%), needle-leaved deciduous (mean establishment index = 14.9%) and herbaceous annuals (mean establishment index = 21.8%). Herbaceous annuals and needle-leaved evergreens are significantly different from five other groups, broad-leaved evergreens, broad-leaved deciduous, herbaceous perennials, succulent evergreens and aquatics (multiple comparison test after Kruskal-Wallis, Table 5.5).

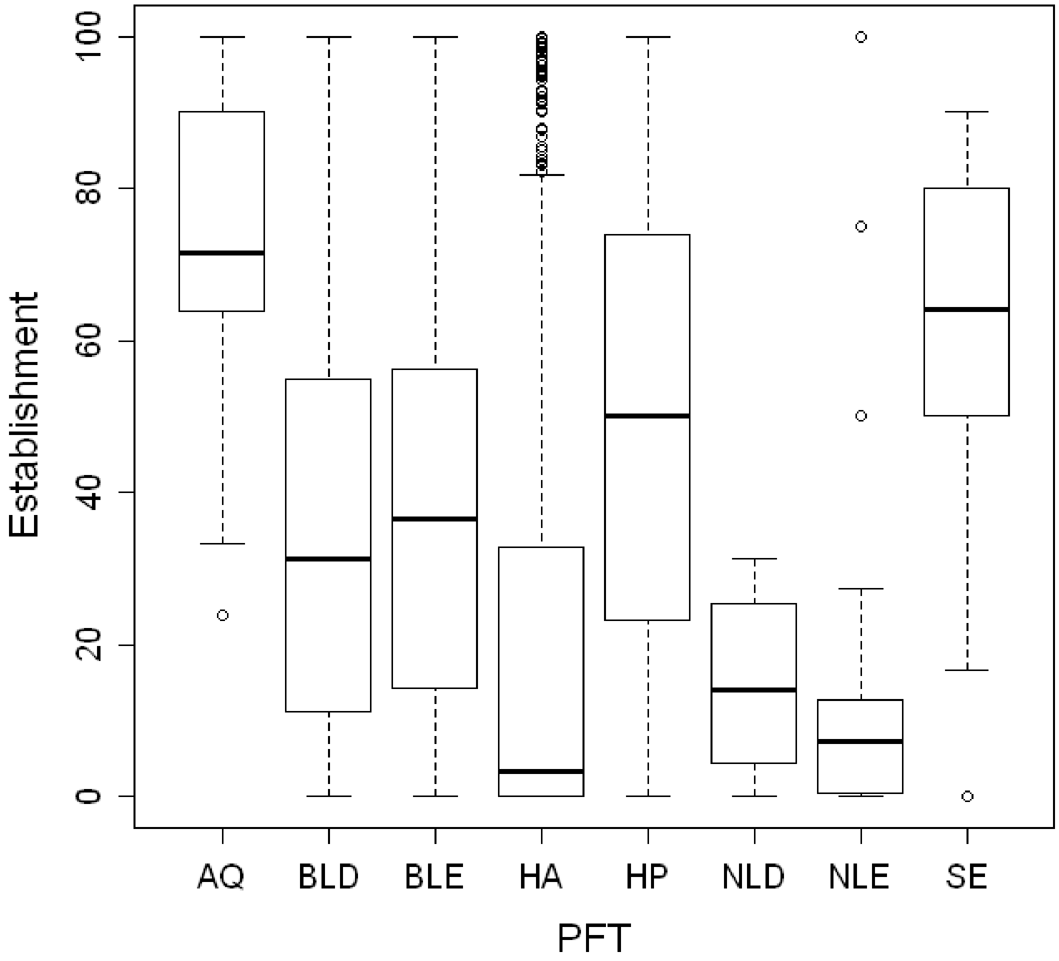


Figure 5.11. Establishment index of species within each broad PFT (AQ = Aquatic, BLD = Broad-leaved deciduous, BLE = Broad-leaved evergreen, HA = Herbaceous annual, HP = Herbaceous perennial, NLD = Needle-leaved deciduous, NLE = Needle-leaved evergreen, SE = Succulent evergreen). Significant differences between groups (Kruskal-Wallis chi-squared = 256.2, N=8, $p < 0.0001$).

Table 5.5. Comparisons of establishment index values for broad plant functional types with significant differences from multiple comparison test after Kruskal-Wallis (Kruskal-Wallis chi-squared = 256.2, N=8, $p < 0.0001$). Broad PFT abbreviations are: AQ = Aquatic, BLD = Broad-leaved deciduous, BLE = Broad-leaved evergreen, HA = Herbaceous annual, HP = Herbaceous perennial, NLE = Needle-leaved evergreen, SE = Succulent evergreen.

| Comparison | N | Observed difference | Critical difference | Significance |
|---|---|---|---|---|
| AQ-BLD | AQ=19, BLD=218 | 467.2 | 334.7 | p<0.05 |
| AQ-BLE | AQ=19, BLE=128 | 423.5 | 344.0 | p<0.05 |
| AQ-HA | AQ=19, HA=484 | 685.9 | 327.2 | p<0.05 |
| AQ-NLE | AQ=19, NLE=40 | 767.2 | 389.8 | p<0.05 |
| BLD-HA | BLD=218, HA=484 | 218.6 | 114.1 | p<0.05 |
| BLD-HP | BLD=218, HP=648 | 170.4 | 109.5 | p<0.05 |
| BLD-NLE | BLD=218, NLE=40 | 299.9 | 240.7 | p<0.05 |
| BLE-HA | BLE=128, HA=484 | 262.4 | 139.1 | p<0.05 |
| BLE-NLE | BLE=128, NLE=40 | 343.7 | 253.4 | p<0.05 |
| HA-HP | HA=484, HP=648 | 389.0 | 84.1 | p<0.05 |
| HA-SE | HA=484, SE=10 | 491.4 | 447.0 | p<0.05 |
| HP-NLE | HP=648, NLE=40 | 470.3 | 227.9 | p<0.05 |
| NLE-SE | NLE=40 , SE=10 | 572.7 | 494.6 | p<0.05 |

### *Establishment and importance of climate and land use*

The most established PFTs have the largest proportion of variance in species richness explained by climate variables and the least established groups by land cover variables. Figure 5.12 shows the proportion of total variance explained by climate variables from hierarchical partitioning against mean establishment index of species for each PFT; the relationship between the two (Spearman's rank correlation coefficient 0.672, N = 11, $p<0.028$) indicates that climate is more important for more established groups. However, caution should be taken in interpretation of the significance because the plot includes both types of functional group, and some individual species are represented in more than one of the data points.

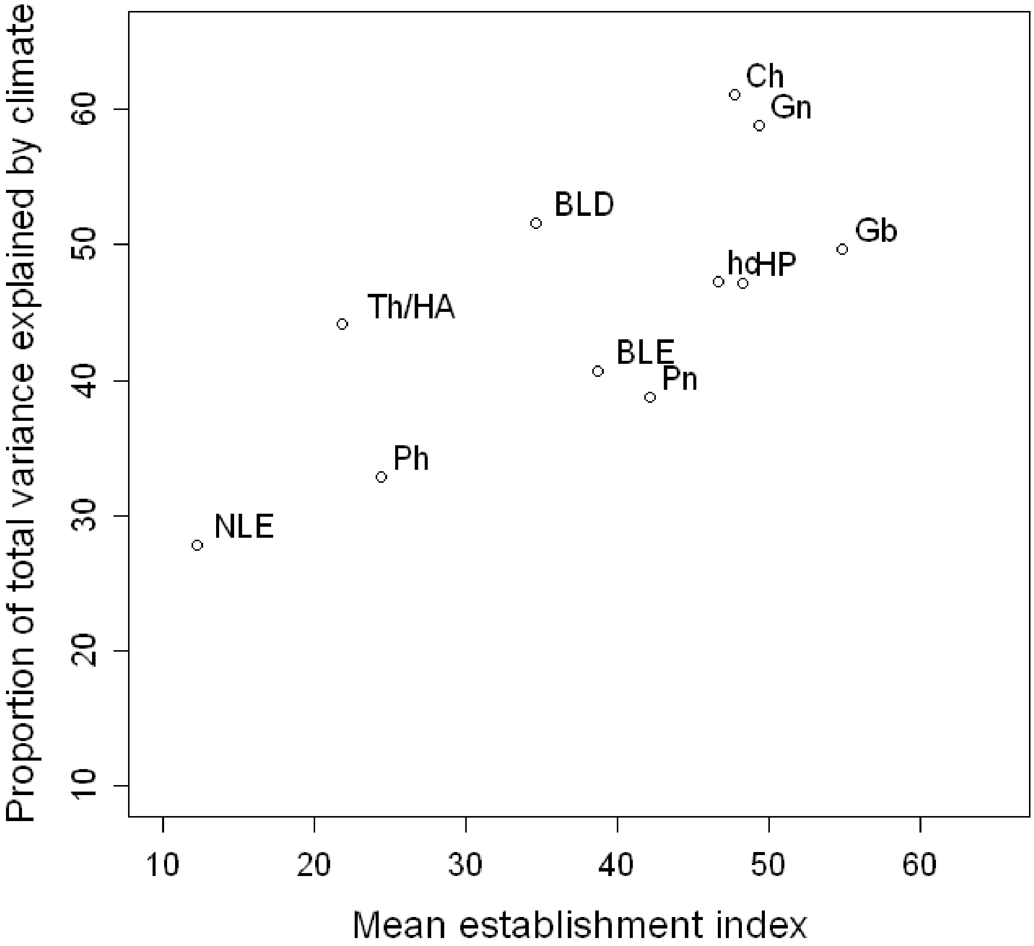


Figure 5.12. Proportion of total variance explained by climate variables from hierarchical partitioning against mean establishment index of species for each PFT (Ch = Chamaephyte, Gb = Bulbous geophyte, Gn = Non-bulbous geophyte, hc = Hemicryptophyte, Ph = Phanerophyte, Pn = Nanophanerophyte, Th/HA = Therophyte/ Herbaceous annual, BLD = Broad-leaved deciduous, BLE = Broad-leaved evergreen, HP = Herbaceous perennial , NLE = Needle-leaved evergreen).

## 5.5 Discussion

### *5.5.1 Patterns of PFTs with climate and land use*

General patterns with climate and land use show that species richness of all Plant Functional Types appear to have similar results with climate and all groups are positively associated with urban land cover; however, some PFTs are less associated with urban areas than with other land cover types.

Species richness of all PFTs is greater in warmer, drier, more urban parts of Britain, reflecting the overall species richness gradients of introduced plants in Britain. The results from the GLMs (Table 5.2 and 5.3) show all groups have a positive slope with urban land cover and with the majority of groups having the highest z value with urban land cover (all $N=291$, $p<0.001$) out of all climate and land cover variables used in the models. Significant results with climate variables show positive 1st order effects with MTWA and negative with APET. Marini *et al*. (2012) found an absence of life-form-dependent responses among non-native species along an elevation gradient, with non-native species richness showing a consistent positive relationship with temperature across all life forms. However, Hulme (2009b) found some distinct patterns for life forms when looking at a limited number of non-native species, with chamaephytes associated with cool, wet areas and bulbous geophytes and therophytes more associated with warm and dry areas. Results of this study indicate that species richness of different PFTs is not forming distinct patterns with climate variables and urban land cover, but are forming some patterns with other types of land cover, suggesting species richness is related to where species are likely to be introduced and can become established, rather than to climatic filtering.

The importance of different land cover variables varies for predicting species richness of different PFTs. The GLM urban slope estimate is positive for all Raunkiaer life forms and all broad PFTs, indicating that non-native species richness is positively associated with urban land cover for all modelled groups (Figures 5.6 and 5.7). Accidental introductions of non-native species are more likely to occur in areas with high levels of human activity, especially in urban areas that contain gardens and parks, from which many non-native species may escape (Pyšek, 1998; Dehnen-Schmutz *et al*., 2007; Botham *et al*., 2009; Roy *et al*., 2012). The PFTs with the strongest associations between species richness and urban land cover are broad-leaved evergreens (slope estimate 0.41, N=291, p<0.001) and nanophanerophytes (slope estimate 0.40, N=291, p<0.001). The results from Hierarchical Partitioning also support the importance of urban land cover for these two groups, with broad-leaved evergreens and nanophanerophytes having the largest proportions of variance explained by urban land cover out of all groups (at 13.99 and 13.86% respectively). Many broad-leaved evergreen and nanophanerophyte species are introduced as ornamentals and are grown in urban areas; examples include *Cotoneaster* spp., *Hebe* spp., *Cornus* spp., *Symphoricarpos* spp., *Berberis* spp. and *Hypericum* spp., which are frequently used in amenity planting and grown in gardens (Stace, 1997; Preston *et al*., 2002). Shrubs and species with mesomorphic leaves (those adapted to moist conditions) have been found to be over-represented among introduced neophytes in a study of an urban flora in Germany (Knapp *et al*., 2010), and it was suggested that this was due to species likely to be chosen for planting in parks and gardens.

Other studies have predicted that species which are herbaceous annuals or therophytes are most likely to benefit from urban environments (e.g. Knapp *et al*., 2008), due to a high proportion of unstable habitats such as brownfield sites and warmer and drier conditions associated with well-drained substrates and the 'urban heat island' effect (e.g. Oke, 1982). Urban land cover is positively associated with annuals in this study (GLM slope estimate 0.18, N=291, p<0.001); however, a positive association with arable land cover also important, explaining the most variation in HP (arable 12.3%, urban 10.01%). Therophytes are expected to be associated with urban environments as habitats are often dry and disturbed and this would favour species with short life-cycle and reproduction by seed; arable land could be predicted to favour this group for similar reasons, as also subject to disturbance from human activities such as ploughing etc. Examples of species which occur in both urban and arable areas are *Matricaria discoidea*, *Veronica persica*, *Coronopus didymus* and *Conyza canadensis*, which are weeds of cultivated land that occur in open, disturbed ground found in urban areas (Clement and Foster, 1994; Preston *et al*., 2002). However, more annual species are likely to have been introduced in agricultural areas in Britain: out of 530 annual non-natives in Britain, 317 (59.8%) have been intentionally introduced as an agricultural crop or unintentionally as an agricultural seed contaminant, while 130 (24.5%) have been intentionally introduced as an ornamental or unintentionally as an ornamental seed contaminant (GB Non-native species secretariat, 2011b). This indicates more annual species are likely to have been introduced into arable areas than into urban areas as garden plants.

Another group with urban land cover less important than other land cover types is needle-leaved evergreens. The results from the GLM (Table 5.3) and from Hierarchical Partitioning (Figure 5.9 and Table A3.4) indicate that broad-leaved woodland, coniferous woodland and heathland are more important than urban land cover. This is likely to be related to where deliberate planting may occur, as introduced needle-leaved evergreen species are frequently used for forestry and grown plantations (Preston *et al*., 2002), and are therefore less likely to be introduced in urban areas than other groups. This is shown in the map of species richness (Figure 5.3), with higher species richness most frequent in the north and west with urban areas less obvious than for other PFTs. However, there is still a positive relationship with urban areas for this group, as species are also planted as ornamentals in parks and gardens and may also establish from these areas.

### *5.5.2 Establishment of PFTs*

The PFTs with the most established species on average are hydrophytes (mean establishment index 72.1%), succulent evergreens (56.4%), bulbous geophytes (54.8%) and non-bulbous geophytes (49.3%) (Figure 5.10 and Figure 5.11). These groups all contain species which can reproduce vegetatively (Hill *et al*., 2004): previous studies have suggested that non-native species which can spread clonally are more likely to be able to invade semi-natural vegetation, with clonal growth becoming more important as the invaded habitat becomes more isolated, colder, wetter and less influenced by man (e.g. Thompson *et al*., 1995). Species able to spread vegetatively are more likely to be competitive in semi-natural vegetation, as they are less reliant on being able to reproduce by seed in a climate possibly less suitable for growth than in their native region. Hydrophytes can frequently regenerate from fragments; for example, *Myriophyllum aquaticum*, *Elodea canadensis* and *E. nuttallii*, or can produce specialised buds or turions in some genera. Succulent evergreens can spread from creeping and rooting at nodes, like *Carpobrotus edulis* and *Disphyma crassifolium*, and from fragments e.g. in some *Sedum* species. Geophytes can reproduce from bulbs, rhizomes, corms and tubers, with non-bulbous geophytes such as *Fallopia japonica* and *F. sachalinensis* having far-creeping rhizomes and being able to regenerate from rhizome fragments, while bulbous geophytes such as *Allium* species regenerate by slowly cloning by offsets of below-ground bulbs and also by detaching ramets on inflorescences in some species.

The PFTs with the least established species are needle-leaved evergreen (12.3%), needle-leaved deciduous (14.9%) and therophytes (21.8%). Needle-leaved evergreen and deciduous species with low establishment (<10%) include tree species widely planted as ornamentals or in plantations which are only occasionally self-sown, such as *Picea abies, Abies nordmanniana* and *Larix kaempferi* (Stace, 1997). Therophytes with low establishment (<10%) include crops such as *Brassica* spp., *Triticum* spp., *Pisum sativum*, *Raphanus sativus*, *Linum usitatissimum* and *Cucurbita* spp., and other annual species grown in gardens and amenity areas as e.g. bedding plants, such as *Nigella damascena, Limnanthes douglasii* and *Nicotiana alata*. Dehnen-Schmulz *et al*. (2007) found that ornamental species with an annual life form are more likely to escape from gardens than other life forms, but were less likely to become established than other garden plants. This was suggested to be because many annuals have a ruderal or competitive ruderal strategy (Grime, 1979), which may give them an advantage in finding suitable habitats outside cultivation but may also explain why they are less likely to establish in the wild than non-annual species grown in gardens. In contrast to the most established groups (hydrophytes, succulent evergreens, bulbous geophytes and non-bulbous geophytes), species within needle-leaved evergreen and deciduous and therophyte groups reproduce by seed. This may cause difficulties if the climate is less suitable for growth than in native regions e.g. lower growing degree days resulting in less time to complete life cycles in Britain compared to Mediterranean climates for annuals, or insufficient winter chilling for some boreal needle-leaved evergreen or deciduous species.

The most established PFTs have the largest proportion of variance in species richness explained by climate variables and the least established groups by land cover variables (Figure 5.12). The most established life forms modelled are chamaephytes, geophytes and hemicryptophytes. Life forms found to be more likely to be successful invaders in semi-natural and man-made habitats in the Czech flora were geophytes, hemicryptophytes and therophytes (Pyšek *et al*., 1995), with geophytes and hemicryptophytes more likely to be successful in semi-natural vegetation and therophytes in man-made habitats. Geophytes and hemicryptophytes were found to be more likely to be established, but therophytes were not; a large number of annual species which occur in the wild are casual escapes from crops or accidental introductions which do not necessarily become established.

### *5.5.3 Predicting distributions using models*

The results of the GLMs indicate that the species richness of Raunkiaer life forms can be predicted well; all Spearman's rank correlations between modelled and recorded species richness are over 0.741 (N = 2499, $p<0.0001$). Therophytes have the strongest correlation (Spearman's rank correlation coefficient 0.890, N = 2499, $p<0.0001$). The results of the GLMs for broad PFTs give a wider range of correlations between modelled and recorded species richness from 0.545 to 0.890 (N = 2499, $p<0.0001$). Needle-leaved evergreen have the weakest correlation between modelled and recorded species richness (Spearman's rank correlation coefficient 0.545, N = 2499, $p<0.0001$). These two groups are among the least established groups (Figures 5.10 and 5.11), and are both have more variance explained by land cover than by climate variables (Figure 5.12). Annuals are intentionally introduced as crops or ornamentals, or unintentionally introduced as seed contaminants or with raw material such as wool shoddy, and are therefore more likely to be associated with arable and urban habitats. Needle-leaved evergreens are introduced into urban areas as ornamentals, but also deliberately planted in plantations; it is possible that models are less able to predict this group due to deliberate planting in a range of land cover types.

### *5.5.4 Implications and conclusions*

In conclusion, the distributions of different groups in Britain appear predictable, in relation to climatic patterns and land use, but not in a way that was predicted a priori by the characteristics of the functional groups directly.  Rather, all groups are more diverse in warmer, drier and more urban areas. This reflects species richness gradients and means of introduction, with the distributions of the groups then modified relative to this overall pattern, depending on the species' characteristics. Some PFTs are less associated with urban areas than with other land cover types: annual species are positively associated with arable and urban land cover, with this pattern likely to be due to where species are introduced and to the occurrence of suitable habitats. The majority of annual species have been introduced as intentionally as crops or accidentally as arable weeds, with a smaller number of species introduced as ornamentals, and arable and urban land cover also provide disturbed habitats that favour reproduction by seed. Species richness of needle-leaved evergreens is positively associated with heath, acid grassland, broad-leaved woodland and coniferous woodland. These species are frequently used for forestry, and would therefore be less likely to be associated with urban. The least established groups show greater associations with land cover than with climate (therophytes and needle-leaved evergreens), while more established groups (chamaephytes, geophytes and hemicryptophytes) show a greater association with climate. Positive relationships with temperature and urban suggests all groups have potential to increase with future urbanisation and climate change.

# Chapter 6: General discussion

## 6.1 Summary of findings

This thesis has examined the establishment of non-native plant species in relation to climate and land use in Britain. The primary aims of this thesis were:
1) to determine patterns of non-native species richness with climate and land use;
2) to quantify the level of establishment of non-native species; and
3) to examine the distributions and establishment of Plant Functional Types.

Chapter 3 examined patterns of non-native species richness with climate and land use, to test whether different groups (natives, non-natives, neophytes and archaeophytes) show distinct patterns with climate and land use variables and whether current species richness can be modelled from climate and land use variables. It was found that current species richness of different groups can be predicted well using climate and land use variables. Non-native species richness is positively related to temperature and urban land cover, and negatively related to rainfall. Patterns for archaeophytes and neophyte species richness show that archaeophytes are less associated with urban areas than neophytes, with patterns more related to climate variables, although a negative association with heathland and a positive association with arable land cover are also important. Neophytes show the strongest positive association with urban land cover. Comparing differences in predicted and recorded species richness suggests that patterns are related to recorder effort at the vice-county level, with similar patterns for native and non-natives, and is related to additional recording for floras. Models using projected climate data do not suggest large increases in the proportion of non-native species in the flora; however, as the models are predicting climates not represented in the original data in the south, non-native species previously unable to survive or reproduce may become established compensating for the loss of native species in some areas.

In Chapter 4, an establishment index was calculated to quantify establishment of non-native species; this was used to test whether level of establishment increases with greater time since introduction and whether range size increases with level of establishment. It was found that date of introduction and range size are not necessarily good predictors of level of establishment, with no significant relationship between establishment and time since introduction and a weak significant relationship between establishment and range size. Models were used to test the hypothesis that species richness of poorly established species is more associated with urban land use than for well-established species and that well-established species are more associated with climate than land use. It was found that well established species are less likely to be associated with urban areas than poorly established species; however, patterns with other land cover variables and climate were less clear.

In Chapter 5, distributions and establishment of Plant Functional Types were examined. Analyses were used to test whether non-native PFTs are forming distinct patterns with climate and land use variables. It was found that distributions of different groups in Britain appear predictable in relation to climate and land use; however, all groups are most diverse in warmer, drier, more urban areas. It was predicted that PFTs with more well-established species are forming patterns associated with climate, while PFTs with more poorly established species are more associated with land use due to methods of introduction. The least established groups (therophytes, needle-leaved evergreen and needle-leaved deciduous) show greater associations with land cover than with climate. More established groups (chamaephytes, geophytes and hemicryptophytes) show a greater association with climate. Positive relationships with temperature and urban land cover suggests all groups have potential to increase with future urbanisation and climate change.

Therefore, this thesis has provided information on climate and land use variables which influence distributions and establishment of non-native plant species and on which factors are most important for different groups. Determining current patterns allows prediction of possible future changes, helping to identify groups of species which may increase with climate or land use change. Discussion of specific issues and possible further work are presented below.

## 6.2 Botanical recording

The plant data used were records on a hectad (10 x 10 km grid square) scale, provided by the Botanical Society of the British Isles. There are some limitations relating to the data set of plant records used, including variation in recorder effort in different areas of Britain (Preston *et al*., 2002). Records are from a variety of sources, including recording by members of the Botanical Society of the British Isles (www.bsbi.org.uk), and more targeted recording for vice-county floras and the New Atlas of the British and Irish Flora (Preston *et al*., 2002). This study used a subsample of well-recorded grid squares for statistical model building, with a systematic recording system, to minimise differences in recorder effort. These are the BSBI Monitoring Scheme (or Local Change) grid squares (Braithwaite *et al*., 2006): 293 squares regularly arranged in a systematic grid of 1 in 9 which have had additional recording in 1987/1988 and 2003/2004 (Figure 2.1). Comparing predicted and recorded species richness for other grid squares (Figures 3.13 and 3.14) indicates that recorder effort varies on a vice-county level (Figures 3.15 and 3.17), and is related to whether additional recording was undertaken for County Floras in the time period studied. Analysis showed similar patterns for non-native and natives for the time period studied, indicating that the same areas are well recorded for both groups (Figure 3.16).

There has been an increase in interest in recording non-natives over time, with some recent schemes to encourage wider recording in order to help determine if new non-native species are appearing in the wild or if species are spreading to new areas. This is also to aid monitoring of species considered to be problematic and to help with targeting management. For example, the Recording Invasive Species Counts project (GB Non-native species secretariat, 2011d), a web-based scheme with online recording starting in 2010, requests records for a list of species considered to be invasive. The species were selected based on criteria such as level of invasiveness, ease of identification for the general public and usefulness of the extra data to the recording scheme. Other more general schemes to encourage recording allow submission of records with photos to help with identification and verification of records; examples include iSpot (www.ispotnature.org) and iRecord (www.brc.ac.uk/irecord).

This study looked at large scale associations with land cover and climate data. The records used are presence on a 10 x 10 km grid scale; this means that when looking at land cover, species richness associations are with the proportion of broad land cover types present in each grid square, or related to the heterogeneity/homogeneity of squares. It would be necessary to use data on finer scale (e.g. records with GPS coordinates or tetrad data) or quadrat data to look at individual species associations with land cover types or habitats.

There are some large scale data sets with quadrat or habitat association data; for example, quadrat data assembled for projects such as the National Vegetation Classification (Rodwell, 1991 to 2000) and the vegetation plots recorded for the Countryside Survey (www.countrysidesurvey.org.uk). There is also information on habitat preferences for a limited number of non-native species included in PLANTATT (Hill *et al*., 2004). Finer scale data or information on habitat preferences could be used to study the level of establishment of species within different habitat types, which may help to identify habitats which could potentially have greater increases in non-native species.

Records used to calculate the establishment index used in this study were those assigned a status (Macpherson *et al*., 1996; Macpherson, 1997) by recorders: established, casual, planted or surviving (Table 4.1). Recorders assigning a status follow the status definitions and make an informed decision based on a number of factors including population size, evidence of regeneration, available habitat, and how a species was likely to have been introduced into the area. The Botanical Society of the British Isles is currently developing a new scheme to classify records by status, to allow more information on the degree of regeneration and the extent to which they are invading semi-natural habitats to be collected. The potential new categories are: survivor, casual, ruderal, established and transforming. More informative ways of quantifying establishment of non-native species in the future could include classifying species establishment while taking into account whether a species is producing seed or seedlings, population size, distance from point of origin and method of introduction. Recording habitats will also give additional information on where non-native species may be most likely to spread or become invasive.

## 6.3 Climate and land use

Climate and land use variables are important determinants for non-native species richness. Climatic conditions of a new area will influence the survival and reproduction of an introduced species, depending on similarity between the native and introduced ranges (e.g. Sakai *et al*., 2001). Land use influences where species are likely to be introduced in a new area, whether they can establish and can also affect rate of spread. Non-native species are known to be more likely to be introduced in areas with higher human population densities, as accidental introductions are more likely with high levels of human activity and many non-native species are grown in habitats associated with urban areas (Pyšek, 1998; Dehnen-Schmutz *et al*., 2007; Botham *et al*., 2009; Roy *et al*., 2012). Human disturbance can facilitate establishment and invasion (e.g. Burke and Grime, 1996), and human activity can aid dispersal allowing range expansion (e.g. Pyšek and Hulme, 2005). Previous studies analysing the spatial distributions of non-native species richness or individual species have generally found both land use and climate variables to be important factors in determining distributions (e.g. Pyšek *et al.*, 2010; Albuquerque *et al.*, 2011).

When examining patterns of species richness with climate and land cover in this study, all non-native species in Britain included in the New Atlas of the British and Irish Flora (Preston *et al*., 2002) were used. Well-recorded 10 x 10 km grid squares with a systematic sampling strategy were used to build the GLMs to minimise variation in recorder effort, and the models were then tested against the rest of the grid cells. Hierarchical Partitioning was also used to compare patterns with those from the GLMs. When the results from this study are compared to other studies examining non-native species distributions in relation to environmental variables (Hulme, 2009b; Albuquerque *et al*., 2011), the general patterns are similar with higher non-native species richness in warmer, drier, more urban areas of Britain. Previous studies have also shown that the distributions of archaeophytes are more likely to be related to climate and less likely to be related to urban land cover than neophytes (Hulme, 2009b; Albuquerque *et al*., 2011), with negative associations with urban having been shown for some archaeophytes when examining patterns for individual species (Botham *et al*., 2009). In this study, neophyte and archaeophyte species richness were both found to have positive relationships with proportion of urban land cover, with neophytes more associated with urban land cover than archaeophytes.

However, archaeophytes and neophytes vary in their levels of establishment, with some archaeophytes being poorly established while some neophytes are very well established (Figures 4.1 and 4.2). The reasons for this include wide variations in lag times (Kowarik, 1995; Caley *et al*., 2008; Daehler, 2009; Aikio *et al*., 2010) and rates of spread (Williamson *et al*., 2003; Williamson *et al*., 2005; Pyšek and Hulme, 2005), with some species taking many years between introduction or establishment and then spreading widely and others spreading almost immediately. Land use changes have also had an impact on the level of establishment of many archaeophytes, with changes in agricultural practices causing some previously well established species to become reliant on deliberate introductions to maintain their populations (Preston *et al*., 2002; Braitwaite *et al*., 2006). This is reflected in the patterns with date of introduction and establishment index, with little relationship between the two (Figure 4.1). This suggests that using date of introduction to separate species when studying patterns with climate and land use will not necessarily produce groups of species with similar characteristics. Well established species are less associated with urban areas than poorly established species (Figures 4.7 and 4.8); however, archaeophyte and neophyte categories contain both well and poorly established species, potentially giving different patterns with climate and land use depending on the number and subset of species being studied.

## 6.4 Establishment

Non-native species are frequently separated into 'casual' and 'established', with casual species not reproducing or spreading in the wild and remaining dependent on repeated introductions (Preston *et al*., 2002). The establishment index calculated for this study attempts to further quantify level of establishment for introduced species using records assigned a status (Macpherson *et al.*, 1996; Macpherson, 1997) by recorders: established, casual, planted or surviving (Table 4.1). Using this establishment index gave some clear patterns with urban land use, with poorly established species more associated with urban land cover than well established species (Figures 4.7 and 4.8). The relationships of time since introduction and time first recorded in the wild with the calculated establishment index used in this study suggests that residence time is not a good predictor of level of establishment (Figure 4.1), due to factors such as wide variations in lag times (Kowarik, 1995; Caley *et al*., 2008; Daehler, 2009; Aikio *et al*., 2010), rates of spread (Williamson *et al*., 2003; Williamson *et al*., 2005; Pyšek and Hulme, 2005) and declines caused by land use changes (Preston *et al*., 2002; Braitwaite *et al*., 2006). Range size is also not necessarily a reliable indicator of level of establishment (Figure 4.3) as this will be dependent on factors such as dispersal ability and availability of suitable habitat; a species can be well-established (reproducing successfully in the wild) within a small range, or occupy a large range but be entirely dependent on planting or repeated introductions.

Although only a small proportion of introduced species are likely to invade semi-natural vegetation and become problematic (Williamson and Brown, 1986; Williamson, 1993;

Kowarik, 1995), identifying which species they are likely to be is challenging. Previous studies attempting to distinguish successful or invasive non-natives from unsuccessful non-native or native species using traits have generally found no definitive set of characteristics describing successful non-native species (e.g. Noble, 1989; Roy, 1990; Pyšek *et al*., 1995; Tecco *et al*., 2010). Risk assessments are used to identify potentially problematic species before they are introduced, or to select species which have already been introduced which need to be prioritised for management (GB Non-native species secretariat, 2011c). The potential for escape, establishment, spread, hybridisation with natives, ecological consequences, and potential for control and risk management all need to be considered (e.g. Manchester and Bullock, 2000; Baker *et al*., 2008). Quantifying establishment in this way could help to identify recently introduced species which could potentially spread and cause problems. Species which have only recently been introduced or have been recorded in only a few places in the wild and are established in all locations may be likely to be ones that will spread widely and will require monitoring or management.

### 6.5 Plant Functional Types

PFT classifications based on life form (e.g. Raunkiaer, 1934) have been used to study distributions of non-native species in relation to climate and land use (Pyšek *et al*., 1995; Hulme, 2009; Smith, 2010; Marini *et al.*, 2012). Life forms have been shown to have predictable responses to changes in environmental variables such as water availability and temperature (e.g. Chapin *et al*., 1996; Diaz and Cabido, 1997) and disturbance (e.g. McIntyre *et al.*, 1995). It was expected that different life forms would show predictable patterns with climate; a small study looking at non-native life forms with climate found some associations (Hulme, 2009b). However, in this study all groups were found to be more diverse in warmer, drier and more urban areas, with some differences in association with types of land cover for a few groups, mainly related to where species are likely to be introduced.

Using the calculated establishment index, the least established groups show greater associations with land cover than with climate (therophytes and needle-leaved evergreens), while more established groups (chamaephytes, geophytes and hemicryptophytes) show a greater association with climate (Figure 5.12). Positive relationships with temperature and urban land cover suggests all groups have potential to increase with future urbanisation and climate change. However, the more established groups (chamaephytes, geophytes and hemicryptophytes) may have more potential to cause problems. Further study on traits related to establishment for these groups may be beneficial; these groups all contain species capable of vegetative spread or multiple methods of reproduction (Hill *et al*., 2004), while the least established groups rely on seed to reproduce (therophytes and needle-leaved evergreens). Examination of traits such as method of reproduction or dispersal mechanisms in relation to establishment may help to identify species which may spread from man-made habitats to semi-natural vegetation.

## 6.6 Climate change

Projected climate data was used to predict possible changes in species richness for natives and non-natives; all five SRES and climate model combinations showed similar patterns, with a predicted increase in species richness of natives and non-natives in the west and north and the greatest decrease in the south and east (Figures 3.21 to 3.25). Similar patterns were also shown when studying potential changes in the proportion of non-native species in the flora, with a predicted increase in proportion of non-natives in upland areas in the north and west and a decrease in the east and south (Figures 3.21 to 3.25). This does not indicate a predicted increase in the proportion of non-native species in the flora for much of Britain, as native species richness is also predicted to increase. Northern and upland areas are predicted to become more like the relatively species-rich south, with increases in temperature leading to an increase in species richness of both natives and non-natives. However, the climate in the south, which was not included in the original models, is shown to lead to a decline in native species richness but could potentially lead to a greater increase in non-native species than shown. Non-natives which are currently not able to become established may be able to establish and spread in these areas (e.g. Simberloff, 2000; Theoharides and Dukes, 2007), while species richness of natives in southern areas will depend on adaptability to new climatic conditions. Change in species richness will depend on many other factors, including land use change, habitat availability and fragmentation (e.g. Theoharides and Dukes, 2007) and dispersal ability of these species (Bullock *et al*., 2012; Travis *et al*., 2013). Potential future increases in urbanisation are also likely to favour higher non-native species richness due to the positive association between non-native species and urban land cover (Figure 3.19, Table 3.2).

Introduced species can have significant ecological impacts outside their native ranges (e.g. Millenium Ecosystem Assessment, 2005; Defra, 2008) on survival of resident biota, activity of animals, community productivity, fire frequency and nutrient cycling (Pysek *et al*., 2012). 'Invasive' non-natives have been defined as those which have a detrimental impact in their area of introduction either ecologically, socially or economically (GB Non-native species secretariat, 2011a). Future climate and land use changes could lead to increased problems with some invasive species, or allow some established species to become invasive. However, only a small proportion of introduced species are likely to invade semi-natural vegetation and become problematic (Williamson and Brown, 1986; Williamson, 1993; Kowarik; 1995). Some non-native species also have positive impacts; many species are intentionally introduced as they are economically valuable for agriculture, horticulture or forestry (Gozlan and Newton, 2009; Pejchar and Mooney, 2009). Positive ecological impacts can include increased carbon stocks in the vegetation, meaning some invaded communities can sequester more carbon than native communities (Liao *et al*., 2007) and provision of increased food resources for native invertebrate populations (Schweiger *et al*., 2010). Presence of some non-native species may lead to the loss of species diversity on a local scale but can lead to an increase in total species richness on a larger scale: non-native species are an important part of the British flora, providing a significant contribution to overall biodiversity at 44% of the British Flora (Figure 1.1; Preston *et al*., 2002).

### 6.7 Further work

This study used records assigned statuses giving information on whether or not a species is reproducing in the wild to quantify level of establishment (Chapter 4). Identifying species when they first become established in the wild and monitoring their level of establishment may help to give an indication of which species might become invasive or spread. Species which have only recently been introduced or have been recorded in only a few places in the wild and are established in all locations may be likely to be ones that will spread widely and will require monitoring or management. More informative ways of quantifying establishment of non-native species in the future could include classifying species' establishment while taking into account whether a species is producing seed or seedlings, population size, distance from point of origin and method of introduction. Recording habitats or using data on a finer scale or quadrat data to look at individual species associations with land cover types or habitats could be used to study the level of establishment of species within different habitat types, which may help to identify habitats which could potentially have greater increases in non-native species. Examination of traits such as method of reproduction or dispersal mechanisms in relation to level of establishment may also aid identification of species which may spread from man-made habitats to semi-natural vegetation.

Projected climate data were used to examine possible future changes in species richness in native and non-native species (Chapter 3). However, climate in the south, which was not included in the original models, is shown to lead to a decline in native species richness but could potentially lead to a greater increase in non-native species than shown. Non-natives which are currently not able to become established may be able to establish and spread in these areas (e.g. Simberloff, 2000; Theoharides and Dukes, 2007), while species richness of natives in southern areas will depend on adaptability to new climatic conditions. More accurate prediction with climate envelope modelling would have to include species not currently in the wild that are likely to increase based on climate of native areas i.e. garden plants: this would involve looking at potential future levels of establishment based on climates in their native ranges. PFT classifications used in Chapter 5 were selected based on those shown to be useful for climate modelling; current distribution can be modelled well, however, examining predicted changes with projected climate data could indicate which groups are most likely to increase in the future. Analyses showed land cover to be important, particularly urban land cover, suggesting predictions with projected land cover change would be valuable as further urbanisation is likely to cause increases in non-native species richness. This would require examining possible changes in species richness with projected land use change data (e.g. Rounsevell *et al*., 2006) based on interpretation of the global storylines presented in the IPCC report on emissions scenarios (IPCC, 2000). However, obtaining data with corresponding time periods and at a similar scale to the projected climate data used was difficult at the time of this study, therefore only climate data were used to assess possible future changes (see Chapter 3). Comparing these predictions with those using projected climate data, in addition to both together, could help to determine the relative importance and potential impacts of future changes in different environmental variables.

## 6.8 Concluding remarks

Non-native species are an important part of the British flora with non-native species currently accounting for 44% of species in the flora following a dramatic increase from 1500AD onwards due to large numbers of neophyte introductions (Figure 1.1). Non-native species are often viewed negatively, with a societal and scientific bias (e.g. Schlaepfer *et al*., 2010), and can have significant negative impacts outside their native ranges (e.g. Millenium Ecosystem Assessment, 2005; Defra, 2008; Pysek *et al*., 2012). However, most impacts can be potentially positive or negative, including effects on survival of resident biota, activity of animals, community productivity, fire frequency and nutrient cycling (Pysek *et al*., 2012). Many non-native species have been introduced due to their economic importance as crops or ornamental species, and some non-native species are considered to be of conservation concern with many arable weed archaeophytes identified as priority species requiring conservation action under the UK Biodiversity Action Plan (JNCC, 2007).

Climate and land use are major determinants of non-native species distributions (Carboni *et al*., 2010; Pyšek *et al*., 2010; Albuquerque *et al*., 2011; Polce *et al*., 2011) and there is potential for future changes in land use and climate to have an impact on distributions of non-native species. Future environmental conditions may favour invasions due to possible changes to transport, establishment and spread of non-native species (Theoharides and Dukes, 2007; Burgiel and Muir, 2010). This thesis has used data provided by the Botanical Society of the British Isles to determine patterns of non-native species richness with climate and land use, predict possible changes with climate change, quantify establishment of non-native species and to examine levels of establishment for different groups of non-native species in relation to environmental variables.

Non-native species richness is positively related to temperature and urban land cover, and negatively related to rainfall. Patterns for archaeophytes and neophyte species richness show that archaeophytes are less associated with urban areas than neophytes, with patterns more related to climate variables. Models using projected climate data do not suggest large increases in the proportion of non-native species in the flora; however, as the models are predicting climates not represented in the original data in the south, non-native species previously unable to survive or reproduce may become established compensating for the loss of native species in some areas. Date of introduction and range size are not necessarily good predictors of level of establishment, with no significant relationship between establishment and time since introduction and a weak significant relationship between establishment and range size. It was found that well established species are less likely to be associated with urban areas than poorly established species; however, patterns with climate were less clear. Distributions of different PFTs in Britain appear predictable in relation to climate and land use; however, all groups are most diverse in warmer, drier, more urban areas. The least established groups show greater associations with land cover than with climate while more established groups show a greater association with climate. Positive relationships with temperature and urban land cover suggests all groups have potential to increase with future urbanisation and climate change.

# Appendix 1

Table A1.1. Spearman's rank correlation coefficients between species richness and climate and land cover variables using BSBI monitoring squares (n=291). All significant (p<0.05) except those indicated by brackets.

| | Native | Non-native | Neophytes | Archaeophytes |
|---|---|---|---|---|
| GDD5 | 0.63 | 0.77 | 0.71 | 0.84 |
| MTCO | 0.33 | 0.38 | 0.34 | 0.43 |
| MTWA | 0.66 | 0.83 | 0.77 | 0.90 |
| APET | -0.57 | -0.78 | -0.71 | -0.87 |
| SPRE | -0.36 | -0.63 | -0.56 | -0.75 |
| WPRE | -0.33 | -0.61 | -0.55 | -0.71 |
| Standing water | -0.13 | -0.22 | -0.19 | -0.25 |
| Heath | -0.51 | -0.72 | -0.66 | -0.81 |
| Broad-leaved woodland | 0.67 | 0.62 | 0.64 | 0.55 |
| Coniferous woodland | (-0.01) | -0.20 | -0.13 | -0.32 |
| Improved grassland | 0.41 | 0.34 | 0.35 | 0.31 |
| Neutral grassland | 0.14 | (0.00) | (0.02) | (-0.03) |
| Calcareous grassland | 0.52 | 0.55 | 0.52 | 0.57 |
| Acid grassland | -0.33 | -0.58 | -0.53 | -0.65 |
| Arable | 0.39 | 0.65 | 0.59 | 0.75 |
| Urban | 0.64 | 0.82 | 0.81 | 0.79 |
| Inland rock | 0.13 | (0.11) | 0.13 | (0.06) |

Table A1.2. Percentage of total variance explained from Hierarchical Partitioning using climate and land cover variables from GLMs.

| **Climate and land cover variables** | **Natives** | **Non-natives** | **Neophytes** | **Archaeophytes** |
|---|---|---|---|---|
| GDD5 | | 6.33 | 6.72 | 17.13 |
| MTCO | 7.31 | 7.12 | 7.53 | |
| MTWA | 5.66 | 6.31 | 6.71 | 26.83 |
| **Temperature (total GDD5, MTCO, MTWA)** | **12.97** | **19.76** | **20.95** | **43.97** |
| APET | 22.95 | 15.30 | 13.31 | 10.53 |
| SPRE | 5.25 | 6.35 | 6.76 | |
| WPRE | | 6.39 | 6.77 | |
| **Rainfall (total APET, SPRE, WPRE)** | **28.21** | **28.03** | **26.84** | **10.53** |
| **Total for all climate** | **41.18** | **47.79** | **47.79** | **54.50** |
| Acid grassland | 7.66 | | | |
| Arable | | 9.14 | 8.05 | 8.08 |
| Broad-leaved woodland | 18.54 | 10.58 | 10.62 | 4.76 |
| Calcareous grassland | | | | |
| Coniferous woodland | 5.04 | 7.62 | 7.27 | 4.66 |
| Heath | | | | 16.74 |
| Improved grassland | 8.06 | 6.52 | 6.66 | 3.78 |
| Inland rock | 4.52 | | | |
| Neutral grassland | 4.55 | 6.68 | 6.99 | 2.56 |
| Standing water | | | | |
| Urban | 10.46 | 11.67 | 12.61 | 4.92 |
| **Total for all land cover** | **58.82** | **52.21** | **52.21** | **45.50** |

# Appendix 2

Figure A2.1. Relationships between modelled species richness and recorded species richness for each 10 x 10 km grid square (excluding model-building squares), using species grouped by level of establishment (5% to 60%).

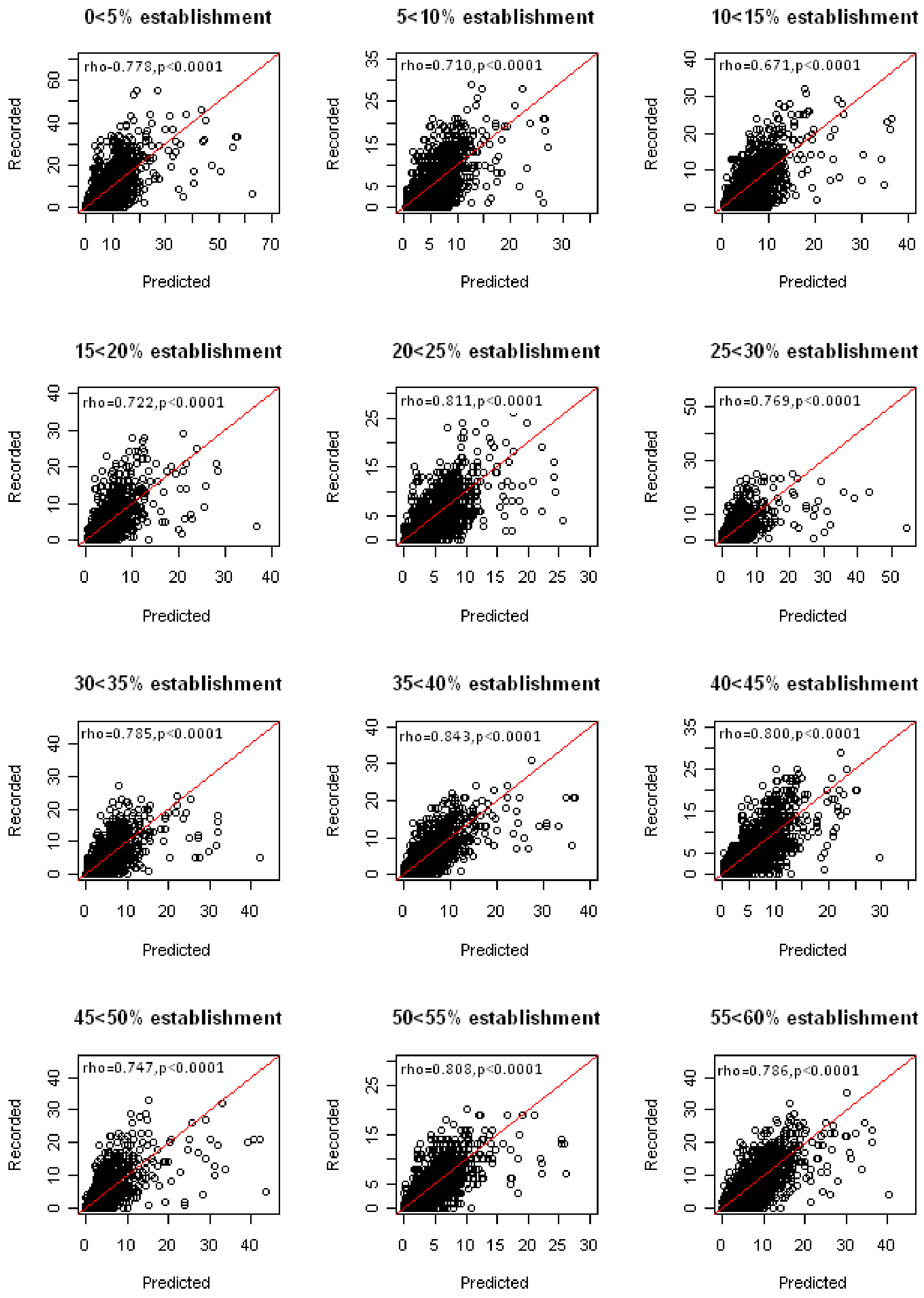


Figure A2.1. (continued) Relationships between modelled species richness and recorded species richness for each 10 x 10 km grid square (excluding model-building squares), using species grouped by level of establishment (65% to 100%).

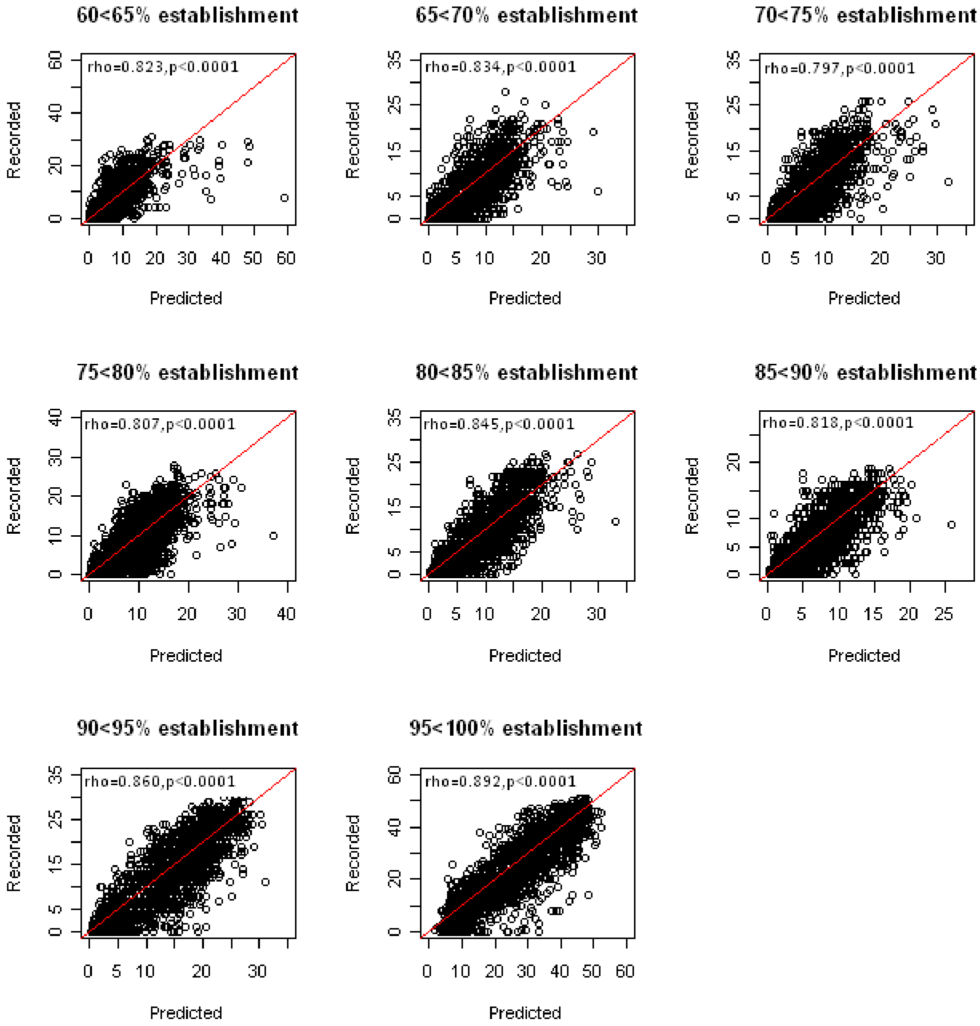


Table A2.1. GLMs for groups with different levels of establishment (2 to 20%). Slope estimate, standard error, Z value and significance are shown for each climate and land cover variable included (after elimination using AIC). Predictor variables were standardised to allow comparison of relative importance.

| | 5 | | | | | 10 | | | | | 15 | | | | | 20 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. |
| poly(GDD5, 2)1 | 20.93 | 24.62 | 0.85 | 0.3952 | | -16.26 | 4.86 | -3.35 | 0.0008 | *** | -2.18 | 4.65 | -0.47 | 0.6386 | | | | | | |
| poly(GDD5, 2)2 | 1.90 | 4.85 | 0.39 | 0.6952 | | 6.40 | 1.88 | 3.41 | 0.0006 | *** | 3.01 | 1.81 | 1.66 | 0.0969 | . | | | | | |
| poly(MTCO, 2)1 | -7.07 | 7.12 | -0.99 | 0.3205 | | | | | | | | | | | | -4.07 | 1.51 | -2.71 | 0.0068 | ** |
| poly(MTCO, 2)2 | -3.46 | 2.84 | -1.22 | 0.2218 | | | | | | | | | | | | 1.04 | 1.14 | 0.91 | 0.3622 | |
| poly(MTWA, 2)1 | 3.26 | 21.02 | 0.16 | 0.8769 | | 18.76 | 5.53 | 3.39 | 0.0007 | *** | 8.95 | 5.48 | 1.63 | 0.1023 | | 12.76 | 3.12 | 4.10 | 0.0000 | *** |
| poly(MTWA, 2)2 | -5.41 | 4.09 | -1.32 | 0.1857 | | -6.53 | 1.97 | -3.32 | 0.0009 | *** | -3.72 | 1.98 | -1.88 | 0.0601 | . | -3.63 | 1.45 | -2.51 | 0.0122 | * |
| poly(APET, 2)1 | | | | | | -5.02 | 2.34 | -2.15 | 0.0316 | * | -3.59 | 2.35 | -1.53 | 0.1263 | | -3.68 | 2.34 | -1.58 | 0.1147 | |
| poly(APET, 2)2 | | | | | | -1.36 | 0.90 | -1.52 | 0.1294 | | -0.54 | 0.89 | -0.61 | 0.5436 | | -0.31 | 0.98 | -0.32 | 0.7496 | |
| poly(SPRE, 2)1 | 1.76 | 2.20 | 0.80 | 0.4228 | | 2.75 | 4.59 | 0.60 | 0.5498 | | 5.98 | 4.53 | 1.32 | 0.1869 | | 3.76 | 1.75 | 2.15 | 0.0313 | * |
| poly(SPRE, 2)2 | -1.28 | 1.77 | -0.72 | 0.4700 | | -4.81 | 2.68 | -1.80 | 0.0720 | . | -4.89 | 2.61 | -1.87 | 0.0609 | . | -1.06 | 1.40 | -0.75 | 0.4508 | |
| poly(WPRE, 2)1 | | | | | | 0.84 | 4.27 | 0.20 | 0.8436 | | -3.54 | 4.24 | -0.84 | 0.4031 | | | | | | |
| poly(WPRE, 2)2 | | | | | | 4.06 | 2.50 | 1.62 | 0.1047 | | 4.69 | 2.49 | 1.88 | 0.0600 | . | | | | | |
| acid | 0.11 | 0.11 | 1.06 | 0.2878 | | 0.11 | 0.07 | 1.59 | 0.1113 | | 0.18 | 0.07 | 2.54 | 0.0111 | * | 0.18 | 0.08 | 2.18 | 0.0296 | * |
| arable | 0.51 | 0.13 | 3.96 | 0.0001 | *** | 0.51 | 0.09 | 5.48 | 0.0000 | *** | 0.44 | 0.11 | 3.93 | 0.0001 | *** | 0.44 | 0.13 | 3.49 | 0.0005 | *** |
| bwood | 0.06 | 0.04 | 1.33 | 0.1836 | | 0.12 | 0.04 | 3.21 | 0.0013 | ** | 0.16 | 0.04 | 4.07 | 0.0000 | *** | 0.13 | 0.04 | 3.00 | 0.0027 | ** |
| calc | | | | | | | | | | | | | | | | | | | | |
| cwood | 0.33 | 0.07 | 4.62 | 0.0000 | *** | 0.26 | 0.05 | 5.38 | 0.0000 | *** | 0.30 | 0.05 | 5.90 | 0.0000 | *** | 0.26 | 0.06 | 4.38 | 0.0000 | *** |
| heath | 0.20 | 0.19 | 1.05 | 0.2930 | | | | | | | 0.22 | 0.12 | 1.84 | 0.0663 | . | 0.29 | 0.14 | 2.08 | 0.0377 | * |
| improved | 0.36 | 0.10 | 3.55 | 0.0004 | *** | 0.38 | 0.07 | 5.43 | 0.0000 | *** | 0.38 | 0.09 | 4.25 | 0.0000 | *** | 0.39 | 0.10 | 3.97 | 0.0001 | *** |
| inrock | 0.09 | 0.07 | 1.31 | 0.1902 | | 0.10 | 0.05 | 1.77 | 0.0767 | . | 0.09 | 0.05 | 1.80 | 0.0719 | . | | | | | |
| neutral | 0.11 | 0.08 | 1.36 | 0.1727 | | 0.15 | 0.06 | 2.63 | 0.0085 | ** | 0.16 | 0.06 | 2.53 | 0.0113 | * | 0.14 | 0.07 | 2.01 | 0.0443 | * |
| swater | | | | | | | | | | | | | | | | | | | | |
| urban | 0.41 | 0.06 | 6.55 | 0.0000 | *** | 0.40 | 0.05 | 8.16 | 0.0000 | *** | 0.39 | 0.06 | 7.01 | 0.0000 | *** | 0.43 | 0.06 | 6.82 | 0.0000 | *** |

Table A2.1. (continued) GLMs for groups with different levels of establishment (25 to 40%).

| | 25 | | | | | 30 | | | | | 35 | | | | | 40 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. |
| poly(GDD5, 2)1 | -19.47 | 26.06 | -0.75 | 0.4550 | | 1.68 | 28.36 | 0.06 | 0.9527 | | 31.84 | 20.91 | 1.52 | 0.1278 | | 27.91 | 20.66 | 1.35 | 0.1766 | |
| poly(GDD5, 2)2 | 14.44 | 5.65 | 2.55 | 0.0106 | * | 11.52 | 5.12 | 2.25 | 0.0244 | * | 2.05 | 3.72 | 0.55 | 0.5814 | | 11.10 | 4.24 | 2.62 | 0.0088 | ** |
| poly(MTCO, 2)1 | 3.53 | 7.53 | 0.47 | 0.6391 | | -0.26 | 8.26 | -0.03 | 0.9753 | | -8.22 | 6.02 | -1.37 | 0.1717 | | -9.28 | 6.04 | -1.54 | 0.1242 | |
| poly(MTCO, 2)2 | -8.05 | 3.43 | -2.35 | 0.0190 | * | -5.31 | 3.29 | -1.61 | 0.1065 | | -4.21 | 2.33 | -1.81 | 0.0705 | . | -9.61 | 2.49 | -3.87 | 0.0001 | *** |
| poly(MTWA, 2)1 | 31.53 | 21.62 | 1.46 | 0.1448 | | 13.31 | 23.52 | 0.57 | 0.5714 | | -15.15 | 17.54 | -0.86 | 0.3878 | | -3.48 | 17.55 | -0.20 | 0.8427 | |
| poly(MTWA, 2)2 | -16.38 | 4.46 | -3.67 | 0.0002 | *** | -12.57 | 4.04 | -3.11 | 0.0019 | ** | -3.87 | 2.89 | -1.34 | 0.1808 | | -12.06 | 3.35 | -3.60 | 0.0003 | *** |
| poly(APET, 2)1 | -7.12 | 2.84 | -2.51 | 0.0121 | * | -0.20 | 0.14 | -1.47 | 0.1423 | | | | | | | | | | | |
| poly(APET, 2)2 | -1.64 | 1.06 | -1.55 | 0.1217 | | | | | | | | | | | | | | | | |
| poly(SPRE, 2)1 | -7.25 | 7.40 | -0.98 | 0.3271 | | -10.81 | 8.07 | -1.34 | 0.1802 | | -0.12 | 0.10 | -1.29 | 0.1974 | | -9.70 | 6.33 | -1.53 | 0.1256 | |
| poly(SPRE, 2)2 | -12.59 | 4.60 | -2.74 | 0.0061 | ** | -16.93 | 5.25 | -3.22 | 0.0013 | ** | | | | | | -11.06 | 3.56 | -3.11 | 0.0019 | ** |
| poly(WPRE, 2)1 | 8.03 | 6.54 | 1.23 | 0.2199 | | 7.58 | 7.03 | 1.08 | 0.2808 | | | | | | | 6.45 | 5.56 | 1.16 | 0.2463 | |
| poly(WPRE, 2)2 | 10.41 | 3.85 | 2.71 | 0.0068 | ** | 11.26 | 4.20 | 2.68 | 0.0074 | ** | | | | | | 9.77 | 3.29 | 2.97 | 0.0030 | ** |
| acid | | | | | | 0.14 | 0.11 | 1.29 | 0.1981 | | | | | | | | | | | |
| arable | 0.35 | 0.11 | 3.26 | 0.0011 | ** | 0.44 | 0.12 | 3.68 | 0.0002 | *** | 0.34 | 0.09 | 3.79 | 0.0002 | *** | 0.24 | 0.08 | 2.84 | 0.0045 | ** |
| bwood | 0.08 | 0.04 | 1.99 | 0.0462 | * | 0.10 | 0.05 | 2.06 | 0.0390 | * | 0.09 | 0.04 | 2.40 | 0.0162 | * | 0.09 | 0.03 | 2.61 | 0.0091 | ** |
| calc | 0.08 | 0.05 | 1.47 | 0.1415 | | | | | | | -0.10 | 0.05 | -1.87 | 0.0622 | . | | | | | |
| cwood | 0.34 | 0.07 | 4.98 | 0.0000 | *** | 0.28 | 0.07 | 3.73 | 0.0002 | *** | 0.18 | 0.06 | 2.76 | 0.0057 | ** | 0.18 | 0.06 | 3.05 | 0.0023 | ** |
| heath | | | | | | | | | | | | | | | | | | | | |
| improved | 0.31 | 0.08 | 3.79 | 0.0002 | *** | 0.37 | 0.10 | 3.89 | 0.0001 | *** | 0.26 | 0.07 | 3.97 | 0.0001 | *** | 0.26 | 0.07 | 3.99 | 0.0001 | *** |
| inrock | 0.14 | 0.07 | 2.16 | 0.0306 | * | | | | | | 0.08 | 0.06 | 1.38 | 0.1683 | | | | | | |
| neutral | 0.17 | 0.08 | 2.24 | 0.0251 | * | 0.19 | 0.08 | 2.41 | 0.0161 | * | 0.12 | 0.06 | 2.01 | 0.0449 | * | 0.18 | 0.06 | 3.01 | 0.0026 | ** |
| swater | 0.07 | 0.06 | 1.31 | 0.1912 | | 0.07 | 0.06 | 1.19 | 0.2356 | | | | | | | | | | | |
| urban | 0.35 | 0.05 | 6.34 | 0.0000 | *** | 0.46 | 0.06 | 7.52 | 0.0000 | *** | 0.34 | 0.05 | 7.35 | 0.0000 | *** | 0.31 | 0.04 | 7.33 | 0.0000 | *** |

Table A2.1. (continued) GLMs for groups with different levels of establishment (45 to 60%).

| | 45 | | | | | 50 | | | | | 55 | | | | | 60 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. |
| poly(GDD5, 2)1 | | | | | | | | | | | -16.22 | 22.11 | -0.73 | 0.4632 | | -7.74 | 21.01 | -0.37 | 0.7127 | |
| poly(GDD5, 2)2 | | | | | | | | | | | 12.50 | 4.42 | 2.83 | 0.0047 | ** | 9.72 | 4.03 | 2.41 | 0.0159 | * |
| poly(MTCO, 2)1 | | | | | | | | | | | 2.03 | 6.32 | 0.32 | 0.7488 | | 1.63 | 5.95 | 0.28 | 0.7836 | |
| poly(MTCO, 2)2 | | | | | | | | | | | -6.09 | 2.79 | -2.18 | 0.0291 | * | -5.09 | 2.65 | -1.92 | 0.0544 | . |
| poly(MTWA, 2)1 | 7.49 | 1.93 | 3.89 | 0.0001 | *** | 11.54 | 3.64 | 3.17 | 0.0015 | ** | 23.94 | 18.20 | 1.32 | 0.1885 | | 14.50 | 17.36 | 0.84 | 0.4036 | |
| poly(MTWA, 2)2 | -3.61 | 0.98 | -3.70 | 0.0002 | *** | -4.41 | 1.72 | -2.57 | 0.0103 | * | -12.73 | 3.42 | -3.73 | 0.0002 | *** | -10.46 | 3.16 | -3.31 | 0.0009 | *** |
| poly(APET, 2)1 | -4.03 | 1.57 | -2.57 | 0.0102 | * | -7.08 | 3.39 | -2.09 | 0.0368 | * | -9.76 | 2.54 | -3.85 | 0.0001 | *** | -5.28 | 2.38 | -2.22 | 0.0264 | * |
| poly(APET, 2)2 | -1.03 | 0.70 | -1.48 | 0.1397 | | -0.87 | 1.16 | -0.75 | 0.4541 | | -2.12 | 0.94 | -2.26 | 0.0238 | * | -1.12 | 0.92 | -1.22 | 0.2224 | |
| poly(SPRE, 2)1 | 1.03 | 1.31 | 0.79 | 0.4315 | | 5.09 | 8.27 | 0.62 | 0.5383 | | -2.50 | 6.13 | -0.41 | 0.6832 | | 0.43 | 5.31 | 0.08 | 0.9354 | |
| poly(SPRE, 2)2 | -2.51 | 1.28 | -1.97 | 0.0493 | * | -12.28 | 6.24 | -1.97 | 0.0493 | * | -16.11 | 4.19 | -3.84 | 0.0001 | *** | -9.70 | 3.41 | -2.84 | 0.0045 | ** |
| poly(WPRE, 2)1 | | | | | | -9.32 | 7.39 | -1.26 | 0.2071 | | 1.45 | 5.38 | 0.27 | 0.7872 | | 0.29 | 4.79 | 0.06 | 0.9510 | |
| poly(WPRE, 2)2 | | | | | | 2.91 | 4.84 | 0.60 | 0.5469 | | 9.08 | 3.35 | 2.71 | 0.0067 | ** | 7.02 | 2.98 | 2.36 | 0.0185 | * |
| acid | | | | | | | | | | | | | | | | | | | | |
| arable | 0.33 | 0.07 | 4.99 | 0.0000 | *** | 0.23 | 0.12 | 1.96 | 0.0502 | . | 0.29 | 0.09 | 3.37 | 0.0008 | *** | 0.33 | 0.09 | 3.46 | 0.0005 | *** |
| bwood | 0.10 | 0.03 | 3.57 | 0.0004 | *** | 0.10 | 0.04 | 2.23 | 0.0260 | * | 0.10 | 0.04 | 2.83 | 0.0047 | ** | 0.15 | 0.04 | 4.20 | 0.0000 | *** |
| calc | | | | | | -0.10 | 0.06 | -1.50 | 0.1332 | | | | | | | | | | | |
| cwood | 0.21 | 0.04 | 4.92 | 0.0000 | *** | 0.24 | 0.07 | 3.40 | 0.0007 | *** | 0.23 | 0.05 | 4.25 | 0.0000 | *** | 0.24 | 0.05 | 4.56 | 0.0000 | *** |
| heath | | | | | | | | | | | | | | | | 0.13 | 0.12 | 1.11 | 0.2691 | |
| improved | 0.23 | 0.05 | 4.58 | 0.0000 | *** | 0.16 | 0.09 | 1.85 | 0.0649 | . | 0.33 | 0.07 | 5.02 | 0.0000 | *** | 0.31 | 0.07 | 4.22 | 0.0000 | *** |
| inrock | | | | | | | | | | | | | | | | 0.08 | 0.06 | 1.38 | 0.1664 | |
| neutral | 0.13 | 0.04 | 2.97 | 0.0030 | ** | 0.11 | 0.08 | 1.29 | 0.1969 | | 0.16 | 0.06 | 2.72 | 0.0066 | ** | 0.15 | 0.06 | 2.47 | 0.0137 | * |
| swater | | | | | | | | | | | | | | | | | | | | |
| urban | 0.32 | 0.04 | 8.71 | < 2e-16 | *** | 0.38 | 0.06 | 6.45 | 0.0000 | *** | 0.32 | 0.04 | 7.12 | 0.0000 | *** | 0.34 | 0.05 | 7.01 | 0.0000 | *** |

Table A2.1. (continued) GLMs for groups with different levels of establishment (65 to 80%).

| | 65 | | | | | 70 | | | | | 75 | | | | | 80 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. |
| poly(GDD5, 2)1 | -9.83 | 20.83 | -0.47 | 0.6370 | | 16.42 | 16.05 | 1.02 | 0.3062 | | | | | | | 2.21 | 14.52 | 0.15 | 0.8792 | |
| poly(GDD5, 2)2 | 11.43 | 4.18 | 2.74 | 0.0062 | ** | 8.39 | 3.03 | 2.77 | 0.0056 | ** | | | | | | 6.00 | 2.62 | 2.29 | 0.0220 | * |
| poly(MTCO, 2)1 | 3.00 | 5.97 | 0.50 | 0.6147 | | -6.44 | 4.63 | -1.39 | 0.1645 | | | | | | | -1.93 | 4.09 | -0.47 | 0.6370 | |
| poly(MTCO, 2)2 | -6.58 | 2.63 | -2.50 | 0.0124 | * | -5.67 | 1.90 | -2.99 | 0.0028 | ** | | | | | | -3.68 | 1.72 | -2.15 | 0.0318 | * |
| poly(MTWA, 2)1 | 17.10 | 17.35 | 0.99 | 0.3243 | | 3.58 | 13.45 | 0.27 | 0.7901 | | 7.38 | 1.60 | 4.61 | 0.0000 | *** | 9.18 | 12.13 | 0.76 | 0.4492 | |
| poly(MTWA, 2)2 | -11.22 | 3.30 | -3.39 | 0.0007 | *** | -11.30 | 2.32 | -4.87 | 0.0000 | *** | -3.02 | 0.82 | -3.70 | 0.0002 | *** | -7.93 | 1.99 | -3.98 | 0.0001 | *** |
| poly(APET, 2)1 | -5.27 | 2.33 | -2.26 | 0.0239 | * | | | | | | -2.21 | 1.37 | -1.61 | 0.1080 | | | | | | |
| poly(APET, 2)2 | -1.01 | 0.86 | -1.17 | 0.2410 | | | | | | | -0.37 | 0.61 | -0.61 | 0.5409 | | | | | | |
| poly(SPRE, 2)1 | -1.21 | 5.70 | -0.21 | 0.8319 | | -5.22 | 4.39 | -1.19 | 0.2343 | | 2.77 | 0.97 | 2.86 | 0.0043 | ** | | | | | |
| poly(SPRE, 2)2 | -9.50 | 3.72 | -2.55 | 0.0107 | * | -6.52 | 2.50 | -2.61 | 0.0091 | ** | -0.66 | 0.88 | -0.76 | 0.4496 | | | | | | |
| poly(WPRE, 2)1 | 0.39 | 5.13 | 0.08 | 0.9394 | | 3.41 | 4.03 | 0.85 | 0.3976 | | | | | | | | | | | |
| poly(WPRE, 2)2 | 4.76 | 3.16 | 1.51 | 0.1316 | | 5.39 | 2.42 | 2.22 | 0.0261 | * | | | | | | | | | | |
| acid | | | | | | | | | | | | | | | | | | | | |
| arable | 0.26 | 0.08 | 3.12 | 0.0018 | ** | 0.15 | 0.06 | 2.47 | 0.0134 | * | 0.28 | 0.06 | 4.95 | 0.0000 | *** | 0.26 | 0.05 | 4.87 | 0.0000 | *** |
| bwood | 0.12 | 0.03 | 3.68 | 0.0002 | *** | 0.06 | 0.03 | 2.30 | 0.0214 | * | 0.12 | 0.02 | 4.72 | 0.0000 | *** | 0.08 | 0.03 | 3.17 | 0.0015 | ** |
| calc | | | | | | | | | | | | | | | | | | | | |
| cwood | 0.22 | 0.05 | 4.36 | 0.0000 | *** | 0.18 | 0.04 | 4.33 | 0.0000 | *** | 0.19 | 0.04 | 5.32 | 0.0000 | *** | 0.14 | 0.04 | 3.36 | 0.0008 | *** |
| heath | -0.19 | 0.14 | -1.38 | 0.1680 | | | | | | | | | | | | | | | | |
| improved | 0.17 | 0.07 | 2.49 | 0.0130 | * | 0.13 | 0.05 | 2.78 | 0.0055 | ** | 0.23 | 0.04 | 5.40 | 0.0000 | *** | 0.22 | 0.04 | 4.86 | 0.0000 | *** |
| inrock | | | | | | | | | | | 0.08 | 0.04 | 2.01 | 0.0442 | * | | | | | |
| neutral | 0.11 | 0.06 | 1.92 | 0.0546 | . | 0.09 | 0.05 | 1.95 | 0.0518 | . | 0.13 | 0.03 | 3.91 | 0.0001 | *** | 0.15 | 0.04 | 3.94 | 0.0001 | *** |
| swater | | | | | | | | | | | | | | | | | | | | |
| urban | 0.32 | 0.04 | 7.38 | 0.0000 | *** | 0.19 | 0.03 | 5.65 | 0.0000 | *** | 0.28 | 0.03 | 8.83 | < 2e-16 | *** | 0.24 | 0.03 | 7.65 | 0.0000 | *** |

Table A2.1. (continued) GLMs for groups with different levels of establishment (85 to 100%).

| | 85 | | | | | 90 | | | | | 95 | | | | | 100 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. | Slope | S.E. | Z | P | Signif. |
| poly(GDD5, 2)1 | 3.01 | 12.86 | 0.23 | 0.8146 | | -7.74 | 14.50 | -0.53 | 0.5936 | | -1.08 | 10.00 | -0.11 | 0.9141 | | -8.65 | 1.35 | -6.39 | 0.0000 | *** |
| poly(GDD5, 2)2 | 5.53 | 2.28 | 2.43 | 0.0152 | * | 9.92 | 2.48 | 4.00 | 0.0001 | *** | 6.36 | 1.76 | 3.61 | 0.0003 | *** | 3.23 | 0.56 | 5.82 | 0.0000 | *** |
| poly(MTCO, 2)1 | -2.58 | 3.61 | -0.71 | 0.4751 | | -1.49 | 4.08 | -0.37 | 0.7153 | | -2.30 | 2.79 | -0.83 | 0.4096 | | | | | | |
| poly(MTCO, 2)2 | -3.47 | 1.49 | -2.34 | 0.0196 | * | -3.61 | 1.66 | -2.17 | 0.0302 | * | -3.35 | 1.17 | -2.87 | 0.0041 | ** | | | | | |
| poly(MTWA, 2)1 | 8.14 | 10.70 | 0.76 | 0.4466 | | 17.79 | 11.86 | 1.50 | 0.1337 | | 10.91 | 8.31 | 1.31 | 0.1893 | | 16.68 | 1.56 | 10.71 | < 2e-16 | *** |
| poly(MTWA, 2)2 | -6.40 | 1.71 | -3.74 | 0.0002 | *** | -10.61 | 1.85 | -5.74 | 0.0000 | *** | -7.46 | 1.31 | -5.70 | 0.0000 | *** | -5.00 | 0.57 | -8.75 | < 2e-16 | *** |
| poly(APET, 2)1 | | | | | | -0.13 | 0.07 | -1.88 | 0.0604 | . | | | | | | | | | | |
| poly(APET, 2)2 | | | | | | | | | | | | | | | | | | | | |
| poly(SPRE, 2)1 | | | | | | 6.18 | 3.34 | 1.85 | 0.0644 | . | | | | | | | | | | |
| poly(SPRE, 2)2 | | | | | | -3.93 | 2.05 | -1.92 | 0.0546 | . | | | | | | | | | | |
| poly(WPRE, 2)1 | | | | | | -5.37 | 3.10 | -1.73 | 0.0830 | . | | | | | | | | | | |
| poly(WPRE, 2)2 | | | | | | 1.29 | 1.95 | 0.66 | 0.5065 | | | | | | | | | | | |
| acid | | | | | | 0.07 | 0.04 | 1.58 | 0.1146 | | 0.07 | 0.03 | 2.22 | 0.0262 | * | | | | | |
| arable | 0.20 | 0.05 | 4.26 | 0.0000 | *** | 0.22 | 0.05 | 4.15 | 0.0000 | *** | 0.20 | 0.04 | 5.13 | 0.0000 | *** | 0.09 | 0.02 | 3.57 | 0.0004 | *** |
| bwood | 0.09 | 0.02 | 3.91 | 0.0001 | *** | 0.13 | 0.02 | 5.64 | 0.0000 | *** | 0.11 | 0.02 | 5.73 | 0.0000 | *** | 0.03 | 0.01 | 2.64 | 0.0084 | ** |
| calc | | | | | | | | | | | | | | | | | | | | |
| cwood | 0.14 | 0.03 | 3.92 | 0.0001 | *** | 0.12 | 0.03 | 3.58 | 0.0003 | *** | 0.07 | 0.03 | 2.42 | 0.0156 | * | 0.05 | 0.02 | 2.68 | 0.0073 | ** |
| heath | | | | | | | | | | | | | | | | -0.06 | 0.03 | -1.82 | 0.0690 | . |
| improved | 0.19 | 0.04 | 4.83 | 0.0000 | *** | 0.22 | 0.04 | 5.29 | 0.0000 | *** | 0.20 | 0.03 | 6.24 | 0.0000 | *** | 0.07 | 0.02 | 3.58 | 0.0003 | *** |
| inrock | | | | | | 0.06 | 0.04 | 1.57 | 0.1162 | | | | | | | 0.04 | 0.02 | 2.09 | 0.0363 | * |
| neutral | 0.08 | 0.03 | 2.41 | 0.0161 | * | | | | | | 0.10 | 0.03 | 3.95 | 0.0001 | *** | 0.03 | 0.02 | 1.70 | 0.0884 | . |
| swater | | | | | | | | | | | | | | | | -0.03 | 0.02 | -1.60 | 0.1090 | |
| urban | 0.19 | 0.03 | 6.69 | 0.0000 | *** | 0.19 | 0.03 | 6.24 | 0.0000 | *** | 0.14 | 0.02 | 5.79 | 0.0000 | *** | 0.06 | 0.01 | 3.75 | 0.0002 | *** |

Table A2.2. Percentage of total variance explained from Hierarchical Partitioning using climate and land cover variables from GLMs for species grouped by level of establishment (5% to 50%).

| **Climate and land cover variables** | **Level of establishment (%)** | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **>0, ≤5** | **>5, ≤10** | **>10, ≤15** | **>15, ≤20** | **>20, ≤25** | **>25, ≤30** | **>30, ≤35** | **>35, ≤40** | **>40, ≤45** | **>45, ≤50** |
| GDD5 | | 18.19 | | | 6.74 | 7.64 | 18.25 | 7.17 | | |
| MTCO | 13.77 | | | 5.94 | 7.83 | 7.12 | 15.75 | 17.75 | | |
| MTWA | 7.75 | 23.57 | 6.93 | 23.13 | 7.14 | 7.95 | 6.81 | 7.92 | 22.79 | 21.40 |
| **Temperature (total GDD5, MTCO, MTWA)** | **21.53** | **41.75** | **6.93** | **29.06** | **21.71** | **22.72** | **40.81** | **32.83** | **22.79** | **21.40** |
| APET | | 1.26 | | | 16.63 | 13.84 | | | 18.37 | 9.67 |
| SPRE | | 5.53 | 7.16 | 9.30 | 6.22 | 6.75 | | 6.77 | 17.44 | 6.28 |
| WPRE | | | 6.67 | | 6.51 | 6.74 | | 7.59 | | 1.94 |
| **Rainfall (total APET, SPRE, WPRE)** | | **6.79** | **13.83** | **9.30** | **29.36** | **27.33** | | **14.35** | **35.80** | **17.90** |
| **Total for all climate** | **21.53** | **56.87** | **20.61** | **38.27** | **51.04** | **48.61** | **40.81** | **46.65** | **58.10** | **48.04** |
| Acid grassland | 12.32 | | 9.63 | 7.84 | | | | | | |
| Arable | 7.84 | 7.88 | 7.58 | 6.77 | 9.35 | 7.58 | 8.43 | 8.79 | 7.11 | 7.29 |
| Broad-leaved woodland | 7.55 | 7.75 | 9.94 | 8.04 | | 8.71 | 7.57 | 9.68 | 7.89 | 8.22 |
| Calcareous grassland | | | | | | | 6.18 | | | 6.14 |
| Coniferous woodland | 6.81 | 5.68 | 6.21 | 5.77 | 7.59 | 8.24 | 7.50 | 8.84 | 5.89 | 6.30 |
| Heath | 16.01 | | 14.84 | 11.35 | | | | | | |
| Improved grassland | 5.79 | 5.33 | 6.40 | 4.99 | 6.58 | 6.61 | 5.79 | 6.11 | 5.62 | 5.85 |
| Inland rock | 5.06 | | 5.73 | | 6.00 | | 5.95 | | | |
| Neutral grassland | 5.54 | 5.37 | 6.00 | 5.26 | 6.68 | 7.08 | 5.65 | 6.88 | 5.21 | 5.52 |
| Standing water | | | | | | | | | | |
| Urban | 11.56 | 11.12 | 13.07 | 11.70 | 12.75 | 13.16 | 12.12 | 13.04 | 10.19 | 12.64 |
| **Total for all land cover** | **78.47** | **43.13** | **79.39** | **61.73** | **48.96** | **51.39** | **59.19** | **53.35** | **41.90** | **51.96** |

Table A2.2. (continued) Percentage of total variance explained from Hierarchical Partitioning using climate and land cover variables from GLMs for species grouped by level of establishment (55% to 100%).

| | **Level of establishment (%)** | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Climate and land cover variables** | **>50, ≤55** | **>55, ≤60** | **>60, ≤65** | **>65, ≤70** | **>70, ≤75** | **>75, ≤80** | **>80, ≤85** | **>85, ≤90** | **>90, ≤95** | **>95, ≤100** |
| GDD5 | 6.26 | 6.65 | 6.66 | 6.41 | | 2.73 | 21.36 | 5.12 | 4.22 | 18.97 |
| MTCO | | 7.56 | 7.33 | 18.15 | | 12.88 | 12.42 | 5.77 | 11.29 | |
| MTWA | 6.83 | 6.61 | 6.84 | 6.57 | 24.46 | 26.87 | 27.95 | 4.99 | 33.55 | 28.27 |
| **Temperature (total GDD5, MTCO, MTWA)** | **13.09** | **20.83** | **20.84** | **31.13** | **24.46** | **42.48** | **61.73** | **15.88** | **49.05** | **47.24** |
| APET | 24.96 | 13.46 | 14.57 | | 1.48 | | | 12.26 | | |
| SPRE | 6.12 | 6.70 | 6.59 | 6.58 | 16.60 | | | 17.74 | | |
| WPRE | 6.26 | 6.66 | 6.55 | 6.83 | | | | 12.97 | | |
| **Rainfall (total APET, SPRE, WPRE)** | **37.34** | **26.82** | **27.72** | **13.41** | **18.08** | | | **42.98** | | |
| **Total for all climate** | **50.38** | **47.56** | **48.46** | **44.53** | **50.59** | **59.70** | **61.73** | **58.77** | **48.85** | **47.24** |
| Acid grassland | | | | | | | | | 11.60 | |
| Arable | 8.54 | 8.11 | 8.18 | 10.95 | 6.90 | 8.03 | 7.89 | 7.44 | 9.04 | 8.73 |
| Broad-leaved woodland | 9.47 | 11.07 | 10.15 | 11.24 | 9.51 | 7.32 | 7.84 | 12.33 | 9.85 | 6.06 |
| Calcareous grassland | | | | | | | | | | |
| Coniferous woodland | 7.51 | 7.24 | 7.58 | 8.27 | 5.82 | 5.92 | 5.17 | 5.29 | 5.26 | 4.11 |
| Heath | | | | | | | | | | 19.44 |
| Improved grassland | 6.08 | 6.62 | 6.30 | 6.23 | 5.71 | 5.22 | 5.00 | 6.33 | 4.85 | 3.81 |
| Inland rock | | | | | 5.67 | | | | | 3.24 |
| Neutral grassland | 6.41 | 6.85 | 6.92 | 6.89 | 4.94 | 4.53 | 4.12 | | 3.65 | 2.37 |
| Standing water | | | | | | | | | | |
| Urban | 11.62 | 12.55 | 12.41 | 11.90 | 10.87 | 9.28 | 8.25 | 9.83 | 6.89 | 5.00 |
| **Total for all land cover** | **49.62** | **52.44** | **51.54** | **55.47** | **49.41** | **40.30** | **38.27** | **41.23** | **51.15** | **52.76** |

# Appendix 3

Table A3.1. Spearman's rank correlation coefficients for species richness of Raunkiaer life forms with climate and urban land cover using BSBI monitoring squares. All correlation coefficients are significant at *P* < 0.0001(N = 291 grid cells in each case).

| | GDD5 | MTCO | MTWA | APET | SPRE | WPRE | Urban |
|---|---|---|---|---|---|---|---|
| Therophyte (503 species) | +0.836 | +0.438 | +0.892 | -0.857 | -0.736 | -0.708 | +0.804 |
| Hemicryptophyte (501 species) | +0.723 | +0.335 | +0.783 | -0.720 | -0.577 | -0.566 | +0.822 |
| Bulbous geophyte (80 species) | +0.659 | +0.373 | +0.680 | -0.663 | -0.530 | -0.508 | +0.677 |
| Non-bulbous geophyte (89 species) | +0.660 | +0.384 | +0.684 | -0.624 | -0.474 | -0.456 | +0.729 |
| Chamaephyte (121 species) | +0.764 | +0.432 | +0.792 | -0.733 | -0.556 | -0.510 | +0.771 |
| Nanophanerophyte (196 species) | +0.595 | +0.332 | +0.618 | -0.548 | -0.401 | -0.400 | +0.729 |
| Phanerophyte (219 species) | +0.650 | +0.251 | +0.725 | -0.664 | -0.532 | -0.540 | +0.757 |
| Hydrophyte (19 species) | +0.729 | +0.382 | +0.771 | -0.703 | -0.559 | -0.525 | +0.749 |
| All non-natives (1728) | +0.773 | +0.384 | +0.829 | -0.776 | -0.631 | -0.613 | +0.824 |

Table A3.2. Spearman's rank correlation coefficients for species richness of broad PFTs with climate and urban land cover using BSBI monitoring squares. Correlation coefficients significant (N = 291, *P* < 0.001) except where given.

| | GDD5 | MTCO | MTWA | APET | SPRE | WPRE | Urban |
|---|---|---|---|---|---|---|---|
| Herbaceous annual<br>(503 species) | +0.836 | +0.438 | +0.892 | -0.857 | -0.736 | -0.708 | +0.804 |
| Herbaceous perennial<br>(742 species) | +0.732 | +0.365 | +0.781 | -0.723 | -0.568 | -0.550 | +0.808 |
| Aquatic<br>(19 species) | +0.729 | +0.382 | +0.771 | -0.703 | -0.559 | -0.525 | +0.749 |
| Succulent evergreen<br>(10 species) | +0.259 | +0.267 | +0.154<br>p=0.008 | -0.179<br>p=0.002 | -0.048<br>p=0.410 | +0.052<br>p=0.376 | +0.137<br>p=0.019 |
| Needle-leaved deciduous<br>(5 species) | +0.062<br>p=0.292 | -0.159<br>p=0.006 | +0.113<br>p=0.054 | -0.047<br>p=0.42 | +0.072<br>p=0.221 | +0.005<br>p=0.926 | +0.237 |
| Needle-leaved evergreen<br>(43 species) | +0.248 | -0.012<br>p=0.835 | +0.312 | -0.274 | -0.157<br>p=0.007 | -0.186<br>p=0.001 | +0.313 |
| Broad-leaved deciduous<br>(256 species) | +0.693 | +0.301 | +0.762 | -0.699 | -0.581 | -0.592 | +0.819 |
| Broad-leaved evergreen<br>(150 species) | +0.684 | +0.418 | +0.696 | -0.623 | -0.442 | -0.403 | +0.752 |
| All non-natives<br>(1728) | +0.773 | +0.384 | +0.829 | -0.776 | -0.631 | -0.613 | +0.824 |

Table A3.3. Percentage of total variance explained from Hierarchical partitioning using climate and land cover variables from GLMs for Raunkiaer life forms (Ch = Chamaephyte, Gb = Bulbous geophyte, Gn = Non-bulbous geophyte, hc = Hemicryptophyte, Hy = Hydrophyte, Ph = Phanerophyte, Pn = Nanophanerophyte, Th = Therophyte).

| **Climate and land cover variables** | **Raunkiaer life form** | | | | | | |
|---|---|---|---|---|---|---|---|
| | **Ch** | **Gb** | **Gn** | **hc** | **Ph** | **Pn** | **Th** |
| GDD5 | 20.22 | 6.12 | 6.12 | 6.57 | 6.10 | 7.08 | |
| MTCO | | | 6.67 | 7.45 | 7.63 | 7.61 | 8.28 |
| MTWA | 25.70 | 6.24 | 6.06 | 6.49 | 6.10 | 7.08 | 5.84 |
| **Temperature (total GDD5, MTCO, MTWA)** | **45.93** | **12.36** | **18.85** | **20.51** | **19.83** | **21.76** | **14.13** |
| APET | 10.47 | 25.14 | 19.28 | 13.64 | | 9.95 | 18.42 |
| SPRE | 4.67 | 6.17 | 10.32 | 6.58 | 13.06 | 7.08 | 5.54 |
| WPRE | | 6.04 | 10.38 | 6.60 | | | 6.04 |
| **Rainfall (total APET, SPRE, WPRE)** | **15.14** | **37.35** | **39.97** | **26.81** | **13.06** | **17.03** | **30.00** |
| **Total for all climate** | **61.07** | **49.72** | **58.82** | **47.32** | **32.89** | **38.80** | **44.13** |
| Acid grassland | | | | | 11.12 | 9.32 | |
| Arable | 6.45 | 8.69 | 7.28 | 8.30 | 8.55 | 7.35 | 12.32 |
| Broad-leaved woodland | 7.18 | 9.87 | 9.93 | 10.77 | 11.41 | 9.92 | 8.88 |
| Calcareous grassland | | | | | | | |
| Coniferous woodland | 5.61 | 6.54 | 5.77 | 7.92 | 6.34 | 7.13 | 8.50 |
| Heath | | | | | | | |
| Improved grassland | 6.15 | 7.20 | 6.27 | 6.61 | 6.13 | 6.51 | 5.50 |
| Inland rock | | | | | 5.71 | | 5.22 |
| Neutral grassland | 4.79 | 7.26 | | 6.75 | 6.05 | 7.13 | 5.44 |
| Standing water | | | | | | | |
| Urban | 8.75 | 10.72 | 11.93 | 12.33 | 11.80 | 13.86 | 10.01 |
| **Total for all land cover** | **38.93** | **50.28** | **41.18** | **52.68** | **67.11** | **61.20** | **55.87** |

Table A3.4. Percentage of total variance explained from Hierarchical partitioning using climate and land cover variables from GLMs for broad PFTs (AQ = Aquatic, BLD = Broad-leaved deciduous, BLE = Broad-leaved evergreen, HA = Herbaceous annual, HP = Herbaceous perennial, NLE = Needle-leaved evergreen).

| **Climate and land cover variables** | **Broad PFT** | | | | |
|---|---|---|---|---|---|
| | **BLD** | **BLE** | **HA** | **HP** | **NLE** |
| GDD5 | 6.21 | 7.10 | | 6.49 | |
| MTCO | 7.43 | 7.29 | 8.28 | 7.21 | 4.64 |
| MTWA | 6.17 | 7.14 | 5.84 | 6.45 | 17.63 |
| **Temperature (total GDD5, MTCO, MTWA)** | **19.81** | **21.53** | **14.13** | **20.15** | **22.27** |
| APET | | 12.08 | 18.42 | 14.02 | |
| SPRE | 18.55 | 7.07 | 5.54 | 6.53 | |
| WPRE | 13.24 | | 6.04 | 6.51 | 5.56 |
| **Rainfall (total APET, SPRE, WPRE)** | **31.79** | **19.14** | **30.00** | **27.07** | **5.56** |
| **Total for all climate** | **51.61** | **40.67** | **44.13** | **47.22** | **27.82** |
| Acid grassland | | | | | 3.69 |
| Arable | 7.82 | 7.23 | 12.32 | 8.31 | 6.50 |
| Broad-leaved woodland | 9.64 | 10.12 | 8.88 | 10.84 | 24.55 |
| Calcareous grassland | | | | | |
| Coniferous woodland | 6.92 | 7.38 | 8.50 | 7.72 | 5.44 |
| Heath | | | | | 16.05 |
| Improved grassland | 5.60 | 7.18 | 5.50 | 6.91 | 5.20 |
| Inland rock | | 6.54 | 5.22 | | 2.62 |
| Neutral grassland | 6.42 | 6.88 | 5.44 | 6.88 | 3.16 |
| Standing water | | | | | |
| Urban | 12.00 | 13.99 | 10.01 | 12.11 | 4.98 |
| **Total for all land cover** | **48.39** | **59.33** | **55.87** | **52.78** | **72.18** |

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