Unexplained limits on species distributions: how important is climate in defining species' range edges?

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

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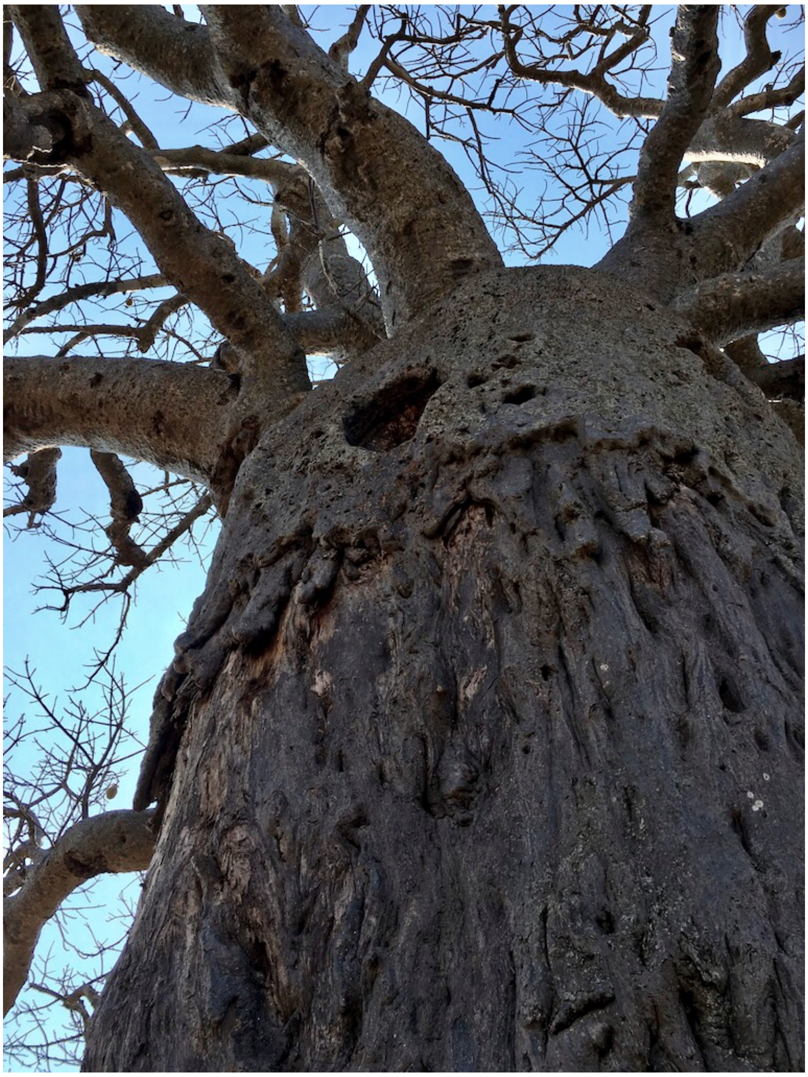

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Abstract

The study of species' range margins has a long history of academic interest, but is of particular relevance today due to its applications in modelling species range shifts induced by climate change, and predicting the spread of invasive species. Climate has long been assumed to structure species' ranges over broad scales, but this consensus has recently been challenged by work on non-climatic factors, such as dispersal, biotic interactions and gene flow. It remains unclear how and where non-climatic factors can structure species' ranges, and to what extent species' ranges will consistently match sets of climatic conditions.

In this thesis I investigate what can lead to a species underfilling its climatic niche (when a species fails to colonise all climatically suitable areas), or expanding its climatic niche (when a species is able to colonise new types of climate). I find evidence that several non-climatic factors can slow or prevent non-native species colonising all climatically suitable areas in their naturalised regions, including dispersal, fragmentation of climatically suitable areas and the area of introduction. I also find that species will readily spread into new precipitation regimes with which they have not been previously associated. This suggests that species ranges can be constrained by non-climatic factors in the wettest part of their native range, and these constraints are frequently lifted in their naturalised range. I find evidence that species range limits set by temperature, in particular temperature maxima and minima, are more conserved and species will rarely expand into new thermal regimes. I also find evidence that species have different phenotypic responses to temperature across their range. Together these results indicate that a species' current range frequently does not indicate its overall climatic tolerance, particularly in relation to precipitation, hence predictions that rely on associations between occurrence and environmental variables will frequently be flawed. Future work should consider a systematic way of detecting and including non-climatic factors that constrain the edges of species' ranges.

Acknowledgements

“The king forbade my tongue to speak of Mortimer. But I will find him when he is asleep, and in his ear I’ll holler ‘Mortimer!’ Nay I’ll have a starling shall be taught to speak nothing but Mortimer, and give it to him to keep his anger still in motion”
-Henry IV. Part I, Act I, Scene III

I write these acknowledgements as the very last part of my thesis, so I write this in a reflective frame of mind. When I think of the variety of things I have learned, some expected and some unanticipated, I am mildly surprised my brain hasn’t quietly exploded. Ultimately, I cannot possibly claim credit for everything I have learned, and a great deal of thanks goes to all those who have taught me and helped me throughout my PhD. Whether that is patiently explaining a Bayesian prior to me again (and again), elaborating on the finer points of grass taxonomy, or teaching me the basics of incubator repair, thank you to everyone at Penryn Campus and elsewhere.

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Chapter 1: General Introduction

1.1 Introduction

There is a land-mark in South Africa for the southern-most Baobab tree on the African continent (see frontispiece). It lies approximately fifty kilometres south of its nearest relative, and is likely over a thousand years old. The enormous ten-meter diameter tree standing as the last outpost of its species is a poignant image, and begs the question of why it is the southernmost example of its kind. There is no easily discernible barrier to more southerly spread and the habitat surrounding this Baobab does not differ greatly from that found further south. The mechanism that limits species range ranges is not always easily recognisable. Why species exist in some places but not in others is one of the earliest questions raised by travelling naturalists (Buffon, 1767, Humboldt, 1838), and the attempts to answer such questions have given rise to the field of biogeography and a huge body of research. Despite this, there are still many unanswered questions about what factors structure species ranges, and the best way to discern how these factors affect different species. The study of species range margins has long been of academic interest, but it has received an intense amount of recent attention for practical applications. Global anthropogenic change is driving rapid redistribution of many species ranges, in particular because of climate change (Pecl et al., 2017) and human introduction of species into new areas (Dawson et al., 2017). There is therefore a need to understand what structures species ranges and predict how species ranges will change in the future. In this introduction I will provide a brief overview of the history and concepts in the study of species range margins and establish the main questions that this thesis addresses.

1.2 Historical perspective

Early naturalists documented the biodiversity they encountered on their voyages, and these early maps of species distributions, typically in the form of checklists, were the first basis of understanding where and when species can and cannot exist. Early studies of species ranges frequently focussed on island endemic species, and more broadly on how physical barriers such as coastline and mountain ranges could prevent species spreading beyond a certain point (Darwin, 1859; Hooker, 1847; Wallace, 1876). Famously, an understanding of the physical barriers that could separate species populations led to the theory of natural selection and speciation (Darwin, 1859). There was also an early recognition that species ranges could be formed by more than physical barriers. Early biogeographers noted transitions in ecotone and species composition across altitudinal and latitudinal gradients over 150 years ago (Humboldt, 1838). As with many other concepts in biogeography, Darwin provided an early hypothesis to explain why species had an upper and lower altitudinal boundary. Darwin proposed that a species' upslope range edge was defined by climate, typically a species' cold tolerance, and the downslope range edge was defined by a species' ability (or lack thereof) to compete with other species (Darwin, 1859). This idea was later expanded to include latitudinal gradients, where a species' poleward range margin was set by climatic factors and the equatorward range margin was set by competition. These early hypotheses were the first attempt of many to identify what factors can structure species ranges, how several different factors can act on different range edges within a single species, and how factors can vary between different species.

Early studies of species range edges typically focussed on a particular study system, composed of one or a few species, and on one specific margin of a species range. Work on how species assemblages could change over latitude demonstrated that species assemblage strongly correlated to temperature, and concluded temperature alone could structure species ranges (Merriam, 1894). Other early studies focussed on the tree-line at high altitudes or latitudes, and found similar strong correlations of tree range edges to temperature in multiple locations (e.g. Grace, Berninger, & Nagy, 2002; Köppen, 1931). Study systems such as these have emphasised the role of climate on species range edges, and have been influential on the early development of general principles of range limits. Study systems however have limitations. They typically focus on one or a few taxonomic groups, and on one specific range margin, and as such are not necessarily representative of general ecological principles.

In contrast to the role of climate, the role of competition and other biotic interactions have received limited attention in predictions of species ranges. This is despite Darwin's early hypothesis, that competition was as important as climate in limiting species ranges (Darwin, 1859), and the fact that competition has been revisited several times as an important range limitation in theoretical work (Brown, 1995; Gaston, 2003; Grinnell, 1917; MacArthur, 1972; Walter, 1979). It has been notoriously difficult to measure competition in the laboratory in a manner that represents interactions in the field (MacArthur, 1972). Correlative studies that link non-overlap of species ranges to competitive exclusion have been controversial (Connor & Simberloff, 1979; Connor, Collins, & Simberloff, 2013; Diamond, 1975; Early & Keith, 2019), and been criticised for not providing proof of causation. While examples of competition as a range limit do exist, field studies of competition often have to be long-term, work-intensive and focus on one or a few taxa (Wisz et al., 2013). As a result, the broad multi-taxa studies that demonstrate the role of climate in species range limits, have historically been lacking for competition and for other biotic interactions.

This demonstrates some of the difficulties in directly measuring biotic interactions, and perhaps why the role of biotic interactions and other non-climatic factors have lagged behind that of climate (Sexton, McIntyre, Angert, & Rice, 2009). Partly as a result of evidence from early study systems, there has long been a general consensus that on a global level climate is the dominant structuring force of species ranges. (Gleason & Cronquist, 1964; Good, 1964; Grace, 1987).

1.3 The niche

In the time since these early hypotheses, a number of core concepts have been developed to help understand and frame species range limits. The first, and most important, is the definition of a species range. With the exception of coastlines and other physical barriers there is typically not an obvious line that marks the edge of a species range, but a gradual decline in population density and/or fitness until the species is no longer found (Gaston, 2003). The position of peripheral populations may vary through time as populations appear and die out. Generally, a defined species range includes only populations which are permanent and not prone to local extinctions, and temporary populations are usually not included in a species range. Using this definition, it is possible to characterise where a species lives and what factors contribute to its presence or absence.

One key concept in biogeography, and one that will be used extensively in this thesis, is the niche. The niche in its original formulation simply described the habitats and conditions in which a species can persist (Grinnell, 1917), and its accompanying adaptations. Later work formalised the niche concept into a mathematical framework, where species ranges were correlated with their environmental conditions to form a multidimensional "hyperspace" (Hutchinson, 1957). Niche space is an abstract representation of the species' physical range, and describes the environmental range of conditions in which a species can persist. There is a further distinction between the fundamental niche, which are all conditions a species could theoretically persist in, and the realised niche, which are the conditions in which a species actually currently lives. In its original formulation the fundamental niche described the physiological limits of a species, while the realised niche took into account biotic interactions (Hutchinson, 1957).

Under the assumption that climate is the dominant limitation of species range, a species should colonise all climatically suitable areas and fill most or all of its fundamental niche. A species' fundamental niche can be estimated through laboratory experiments that discern the physiological limits of a species. Once the fundamental niche is known, the total climatically suitable area can be identified and compared to a species actual range. If a species does not fill its potential range, then further experimentation can identify the non-climatic factors that are limiting it. However, for practical reasons it is not possible to carry this out for every species' range edge. Climatic niche models are a much less labour-intensive way to characterise a species range, as they do not require any knowledge of mechanistic links between species and their environment, and have been used for a wide number of applications in a number of different fields, including climate change ecology, invasion ecology, paleoecology, and evolutionary ecology (Araújo & Peterson, 2012; Elith, Kearney, & Phillips, 2010). Climatic niche models correlate a species' current range to environmental conditions, usually temperature and precipitation, and characterise the types of climate in which a species lives. Any climate that falls within the climate niche is assumed to be suitable for colonisation by the species. It is worth noting that a species niche is an abstraction, if a species fills its climate niche it does not mean it occurs in all climatically suitable areas in its range. Species ranges frequently shift over time and space, as populations go extinct and colonise new areas (Gaston, 2003), but climatic niche models assume that broadly, species ranges represent all the climatic conditions in which a species can persist. Therefore, for climatic niche models to be widely applicable, species ranges need to consistently correlate to a particular set of climatic conditions, and climatic niches need to be relatively stable over space and time. For both of these to be true, climate needs to be the primary limitation of species ranges.

1.4 Evidence for climate as a primary limitation of species ranges

There is ample evidence to suggest climate is an important factor in limiting species ranges. Species commonly are observed with boundaries that coincide with identifiable sets of climatic conditions (e.g. Salisbury 1926; Iversen 1944; Pigott 1975; Anadón et al. 2006). Comparisons of species ranges have shown that in some species they consistently coincide with the same climatic limits through time (Tingley, Monahan, Beissinger, & Moritz, 2009) and across different parts of their range (Petitpierre et al., 2012; Thomas, 2010).

Comparisons from physiological experiments show that some species range extend to the very edge of their physiological tolerances, and fail to survive in the long term outside their current ranges (Kearney & Porter, 2009; Sexton et al., 2009). Species ranges can be defined by a wide variety of climatic factors, from thermal maxima and minima (Sunday, Bates, & Dulvy, 2012), to precipitation levels (Normand et al., 2009; Tingley et al., 2009), or timing of climate events in relation to phenology (Chuine, 2010). In addition, historical evidence from broad climatic changes in the quaternary show that many species ranges shift to match certain climatic conditions (Hewitt, 2000; Huntley, 1991), Similarly, recent anthropogenic climate change is driving a large number of species range shifts (Pecl et al., 2017), and many species shift their range to match a certain set of climatic conditions.

1.5 Evidence for non-climatic factors as limitations of species ranges

For every one of the study systems that support climate as a range limitation, from correlative evidence, transplant experiments, historical evidence, climate change induced range shifts or physiological data, there are counter-examples of species that do not consistently coincide their range limits with certain climatic conditions.

Transplant experiments have frequently shown that species can survive outside of their current ranges, even in the long term (Hargreaves, Samis, & Eckert, 2014; Prince & Carter, 1985). Analysis of species ranges have shown many species do not occupy all climatically suitable areas, even if they fill their climatic niche (Bradley, Early, & Sorte, 2015). Physiological studies have shown that many species' ranges do not extend to their physiological limits, so do not fill all of their fundamental niche or occur in all climatically suitable areas (Sunday et al., 2012).

There are numerous examples of species that have been introduced to new areas outside of their native range and have successfully colonised new types of climate, thus demonstrating that climatic niches are not constant (Early & Sax, 2014; Gallagher, Beaumont, Hughes, & Leishman, 2010; Hill, Gallardo, & Terblanche, 2017; Li, Liu, Li, Petitpierre, & Guisan, 2014). Analysis of species ranges historically have also shown that species ranges can grow or shrink in ways that do not correlate to changes in climate (Early & Sax, 2014; Gallagher et al., 2010; Hill et al., 2017; Li et al., 2014). Range shifts induced by climate change are very variable from species to species. While some shift their range to match climatic conditions, others have shrunk their ranges (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011), or shifted their ranges in a manner that does not match their previous thermal niche (Lenoir et al., 2010).

The body of evidence suggests that in many cases simply correlating a species' current range with climate is not enough to understand species ranges and what factors limit species distribution. There is therefore a need to identify what other factors can set a species' range edge.

1.5.1 Dispersal

Dispersal plays an important role in species ranges, as it allows species to colonise new areas and to allow gene flow between existing populations. If a species has low dispersal then it may not be able to colonise all climatically suitable areas, and therefore not colonise all types of climate it could occupy. Barriers to dispersal can be physical barriers such as mountains and water-ways, or high fragmentation of habitat, or very low dispersal ability (Gaston, 2003). There is some evidence that species ranges are frequently dispersal limited. Transplant experiments have found that many species can survive outside of the current range if introduced (Hargreaves et al., 2014). Historical studies have shown that species may also not match their climatic tolerances due to dispersal limitations, for instance tree species that recolonised Europe after the last period of glaciation still lag behind their climatic potential range (Svenning, Normand, & Skov, 2008). Some studies have even concluded that most species are dispersal limited, and climate acts as a secondary range limit (Gaston, 2009). Studies of species range filling (whether species ranges extend to all climatic limits) have shown that many species with low dispersal do not fill most climatically suitable areas (Bradley et al., 2015). If dispersal is the primary limiting factor for species range edges, we would expect species with the highest dispersal ability to fill the most (or all) climatically suitable areas, and species with large ranges would be most likely to exist up to their physiological limit.

1.5.2 Biotic interactions

There is now wide-spread evidence that biotic interactions can structure species range on a broad scale. Transplant and exclusion experiments have shown that competition between species can exclude species from climatically suitable areas (Price & Kirkpatrick, 2009), as can predation/parasitism (Holt & Barfield, 2009) and resource abundance (Quinn, Gaston, & Roy, 1997). Biotic interactions, such as facilitation and mutualism, can also help species colonise climate that they would not otherwise (Afkhami, McIntyre, & Strauss, 2014; Crotty & Bertness, 2015).

Biotic interactions may restrict species from specific portions of their climate niche, as well as specific areas of their potential range. For example, the mosquito species *Aedes aegypti* is outperformed by a competing species, *Aedes albopictus*, at temperatures under 24°C (Lounibos et al., 2002). If this competitor is removed, for example if *Aedes aegypti* is introduced to a new region, then it could colonise more types of climate and expand both its range and its realised niche. It is possible to look for evidence of species colonising new types of climate (also known as “niche expansion”) by comparing species niche between the native and naturalised ranges. When species are introduced to new areas without their native competitors or predators, they can colonise new types of climate they are excluded from in their native range. There is evidence of “enemy release” across a wide number of introduced species (Heger & Jeschke, 2014; Liu & Stiling, 2006), most commonly from the removal of a native predator.

As a result of examples such as these, there now stands a wide evidence base for biotic interactions and how they can limit species ranges (Early & Keith, 2019).

1.5.3 Gene flow

If a population at a range edge suffers declined fitness due to climatic factors, there should be selection pressure to adapt to those conditions. Local adaptation is common across many taxonomic groups (Kawecki & Ebert, 2004; Savolainen, Lascoux, & Merilä, 2013), and although the limits of adaptation are not infinite it can assist species to expand their range. However, a number of factors can restrict adaptation and therefore species niches and ranges. Genetic exchange with more central populations that are adapted to climate at the centre of a species range can promote maladaptive phenotypes in populations at range margins. This process, also known as “gene swamping” restricts the development of adaptation to local conditions (Gaston, 2009; Lenormand, 2002). While there is theoretical support for gene swamping as a range limitation, empirical examples are limited (Bridle, Gavaz, & Kennington, 2009; Gaston, 2003), as is evidence that changes in geneflow can lead to range expansions or contractions. There is some indirect evidence that novel adaptations can take place in non-native populations due to either a mixing of genotypes that were not commonly found together in the native range, or a removal of maladaptive gene flow (Alexander & Edwards, 2010).

1.5.4 Combined effects

It is very likely that for many species no one factor acts in isolation, and different factors can structure different range edges in a single species. There are unfortunately few studies of multiple range edges that directly test this, however there a few examples illustrate how range margins can be set by a variety of factors. *Arabidopsis lyrata* is locally adapted to cope with frost damage at its northern range edge, but adapted to cope with increased predation pressure at more southerly latitudes (Vergeer & Kunin, 2013), providing an example of local adaptation and of a species that appears to have different factors controlling its northern and southern range edges. In the case of the Baobab, trees can survive a reasonably broad range of temperature and precipitation conditions, but young specimens are vulnerable to frost, flooding and elephant grazing (Sanchez, 2010). The combination of these factors restricts recruitment at the southern range margin, and forms an effective range margin on this edge of the species range.

It is becoming increasingly clear that multiple factors, rather than just climate, can be important for setting the edges of species ranges. The field of biogeography has moved on from the paradigm that climate dominates species range edges, and there are numerous examples of species that demonstrate the role of non-climatic factors, including dispersal, biotic interactions and gene flow. The problem that still remains for ecologists is understanding which factors are dominant at different species range edges, and the development of general macroecological principles that can describe these patterns. To answer this problem, Darwinian principles have been recently revisited (Louthan, Doak, & Angert, 2015) in relation to broad scale patterns of species ranges, in particular that a species' physiologically stressful range edge is set by climate, and less stressful ranges edges are set by biotic interactions. An alternative theory suggests biotic interactions may be more important at physiologically stressful range margins as they can further stress populations and lower fitness (Silliman & He, 2018). Other studies have suggested range margins are set by climate in widely dispersed species, and are more likely to be set by dispersal if ranges are smaller (Gaston, 2003). Testing such large scale hypotheses is challenging, but is now easier than ever thanks to the development of large online databases, the recent recognition of non-climatic factors at range edges (Pigot & Tobias, 2013; Wisz et al., 2013), and the development of more sophisticated statistical frameworks (Early & Keith, 2019). These recent advancements allow us to test large-scale macroecological hypotheses with global datasets.

1.6 Using naturalised species to study species range limits

Human activity has resulted in a huge number of species introductions globally (Dawson et al., 2017), and species now exist where they have never lived historically. While non-native species have many documented negative impacts (Simberloff et al., 2013), they also provide a useful model system for studying species range edges and species' climatic niches. By comparing the climatic conditions a species occupies in its native and naturalised regions, we can test if a species' climatic niche remains the same, and what factors set range edges in species' native and naturalised ranges. If a species' native range represents all the climatic conditions a species can occupy (i.e. its range edges are entirely set by climate), we would expect a species' naturalised range to represent the same set of climatic conditions, or a subset of those conditions. This is especially true if the species has only been recently introduced and has not had time to disperse from the site of establishment. If, on the other hand, a species' native range is limited by one of the non-climatic factors discussed above, namely dispersal, biotic interactions, or gene flow, then a species' naturalised niche may show changes.

Human assisted dispersal may introduce species to climate it has never been associated with previously (Tingley, Thompson, Hartley, & Chapple, 2016), and reveal a species has a broader physiological tolerance than its native range would suggest. If biotic interactions prevent species colonising all climatically suitable areas in their native region, and these interactions change or are removed in a species' naturalised region, species may spread into new types of climate. Predator release has been observed in multiple species (Heger & Jeschke, 2014; Liu & Stiling, 2006), and there are several examples of species that have shown niche expansion when competitors are absent (Bolnick et al., 2010). Introduced species have also shown changes in their physiological tolerances as compared to their native range, and have been used as possible evidence of genetic flow limiting adaptation in the native range (Alexander & Edwards, 2010). Naturalised and native species ranges therefore allow us to compare two species ranges with similar physiological tolerances, similar climate and an independent set of non-climatic factors. Comparisons between the two ranges can therefore illuminate which factors most structure native species ranges.

Studies of naturalised species' ranges can also provide information on which factors lead to a species successfully colonising climatically suitable areas. After a species is established, if it is successful it will spread from its original site, frequently after a time lag (Aikio, Duncan, & Hulme, 2010). If there is nothing that limits a species filling all climatically suitable areas, then it will disperse until it colonises all areas. Species' range size would be therefore tied to time since introduction and dispersal. However, a number of other factors can help or hinder species spread, such as species traits and fragmentation of habitat (Blackburn et al., 2009; Estrada, Morales-Castilla, Meireles, Caplat, & Early, 2017; Vall-llosera & Sol, 2009). The factors that may assist a species colonise all climatically suitable areas in the naturalised range are parallel to factors that lead to native species filling their climatically suitable area.

Naturalisation studies are not without limitations. There is a great deal of stochasticity to the process of naturalisation. The success of an introduced species can vary depending on the size of the founding population, its genetic makeup and how climatically suitable the area of establishment is (Blackburn et al., 2009; Simberloff, 2009). The range size and degree of successful spread of a naturalised species may be linked to these processes rather than other range limiting factors. In addition, native and naturalised regions are not truly independent. A naturalised region may share some competitors, diseases, predators etc. with the native region, and the factors that are shared and which are important for particular species are often not known (Early & Keith, 2019). Finally, non-native species are not randomly selected, traits that allow a species to be successful at establishing may also allow them to spread successfully. A great number of non-native species have a high reproductive rate and dispersal ability, with a large native range (Higgins & Richardson, 2014; Richardson & Pyšek, 2012). Therefore, conclusions regarding the range limits of non-native species may not be generally applicable, especially when applying similar principles to native species, in particular to endemic species with small ranges. Despite these drawbacks, a study that uses a broad multi-taxonomic approach, and considers species with a wide variety of traits, life-history and range sizes, can mitigate some of these biases.

1.7 Applications of species range limit studies

By understanding what causes species range limits, we can project species ranges in the past, the future or into new areas.

1.7.1 Range shifts caused by climate change

Anthropogenic climate change is currently inducing a huge number of species range shifts (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Parmesan, 2006; Walther et al., 2002), with potentially huge impacts for native ecosystems and humans alike (Pecl et al., 2017). For mitigation and conservation, it is crucial to understand species range shifts. As climate change is driving these range shifts, a large number of models assume that species range will shift to match their current climate niche. However, species often fail to move to match their previous climate niche (Bertrand et al., 2011; Crimmins, Dobrowski, Greenberg, Abatzoglou, & Mynsberge, 2011), and can even demonstrate range shifts in multiple or contrasting directions (Davis & Shaw, 2001; Hodkinson, 1997; Taper, Bohning-Gaese, & Brown, 1995). Conservation areas may increase or decrease in value, depending on how species shift their ranges in response to climate change (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011). Range-shifting species may also impact other native species and native ecosystem functioning (Pecl et al., 2017). Planning is required to mitigate these impacts. As such, we need to understand what is driving range shifts, and in order to do so we need to know what structures species ranges currently. Predictions of range shifts can then incorporate how these factors will change, along with climate change, into the future.

1.7.2 Invasive species

Invasive species have a huge impact on native ecosystems, agriculture and human infrastructure (Simberloff et al., 2013). Predicting the spread of invasive species is a crucial part of preventing and mitigating the impact of invasive species. Climatic niche modelling has been used widely to predict the spread of species, often with great success, particularly with wide-spread species (Early, González-Moreno, Murphy, & Day, 2018). Invasive species predictions typically have two main goals. One, to identify the maximum potential range of an invasive species. Two, to predict how quickly an invasive species can spread. Work on species range limits can help improve both aspects.

Climatic niche models typically assume that an invasive species will colonise similar climate to that found in its native range. However, introduced species may show niche expansions when introduced to new areas (Early & Sax, 2014; Gallagher et al., 2010; Hill et al., 2017; Li et al., 2014). Niche expansions can result in species spreading much further than predicted by climatic niche models, and therefore have a higher impact than predicted (Bacher et al., 2018). At the moment there is no real knowledge about how niche expansions occur, only that they do occur. There is a real need to understand what factors can drive niche expansions, and evidence on what drives niche expansions can inform mitigation and conservation strategy. Understanding what can limit a species range and a species' spread can also help improve predictions on which species are most likely to spread quickly and why. It is still unclear which factors contribute most to invasive species success. Candidate factors include dispersal, life-history traits, presence or absence of biotic interactions, landscape-scale factors (e.g. habitat fragmentation) or genetic changes in the introduced population. Understanding which of these factors contributes to invasive success can inform conservation strategy by either prioritising species that have the traits that contribute to successful spread, or prioritising areas that are particularly prone to invasion.

1.7.3 Evolution and range margins

The study of species range margins can also provide useful information to the study of speciation and adaptive radiation. Speciation and divergence of species often begins with locally adapted populations and peripheral populations that become separated from the main population (Sexton et al., 2009). It is a central goal in evolutionary ecology to determine what factors can promote adaptive diversification or alternatively promote species stability. Species range margins provide a model system for investigating the relative importance of the factors that cause local adaptation, and what is driving selection pressure. The relative role of climate, dispersal, biotic factors and gene flow in creating species range margins can therefore link ecological processes to broader evolutionary processes

1.7.4 Paleoecology

Paleoecological models frequently wish to reconstruct past ecosystems. Such models use knowledge of past climate to predict historical species ranges (Nogués-Bravo, 2009), on the assumption that a species' current range describes its climatic preference and this will be the same over time. In the absence of reliable climate data, studies also use evidence of species presence (e.g. pollen records) to reconstruct past climate, based upon knowledge of a species' climatic preference (Mauri, Davis, Collins, & Kaplan, 2015). While correlating species range edges to climate can be effective, dispersal limitations and range limits caused by other non-climatic factors jeopardises the accuracy of these models (Ivory, Russell, Early, & Sax, 2019). Understanding what structures a species range now, and how this translates into a species realised niche, can therefore drastically improve paleoecological models

1.8 Aims of this thesis

Several key questions raised in this introduction are addressed in this thesis.

1) What factors can contribute to naturalised species spread once they are established, and what can restrain species from reaching all climatically suitable areas?
In chapter two I collated the native and naturalised ranges of a wide selection of non-native birds, mammals and plants into a global database. I then used species' native ranges to estimate climatically suitable areas that are adjacent to known established populations of non-native birds, mammals and plants. I overlaid species' potential ranges, along with a measure of vulnerability, to highlight areas that are likely to face a large number of colonisations in the near future.
In chapter three I investigated what factors can help or hinder species colonise their climatic potential range, beyond simply time since introduction and dispersal. I correlated species range filling (the proportion of climatically suitable area a species inhabits) to a variety of factors that have been suggested to help species colonise available areas. These candidate factors included i) introduction history ii) species traits iii) the spatial distribution of suitable areas and iv) interactions between the invader and native landscape.

2) How commonly can species colonise climate that is dissimilar to their native range (i.e. species expand their climatic niche), and what processes are driving this?
In chapter four, I have compared native and naturalised climatic niches in over 600 terrestrial plants, and investigated how frequently species niche expansions occur, and whether there is a pattern to niche expansion. I consider whether patterns of niche expansions provide evidence of non-climatic range limits in the native range. In particular, I discuss potential dispersal limitations in the native range, the release of biotic interactions, flaws in the modelling process, or an expansion of a species' fundamental niche.

3) Are species consistently adapted to local climate across different range edges and what information can this provide on selection pressure at species range edges?
In chapter five I carried out common garden experiments using *Iberis amara* seeds from multiple range edges, and measured a number of germination and growth traits to compare fitness between populations and temperature regimes. I then discuss whether local adaptation is evidence that species range edges are set by climate, and whether the recent range expansion of *I. amara* (L.) was facilitated by adaptation. This work also lays groundwork to investigate adaptation to non-temperature factors and to assess species ranges (e.g. with transplants).

Chapter 2: The spread of already established species threatens areas with little capacity to mitigate their impacts

Abstract

Thousands of species have been introduced outside their native range by humans. Established non-native species are likely to spread from their current locations, assisted by natural or human dispersal. Therefore, native ecosystems, agriculture and industry in many areas will be affected by the spread of large numbers of non-native species in the near future. I highlight climatically suitable areas that are adjacent to known established populations of non-native birds, mammals and plants. Areas in eastern Europe, Australia and the south-eastern United States in particular are likely to face a large number of colonisations in the near future. I further highlight areas that lack the response capacity to mitigate the impacts of non-native species, and especially where this lack of capacity overlaps with high colonisation threat. Areas in China, central Africa and South America lack the response capacity to mitigate the impacts of non-native species, and in addition will also face colonisation by a large number of species.

2.1 Introduction

Invasive species pose a threat to native ecosystems, agriculture and human infrastructure (Simberloff et al., 2013). There are more species currently living outside their native range than at any point in human history (Seebens et al., 2017), and the number is only likely to rise. While there is considerable attention on how to slow the introduction of new species, there is still the problem of species that have already naturalised outside their native range. Even if no new species ever successfully establish again, there are still thousands of species already established outside of their native range. It is likely at least some of these species will expand their naturalised range, so the impact of non-native species will only increase over time.

Areas close to international trading points of entry typically have the highest concentration of new introductions (Chapman, Purse, Roy, & Bullock, 2017) and thus suffer more impact from non-native and invasive species than other areas (Muirhead, Minton, Miller, & Ruiz, 2015). Naturalised species usually spread more widely from the initial site of introduction, but this typically happens after a latency period, also known as an invasion lag (Aikio et al., 2010; Crooks, 2005). For example, non-native plants in New Zealand on average have a lag period of 20-30 years before any noticeable increase in their range (Aikio et al., 2010). In order to proactively manage impacts from non-native species, we need to identify areas at the highest risk of colonisation in the future, even if the species in question is not currently spreading.

Although only a low proportion of non-native species typically become invasive (Jeschke, 2014), there are four reasons it is crucial to understand the potential ranges of all naturalised species, even those not known to be invasive. First, it has proved very difficult to identify the species that will have invasive impacts before the species are introduced or naturalised, or even when those impacts are in their early stages (Jeschke et al., 2014; Ricciardi, Hoopes, Marchetti, & Lockwood, 2013). This means many “sleeper species” that have not yet spread widely could become invasive in future. Second, a naturalised species’ range size is itself often key to quantifying its invasive impact (Hawkins et al., 2015; Parker, Simberloff, & Lonsdale, 1999). Third, the impacts of invasive species vary greatly between ecosystems and thus geographic location (Ricciardi et al., 2013), so an impact assessment conducted in one region may under- or over-estimate impacts elsewhere. Fourth, native ecosystems can be impacted by the cumulative effects of many non-native species, not just a few high-impact invasive species, i.e. ‘invasional meltdown’. Rather, the impacts from naturalised species are often non-additive, and positive interactions between naturalised species can enhance their invasive impacts (Simberloff & Von Holle, 1999). It is therefore important to know not just where known high-impact invasive species will colonise, but which areas will be under threat by a large number of non-native species. Further, the degree of threat these naturalised species pose will be modified by how well conservation, land-management, and infrastructure agencies can mitigate the spread and impact of a species. National capacity to proactively prevent the introduction of non-native species and reactively manage established species varies greatly across the world (Early et al., 2016). It is therefore important to identify which parts of the world face both the spread of large number of non-native species, and low capacity to mitigate the resulting impact.

I identified the terrestrial areas of the world that are threatened by imminent colonisation of large numbers of non-native plant, bird, and mammal species that have already naturalised. I identified 649 plants, 114 birds and 70 mammal species using several global check-lists that have formed non-native, self-sustaining populations somewhere in the world following introduction by people. These taxa are amongst the most commonly introduced and are well recorded globally, resulting in good estimates of current range size and areas of first introduction. I used climate matching to calculate the number of already-introduced species that could colonise each part of the world’s land surface, to produce a global map of non-native species threat. Climate matching uses the climate conditions species occupy in their native range to produce a map of climatically suitable areas in the non-native region. This is a widely used technique, particularly for invasive plant and pest risk assessment (Pheloung, Williams, & Halloy, 1999). Climate matching has proved particularly accurate for wide-spread species that are often the worst invaders (Early et al., 2018; Marmion, Luoto, Heikkinen, & Thuiller, 2009; McPherson & Jetz, 2007). However, there is evidence that species can expand their climatic niche following naturalisation, and colonise areas that their native niche would not predict (Early & Sax, 2014; Hill et al., 2017; Li et al., 2014). I considered including naturalised occurrence information, as well as native, to characterise species niches and identify climatically suitable areas, as this would reduce the risk of underestimating the species niche due to limited or incomplete native data. However, this was decided against for several reasons. First, native distributions are assumed to be more stable and should commonly characterise a species climatic niche, as species have been present in their native region for longer and are more likely to have spread to all suitable areas (Early & Sax, 2014). Secondly, several naturalised populations could not be verified as permanently established and were removed from the dataset, and it is possible that several populations retained are not viable in the long-term (though the data was checked and cleaned for this as far as possible). In order to avoid over-estimating species niches by including non-viable populations that temporarily persist in climate outside of the species fundamental niche, I decided to take the more conservative approach and only characterise species' niches based on native data. The estimated ranges here are therefore, if anything, conservative.

2.2 Methods

2.2.1 Collating non-native species data and distribution

I identified birds, plants and mammals that have established on a mainland landmass outside their native continent following introduction by people. Plant species were drawn from Randall (2017) and GISIN (2015), bird species were drawn from Dyer et al. (2017), Lever (2005) and Sol et al. (2012), and mammal species were drawn from Capellini et al. (2015). Species that were introduced pre-Columbus were removed from consideration, as were species that are not confirmed to reproduce in their naturalised range. For a full species list, see the Supplementary Material (Table S1; S2; S3).

For all species I obtained occurrence data from GBIF (downloaded 31st August 2017) using R's dismo package (Hijmans, Phillips, Leathwick, & Elith, 2015). Points were classified as either "native" or "naturalised" based upon sources listed in the Supplementary Materials (Table S4). Species that occupied fewer than 5 grid-cells (at 10 arc-minute resolution) in their native or naturalised range were discarded. In total the database on native and naturalised ranges contains information on 70 mammal species, 114 bird species and 649 plant species.

I restricted predictions of species' potential naturalised ranges to the biogeographic realm/s into which species were introduced. I used biogeographic realms from Holt et al. (2013), but with an additional distinction between western and eastern Palearctic along an approximate line of the Ural mountains (Fig. S1). Species that were found to be native and naturalised in the same biogeographic realm were removed from analysis, due to the difficulty in exactly defining the native and naturalised ranges.

2.2.2 Modelling species' climatically suitable range

I modelled potential ranges using three climate variables: mean temperature of coldest month, mean temperature of warmest month and total annual precipitation. These represent the most universal parsimonious variables that influence species ranges (Early & Sax, 2014). Gridded climate data were downloaded from WorldClim at 10 arc-minute resolution and provided average climatic variables from 1970-2000 (Fick & Hijmans, 2017).

I restricted a species' available climate to only climate shared in both their native and naturalised realms, and used principal components analysis (PCA) to produce a gridded climate space of 100x100 cells on two axes (Broennimann et al., 2012). I estimated species occurrence density in the climate conditions contained in each PCA grid-cell using a kernel smoothed density function. The climate conditions occupied in the native realm/s were defined using a minimum convex hull polygon around all cells in which native density > 0, and the same was done for the naturalised realm/s. In order to identify suitable climate for each species, I identified from the PCA the climatically suitable geographic grid-cells in a species' naturalised realm, i.e. those that have climate the species occupies in its native realm.

I restricted predictions of species' potential naturalised ranges to the climate conditions present in both a species' native and naturalised realms (i.e. analogue climate). To classify species' potential naturalised ranges into colonised and uncolonised I constructed a naturalised range polygon for each species using the point occurrence data and level 4 geographic administrative units from the TDWG scheme (Brummitt, 2001). Within each administrative unit I calculated the colonised area using a convex hull polygon around each species' occurrence data. These polygons were aggregated for each species. Any part of the species' potential naturalised range that was not contained within these range polygons was classed as uncolonised. The resulting range maps of climatically suitable, but uncolonised, areas were then stacked to produce the final global figures.

2.2.3 Compensating for recorder effort

I calculated recorder effort using Meyer et al.'s (2016) approach, which compares the species that have GBIF records in a grid-cell with the species that are known to be in the region from surveys and expert knowledge. These data are used to estimate the likelihood of detecting all known species in a given area. A value of zero indicates no recording effort and no species known to live there are detected, and a value of one indicates recording effort is sufficiently high to give a 100% detection probability, where all species known to occupy the area are detected. To compensate for recording effort I multiplied the number of observed species in a grid-cell multiplied by the reciprocal of the detection probability. Detection probability was given a floor of 0.01% as otherwise the relative number of species once recording effort was accounted for could be hyper-inflated to unrealistic levels.

2.2.4 Combining colonisation threat with capacity shortfall

I created a combined metric of colonisation risk using the measure of the number of species that could colonise each grid-cell and a national measure of response capacity to mitigate the impact of invasive species (Early et al., 2016). The measure of response capacity for each country is qualitative and based the number of measures each country has in place to mitigate invasive species, taken from Early *et al.*, (2018). I selected a subset of reactive and proactive responses that were most directly relevant to mitigating the spread of non-native species, and combined them into a single score. Reactive measures were: recognising invasive species as a threat, a national checklist and the scale of current management policies. Proactive measures were: the level of research and international collaboration, and outreach and monitoring programs in place. The resulting score can range from 0 to 5, but for this analysis was and inverted (5 - total score). The number of species that could colonise a grid-cell was divided into 20% quantiles, creating five threat categories from very low to very high. The same was done for the inverted capacity measure and both metrics were combined to create a heatmap of combined threat.

2.3 Results

2.3.1 Native and non-native species distributions

Every continent on Earth (except Antarctica) has at least one native and naturalised species represented in the dataset (Fig. 2.1). The median native range size of birds was 1.8 million km^2, mammals 1.7 million km^2, and plants 2.0 million km^2. Naturalised range sizes were smaller than native range sizes: 85,000 km^2 for birds, 130,000 km^2 for mammals, and 1.1 million km^2 for plants. For birds, the highest concentration of naturalised species are found in Spain, the UK, Arabian Peninsula, Australia and New Zealand, as well as across numerous pacific islands (Fig. 2.1). For mammals, naturalised species are particularly concentrated in California, the north western U.S. states, Texas, western Europe, and Australia. For plants, naturalised species ranges are particularly concentrated in California, Western Europe, Australia and Japan (Fig. 2.1).

2.3.2 Global threat of colonisation by non-native species

The areas that could face colonisation from the greatest number of non-native birds are in Mexico and the south-eastern United States. Eastern Europe could face colonisation by the greatest number of non-native mammals. The south-eastern United States, Mexico, eastern Europe, and south and west Australia could face colonisation by the greatest number of non-native plant species (Fig. 2.2). These areas are typically adjacent to areas with a high number of currently established naturalised species (Fig. 2.1).

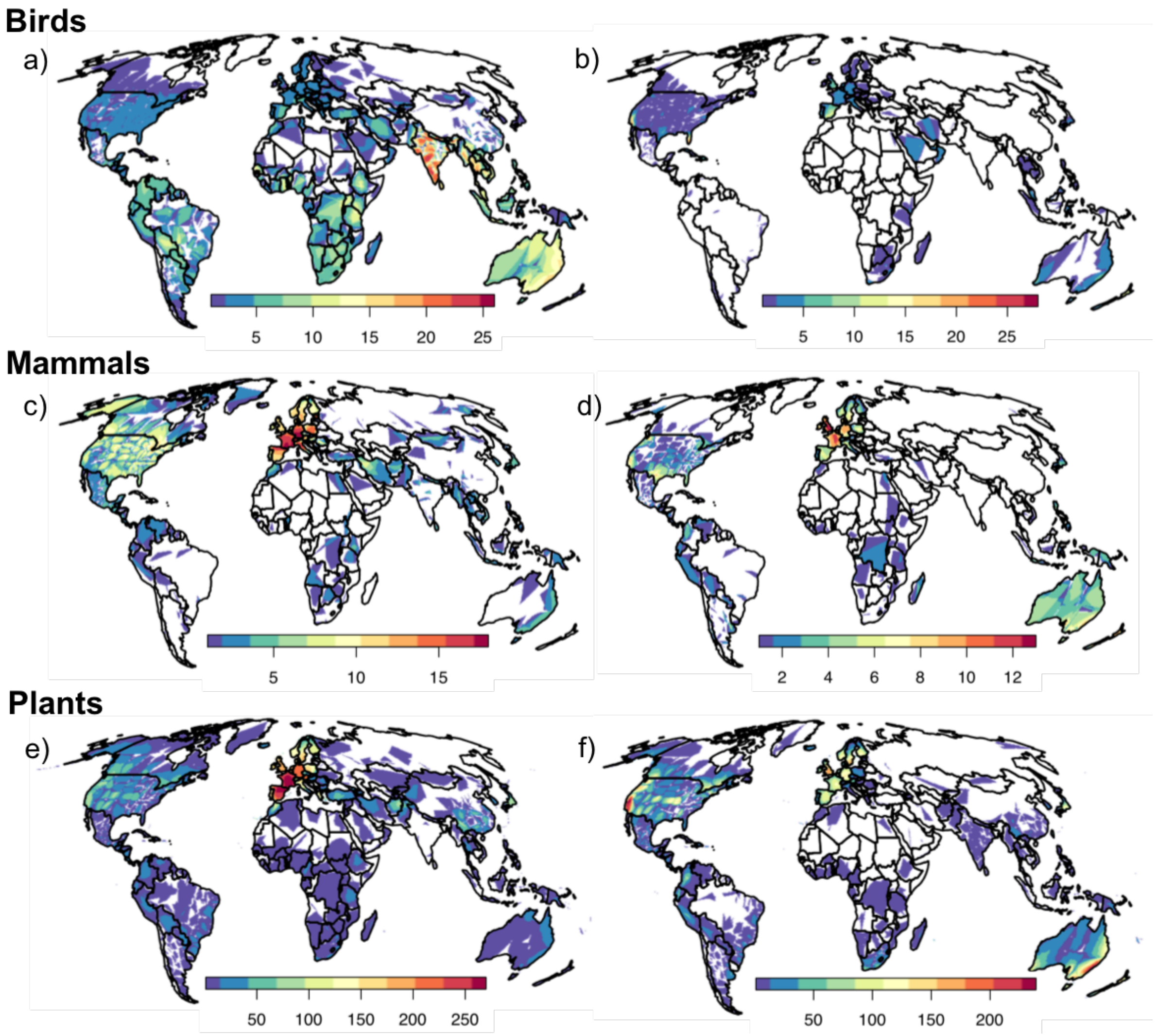
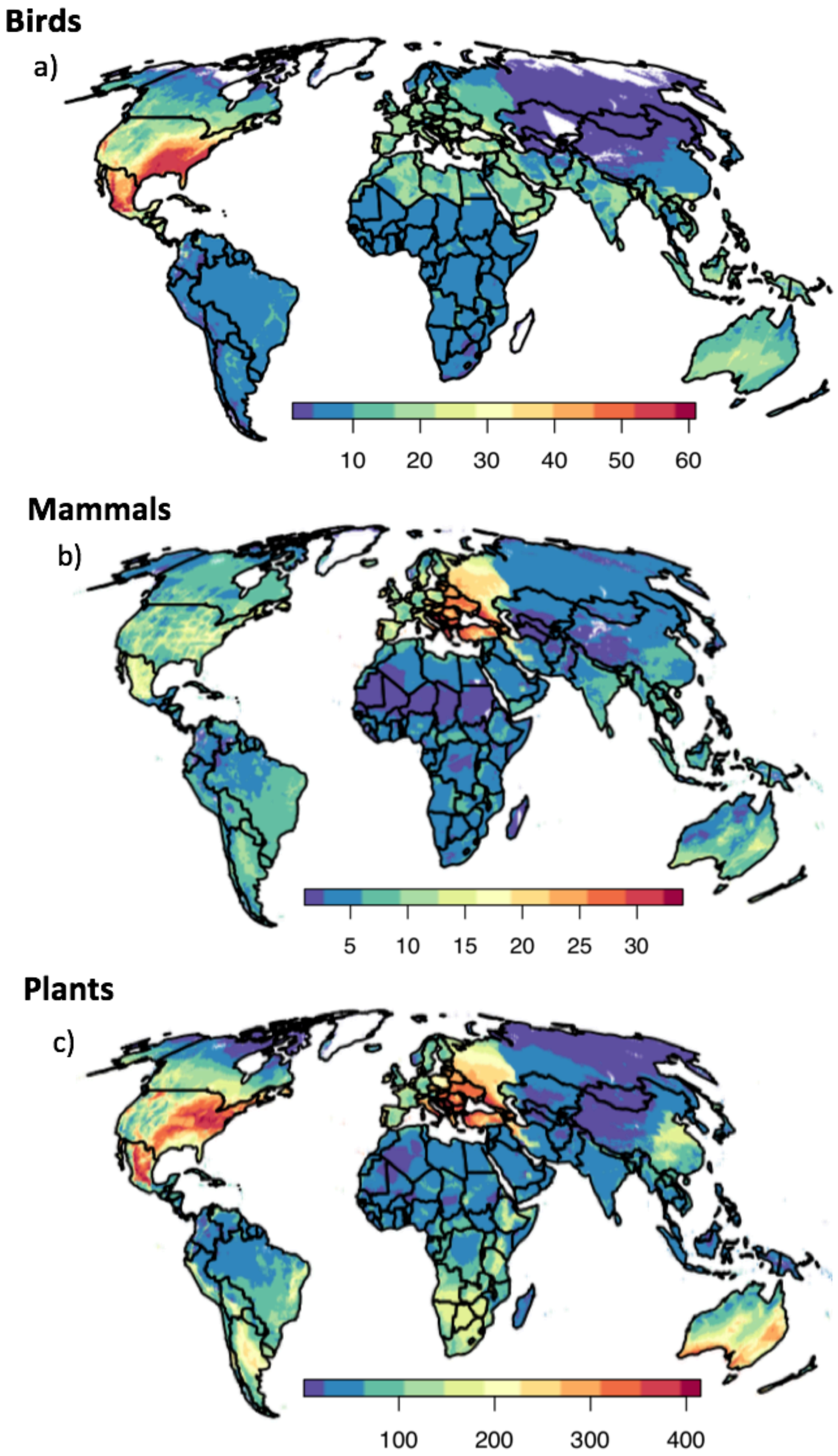


Figure 2.1: Number of study species' native ranges (a,c,e) and naturalised ranges (b, d, f) that fall in each 10 minute grid-cell. Colours represent number of species.

2.3.3 Addressing data bias

To compensate for variation in data availability around the world, I weighted the number of naturalised species in each global grid-cell by taxonomic coverage, a measure of species detection probability (Meyer, Weigelt, & Kreft, 2016). This identified areas where low reporting results in an under-estimate of threat of colonisation than otherwise expected, and where high reporting effort results in over-estimated threat. After accounting for data bias the same hotspots of native, naturalised and potential ranges of species were identified as when recorder effort was not considered. However, further hotspots were revealed in several less-sampled areas, where there are likely to be more non-native species than are



Birds

Mammals

Plants

Figure 2.2: Threat of terrestrial colonisation globally. The numbers of (a) birds, (b) mammals, and (c) plants that could colonise each 10 minute grid-cell based on the cell's climatic suitability for each species.

reported. Notable additional hotspots are the Middle East (birds), Central Africa (mammals and plants), and China (plants) (Supp. Material Fig S3).

2.3.4 National capacity to mitigate non-native species threat

Different parts of the world have different capacities to cope with the impacts of non-native species (Early et al., 2018). I assessed this by combining the metric of invasive species threat with a metric of each nation's reactive and proactive capacities to deal with invasive species from Early et al. (2016). Parts of China, central Africa and South America face a high colonisation threat and low capacity to mitigate impacts of colonising species (Fig. 2.3).

2.4 Discussion

Nearly all introduced species have not filled the areas that are climatically suitable for them. Species colonisation in the near future will be highest in regions that already have many introduced species, e.g. North America, Australia and Europe (Fig. 2.2). Other areas of the world, which have not been colonised by a large number of introduced species up until this point, will also likely face a large number of spreading species in the near future. These include notable hotspots of colonisation threat in southern Africa and South America (Fig. 2.2).

Areas with few resources to prevent colonisations are particularly at risk from invasive species. I note several areas in central Africa, eastern Asia, and South America that face a large number of future colonisations and have a low response capacity (Fig. 2.3). These areas lack the proactive or reactive response capabilities to cope with new introductions, or to mitigate the impacts of already-established species (Early et al., 2016). I suggest that these areas are also unlikely to have capacity to cope with the spread of non-native species into new areas. Managing these species will be costly, but managing existing ranges will reduce the probability species continue to spread to new areas.

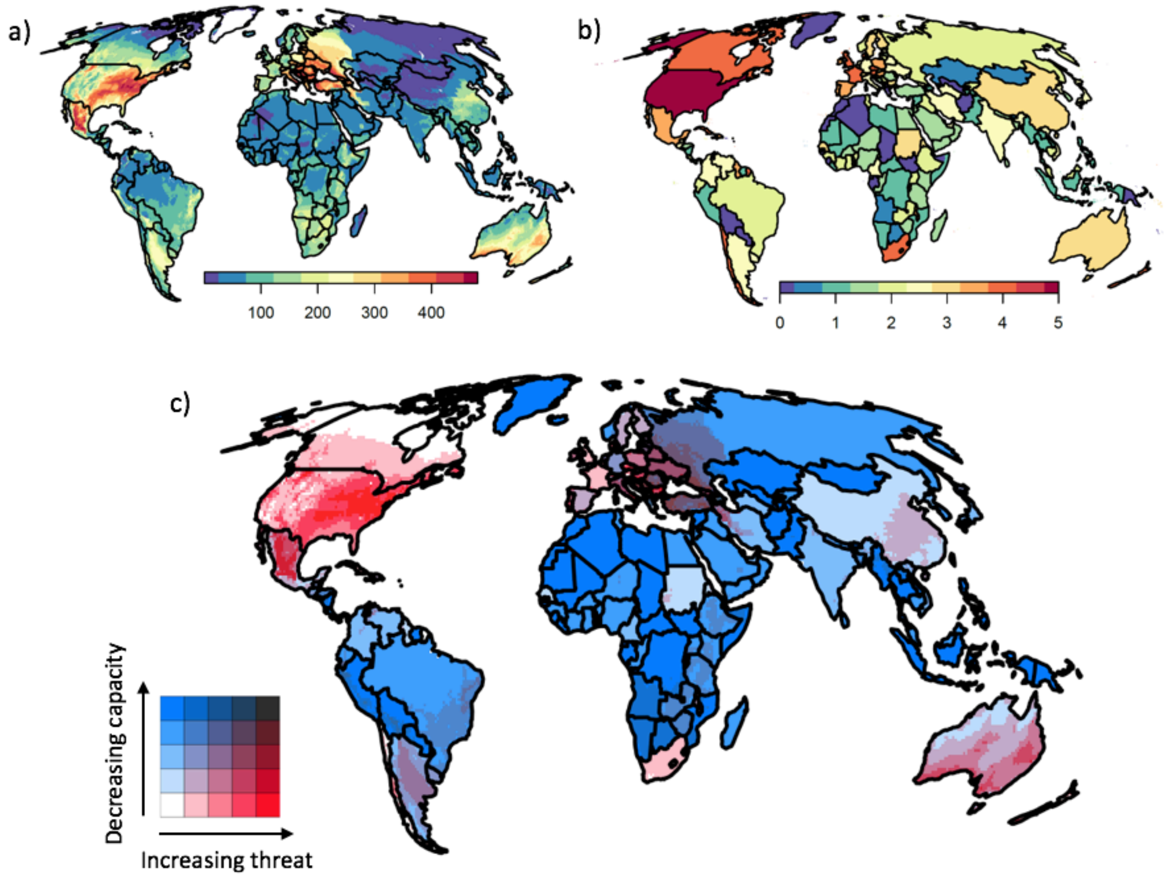


Figure 2.3: a) Threat of terrestrial colonisation globally. The number of species from all three taxonomic groups that could colonise each 10 minute grid-cell based on the cell's climatic suitability. b) the response capacity of each country to act against invasive species (Early et al., 2016). c) The combined threat of non-native species and lack of capacity.

Even if a small percentage of the species that colonise are invasive, it is well documented a single invasive species can cause severe problems for native ecosystems, agriculture, industry (Simberloff et al., 2013). In order to assess the risk of future colonisations, it is important to understand how naturalised species will spread in the future, or alternatively what is preventing them from colonising their potential naturalised range. In addition, more ongoing monitoring, early-warning communication is needed to identify potential sleeper species.

Some of the naturalised species I analysed only established a few decades ago, but others have been established for over a century. Therefore, there is not a straightforward relationship between time since introduction and extent of colonisation. Historically and currently, species introductions tend to centre around points of trade and human activity (Chapman et al., 2017). Areas that have not yet been widely colonised could therefore be due to limited historical trade. For example, high colonisation threat in eastern Europe may be due to the cold war, when the separation between western and Soviet countries may have stifled movement of introduced species for decades (Chiron, Shirley, & Kark, 2010; Roques et al., 2016). This barrier is now lifted and allowing species to spread further East (Roques et al., 2016), meaning that eastern Europe is an area of particular concern for future colonisations. However, historical reasons are less apparent in other areas facing a high colonisation threat. Birds have been introduced in high numbers to Florida, but they have not spread effectively through the US despite extensive transportation infrastructure and high dispersal ability. There is some doubt that some of these species are truly self-sustaining, and may be instead be supplemented by ongoing accidental releases (Dyer et al., 2017), but nevertheless there seems to be a large number of bird species that have not spread far from the site of establishment in Florida. This, however, does not mean that birds will never spread beyond their current range, and depends on what factor is currently preventing their spread.

Following introduction, human transport within the colonised region can greatly assist the spread of naturalised species, and species established in areas with a great deal of human trade may be more likely to fill their climatically suitable area more rapidly. For example *Didemnum vexillum* is a marine tunicate with very poor natural dispersal but has a large non-native range due to shipping activity and spread through ballast water (Herborg, O'Hara, & Therriault, 2009). In plants the range size of a non-native or invasive species in central Europe was found to be directly related to the likelihood of human transport, whether deliberately or accidentally (Pyšek, Jarošík, & Pergl, 2011). Therefore, in areas with extensive transportation, such as in the US, Mexico and Australia, it seems likely that with more time many species will expand their range greatly.

It is possible that established, naturalised species are separated from other climatically suitable areas by physical barriers such as mountains or deserts. It is unlikely species will cross these barriers without either being excellent natural dispersers, or being dispersed by humans. Therefore, the true risk of colonisation in areas isolated from introduction locations by physical barriers may be low. This seems to be the case in some regions, for example many plant species have been introduced to California (Fig. 2.1), and are separated from climatically suitable areas in the eastern U.S. by arid areas. While there is transport of introduced species between the western and eastern U.S. (Bradley et al., 2015), this still represents a clear barrier. However, this is not the case in many other examples. For instance, the south-eastern US is a hotspot of colonisation threat from birds (Fig. 2.2), and most of the species that could colonise this area are already established in Florida. If time lags are common, then areas directly adjacent to established species ranges are of huge conservation concern.

I demonstrated that the relative threat of colonisation is not due to under-recording, and globally high levels of colonisation threat are observed in parts of the world with the greatest recording effort, e.g. the U.S. (Fig. 2.2). However, under-reporting could still result in an underestimate of species that could colonise regions. It is likely that in many regions non-native species have established but have not been either recorded or reported. Species often remain in small, localised populations for years after establishment, followed by rapid range expansion (Aikio et al., 2010). This can make detection during the early stages of colonisation very difficult, especially in areas without a systematic recording program. By compensating for reporting effort, we can highlight areas in the Middle East, central Africa and China (Supp. Material Fig. S2), where the number of introduced species is currently much higher than would be expected given the general level of reporting effort. These speculative areas likely have more introduced species than currently reported, and if so are also hotspots of colonisation threat.

If neither trade, transportation, nor recorder effort explain why naturalised species are yet to colonise their potential range, what other factors could be at play? A number of species traits and aspects of introduction history have been linked to the establishment success and subsequent spread of introduced species. Species traits associated with success include natural dispersal ability (Angert et al., 2011; Moravcová, Pyšek, Jarošík, & Pergl, 2015; Václavík & Meentemeyer, 2012; Wilson, Dormontt, Prentis, Lowe, & Richardson, 2009), species niche breadth (Bradley et al., 2015), reproductive speed (Moravcová et al., 2015) and phenotypic plasticity (Angert et al., 2011; Moravcová et al., 2015; Václavík & Meentemeyer, 2012; Wilson et al., 2009). Aspects of introduction history associated with success include the level of human assisted dispersal (Pyšek et al., 2011), repeated introductions that boost populations size and heterogeneity (Blackburn et al., 2009; Vall-llosera & Sol, 2009) and the climatic suitability of initial sites of introduction (Pyšek & Hulme, 2005).

Aspects of the introduced area can also restrict species spread, such as fragmentation of suitable habitat (Kinezaki, Kawasaki, & Shigesada, 2010), biotic resistance (Levine, Adler, & Yelenik, 2004), or human management against invasives (Holmes, Richardson, Van Wilgen, & Gelderblom, 2000; Pyšek & Richardson, 2010). The importance of these explanations remains unknown. If the relative importance of these factors were known, it could help identify when and where species invasion lags are just delays and colonisation is imminent, or where species are unlikely to spread further. Depending on which factors predominate, management could prioritise species that have the potential to spread widely and rapidly and try to control them. Alternatively, management strategy could try to increase ecosystem resistance to non-native species (such as through biotic resistance, disturbance management, landscape structure etc.).

It could be argued that the threat of future colonisation does not immediately translate into future invasive impact. The majority of introduced species have low impact, and only a few exceptional species typically have high impact (Vilà et al., 2010). However, I argue that identifying potential spread of all naturalised species, even species currently classed as “non-invasive”, is important for several reasons.

First, invasional meltdown is common when multiple introduced species co-occur, even if the effect of individual species is small; a recent review found evidence of meltdown in 95 of 150 studies (Braga, Gómez-Aparicio, Heger, Vitule, & Jeschke, 2018). Invasional meltdown can adversely affect native species (Green et al., 2011), and have wide-ranging impacts on native communities (Stanley et al., 2013). Meltdown can occur either directly through facilitation either by a direct interaction (Jackson et al., 2014), or indirectly through one introduced species removing competitors or predators of another introduced species (Green et al., 2011). While invasional meltdown has been observed in a variety of systems, it is extremely difficult to predict how and when the necessary positive interactions will form. Nonetheless, the more co-occurring introduced species in an area, the higher the likelihood that such interactions will form and precipitate an invasional meltdown.

Second, the impact of introduced species increases with disturbance. Invasive species are often extremely effective at colonising disturbed areas (van Kleunen, Dawson, & Maurel, 2015), an ability which is typically associated with fast dispersal and aggressive growth. Disturbance can provide vacant niches through local extinctions, and lower an ecosystem's biotic resistance (Clark & Johnston, 2009; van Kleunen et al., 2015), making it easier for introduced species to establish and proliferate. Therefore, the colonisation hotspots that have a high level of disturbance face greater risk from individual invasive species and from invasional meltdown.

Third, invasive species are often not invasive at the first moment of introduction, and impact comes later after an initial period of lag, spread and population growth (Crooks, 2005). The ultimate impacts of these "sleeper species" are hard to predict ahead of time, and there is a need to identify indicators that can assess the risk of species becoming invasive. A number of frameworks have been developed to quantify impact, including by Parker (Parker et al., 1999) and the EICAT (Hawkins et al., 2015) and SEICAT (Bacher et al., 2018) frameworks. Unfortunately, one of the major criteria for having impact is to have a large introduced range, and thus the frameworks cannot be applied in their entirety to sleeper species. Alternatively, a number of studies have tried to find unifying traits of species or invaded regions that make invasive impacts more likely to occur (Simberloff et al., 2013; Vilà et al., 2010). Identifying species that are not yet invasive, but possess some of the traits of invasive species, would be one way to translate a threat map into one of true future risk.

Chapter 3: What can help or hinder introduced species' spread after establishment?

Abstract

There are a huge number of species across the globe that have established in new areas as a result of human transport. Many introduced species have not yet colonised all climatically suitable areas and their spread could cause substantial impacts on native species, agriculture and human infrastructure. There is therefore a need to understand whether species are still spreading, and if it is only a matter of time until species colonise all climatically suitable areas. In this chapter, I investigate factors that may help or hinder species' spread, and assess how and where species are most likely to spread and cause impact in the near future.

Using a global database of non-native birds, mammals and plants, I investigate the degree to which species have colonised climatically suitable areas. I then assess several factors that could potentially help predict species success in a hierarchical Bayesian model. Candidate explanatory factors included aspects of species' introduction history, species traits, the spatial distribution of climatically suitable areas, and interactions between non-native species and the native landscape. I find that time since introduction, dispersal, fragmentation of climatically suitable areas, and the region of introduction can predict species success at colonising suitable areas, however the effect of these factors varies between taxonomic groups. Species traits poorly predict non-native species spread, and instead find that aspects of the invaded landscape are more important for species success. Landscapes with continuous climatically suitable areas, particularly in Australia, are more vulnerable to invasion.

3.1 Introduction

Understanding and predicting the spread of introduced species is one of the key conservation and ecological challenges of the 21st century (Dawson et al., 2017). However, we know little about what causes the introduced range of some species to increase rapidly, while other species remain in small, isolated populations years after establishing self-sustaining populations (Blackburn et al., 2011; Simberloff & Gibbons, 2004). Species characteristics, introduction history, and the availability and spatial distribution of suitable climate can all influence how successfully a species can spread in its naturalised range (Gallien, Douzet, Pratte, Zimmermann, & Thuiller, 2012), but their relative importance is unknown. This is a major gap in our understanding, given that the extent of the colonised range is considered a prime factor in determining the magnitude of invasive impacts (Parker et al., 1999).

Predictions of the potential range of introduced species typically focus on the importance of climate (Araújo et al., 2011; Early & Sax, 2014), and time since introduction (Byers et al., 2015; Pyšek et al., 2015; Wilson et al., 2007) as the main limiters of introduced species ranges. It is commonly assumed that given enough time, a naturalised species will spread to occupy all areas with climate that matches the climate occupied in the native range (Wilson et al., 2007). The proportion of its potential range a species colonises is termed ‘range filling’ (Bradley et al., 2015). In reality, species have very variable range filling, even long after establishment (Aikio et al., 2010; Crooks, 2005). Understanding what restricts species’ naturalised range, once suitability of the physical environment is accounted for, is therefore a key knowledge gap.

There are a variety of reasons, other than invasion lags, that might explain why species do not colonize all areas that appear climatically suitable. These can be broadly categorised (after Gallien et al., 2012), as 1) introduction history 2) species traits 3) the spatial distribution of suitable areas and 4) interactions between the invader and native landscape. In this study I consider the effect of variables from all four of these groups, and their overall effect on species range filling after they have successfully established.

A species that has been established in an area for longer has had more time to establish, reproduce and spread, and time has been found to be a key factor in predicting naturalised species range size (Byers et al., 2015; Pyšek et al., 2015; Wilson et al., 2007). The number of individuals introduced (‘propagule pressure’) also has an important role in species spread, especially in the first few years following establishment (Blackburn, Cassey, & Lockwood, 2009; Vall-llosera & Sol, 2009). Species introduced into habitat that is similar to their native range are more likely to establish and begin to spread (Pyšek & Hulme, 2005). Human-assisted dispersal is a very effective method of colonising new areas (Pyšek et al., 2015; Wichmann et al., 2009), and species dispersed by humans are frequently more successful at spreading through a novel landscape (Pyšek et al., 2011).

Species that are able to grow and spread quickly, compete effectively, and can quickly colonise new areas, are more likely to become invasive (Moravcová et al., 2015), and similar traits likely contribute to a high level of range filling. Traits that correspond to these characteristics are behavioural flexibility and habitat utilisation, such as habitat generalism (Blackburn et al., 2009; Estrada, Morales-Castilla, Meireles, Caplat, & Early, 2017; Vall-llosera & Sol, 2009) and relative brain mass (Sol, Bacher, Reader, & Lefebvre, 2008a; Vall-llosera & Sol, 2009), which are all linked to establishment success. Traits associated with reproductive rate have been linked to establishment success or invasive status in some species. These include time till sexual maturity (Angert et al., 2011) and seed/clutch size (Capellini et al., 2015; Estrada et al., 2017). Dispersal ability also aids colonisation speed and has been linked to introduced species success (Angert et al., 2011; Moravcová et al., 2015; Václavík & Meentemeyer, 2012; Wilson et al., 2009).

The success of introduced species is an interaction of not just the traits of the introduced species, but also the characteristics of the landscape to which the species is introduced (Thuiller et al., 2010). An introduced species that has little to no phylogenetic relatedness to native genera may be more likely to be successful because they can exploit unused ecological niches, known as “Darwin’s naturalisation hypothesis” (Rejmánek, 1996). Competitors, ecological diversity, predators and soil ecology have all been suggested to contribute to the biotic resistance of the introduced landscape (Levine et al., 2004), and can contribute to how “invadable” the landscape is. If an area has particularly low biotic resistance, and a phylogenetically distinct community, then an introduced species may be more successful there, regardless of the traits the introduced species possesses. For example, due to Australia’s relative evolutionary isolation, many species that are introduced have no native ecological equivalent, and are often more successful due to a lack of natural predators (Harvey, Nipperess, Britton, & Hughes, 2012).

The spatial properties of the introduced area can also be important. In a landscape where suitable climatically suitable areas are extremely continuous, i.e. non-fragmented, it should be much easier for a species to spread than in a landscape with small and isolated fragments of suitable climate (Kinezaki et al., 2010).

To understand and predict invasive impacts, it is important to understand how much of their potential ranges introduced species fill, and what underlies variation in range filling. For example, if low range filling is predominantly driven by invasion time lags and dispersal limitation, then already-introduced species could spread much more widely than they have to date. It would then be crucial to explore what affects the length of invasion time lags, in order to help predict which already-introduced species will invade further in the future, and how quickly species introduced in the future will colonise. If, on the other hand, low range filling corresponds to high fragmentation of climatically suitable areas or biotic resistance, then we can identify regions that are at low or high risk of invasion and manage landscapes appropriately.

Here I undertake the first global assessment of the degree to which introduced birds, mammals, and plants have colonised climatically suitable areas in their introduced ranges. My study is the first to incorporate climatic suitability when investigating invasion lags, and accounting for this major determinant of species’ naturalised ranges frees us to examine the other drivers of colonisation without the complication of unknown climatic suitability. I ask what characteristics of species or geographic regions hasten or slow colonisation and interpret species capacity to spread beyond their current introduced ranges. I consider a wide cross-section of 242 plants, 22 mammals, and 35 birds that have been introduced around the world, ranging from small annual herbs to long-lived large trees, and from tiny herbivores to apex predators.

3.2 Methods

3.2.1 Identifying study species

I identified birds, plants and mammals that have established outside their native range following introduction by people. I included only species confirmed to have established on a mainland landmass outside their native continent. Species that were introduced pre-Columbus were removed from consideration, as were species that are not confirmed to reproduce in their naturalised range. For a full species list, see the Supplementary Material (Table S1; S2; S3).

Plant species were drawn from those not listed as 'Casual Alien', 'unconfirmed naturalisation', 'Contaminant' or 'Native Weed' in Randall (2017). Species listed in the Global Invasive Species Information Network (GISIN, 2015) were also included.

Bird species were compiled from known successful introduction events (Dyer et al., 2017; Lever, 2005; Sol et al., 2012). All migratory birds were removed from the list, due to difficulty defining a species' range and climatic niche. Migratory status was confirmed using Handbook of the Birds of the World (del Hoyo, Elliott, Sargatal, Christie, & de Juana, 2018).

Mammal species were compiled from known successful introduction events (Capellini et al., 2015). A search was made for additional mammal species from various sources, but in final analyses none of these species were included due to either a lack of data on the known naturalised range or because long-term establishment could not be confirmed.

3.2.2 Occurrence data from native and naturalised ranges

For all species I obtained occurrence data from GBIF (downloaded 31st August 2017) using R's dismo package (Hijmans et al., 2015). Points were classified as either "native" or "naturalised" based upon sources listed in the Supplementary Materials (Table S4). Species that occupied fewer than 5 grid-cells (at 10 arc-minute resolution) in their native or naturalised range were discarded. In total the database on native and naturalised ranges has information on 70 mammal species, 114 bird species and 649 plant species.

I restricted predictions of species potential naturalised ranges to the biogeographic realm into which species were introduced. I used biogeographic realms from Holt et al. (2013), but with an additional distinction between western and eastern Palearctic along an approximate line of the Ural mountains (for figure see Supplemental Material Fig. S1). This was done because of the large size of the realm and to separate western Europe and eastern Asia. Species that inhabit both Western Europe and eastern Asia are almost always native to one and naturalised in the other. Species that were found to be native and naturalised in the same biogeographic realm were removed from analysis, due to the difficulty in exactly defining the native and naturalised ranges.

If a species was naturalised in more than one biogeographical realm, I separated this information by realm. Each confirmed breeding population in each separate biogeographic realm was counted as a separate “naturalisation event”. Any introductions prior to 1770 were cropped, because dates prior to this are increasingly uncertain, and to allow equal comparison across all realms (as Australia did not see wide-spread introductions before 1770).

3.2.3 Modelling species potential naturalised ranges using climate

I modelled potential ranges using three climate variables: mean temperature of coldest month, mean temperature of warmest month and total annual precipitation. These represent the most universal parsimonious variables that influence species ranges (Early & Sax, 2014). Including a larger number of variables results in forecasts of smaller potential ranges, and less transferability than the parsimonious set of variables (Early & Sax, 2014). Gridded climate data were downloaded from WorldClim at 10 arc-minute resolution. Each grid-cell contained average climatic variables from 1970-2000 (Fick & Hijmans, 2017).

I restricted a species’ available climate to only climate shared in both their native and naturalised realms, and used principal components analysis (PCA) to produce a gridded climate space of 100x100 cells on two axes (Broennimann et al., 2012). Species occurrence density in each PCA grid-cell was estimated using a kernel smoothed density function. The native occupied niche was defined as an envelope around the occupied native density, and the naturalised likewise around the occupied naturalised density. Any occurrences in non-analogue climate were removed from further analysis.

3.2.4 Measuring niche and range filling

In order to calculate range filling, I identified from the PCA the climatically suitable geographic grid-cells in a species' naturalised realm, i.e. those that have climate the species occupies in its native realm. To calculate the 'filled' areas I constructed a naturalised range polygon for each species using the point occurrence data and level 4 geographic administrative units from the TDWG scheme (Brummitt, 2001). Administrative units are usually countries, but large countries such as the U.S or China are split into states or provinces. Within each administrative unit I created a convex hull polygon around a species' occurrence data of each species, which represents the occupied area. I used these polygons rather than point occurrence data as point data are only a subset of real occurrences, and in themselves points cannot be used to calculate range filling. Without splitting large countries into states/provinces, I found that several clearly separate populations would be incorrectly grouped to construct a range polygon, for example coastal populations in California and Florida, which would overestimate the occupied area. Range filling in each naturalised realm was calculated as the total climatically suitable area that was filled by the naturalised range polygons (km^2). The response variable was the proportion of range filling (from 0 to 1) of each species in their naturalised realm.

3.2.5 Species traits and time of introduction

I assessed species or regional characteristics that may promote or hinder range expansion of introduced species.

The year of introduction is difficult to ascertain for most plants so the first confirmed record of occurrence in a realm was taken as the date of introduction, obtained from Seebens et al. (2017), ALA ("Atlas of Living Australia," 2018), DAISIE (2018) and additional regional sources (see Supp. Table S5).

Mean and maximum dispersal distance is frequently unknown for many plant species, but dispersal distance can be estimated using a number of proxy life history traits (Vittoz & Engler, 2007). Dispersal was estimated as a ranked category from 1-7, which correspond to increasing maximum dispersal distance on an approximately logarithmic scale (Vittoz & Engler, 2007). Estimated dispersal distance varies depending on the species' dispersal mode, plant height, habitat type and taxonomic group (for full definition table see table S6).

I estimated dispersal distance using dispersal mode, plant height and habitat type (Vittoz & Engler, 2007) with data from the TRY database (Kattge et al., 2011). Growth form was obtained from TRY (Kattge et al., 2011) and USDA Plants database. Plants were defined as either herbs, climbers, trees, shrubs or ferns, adapted from the IUCN growth form list (original list IUCN, 2018, see Supp. Material Table S7). The age of a plant at first flowering and the seed number per flowering event were also extracted from the TRY database (Kattge et al., 2011). Previous studies have linked introduced species success to horticultural status (van Kleunen et al., 2018), therefore whether a species was used in horticulture or not was extracted from Dave's Garden PlantFiles (http://davesgarden.com/guides/pf/, accessed 25 May 2018) and from the Plant Information Online database (https://plantinfo.umn.edu/, accessed 25 May 2018).
The year of introduction for birds was estimated using the first confirmed record from GAVIA (Dyer et al., 2017) and Seebens et al. (2017). Natal dispersal distance was estimated using diet, body mass and wingspan (for full method see Garrard, McCarthy, Vesk, Radford, & Bennett, 2012). Bodymass and diet data were gathered from the EltonTraits database (Wilman et al., 2014) and bird wingspan from del Hoyo et al. (2018). If only bird wing-length was available, bird wing-length was extrapolated to wingspan using the method in Garrard et al. (2012). Clutch size and number of clutches per year were obtained from Myhrvold et al. (2015).

The year of introduction for mammals was estimated using the first confirmed record from Long (2003) and Seebens et al. (2017). Natal dispersal distance was estimated using bodymass, home range size and trophic level (for full method see Santini et al., 2013) from PanTHERIA (Jones et al., 2009). Litter size, time till sexual maturity, and interbirth interval were also taken from PanTHERIA. Information on brain residual size were taken from Sol et al. (2008).

For all species, invasive status was determined by their description on GISIN (2015). Bodymass was not used in the analysis as it covaried strongly with the estimated natal dispersal distance (Birds: Pearson’s correlation R-squared = 0.54; Mammals: R-squared = 0.93).

Habitat generalism was obtained for all species using the IUCN Habitat Classification Scheme (accessed IUCN 2018), and quantified as the number of general habitats as an integer and the number of sub-habitats as a decimal (Estrada et al., 2017).

For all species, I also included a measure of median sampling effort. Range filling may be underestimated in areas of low recording effort, as fewer observations are available to construct the true range of the species. To compensate for this, I used a measure of global sampling bias from Meyer, Weigelt, & Kreft (2016), from which I used their measure of taxonomic coverage. For each species I found areas of the naturalised realm that were climatically suitable but not occupied, and took the median taxonomic coverage of all grid-cells within these areas.

The fragmentation of climatically suitable areas was measured in two different ways, the ‘contagion’ of a landscape and the ‘clumpiness’. Both were calculated in the FRAGSTATS program using the same method as described in the program’s documentation (McGarigal, Cushman, Neel, & Ene, 2012). These two metrics measure different aspects of fragmentation, and have different consequences for interpretation (Wang, Blanchet, & Koper, 2014).

Contagion describes how dominant and aggregated suitable grid-cells are over a landscape and how interspersed it is with other types. For the contagion metric calculation, FRAGSTATS estimates the probability that a given cell in a landscape is climatically suitable, and then the conditional probability that an adjacent cell is of a different type (i.e. not climatically suitable). The product of these probabilities equals the probability that two randomly chosen adjacent cells belong to two different types of cell (for full method see McGarigal, Cushman, Neel, & Ene, 2012). Values for contagion range from 0 (climatically suitable grid-cells are completely fragmented and rare) to 100 (climatically suitable grid-cells is completely dominant across the landscape). Contagion is a good measure of fragmentation when comparing within similar areas, such as in the same geographic realm. However, contagion typically correlates with total available area, and as a result it is not a good measure of fragmentation when comparing across geographic realms of different sizes. For this reason, a second measure of fragmentation was also needed to compare fragmentation across realms.

Clumpiness describes how spatially aggregated suitable grid-cells are over a landscape, after accounting for its overall abundance. For the clumpiness metric calculation, FRAGSTATS estimates how many climatically suitable cells would be expected to border each other in a spatially random distribution, given the proportion of climatically suitable area over the whole landscape. It then compares if the actual spatial distribution of climatically suitable grid-cells is more or less randomly aggregated than the estimated random distribution (for full method see McGarigal, Cushman, Neel, & Ene, 2012). Values for clumpiness range between -1 (maximally disaggregated), 0 (spatially randomly distributed) and 1 (maximally aggregated). Clumpiness considers only the number of cell-adjacencies as a proportion of the total number of cells, so does not typically correlate with total available area (Bradshaw et al., 2014).

In total, the final dataset consisted of 484 plant establishment events (242 separate species), 50 bird establishment events (35 species), and 46 mammal establishment events (22 species). The full species list is included in the Supplementary information (Table S1).

3.2.6 Statistical analysis of characteristics corresponding to range filling

For each taxonomic group, the relationships between species' naturalised range filling, traits and introduction characteristics were investigated using a hierarchical Bayesian model based on a beta distribution with a logit link. Realm, invasive status, growth form, horticultural status (in the case of plants) were treated as categorical, all other parameters were continuous. Body mass, home range size, and height were logged to improve linearity. All predictive parameters were centred on their mean and scaled by their standard deviation. I chose to use weakly informative priors throughout which favoured parameter estimates at or near zero, but did not constrain the models from selecting non-zero estimates. For example, priors of continuous parameter effects were specified as a normal distribution with an overall mean of 0 and an overall standard deviation of 2. This reflects the null expectation that a continuous predictor has no correlation with the response parameter (i.e. parameter estimate is zero), and if no information suggests otherwise the parameter estimate will converge at 0. However, a weakly informative prior also has a large standard deviation relative to the scaled continuous parameter, it therefore does not constrain the model from selecting a positive or negative parameter value if this improves the model (Gelman, Jakulin, Pittau, & Su, 2008). For categorial and hierarchical effects I used a weakly informative half-Cauchy distribution for the standard deviation among categorical levels. This reflects the null hypothesis that there is no difference between levels and biases the model towards conservative parameter estimates at or near 0, and therefore avoids overestimating the size of categorical and hierarchical effects. However, the prior distribution retains a long tail to the probability distribution that allows the model to select positive hierarchical effects if this improves the model. An example model with one continuous variables and one hierarchical effect is included in Supplementary Table S8.

Models were run using a Markov chain Monte Carlo (MCMC) method in JAGS through the R package “R2jags” with a burn-in of 10000 samples and checked for convergence after a further 20000 samples, which was extended if estimates did not converge. Models were evaluated using the widely applicable information criterion (WAIC), leave-one-out (LOO) evaluation (Vehtari, Gelman, & Gabry, 2017) and Pearson’s residual fit (Cribari-Neto & Zeileis, 2009). A pseudo R-squared for each model was also calculated as a squared sample correlation between the mean linear predictors and the link-transformed response.

I first investigated the relationship between range filling in each taxonomic group and each predictive variable individually, while also including the naturalised biogeographic realm as a hierarchical effect. Posteriors were checked for a single unimodal peak, and predictive variables whose posterior estimate centred near 0 (meaning the value 0 lay between the 5th or 95th percentile parameter estimates) were not analysed further. The remaining variables were entered into one multivariate model. One parameter was removed from this model at a time, and the more parsimonious model compared to the full model using WAIC, LOO, and Pearson’s residual fit. Models with a lower WAIC were retained, and in cases where models had a similar WAIC (i.e. ±2) the more parsimonious model was selected. In this case, parsimonious refers to the model with a lower number of effective parameters (pD). The posterior distribution of each parameter estimate was taken from the final model. The mean parameter estimates were recorded, as well as the 97.5th and 2.5th percentile estimates. A parameter was classed as having a significant effect when mean, 2.5th and 97.5th percentile estimates fell above or below 0.

3.2.7 Sensitivity analysis for low number of occurrences

Analysis of species range filling is potentially sensitive to bias when including species with extremely low record numbers. I set a threshold of a minimum of five naturalised grid-cells, which allows rarer species and species with small total potential ranges to be included in the analysis. However, species with very few records may reflect a lack of detection rather than a failure to fill their range, and therefore species niches and ranges may not be accurately characterised. I accounted for this by including two forms of sensitivity analysis.

Firstly, I tested for a correlation between range filling and the number of occupied naturalised grid-cells using the same model specification as above (Chapter 3.2.6). The number of grid-cells was logged for normality and treated as a continuous parameter, and region was also included as a hierarchical effect. If species with very low numbers of grid-cells show drastically different patterns in range filling to other species then it suggests that the overall model is very sensitive to species with very small ranges, and a higher threshold should be considered.

As a second sensitivity analysis, I ran a secondary analysis of the final model of range filling in plants, but with a higher cut-off threshold of 20 grid-cells. If the model is robust to species with very low numbers of grid-cells the model output should return similar parameter estimates. Unfortunately, a similar analysis could not be completed for birds or mammals as the smaller sample size associated with a higher threshold caused issues with model convergence.

3.3 Results

3.3.1 Summary of introduced species and range filling

Every continent on Earth (except Antarctica) has at least one native and naturalised species represented in the dataset (Table 3.1). In their native ranges, birds occupied a median of 397 grid-cells, mammals 240, and plants 471 cells. All species had at least 5 occupied grid-cells in their native and naturalised ranges, though only 7% of all species had fewer than 10 occupied grid-cells (Supp. Fig. S4). The maximum number of occupied grid-cells was 8,682,788 (see Supp. Fig. S4). On average naturalised ranges were smaller than native ranges, with birds occupying a median of 28 cells, mammals 43, and plants 202 grid-cells (see Supp. Fig. S4). Using range polygons, birds had a median native range size of 1.8 million km^2, mammals 1.7 million km^2, and plants 2.0 million km^2. In all three taxonomic groups, naturalised range sizes were smaller: median values are 112,000 km^2 for birds, 283,000 km^2 for mammals, and 441,000 km^2 for plants.

The proportion of climatically suitable areas successfully colonised by introduced species was in general low, but highly variable across species (Table 3.1). Mammals occupied a median of 4% of available range, birds 1% and plants 5%. Species niche filling increased with a greater number of grid-cells, but with a very high degree of variability (see Supp. Fig. S5). Species range filling also increased with the number of occupied grid-cells, but range filling was not strongly associated with number of grid-cells when grid-cell count was low (Supp. Fig. S6). The final Bayesian model for plants was re-run with a threshold of 20 grid-cells and produced similar parameter estimates to the final model with the lower threshold (see Table 3.2, S9). There does not seem to be a high sensitivity to species with low numbers of grid-cells, so the threshold of 5 was kept for all further analyses.

3.3.2 Correlation between range filling, traits and time of introduction

Models successfully converged after 20,000 iterations. I confirmed the model was not mis-specified by checking that posterior parameter estimates were normal, as well as residual and LOO evaluation. The effect of realm was consistently important for all three taxa (Table 3.2).

Range filling was particularly high in Australia for plants and mammals, though not for birds (Table 3.2).

For plants, time since introduction had a significant positive effect on range filling globally (Fig. 3.1a). Age at first flowering had a significant negative effect on range filling decreased as first flowering age increased in Australia and the Nearctic. (Fig. 3.1, Table 3.2). Sampling effort had a significant negative effect on range filling in Australia and the Nearctic.

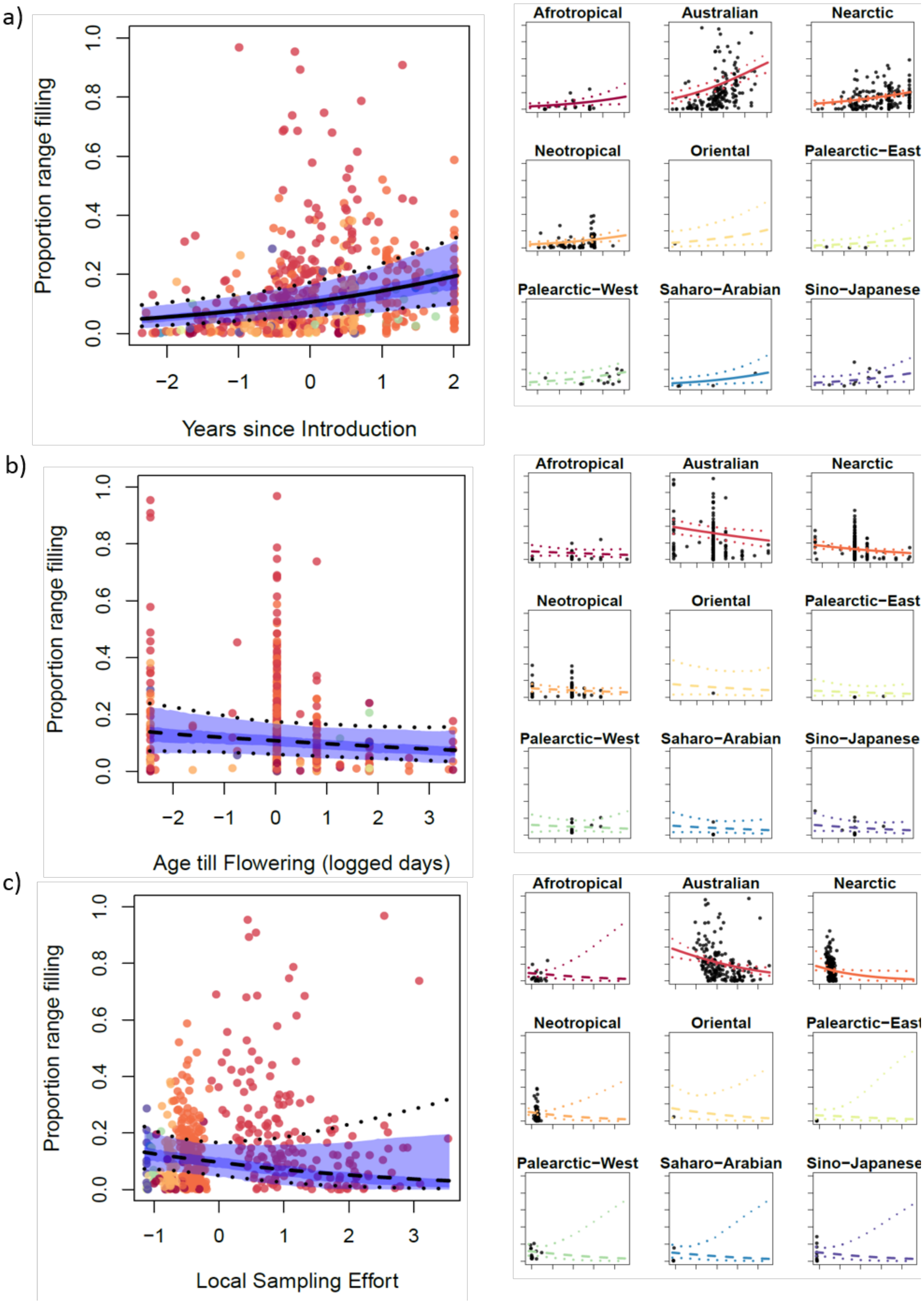

a)
Proportion range filling
0.0
0.2
0.4
0.6
0.8
1.0
−2
−1
0
1
2
Years since Introduction
Afrotropical
Australian
Nearctic
Neotropical
Oriental
Palearctic−East
Palearctic−West
Saharo−Arabian
Sino−Japanese
b)
Proportion range filling
0.0
0.2
0.4
0.6
0.8
1.0
−2
−1
0
1
2
3
Age till Flowering (logged days)
Afrotropical
Australian
Nearctic
Neotropical
Oriental
Palearctic−East
Palearctic−West
Saharo−Arabian
Sino−Japanese
c)
Proportion range filling
0.0
0.2
0.4
0.6
0.8
1.0
−1
0
1
2
3
Local Sampling Effort
Afrotropical
Australian
Nearctic
Neotropical
Oriental
Palearctic−East
Palearctic−West
Saharo−Arabian
Sino−Japanese

Figure 3.1 (overleaf): Plotted plant parameter estimates of all variables kept in the final model to explain species range filling. On the left are global trends for each parameter, on the right are the realm hierarchical effects. a) years since introduction b) age of first flowering event c) the estimated local sampling effort. A solid line signifies the estimate was consistently above or below 0 in >95% of simulations (and therefore judged as significant), a dashed line means it was not. The lighter shaded area shows the 95% probability density interval for the parameter estimate, and the darker shows the 50% interval.

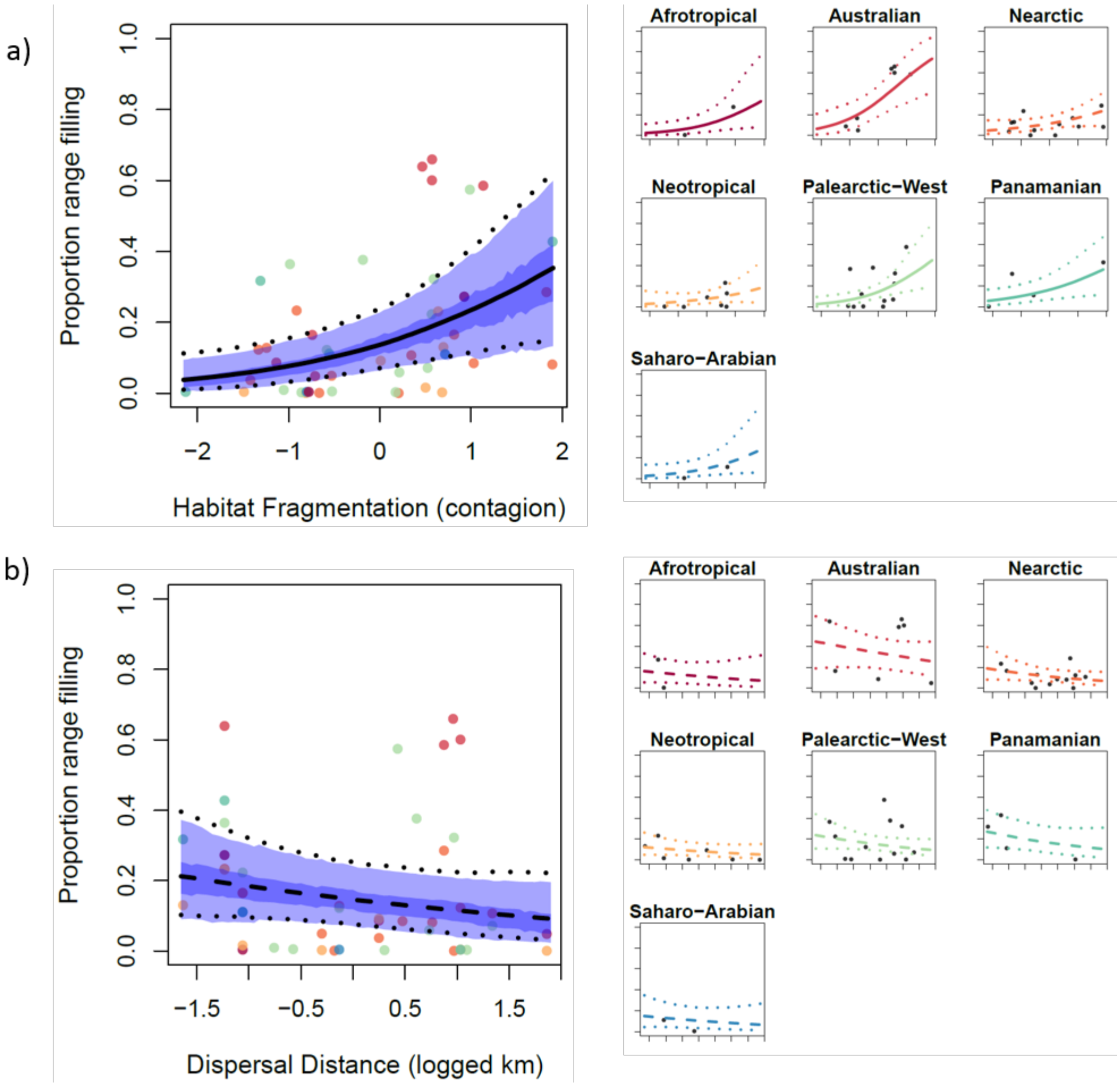


Figure 3.2: Plotted mammal parameter estimates of all variables kept in the final model to explain species range filling. On the left are global trends for each parameter, on the right are the realm hierarchical effects. a) fragmentation of suitable climate (contagion), b) dispersal distance (logged km). A solid line signifies the estimate was consistently above or below 0 in >95% of simulations (and therefore judged as significant), a dashed line means it was not. The lighter shaded area shows the 95% probability density interval for the parameter estimate, and the darker shows the 50% interval.

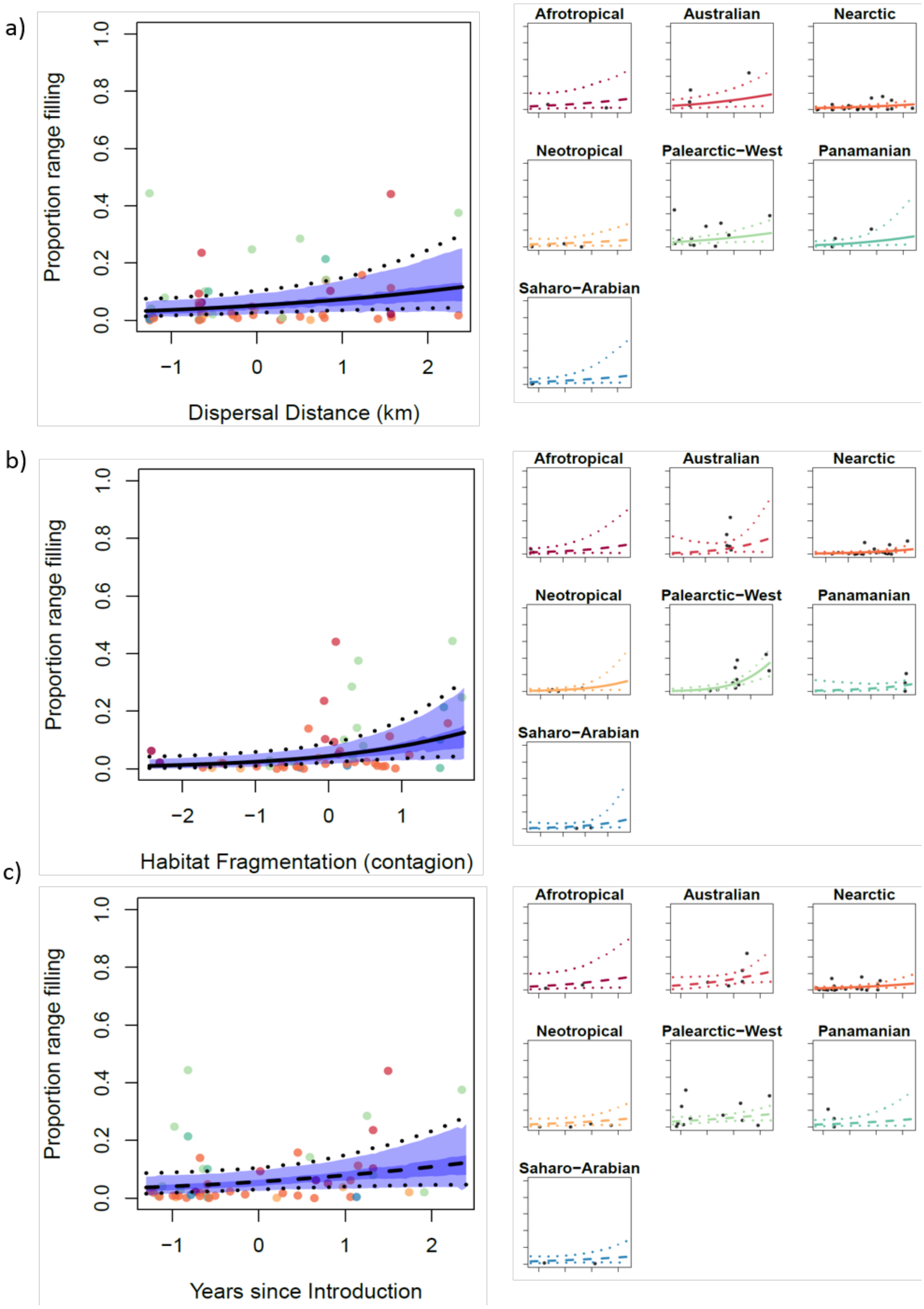


Figure 3.3: Plotted bird parameter estimates of all variables kept in the final mode to explain species range filling. On the left are global trends for each parameter, on the right are the realm hierarchical effects. a) Natal dispersal distance (km), b) fragmentation of suitable climate (contagion) c) years since introduction. A solid line signifies the estimate was consistently above or below 0 in >95% of simulations (and therefore judged as significant), a dashed line means it was not. The lighter shaded area shows the 95% probability density interval for the parameter estimate, and the darker shows the 50% interval.

Table 3.1: Summary statistics of introduced species and range filling for all taxonomic groups across all realms. Biogeographical realms modified from Holt et al. (2013), see Supp. Material (Fig. S1). “Median range size” is the median range size (calculated with minimum convex hull polygon) of all established naturalised species (measured in 1000 km^2). “Median potential range size” is the median area each species has available but has not colonised in each realm (measured in 1000 km^2). For each species the total occupied area is divided by the total available area to return a range filling proportion. “Median proportion of filling” is the median range filling across all species in the given realm.

	Region	**Number of introductions**	**Median Range Size (1000 km^2)**	**Median Potential Range Size (1000 km^2)**	**Median Range Filling Proportion**
Plants	GLOBAL	484	441.45	4487.42	0.10
	Afrotropical	19	145.75	6105.19	0.02
	Australian	171	476.99	2739.75	0.15
	Nearctic	174	887.27	7789.48	0.11
	Neotropical	89	131.06	3625.80	0.34
	Oriental	1	322.71	6260.12	0.05
	Palearctic (East)	3	15.76	8579.61	0.002
	Palearctic (West)	13	511.22	8824.98	0.07
	Saharo-Arabian	4	71.80	9362.50	0.01
	Sino-Japanese	10	145.48	2149.68	0.07
Birds	GLOBAL	50	112.12	5538.15	0.02
	Afrotropical	2	989.46	21991.87	0.04
	Australian	5	744.40	5879.41	0.10
	Nearctic	23	87.26	5276.60	0.01
	Neotropical	4	156.32	12814.93	0.01
	Palearctic (West)	11	320.49	3780.78	0.10
	Panamanian	3	103.24	916.98	0.10
	Saharo-Arabian	2	44.79	6402.21	0.01
Mammals	GLOBAL	46	283.84	3102.15	0.11
	Afrotropical	2	2967.62	14815.67	0.14
	Australian	7	471.68	2529.87	0.59
	Nearctic	12	258.85	4988.17	0.10
	Neotropical	7	247.85	10819.92	0.02
	Palearctic-West	12	571.31	5933.23	0.10
	Panamanian	4	191.94	642.81	0.21
	Saharo-Arabian	2	76.96	2100.02	0.06

Table 3.2: Correlates of range filling for each taxonomic group, and model verification. Estimates for parameters retained in the final model are given as the mean estimate of all posterior draws, with the 5% and 95% estimates as confidence intervals in parentheses. Parameter estimates are given as the linear slope of the logit link equation. When parameter estimates vary across realms, this is indicated by providing the names of the realms in which it varies (Aus = Australian, Nea = Nearctic, Neo=Neotropical). Model verification data are given for the final models, including sample size, Widely Applicable Information Criterion (WAIC) of the model, the effective number of parameters (pD), and correlation of the linear predictor against the link transformed response given as a pseudo R-squared.

	Model Parameter	Estimate	95% CI	Differences between realms?	Model Verification	Estimate
Plants	Intercept	-2.27	(-1.59, -3.02)	Aus	Sample Size	484
	Years since Introduction	0.35	(0.53, 0.15)		DIC	-1065.79
	Days till Flowering (logged)	-0.13	(0.03, -0.26)	Aus, Nea	pD	18.79
	Local sampling effort	-0.29	(0.34, -0.86)	Aus	Pseudo R-Squared	0.31
Birds	Intercept	-2.78	(-2.11, -3.34)		Sample Size	50
	Years since Introduction	0.35	(0.74, 0.00)	Nea	DIC	-199.77
	Dispersal Distance (km)	0.37	(0.73, 0.02)		pD	19.43
	Fragmentation	0.62	(1.12, 0.10)		Pseudo R-Squared	0.59
Mammals	Intercept	-1.83	(-1.14, -2.55)		Sample Size	46
	Dispersal Distance (logged km)	-0.28	(0.10, -0.65)		DIC	-88.75
	Fragmentation	0.66	(1.13, 0.21)		pD	21.36
					Pseudo R-Squared	0.50

For birds, fragmentation of suitable climate (contagion) and natal dispersal distance had a significant positive effect on range filling globally (Table 3.2, Fig. 3.3). The number of years since introduction also had a positive effect in the Nearctic (Table 3.2, Fig. 3.3). For mammals, fragmentation of suitable climate (contagion) had a significant positive effect on range filling globally. Natal dispersal distance was also retained in the final model though it did not have a consistent effect globally or in any particular region (Table 3.2, Fig. 3.2). Removing the parameter reduced overall model fit. Note that as contagion increases the landscape becomes less fragmented, so birds and mammals spread more successfully through less fragmented landscapes.

3.4 Discussion

The world is in no way saturated with naturalised species, even if no further naturalisations occur. Range filling was consistently low (Table 3.1). The results suggest two partially contrasting conclusions regarding species range filling. One, that introduced species will continue to spread and many areas of the world are at risk from colonisation by a large number of introduced species. Two, that many introduced species are being blocked from colonising climatically suitable areas. The results regarding introduction history and species' traits shed light on which conclusion is most likely.

The main factors that influenced plant range filling success were time since introduction, realm (Australia has higher range filling than any other realm), reproductive speed and local sampling effort, though the latter two were only significant in some regions (Fig. 3.1). Of the three taxonomic groups, time seemed to most strongly limit plants. I suggest this is because plants generally have low dispersal characterised by infrequent long distance dispersal events (Tamme et al., 2014), and are therefore most prone to time lags. Even species with a high maximum dispersal distance are apparently no better at filling their range than species with weak dispersal abilities, potentially due to the rarity of such long-distance events. Plants are also more strongly dependent on human assisted dispersal to colonise new areas (Pyšek et al., 2011; Wichmann et al., 2009). However, I tested whether species associated with horticulture have higher range filling on average than non-horticultural species, and did not find any significant effect. This may suggest that species are initially introduced through horticulture, horticulture may not contribute subsequent spread and other methods of human-assisted spread are more important. Naturalised species in Europe often spread very successfully because of accidental movement on clothes, livestock, or vehicles (Pyšek et al., 2009).

Once in a new area a quick reproductive cycle assists rapid range spread, which may explain why younger flowering increased range filling. Since dispersal ability was not significant in plants, but time since introduction was, I suggest that increasing time allows more time for human transportation rather than natural dispersal. This may also explain why time had a particularly strong effect in Australia. Since most recorded introduced species in Australia are found in coastal areas near major cities, these species would be more likely to have a higher frequency of human transportation (Banks, Paini, Bayliss, & Hodda, 2015). Increased sampling effort decreased range filling overall (Fig. 3.1). Many species are introduced near cities and other trade centres (Seebens et al., 2017), and species near their site of establishment have yet to spread, and therefore have smaller ranges. As such, many species near human populations may be expected to have small ranges, and therefore have lower range filling.

Time since introduction, dispersal ability and range fragmentation limit bird range filling (Fig. 3.3). Of the three taxonomic groups studied, birds had by far the highest dispersal ability, and while human transport of bird species is common, the fact birds can disperse long distances naturally may supersede the need for human assisted dispersal. Inclusion of fragmentation in the final model supports this conclusion, as fragmentation of suitable areas is more likely to be important when colonisation is primarily driven by natural dispersal. In contrast to the other two taxonomic groups studied here, birds did not show any variation in range filling between realms (Table 3.1), and in general displayed low range filling. Bird species were found to have large native niche that cover a wide range of climates, and therefore have very large areas of potential range (Table 3.1), which may explain the overall low level of range filling. The lack of variation in range filling between realms may be because birds are generally recorded better than any other taxa (Mair & Ruete, 2016), and their naturalisations are well documented (Dyer et al., 2017), despite regional variation in study effort.

While time since introduction did limit mammal range filling slightly when analysed alone, it was not retained in the final model. Fragmentation of climatically suitable areas predicts mammal range filling more strongly, and mammal species appear to be more successful at filling their potential range when it is continuous and unfragmented. This is against expectations for introduced species as fragmented, heterogenous landscapes are associated with increased disturbance, which has been suggested to increase vulnerability to invasion (Davis, Grime, & Thompson, 2000). In this case, it seems large areas of continuous suitable climate are needed to mammals to spread successfully. This may suggest that introduced mammals require a connected landscape to allow populations to spread, and over a certain level of fragmentation species movement can be restricted (Crooks, Burdett, Theobald, Rondinini, & Boitani, 2011). Strong mammalian dispersers appear to fill less of their potential naturalised ranges than weak dispersers. Mammal dispersal ability is highly correlated to body size (Whitmee & Orme, 2013), and I suggest that it is a larger body size that is limiting mammal naturalised ranges, rather than dispersal ability itself. A large body size typically correlates with a need for larger amounts of unfragmented habitat to incorporate a large home range size (Jones et al., 2009), which limits the available area to colonise, hindering the spread of a species overall. Spread of naturalised mammals thus appears more linked to interactions between mammal traits and human management decisions than to time, natural dispersal or human-assisted dispersal.

Both mammals and plants had strong differences in range filling between realms, with the highest level of range filling in Australia for both taxonomic groups. Low biotic resistance has been suggested in Australia (Harvey et al., 2012), due to the dissimilar ecological assemblage between Australia and most other realms in the world. A lack of ecologically similar species may reduce competition and predation, and promote population growth and spread in the introduced species (Jeschke et al., 2012). Another possibility are the strong human influences on naturalised species ranges in Australia (Mack & Lonsdale, 2001); most species are introduced at or near coastal cities, which are also centres of trade. This could help species spread with human assisted dispersal, particularly in plants, from several population centres, increasing the chance of high range filling (Wilson et al., 2009). Horticultural status was found to not affect range filling in plants, but species are frequently spread accidentally as seeds on clothing or vehicles (Pyšek et al., 2009).

There remains a lot of variation in range filling, that is not explained by the factors analysed here. Some were not included because of strong covariation with other predictive variables (such as body mass), or because of a lack of data. Propagule pressure in particular, which includes the number of individuals introduced and the number of introduced populations, has been noted to have an important role in spread following establishment (Blackburn et al., 2009; Vall-llosera & Sol, 2009). It is possible that where species are likely to be repeatedly introduced to the same realm (Pyšek et al., 2015), differences in range filling between realms could be due to propagule pressure.

In realms where there is a strong link between time since introduction and range filling, already-naturalised species are likely to continue to spread: birds in Australia and the Nearctic, and plants globally. These areas may be particularly prone to range expansions by introduced species in the near future. For example *Hedera helix* is a noted invasive weed in Australia, and can have severe impacts on native vegetation and biodiversity (GISIN, 2015). The first known record in Australia was in 1930, probably introduced and dispersed by humans, and it is now common across large areas of Victoria, New South Wales and South Australia. However, this represents only a proportion of the climatically suitable area available in Australia. I estimate that in ten years, *H. helix* will expand its range by approximately 190,000 km^2, or an area a little smaller than the state of Victoria.

It seems likely that multiple aspects of the introduced realm and the introduced species could affect species success, including the ease of dispersal either naturally or through human assistance (Hulme, 2009), local ecological processes (Alexander & Edwards, 2010), and the fragmentation of climatically suitable areas. Given that range filling was significantly higher in some regions than others in plants and mammals, and fragmentation was significant in mammals and birds, there is evidence that some regions are likely more resistant to invasions than others. Biotic resistance has been suggested to be lower in areas when introduced species are phylogenetically dissimilar to species, as there are more likely to be vacant niches, though the reverse has also been suggested as similar species are more likely to be preadapted (reviewed in Thuiller et al., 2010). Australia is known to be phylogenetically distinct so, if the success of plant and mammal species is due to low biotic resistance, I would suggest the former explanation as more likely. Therefore, species that are introduced to regions that have large, continuous climatically suitable areas and phylogenetically dissimilar native species are more likely to be successful as the regions involved are less resistant to invasion.

Chapter 4: Plants can naturalise in novel precipitation but not temperature regimes

Abstract

Recent research has highlighted multiple examples of climate niche expansion in non-native species, in which species have colonised types of climate with which they have not been previously associated. This may suggest that many species do not colonise climatically suitable areas in their native range, potentially due to non-climatic range limitations. Niche expansion creates challenges for predictions of invasion, as many predictive models assume that a species climatic preference will remain the same in its native and naturalised range. There is therefore a need to understand how common niche expansions are, and what processes drive niche expansions. I compare native and naturalised climatic niches in over 600 terrestrial plants, and find evidence of niche expansion in 45% of introductions. I further find that species predominantly expand into wetter climate than their native niche, and species that expand in this direction also expand further from their native niche. Species also expand into drier climate, but less frequently. Species only rarely show niche expansions towards hotter and colder climate. I also find that species are more successfully able to colonise the wettest and driest portions of their climatic niche. These results suggest that species do not occupy all climatically suitable areas in their native area. This could be because of biotic interactions at wet, productive range edges, which leads to enemy release in the non-native range, or the role of specific precipitation factors at species range edges.

4.1 Introduction

The rise in human-mediated movement of plant species in recent history has resulted in a huge number of plant species introductions (Dawson et al., 2017), many of which have impacted native ecosystems, agriculture and human infrastructure (Simberloff et al., 2013). There is a need to predict the future ranges of introduced species, and until recently it has been assumed that the climatic niche of a species in its native range could serve as a predictor of its potential and realised niche in the naturalised range. Recent work has challenged the assumption that climate in species' current, native ranges accurately represents their climatic tolerances (Bradley et al., 2015; Hill et al., 2017; Li et al., 2014). We must therefore understand if native species' ranges do represent their climatic tolerance, or if native niches are in some way constrained from colonising all climatically suitable areas. Factors that can limit species distributions, such as resource availability, habitat availability, barriers to dispersal and biotic interactions, can vary between species' native and naturalised ranges. Realised ranges might be constrained by geographical boundaries such as coastlines or mountain ranges: these features might exist in the native range but not in the naturalised range. Native ranges may also be constrained by biotic interactions, which are not present in the naturalised range. For example, release from competition or natural enemies in the naturalised range might reveal broader climatic niches than the native range would indicate (Gallien et al., 2012). As a result, a species' realised niche may vary between two ranges, and the realised naturalised niche of any species can expand, as compared to the realised niche in the native range. How frequently niche expansions occur globally, and what mechanisms drive niche expansion remains unknown.

It can be extremely challenging to gather enough evidence on a multi-taxonomic, global scale to draw general conclusions about what best defines species range edges, and how closely species realised niches represent their fundamental niches. Previous empirical work has used transplant experiments (Hargreaves et al., 2014), physiological experiments (Bozinovic, Calosi, & Spicer, 2011; Kearney & Porter, 2009) and common garden experiments (Afkhami et al., 2014; Vergeer & Kunin, 2013) to investigate if species ranges match their physiological tolerances. Other studies have used data on species' native ranges to determine if species fully occupy their climate niche (Araújo & Pearson, 2005; Bocsi et al., 2016; Bradley et al., 2015; Svenning & Skov, 2004), or if climatic niches have changed through time (Tingley et al., 2009; Veloz et al., 2012). While in some cases a species range edge will coincide with its climatic niche edge, this is not universal and the extent to which climate can define a range edge remains unclear. Transplant and physiological studies are an excellent way to test this, but can only be done for a few species, and native range data do not provide independent tests of range limits. Therefore, in this study I use naturalised species ranges as an independent method to test how strongly climate determines species' ranges. If climate is the dominant factor that structures range edges, then the climatic niche should be consistent between the native and naturalised range. Several studies demonstrate that species' naturalised ranges can encompass different climates to those occupied in the native range (i.e. undergo niche 'expansion') (e.g. Early & Sax, 2014; Gallagher, Beaumont, Hughes, & Leishman, 2010; Parravicini, Azzurro, Kulbicki, & Belmaker, 2015). However, there has been little examination of whether species' climatic niches are equally likely to expand in any climatic direction, or if some directions of expansion are more likely than others.

Some climate conditions may impose conserved, impermeable limits on species ranges, while other climatic niche edges may be more permeable. There are few studies that directly test multiple species range edges, but there is some evidence that, within a single species, range edges can be controlled by climatic factors at one edge and biotic factors at another (Vergeer & Kunin, 2013). For example species' cold niche limits are strongly conserved between different parts of species' range (Alexander, van Kleunen, Ghezzi, & Edwards, 2012; Broennimann et al., 2012; Pellissier et al., 2013), suggesting that cold climate can form an impermeable limit to species ranges. Similarly, many species are very sensitive to decreasing precipitation (McCain & Colwell, 2011), again indicating that low precipitation can set the edge of a species range very effectively. It has long been suggested that the physiologically stressful range edge is set by climate, whereas the less stressful range edge (typically the warmer and wetter range edge) is set by factors such as biotic interactions (Darwin, 1859; Louthan et al., 2015). If this is the case, then I would expect naturalised species to undergo niche expansion in the direction where climate plays a weak role in range limitation more frequently than in other directions. Following prevailing theory, I hypothesise that species colonise warmer and wetter conditions than occupied in the native range but not colder and drier conditions. I investigate firstly how common niche expansions are by comparing native and naturalised climatic niches in over six hundred terrestrial plant species across every continent except Antarctica. I then ask whether niche expansion occurs on some climatic axes more commonly than others, by comparing the direction of niche expansion in each species and testing for a directional tendency. Finally, I ask whether species are more successful colonising the hottest, coldest, wettest or driest portions of their potential niche, by comparing niche filling on several climatic axes.

4.2 Methods

4.2.1 Collating non-native species data and distribution

I identified terrestrial plant species that have established on a mainland landmass outside their native continent following introduction by people. I filtered out species that were introduced pre-Columbus, and species that are not confirmed to reproduce in their naturalised range. Species identities were primarily drawn from Randall (2017). All species that were listed as permanently established non-native species were used, i.e. all species that were not listed as 'Casual Alien', 'Unconfirmed naturalisation', 'Contaminant' or 'Native Weed'. Species listed in the Global Invasive Species Information Network (GISIN, 2015) were also added. For a full species list, see the Supplementary Material (Table S1).

For all species I obtained occurrence data from GBIF (downloaded 31st August 2017) using R’s dismo package (Hijmans et al., 2015). Locations of occurrence were classified as either “native” or “naturalised” using regional or national checklists (Supp. Material Table S4). Any occurrences that were not on land were removed, and species that occupied fewer than five 10 arc-minute grid-cells in either their native or naturalised range were discarded as data deficient. In total the completed database contained range information on 606 plant species.

I restricted predictions of species’ potential naturalised ranges to the biogeographic realm into which species were introduced. I used biogeographic realms as defined in Holt et al. (2013), with an additional distinction between western and eastern Palearctic along an approximate line of the Ural mountains (Supp. Material Fig. S1). This was done because species that inhabit both Western Europe and eastern Asia are almost always native to one and naturalised in the other. Species that were found to be native and naturalised in the same biogeographic realm were removed from analysis, due to the difficulty in exactly defining the native and naturalised ranges.

If a species was naturalised in more than one biogeographical realm, each was counted as a separate “naturalisation event” (1852 in total). To produce summary maps of species ranges, I used level 4 geographic administrative units from Brummitt (2001). Administrative units are usually countries, but large countries such as the U.S or China are split into states or provinces. Within each administrative unit I mapped how many native and naturalised species occurred there, and how many species underwent niche expansion.

4.2.2 Modelling species’ climatic niches

I modelled species’ climatic niche using the most universal parsimonious variables that influence species ranges (Early & Sax, 2014): mean temperature of coldest month, mean temperature of warmest month and total annual precipitation. Including a larger number of variables results in forecasts of smaller potential ranges, and less transferability between species than the parsimonious set of variables (Early & Sax, 2014). Gridded climate data were downloaded from WorldClim at 10 arc-minute resolution and provided average climatic variables from 1970-2000 (Fick & Hijmans, 2017). Modelling species’ climatic niches occurred in two stages. Firstly, to find climate that was shared between the native and naturalised realms, and secondly to model niche expansion.

4.2.3 Accounting for analogue climate

I identified climate that was present in both the native and naturalised realms (i.e. analogue climates), and removed any species occurrences in non-analogue climate. Without this correction, species expansions may simply reflect limited climate in the native range and not a true expansion of the realised climatic niche in the naturalised range.

I defined native available climate as any climate present within the native realm, and naturalised available climate as any climate present within the naturalised realm. I used principal components analysis (PCA) to produce a gridded climate space of 100x100 cells on two axes (Broennimann et al., 2012). Species occurrence density in each PCA grid-cell was estimated using a kernel smoothed density function. The native occupied niche was defined as an envelope around the occupied native density, and the naturalised likewise around the occupied naturalised density. Analogue climate was defined as any climate that was present in both the native and naturalised realms, and any occurrences in non-analogue climate were removed from further analysis.

4.2.4 Modelling niche expansion

The disadvantage to restricting available climate to just the native and naturalised realms is that species' niches and directions of niche expansion are not easily comparable, since PCA climate spaces have different orientations. Therefore, the second stage of analysis measured niche expansion using a global climate space. I compared native and naturalised niches, and measured in what direction niche expansion occurred, if it did occur.

All global climate was used to produce a gridded 100x100 cell PCA climate space on two axes, and species' native and naturalised occurrence density were calculated within this global climate space using a kernel smoothed density function. Naturalised species' occurrence density was then corrected by the availability of climate in the naturalised realm and rescaled between 0 and 1 to make it comparable across species. A species' native niche was defined by an envelope around the native occurrences, and the naturalised by an envelope around the naturalised occurrences. Any area of the naturalised niche that occurred outside of the native was defined as expansion, and the occurrence density within this as expansion density. I measured proportion of expansion as the proportion of expansion density over the total summed naturalised occurrence density. Species that had an expansion density of over 10% were deemed to show significant expansion (Petitpierre et al., 2012) and several features of expansion were measured.

If one particular climate is much more common than others, this may introduce bias into models of niche expansion. For example, if a species expands into hotter and colder climate equally well but hotter climate is much more common, an analysis of mean direction would favour expansion towards hot climate. To compensate for this occurrence density in the naturalised niche was corrected for climate availability.

This was done by dividing species occurrence density by climate density in each grid-cell. Corrected occurrence density in a PCA grid-cell therefore represented proportion of occurrence in a particular climate. All analyses were carried out using corrected and uncorrected occurrence densities, however all results presented here use corrected occurrence density.

In order for a species to be included, it needed a minimum of 5 native and naturalised grid-cells. This is a relatively low threshold and patterns of niche expansion could potentially be biased by species with low numbers of records, as such species may have poorly characterised niches. As a form of sensitivity analysis, I carried out a beta regression to test for a correlation between the number of grid-cells and proportion of niche expansion. The number of grid-cells with naturalised occurrences was logged for normality and scaled to a mean of 0 and a standard deviation of 2. Models were run using a Markov chain Monte Carlo (MCMC) method in JAGS through the R package “R2jags” with a burn-in of 10000 samples and checked for convergence after a further 20000 samples, which was extended if estimates did not converge. For a full model specification see Chapter 3.2.6 and Supp. Material Table S8.

4.2.5 Measuring direction and distance of niche expansion

For each species that displayed niche expansion, I wished to measure the direction of niche expansion and how far from the native niche expansions extended.

In order to measure the direction niche expansion, a central point is needed for comparison to describe direction (see Fig. 1). For this I used the centre of a species’ potential naturalised niche, which was defined as the centre of climate density in the naturalised realm that lay within the outline of the native niche. I used this instead of the centre of the native niche as the highest density of occurrence in the native range can vary by climate availability and by recording effort over the native range. I then measured the distance (on PCA axes) from PCA grid-cells in which a species underwent expansion to the centre of the potential naturalised niche, weighted by the naturalised occurrence density in each expansion cell.

I wished to create an overall summary of niche expansion for each species, including overall mean direction, or directions, and variance of expansion. Alternatively, if there is no directional tendency, I wished to include a null model which could describe this. I compared multiple models of circular orientation for each species (Fitak & Johnsen, 2017; Schnute & Groot, 1992), and selected the best model through maximum likelihood. I compared a null uniform model (i.e. expansion is equal in all directions) to several alternative parametric models. Alternative models could be unimodal (expansion occurs in one direction), axial bimodal (expansion occurs in opposite directions), and bimodal (expansion occurs in two directions). Alternative models included information on the circular mean, which describes the direction of expansion (parameter q1 and q2) and the circular variance, or how tightly focussed the direction of expansion was (parameters k1 and k2). Unimodal models can be classified as “modified” if a second random effect component is added to the standard unimodal modal. Bimodal and axial models can be further classified as “homogenous”, where variance is uniform across multiple directions, or “symmetric”, where directional distributions are equal across multiple directions. The best fitting model subset were defined as those with the lowest AIC and ΔAIC<7, as recommended in Fitak & Johnsen (2017). ΔAIC<2 was also considered as a threshold for selecting best fitting models, but it has been noted that while models with ΔAIC>9 have little support, models with models with ΔAIC between 2 and 7 should rarely be dismissed (Burnham & Anderson, 2004; Burnham, Anderson, & Huyvaert, 2011). Therefore, to avoid discarding viable alternative models I used the more inclusive ΔAIC<7.

In cases where the null model was rejected in the previous step, I was interested in how far species expanded in the mean direction of expansion. To summarise niche expansion distance for each species, I used the median distance of each occupied expansion grid-cell from the potential naturalised niche centre. The larger the distance the more dissimilar the occupied expanded niche is from the native niche. Any cells that were more than 45° away from the mean direction of expansion were discounted when calculating niche expansion distance.

4.2.6 Cross-species trends in direction and distance of niche expansion

I also wished to ask if there were trends in expansion across all species. In particular, were species more likely to expand in some climatic directions than others, and if they did expand did some species expand further in some climatic directions? I therefore compiled all species expansions and looked for trends in direction and distance of expansion across all species.

To test if expansion occurred more frequently in some climatic directions than others, I took the overall direction of expansion for each expanding species and used a maximum likelihood approach using parametric models of circular orientation to test for overall tendencies in the direction of expansion. The null model was that expansion is equally likely in any direction in PCA space, and alternative models were the same as listed in section 4.2.5, and the best fitting model subset was again defined as those with the lowest AIC and ΔAIC<7.

I tested whether species, once they expanded, expanded further from the native niche in any particular direction. For this I used a non-parametric circular regression model, which uses a Nadaraya-Watson estimator and the Local-Linear estimator for circular-linear data, taking the von Mises distribution as its kernel (Oliveira et al., 2014). The model does not assume a known parametric distribution, but instead creates a non-parametric smoothed conditional mean response, for which the key parameter is the smoothing parameter. The smoothing parameter was chosen using a least squares cross-validation approach (Di Marzio, Panzera, & Taylor, 2013; Oliveira et al., 2014). A pseudo-R^2 was calculated as the proportional reduction in sum of squared residuals between a null model and the final fitted model.

As a final step, I reperformed both analyses on a regional, rather than global level. Information on naturalised species is not distributed evenly, globally, and I have more information on naturalisation events on some continents than others. I wished to detect if global patterns of niche expansion are truly global or driven by the effect of one or a few realms. To avoid this potential bias, I ran the parametric and non-parametric analyses of niche expansion first globally, and then by naturalisation events in each realm.

4.2.7 Interpreting niche expansion

I wished to test what climatic conditions expansions correspond to, so needed to interpret PCA space in terms of real climatic conditions. I also wanted to test if there was any bias for niche expansion in different types of climate (e.g. species from cold climates are more likely to expand).

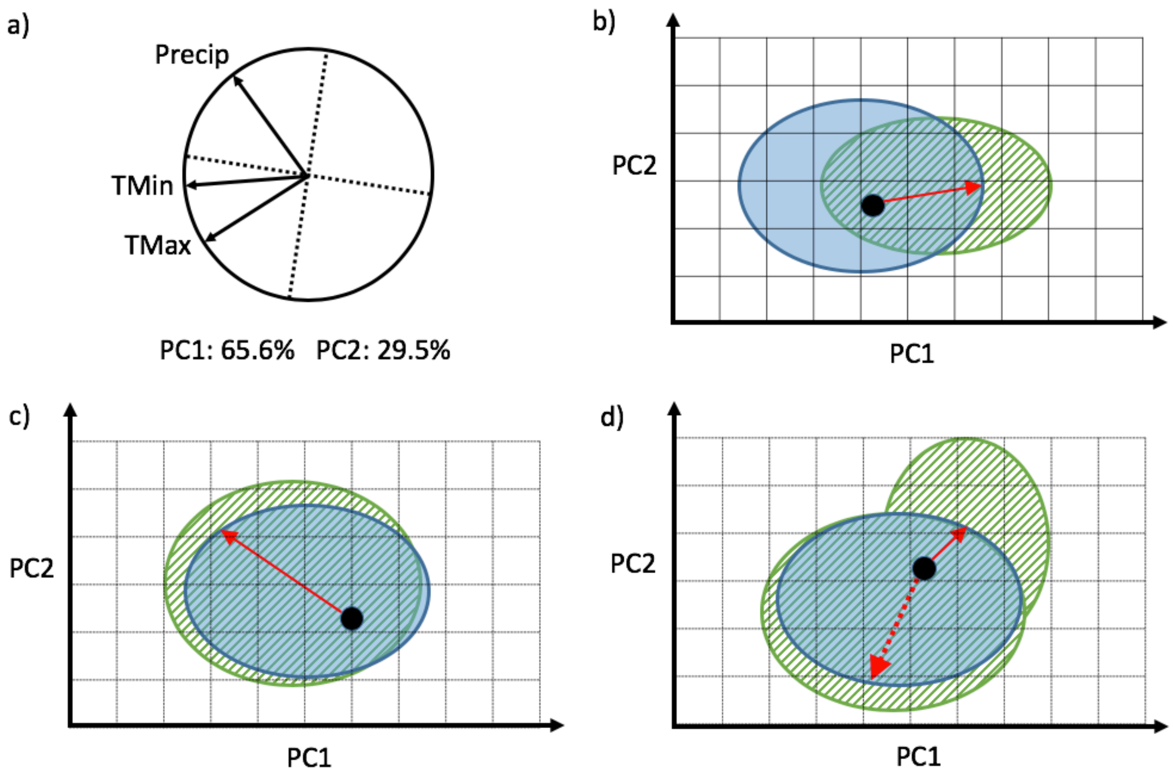


Figure 4.1: a) Global climate PCA correlation circle. Solid arrows are directions in PCA space of increasing precipitation (Precip), maximum temperature (TMax) and minimum temperature (TMin). Dotted lines are quadrants around climate vectors, used in this analysis when considering hottest, wettest, coldest, and driest quadrants. PC (principal component) values are variance explained on each of the two PCA axes. b-d): Types of niche expansion. Green is the occupied native niche, blue is the occupied naturalised niche. Any blue areas that do not overlap with green are areas of niche expansion. Black points are the centre of the potential naturalised niche and red arrows are the measured direction of niche expansion. b) the species has expanded in one specific direction in PCA space. This demonstrates high median distance of expansion, and low variance. c) the species has expanded in one direction but very variably. This demonstrates high distance and a high variance. d) the species has expanded in multiple directions by a large amount. This demonstrates a high distance in both directions, with high variance in one direction (dotted arrow) and low variance in the second direction (solid arrow).

I split the PCA space into four quadrants, based around the directions of increasing temperature and precipitation (Fig. 4.1a). These four quadrants represent the hottest, coldest and wettest quarters of the potential naturalised niche. I measured which quadrant each niche expansion took place in, and the difference between vector of increasing precipitation (∆Precip), increasing temperature (∆Temp), and the direction of niche expansion.

To test whether expansion was more likely to occur under certain climatic conditions, I correlated the position of the native niche to direction of expansion. I carried out a non-parametric circular regression using the Nadaraya-Watson estimator and the

Local-Linear estimator for linear-circular data and tested for a correlation between each of the three climate variables and the direction of expansion. The smoothing parameter was chosen by a least-squares cross-validation approach.

4.2.8 Measuring niche filling

In addition to niche expansion, I wished to investigate if species were able to fill their niche more successfully in some climatic directions than others. I did this by measuring how much of each quadrant of the potential naturalised niche was occupied as a proportion. Within each PCA quadrant (hot, wet, cold, dry) I identified all naturalised occurrence density that occurred within that quadrant. This summed density from each quadrant was then divided by the total naturalised occurrence density. 0 indicates that no naturalised density occurred in that quadrant and 1 that all naturalised density occurred in that quadrant.

4.3 Results

852 naturalisation events showed a niche expansion (45%). Some species were introduced to more than one realm and showed expansion in several realms. In total 404 species showed expansion in at least one of their naturalised realms. Expansions occurred in every continent studied, not including Antarctica (Fig 4.1c). The number of grid-cells with naturalised occurrences did not correlate with the proportion of expansion (Fig. S7), and did not influence how a species niche expanded. 59% of expansions occurred in one direction from the native niche (506 out of 852 expansions), and 41% expanded in multiple directions (346/852). In many cases this involved an overwhelming expansion in one direction, and a minor expansion in a secondary direction. Information on both directions was used for analysis. No species expanded uniformly in every direction.

The type of native climate did not predict the likelihood of niche expansion. Species from cold, dry, hot or wet environments were equally likely to display niche expansion in their naturalised populations. Across all species, species expansion was not equally likely in all directions. Niche expansion was least common towards colder climate and towards hotter climate (as compared to the centre of the potential niche). Niche expansions were most common towards wetter climate, followed by expansion towards drier climate (though less frequently). The highest supported

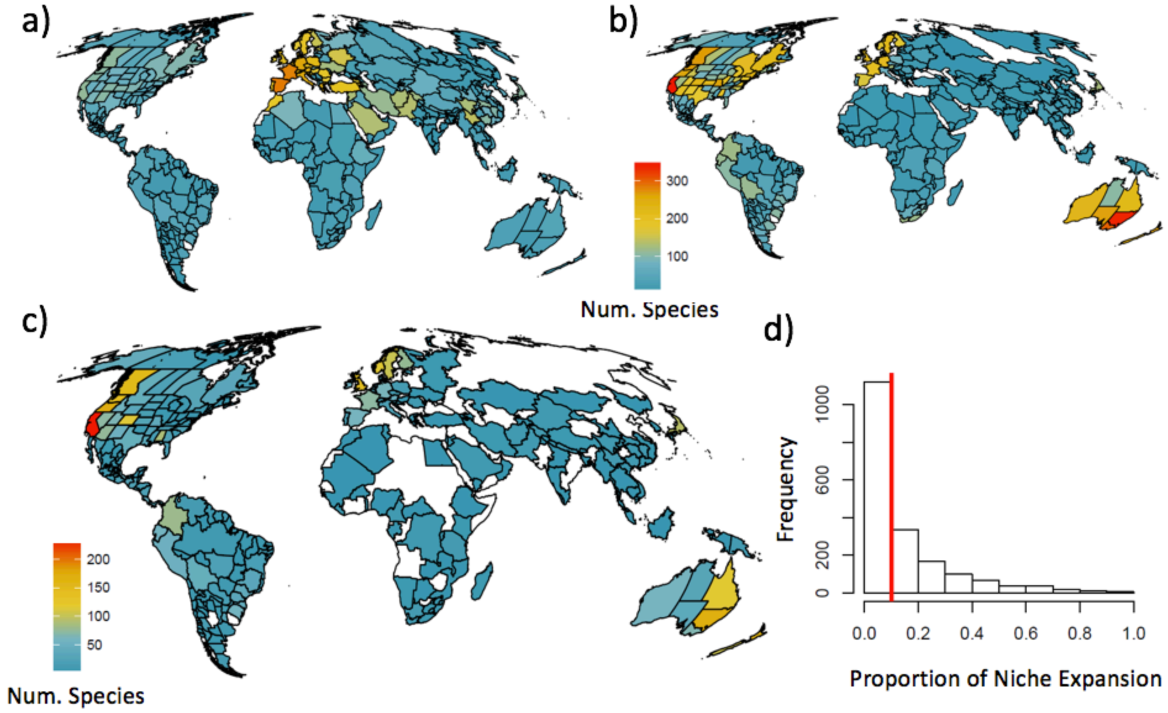


Figure 4.2: a) Number of native species that occur in each administrative area. b) Number of naturalised species that occur each administrative area. c) Number of species that undergo climatic niche expansion in each administrative area. d) The proportion of niche expansion in each naturalised species, measured as the proportion of naturalised occurrence density that occurred outside of the native niche. Any species that underwent more than 10% expansion (red line in figure) was classified as expanding.

parametric model was a symmetrical bimodal model (Model 3B; Fig. 4.3a, Table 4.1). Other models in the best model subset (Table 4.1) were also bidirectional.

Species that expanded towards wetter climate also expanded further than average in that direction (Fig. 4.3b). In all other directions the direction and magnitude of expansion did not correlate with each other and resembled the null model. Species were more successful at filling the wettest parts of their niche, regardless of whether they displayed niche expansion or not (Fig. 4.4). Median niche filling across all species, after correcting for climate availability, was 0.42 in the wettest quadrant of the niche, 0.04 in the hottest, 0.02 in the driest and 0.16 in the coldest.

Table 4.1: Summary of global and regional cross-species trends in direction of niche expansion. Parametric results describe the best fitting circular models of global or regional niche expansion. Model names are as described in Schnute & Groot (1992), and indicate if expansion was primarily in one direction (unimodal), opposite directions (axial bimodal) or two separate directions (bimodal). ∆Precip, ∆TMin and ∆TMax is the difference between the mean direction of expansion and the vector of increasing precipitation, minimum temperature and maximum temperature in PCA space respectively. The best fitting modal for global results (model M3B) is presented in Figure 4.3a. Non-parametric results describe the correlation between direction and distance of expansion in PCA space. Smooth is the smoothing parameter used in the non-parametric regression as optimised with a least-squares cross validation approach. Pseudo R^2 is the proportional reduction in sum squared residuals between the best fit non-parametric model and the null model. Results for the global non-parametric model are illustrated in Figure 4.3b.

		Parametric											**Non-Parametric**	
Region	**n**	**Model Name**	**Model Type**	**Parameters**	**q1**	**k1**	**q2**	**k2**	**∆Precip**	**∆TMax**	**∆TMin**	**AIC Weight**	**Smooth**	**Pseudo-R^2**
Global	**852**	**M3B**	**Symm. Bimodal**	**3**	**1.95**	**7.46**	**5.09**	**0.46**	**0.27**	**1.40**	**1.25**	**0.47**	**47.55**	**0.28**
		M4B	Axial Bimodal	4	5.09	0.37	8.23	8.14	0.27	1.40	1.25	0.30		
		M5B	Bimodal	5	4.90	0.39	1.95	8.16	0.27	1.21	1.25	0.23		
Afro	17	M3A	Homo. Symm. Bimodal	3	1.77	15.37	NA	NA	0.44	1.91	1.42	0.3	49.99	0.82
Aus	123	M2B	Symm. Unimodal	2	1.8	51.75	NA	NA	0.42	1.89	1.4	0.49	50	0.61
Mad	3	M2B	Symm. Unimodal	2	2.05	227	NA	NA	0.17	1.64	1.15	0.6	49.99	0.88
Nea	201	M5B	Bimodal	5	4.39	1.16	2.14	17.83	0.08	0.71	1.06	1	47.39	0.32

Neo	135	M5B	Bimodal	5	5.56	0.98	2.02	6.15	0.2	1.67	1.18	0.53	12.9	0.33
Oce	14	M2A	Unimodal	2	0.52	0.77	NA	NA	1.7	3.17	2.68	0.29	19	0.87
Ori	49	M2B	Symm. Unimodal	2	1.65	33.38	NA	NA	0.56	2.04	1.54	1	15.79	0.47
PalE	12	M2C	Modified Unimodal	2	2.72	87.65	NA	NA	0.5	0.97	0.48	0.24	49.99	0.94
PalW	116	M5B	Bimodal	5	6.28	0.47	1.56	11.98	0.66	2.13	1.64	0.86	49.99	0.53
Pan	66	M5B	Bimodal	5	1.85	15.94	3.52	0.96	0.37	0.17	0.32	0.99	6.15	0.36
Sah	21	M2C	Modified Unimodal	3	0.45	45.19	NA	NA	1.77	3.24	2.75	0.45	31.82	0.72
Sin	95	M2B	Symm. Unimodal	2	2.25	22.36	NA	NA	0.03	1.44	0.95	0.99	12.94	0.11

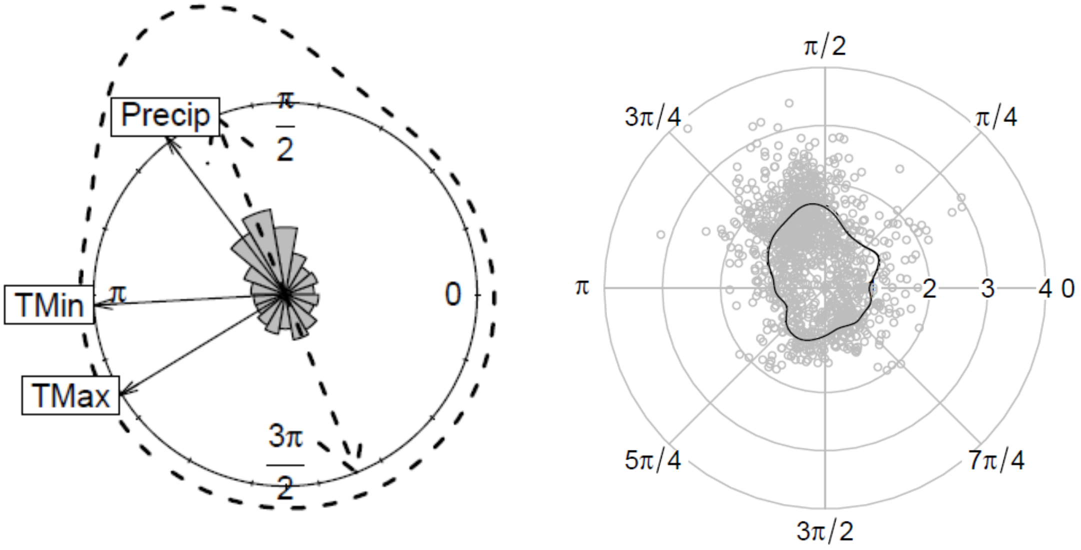


Figure 4.3: a) Circular histogram of the direction of all niche expansions, overlaid with the best fitting parametric circular model (Table 4.1). Fitted model is a symmetrical bimodal model, dotted arrows are the cross-species mean direction of expansion and dotted outline describes the circular variance around the two mean directions. Solid arrows represent directions in PCA space of increasing minimum temperature (Tmin), increasing maximum temperature (TMax) and increasing Precipitation (Precip). b) Circular scatterplot of direction of expansion versus the median distance of niche expansion (distance from the centre). Climatic axes are the same as in Fig. 3a. Outline is the result of the non-parametric regression model, and describes the smoothed circular regression estimate between direction and distance of expansion (Oliveira et al., 2014).

4.4 Discussion

Niche expansions occur in 45% of naturalisation events, can occur in any climatic direction outside the native niche, and naturalised expansions can extend far outside the boundaries of the native niche. However, niche expansions were most frequent towards wetter climates, and secondarily towards drier climates, than towards hotter, or colder climates. Naturalised plants expanded further in the direction of wetter climate than in any other direction (i.e. naturalised climates that were wetter, relative to species’ native ranges, than they were drier, hotter, or colder). Niche expansions occur globally (Fig. 4.1c), and trends in niche expansion do not appear to be driven by data from one particular continent. Niche expansions observed in individual realms follow the same general pattern as niche expansions at a global scale (Table 4.1), excepting realms with a very small sample size. Niche expansions are common globally, and show a clear directional tendency. Species are also more successful at colonising the wettest portions of their potential niche than any other axis. There are several possible mechanisms that describe this pattern of expansion, including dispersal limitations in the native realm, availability of climate, species-specific precipitation factors, evolutionary processes, and the release of non-climatic limitations in the naturalised realm. I discuss the likelihood of each below.

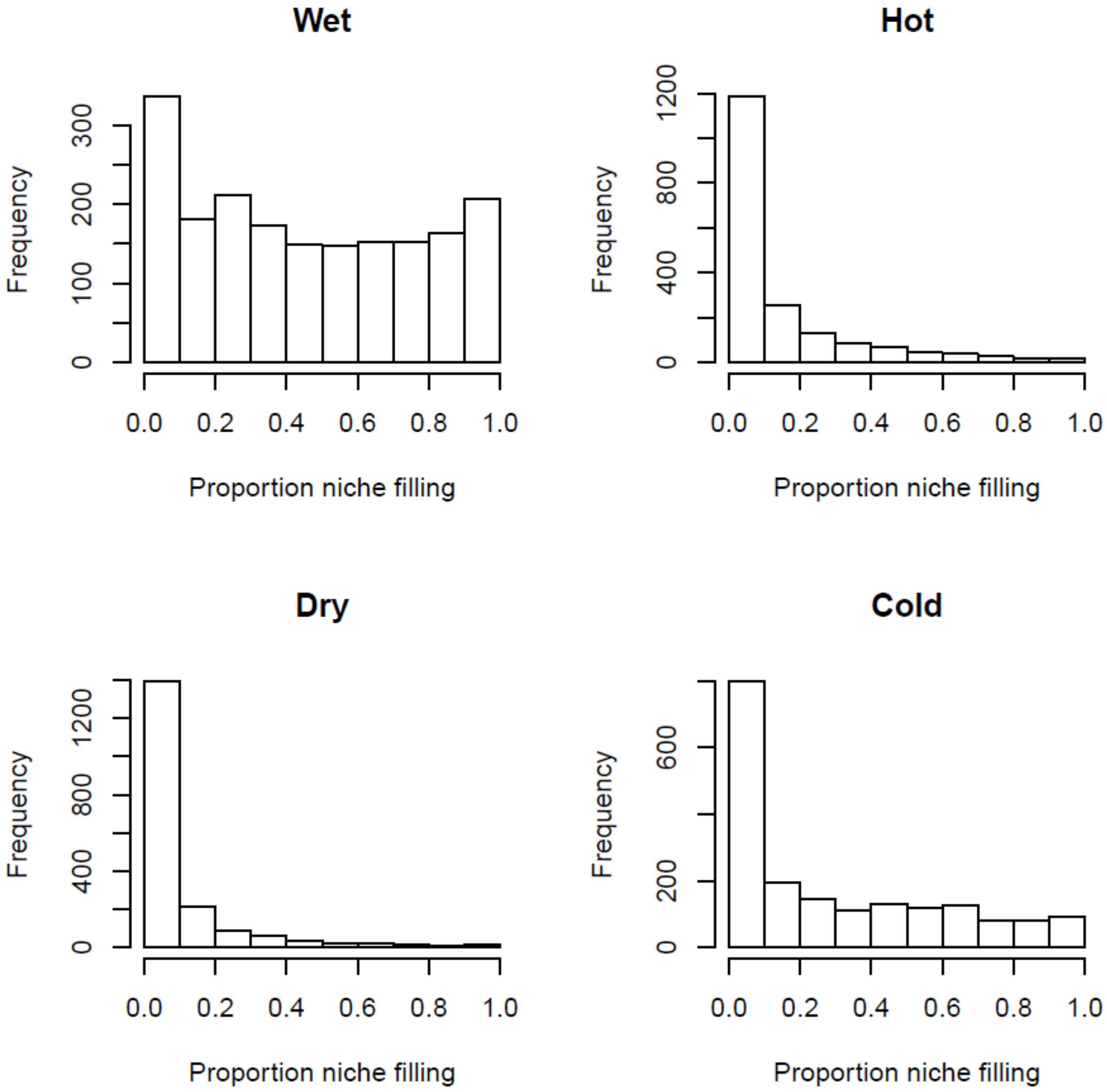


Figure 4.4. Species niche filling in the wettest, hottest, driest and coldest quadrants of species' potential naturalised niche. Proportion of niche filling is the proportion of naturalised occurrence density that occurs in that quadrant as a proportion of total naturalised occurrence density. A proportion of 0 means a species did not occupy any climate the named quadrant. A proportion of 1 means all naturalised occurrences are in the named quadrant.

Many species undergo niche expansion in a new area. One explanation for this expansion is that they have not colonised all suitable climate in their native region (native niche unfilling). I consider only analogue climate in this study, so niche expansion takes place in climate that is available somewhere in the native region, but has not been colonised. Niche unfilling may occur because species cannot reach suitable climate due to physical barriers (Holt et al., 2013), or dispersal limitations (Munguía, Townsend Peterson, & Sánchez-Cordero, 2008; Svenning et al., 2008). However it seems unlikely that physical barriers are present for all species in this study, and equally unlikely that barriers would stop species colonising wetter climates on all continents. Similarly niche unfilling due to dispersal limitation in the native range seems unlikely to be an explanation for all species, since there is no obvious reason why a species would be unable to disperse to locations with the hottest and coldest conditions they can tolerate but not the wettest or driest locations.

It is possible that species expansions are opportunistic, and that observed expansions only occur because climatic conditions in the naturalised realm are predominantly wetter than the native environment. I corrected for this possible bias in several ways. First, I only considered species occurrences in analogue climate space, i.e. in climate that was available in both native and naturalised regions. Second, occurrence densities were corrected for the prevalence of climate conditions in the native and naturalised regions, hence I accounted for any differences in precipitation regimes between native and naturalised ranges. Indeed, without this correction for climate availability, I found species' expansions into drier climate to be much more prevalent. Third, this analysis is global, and I have introductions from every continent and to every continent except Antarctica. Analysis of individual regions and reciprocal analysis shows that species expand towards wetter climates regardless of where they are from, or where they are introduced (Table 4.1), with the exception of realms with very little data on introduced species.

Many species have been shown to be sensitive to much more specific climate factors than those I used. For example, seasonality of rainfall is extremely important for some species (Baltzer & Davies, 2012; Condit, Engelbrecht, Pino, Perez, & Turner, 2013; Reside, Vanderwal, Kutt, & Perkins, 2010), while for others the exact timing of rainfall in species' lifecycles can strongly affect growth

(Franks, Sim, & Weis, 2007; Miranda, Armas, Padilla, & Pugnaire, 2011). It is possible that niche expansions observed here are not a true shift in species' precipitation niche, but simply that total annual precipitation is not an important range limit for these species. If I included a more species-specific precipitation metric, such as rainfall during the flowering period, we may find that although species have shifted to areas with different levels of total annual precipitation, species ranges are limited by specific precipitation factors. Discerning which precipitation factors are important to species range limits is difficult without species-specific information on physiology and ecology.

Temperature and precipitation can occur in specific combinations in a species' native range, and correlate in a different manner than on another continent where species may naturalise. This can mean that species' native niche limits are not formed by precipitation per se, but are formed because those precipitation conditions always co-occur with the thermal limit of their niche. In this case precipitation is not the cause of a species range limit, but a correlate. When the interaction between temperature and precipitation is decoupled in the naturalised range, and species encounter novel combinations of temperature and precipitation, they can display niche expansion. Although this explanation cannot be ruled out, it does not seem likely that this is what drives the global patterns of niche expansion observed here. Since I only considered climate that was analogous to native and naturalised realms, species must have similar combinations of hotter and wetter climate available to them, but are unable to colonise them in the native realm. Additionally, temperature and precipitation tend to be similarly coupled globally, or can couple in one of only a few ways. Temperature and precipitation are not completely independent, and it seems extremely unlikely that all expansions are due to temperature and precipitation coupling in a completely different manner in the naturalised realm as compared to the native realm.

Range expansion may also occur if species develop new adaptive traits. Several empirical examples exist of species showing evolution in their naturalised range, which can occur through a variety of processes (Clements & Ditommaso, 2011; Urban, Phillips, Skelly, & Shine, 2007; Whitney & Gabler, 2008). Adaptations can change a species' fundamental niche and therefore result in niche expansion. If evolutionary processes are the primary drivers behind niche expansions, it appears that adaptations to different precipitation regimes are much more common than those that expand thermal tolerances. There is some evidence that species' physiological thermal tolerances are relatively static over time (Broennimann, Mráz, Petitpierre, Guisan, & Müller-Schärer, 2014; Pellissier et al., 2013; Sunday et al., 2012), and it has been suggested that adaptations that extend the cold niche limit are rare due to the complex genetic and physiological changes involved (Broennimann et al., 2014; Survila, Heino, & Palva, 2009). However, several examples exist of plants extending their range northward into colder latitudes by changes in phenology or life-cycle, either through adaptive or plastic responses (Clements & Ditommaso, 2011). Examples of adaptations to new precipitation regimes also exist (Leger & Rice, 2007; Molina-Montenegro, Quiroz, Torres-Díaz, & Atala, 2011), but there is no wide-spread evidence that adaptations to new precipitation regimes occur more frequently in nature than those related to temperature. Additionally, many species studied here do not only expand into adjacent climate, but expand into climate a large distance from their native niche (Fig. 4.3). This suggests, if adaptation were taking place, species are adapting to drastically different precipitation levels, and in many cases quite rapidly following naturalisation.

It is also possible that species display niche expansion when released from non-climatic range limitations, such as species interactions. If non-climatic factors most strongly constrain species ranges in the wettest parts of their range, and these constraining factors are removed in the naturalised range, it could explain the pattern of niche expansion towards wetter areas. Primary productivity and precipitation correlate strongly globally (Pearson's correlation between global logged precipitation and logged net primary productivity was 0.72), so niche expansion into wetter areas are typically also into more productive areas. Increasing precipitation (and therefore productivity) can correlate with increasing frequency or intensity of a number of different species interactions, all of which can constrain species from the wettest portions of their niche.

Increasing productivity can correlate with increasing competitive pressure (Louthan et al., 2015), and many species are prevented from colonising warmer and wetter conditions at more equatorward latitudes or lower elevations by competitive exclusion (Hargreaves et al., 2014; Roux, Virtanen, Heikkinen, & Luoto, 2012). Increased precipitation and productivity can also correlate with higher disease pathogen load (Hersh, Vilgalys, & Clark, 2012; Pariaud et al., 2009), which can effectively limit a species range (Wisz et al., 2013). There are also several examples that demonstrate that predation incidence increases on species' hot and wet range edges (Pennings et al., 2009; Salazar & Marquis, 2012).

Exclusion experiments on several species, predominantly on warm, productive range edges, have shown that species can spread into climatically new areas if competitors (Price & Kirkpatrick, 2009) or predators (Holt & Barfield, 2009) are excluded. Such observations have led to the general hypothesis that species ranges are constrained by primarily climatic factors at their physiologically stressful limit, and primarily by biotic interactions at less stressful, more productive, range edges (for review see Louthan et al., 2015). Niche limits that appear to be set by precipitation, may therefore coincide with species interactions that actually structure species ranges.

In a naturalised region, species may or may not have similar competitors, predators and diseases as compared to in their native range. Enemy release, in particular, is common during naturalisations (Heger & Jeschke, 2014; Liu & Stiling, 2006) and has been noted to contribute to species success. There is also some, though more limited evidence, for competitive release in some naturalised species (Alexander & Edwards, 2010; Bolnick et al., 2010). Species that are prevented from occupying wet, productive conditions in the native region by biotic factors may therefore display a niche expansion into wetter areas when these limiting factors are removed in their naturalised range.

The secondary peak in niche expansions towards drier climate is not predicted by such a non-climatic range limit hypothesis, and provides possible evidence against the argument presented above that changes in biotic interactions are behind niche expansions. Dry climate is typically more stressful to plants, and standard theory would suggest that the dry edge of a species niche is set by abiotic factors, and therefore that niche expansions due to enemy release or lack of competition should be uncommon in relatively dry climate. Despite this apparent contradiction, I would argue it does not rule out the role of biotic interactions on the driest edge of species range. Biotic interactions can form interactive effects with abiotic stress (Silliman & He, 2018), and drought stress has been shown to increase vulnerability to predators (Silliman, Van Koppel, Bertness, Stanton, & Mendelssohn, 2005), or disease (Carnicer et al., 2011). Therefore, a lack of biotic interactors in the naturalised range may still contribute to niche expansions. If this is the case it suggests biotic and climatic factors can interact on wet and dry niche edges, but this occurs less frequently on hot and cold niche edges.

Species were also more successful at filling their naturalised niches in wetter quarters of their climatic niche, as opposed to the hottest, coldest or driest quarters (Fig. 4.4). If precipitation does not form a strong impediment to growth or spread, species may be highly successful at colonising climate with any level of precipitation as long as it coincides with their thermal optimum and precipitation is above a certain threshold to prevent desiccation. There is some evidence that species can tolerate drought or flooding as long as it coincides with the species' preferred growing temperature (McDowell et al., 2008). Colonising outside of the thermal optimum may be possible, but significantly more difficult, therefore slowing the rate of niche filling on the temperature axis. If this is true, it adds support to conclusions regarding niche expansion that precipitation does not act strongly on structuring species ranges, and species are much less constrained by precipitation than they are by temperature. Interestingly, range filling in the driest quadrant of climate space is low, despite the fact that niche expansions occur more frequently in this direction than in either towards hotter or colder climate (Fig. 4.3a). This could occur when the driest part of a species niche is still above a critical threshold of desiccation, and species are able to colonise the driest available areas and even expand into new climate in the absence of other non-climatic factors that may restrict their range.

In conclusion, plant species more frequently naturalise into wetter and drier climates than they occupy in their native ranges, but much less so into hotter or colder climates. The very large geographic and taxonomic scope of this analyses show this is a global phenomenon in plants. It is not possible to ascertain for certain which explanation is the most likely. However, there are two explanations that are particularly well supported. First, that the widely used metric of annual precipitation cannot capture species' climatic tolerances.

Second, that in their native ranges species are constrained by non-climatic factors, most likely biotic interactions, which are released in the naturalised realm. This does not mean that precipitation cannot form a range limit in plants, but that it does so less frequently than temperature. Species tend to have more conserved thermal limits and rarely expand their niche into hotter and colder climates.

As niche limits defined by temperature are more conserved, it provides evidence temperature is a major constraining factor on species' ranges. This has several consequences for future work in the fields of climate change and invasion ecology. In the case of climate change, shifts in total annual precipitation may not correlate with species range shifts. Instead, species may shift their range in correlation to underlying shifts in more specific precipitation factors, or in correlation to biotic interactors that define species range limits.

Chapter 5: Local population phenotypes of *Iberis amara* (L.) at north and south range margins suggest temperature influences range limits.

Abstract

Although it is frequently assumed that species range margins are set by climatic factors, there is increasing evidence that species range margins do not coincide with the limits of species climatic tolerances. I investigate several range margin populations of *I. amara*, including one that comes from an area of range expansion from its historic native range. I carry out common garden experiments to test for phenotypic differences in response to temperature conditions that correspond to the species' warm and cold range edges in Europe. I look for evidence that species range edges are set by climate, and that the recent range expansion was facilitated by adaptation. I find that germination rate, germination proportion, and plant height vary between populations under different temperature regimes. I also find that a number of other traits, including growth rate, biomass, and root:shoot ratio, do not vary between populations, but do vary between temperature conditions. These variations in response to climate suggest effects of climate on local phenotype, especially on the coldest range edge of *I. amara.* However, there appears to be little evidence that the recent range expansion was facilitated by adaptation to local temperature conditions.

5.1 Introduction

Up until recently there has been a general consensus that climate sets species range edges at a broad spatial scale (Araújo & Guisan, 2006; Pearson & Dawson, 2003). Models that wish to characterise a species range will commonly correlate species' current distribution to environmental factors to estimate a species' climatic tolerances, known as its climatic niche (Guisan & Thuiller, 2005). Climatic niche models are widely used, notably to predict climate change induced range shifts (Araújo et al., 2011; Pecl et al., 2017) and the spread of invasive species (Guisan, Petitpierre, Broennimann, Daehler, & Kueffer, 2014; Jiménez-Valverde et al., 2011).

Models that wish to predict species ranges based on their current climatic niche rely on two main assumptions, 1) that species current distributions represent the full climatic tolerance of a species, 2) that species' climatic niches are stable. Recent work has challenged these assumptions. Species ranges can be set by non-climatic factors (Sexton et al., 2009) and thus species are prevented from colonising all climatically suitable areas (Bradley et al., 2015). In addition, there is evidence species' climatic niches are not stable across their range. Species frequently display local phenotypic differences in response to climate across different populations (Kawecki & Ebert, 2004; Leimu & Fischer, 2008), and have different climatic tolerances across their range (Gallien et al., 2012).

There is therefore a need to assess the assumptions of climatic niche models. For climatic niche models to be accurate, species distributions should be primarily set by climate on all range edges, and climatic tolerances need to be stable across populations. However, there are still relatively few studies that compare the role of climate (or lack of it) and climatic tolerances at multiple range edges. Common garden studies that investigate population phenotypes at species range edges can address this deficiency and can assess the two main assumptions of climatic niche models.

There are compelling reasons to believe that climate can set species range edges. Many species range edges coincide with their physiological limit, as confirmed by transplant and physiological experiments (for examples see Angert & Schemske, 2005; Grace, Berninger, & Nagy, 2002; Hargreaves, Samis, & Eckert, 2014; Sexton, McIntyre, Angert, & Rice, 2009; Van Der Veken, Rogister, Verheyen, Hermy, & Nathan, 2007). Species distributions also frequently correlate with a consistent set of climatic conditions across time and different parts of a species range (Petitpierre et al., 2012; Thomas, 2010; Tingley et al., 2009). Temperature in particular is conserved in many species across range edges and across time (Sunday et al., 2012; Tingley et al., 2009).

Species typically have lower fitness at the edge of their range (Kawecki, 2008), and this has been linked in many species to physiological stress caused by climate conditions (Alexander & Edwards, 2010; Sexton et al., 2009). As such, if climate is lowering fitness at a species' range edge, local populations are under selection pressure to adapt to local climatic conditions. A standing question in biogeography is when and where can species locally adapt to mitigate physiological stress. Multiple factors can promote local adaptation, such as low to medium gene flow (correlated with low dispersal and/or strong habitat fidelity), strong selection, little temporal variation in selection pressure, low plasticity and sufficient standing genetic variation (Bridle & Vines, 2007; Kawecki & Ebert, 2004).

Local adaptation is common in terrestrial plants (Blanquart, Kaltz, Nuismer, & Gandon, 2013), particularly under strong selection pressure. Populations of plants frequently show differences in a variety of traits that increase fitness to local climatic conditions (Leimu & Fischer, 2008), such as survival rate, growth rate, reproductive rate, or phenology. Evidence of local adaptation to climate in range margin populations does not prove that species ranges are set by climate alone, but it does show species are under selection pressure to adapt to climatic conditions. If there is selection pressure then climate is lowering fitness in range margin populations, and hence the species range margin is, at least partially, set by climate.

Increasingly, the role of non-climatic factors has been emphasised on setting species range limits. Species ranges can be set by non-climatic factors, such as dispersal (Bradley et al., 2015; Svenning et al., 2008), biotic interactions (R. Early & Keith, 2019; Wisz et al., 2013) and gene flow (Alexander & Edwards, 2010; Gaston, 2003). In such cases we would expect selection pressure to promote adaptation to these non-climatic factors, rather than climate. Species have shown local adaptation to herbivory (Garrido, Andraca-Gómez, & Fornoni, 2012; Vergeer & Kunin, 2013), to soil factors (Pregitzer, Bailey, Hart, &

Schweitzer, 2010; Smith et al., 2012; Turner, Bourne, Von Wettberg, Hu, & Nuzhdin, 2010), and to parasites (Brown & Tellier, 2011; Kawecki & Ebert, 2004). In some cases species may be adapted to local climate conditions and to non-climatic factors, suggesting that more than one factors can set a range edge (Vergeer & Kunin, 2013).

Species’ response to climate can vary between populations through processes unrelated to climatic factors. Differences between populations can also arise from maternal effects, plasticity or genetic drift (Kawecki & Ebert, 2004). Maternal effects and plastisicity can be adaptive (Donohue, 2009; Nicotra et al., 2010), but are typically reversible, and can be ruled out with multi-generational experiments (Kawecki & Ebert, 2004). However, non-adaptive differences in response to climate that arise from genetic drift represent permanent changes in a population genetic variation. Differences between populations that arise from genetic draft can result in a change in species’ climatic niche, particularly in fragmented small populations (Hereford, 2009; Kunin et al., 2009). While these changes in a species’ climatic niche are not adaptive, they still violate one of the main assumptions of climatic niche modelling. Predictions of a species’ future range based on a species’ current climatic niche are unreliable if a species’ climatic niche is liable to change.

If local adaptation occurs, then fitness should be higher in local conditions than at other range margins. Fitness, however, can be measured in several different ways. Fitness is often equated to survival rate and number of offspring when carrying out local adaptation experiments (Leimu & Fischer, 2008; Sexton et al., 2009). However, species can increase their fitness through a large variety of adaptations. Plants have shown local adaptation in biomass and flower morphology (Olsson & Ågren, 2002), plant size (such as biomass, leaf size, or plant height) (Leimu & Fischer, 2008), biomass allocation (Olsson & Ågren, 2002), germination rate (Bischoff, Vonlanthen, Steinger, & Müller-Schärer, 2006) and phenology (Chuine, 2010). Species may also display trade-offs between different traits to maximise fitness over the short and long term (Leimu & Fischer, 2008). Therefore, to get a full understanding of differences in fitness between populations, many potential candidate traits should be measured to observe differences between populations, and in particular possible differences in adaptive fitness.

In this study I consider three major populations of *Iberis amara* (L.) from three of its range edges in Europe. *I. amara* faces different selection pressures on different range edges, but it is not known if it is climatically limited on any of its range edges. *I. amara* is also classified as a non-native species in Sweden (DAISIE, 2018), though the mode of first introduction is not known. This recent range expansion of *I. amara* is likely due to one of two reasons. One, the species has been previously able to colonise all climatically suitable areas due to a non-climatic range limit, such as low dispersal ability. Two, adaptive traits have recently developed that have allowed the species to expand its climatic tolerance and it has subsequently spread to new areas.

I therefore asked: does *I. amara* have different phenotypic responses to climate across range margin populations, and are these trait differences adaptive? I conducted a common garden experiment was, growing seeds taken from populations at north and south range edges. I compared germination and growth traits in two different temperature treatments, one which represented conditions from the coldest range edge of *I. amara,* and one from the warmest range edge of *I. amara*. Local adaptation to climate can be expressed through a number of traits (Leimu & Fischer, 2008), so I therefore measured multiple life-history traits to ask what traits, if any, of *I. amara* vary between populations, and consider how this may benefit overall fitness.

This experiment provides information on two basic assumption of climatic niche modelling. Firstly, do species range edges coincide with their climatic niche limit. If local adaptation is detected to temperature and populations in Sweden perform better to local thermal conditions, then this provides evidence that climate applies at least some selection pressure at range edge and adaptation may have contributed to range expansion. Secondly, are species' climatic niche consistent across their range, and can changes in the climatic niche contribute to species range expansion. If responses to climate vary between populations, whether these differences are adaptive or not, it suggests that species' climatic niches can vary even over short geographical distances and relatively short periods of time.

5.2 Methods

5.2.1 Study system

Iberis amara (L.) is an annual, herbaceous member of the Brassica family, growing approximately 15-30cm tall. It is occasionally grown horticulturally but occurs naturally in Europe from southern Sweden to northern Spain (Fig. 5.1). *I. amara* is also classified as a introduced species in Sweden (DAISIE, 2018), though the mode of first introduction is not known. The earliest confirmed herbarium record is from 1881 in Gotland, where it was found by the side of a road (SVH, 2019). *I. amara* also occurs as a naturalised species in eastern Europe, North America and China (POWO, 2019). It occurs specifically on chalk grassland or other alkali substrate rich in calcium, it prefers patches of bare ground and rarely grows on any other substrate. Local populations were identified using recent records of *I. amara* from several European sources (Anthos, 2016; Artportalen, 2016; Font et al., 2010; Stroh & Pearman, 2016).

Between the summer of 2016 and the summer of 2018, a number of seed samples were collected from populations in the Chilterns, Gotland and the Valencia region (Fig. 5.1). Only a single seed head was taken from each plant and only a few plants from each local population. Where possible several small populations were sampled to include as much of the meta-population as possible. The exception was in Gotland, as the only population found comprised of several thousand individuals spread over approximately half a kilometre of shore-side rubble, and this was the only population sampled. All seeds were desiccated and stored at 4°C until the beginning of the experiment. *I. amara’*s germination potential is not significantly affected by cold storage, and does not drop by more than a few percentage points even after years of cold storage (Royal Botanic Gardens Kew, 2019).

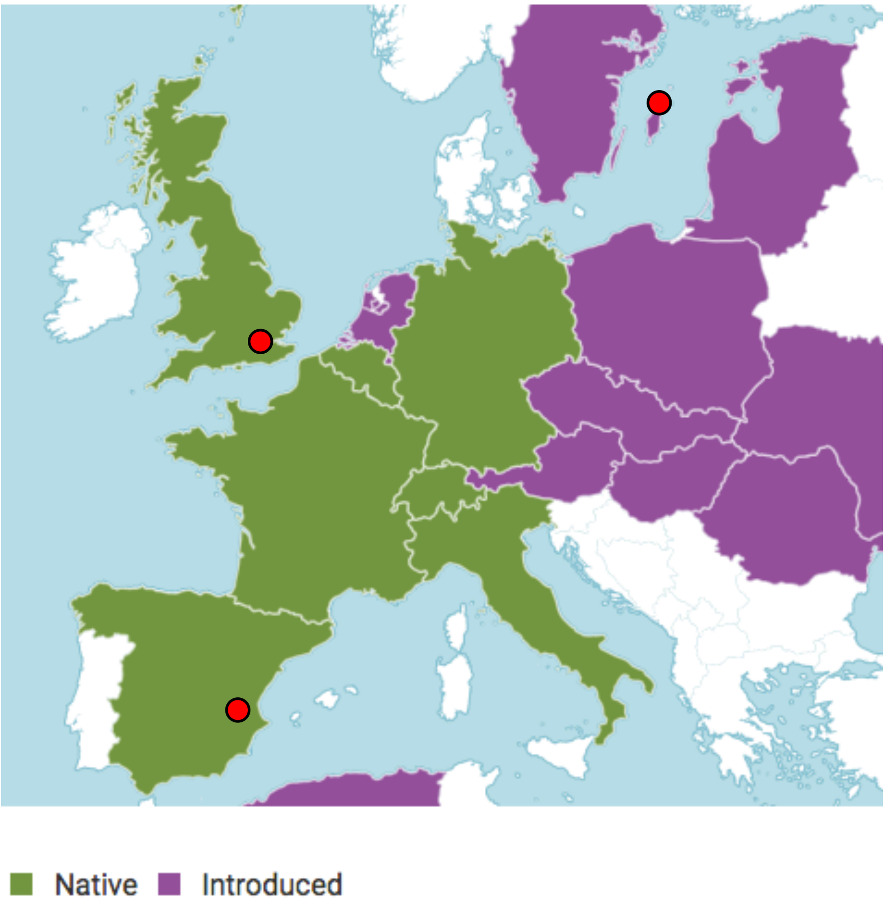


Figure 5.1: Range map of *I. amara* in Europe (POWO, 2019), red points are sources of seeds used in the experiment

5.2.2 Incubation protocol

I wished to simulate the temperature conditions at each range edge of *I. amara* within Europe. To do this, I estimated germination and flowering conditions from the warmest area of its range (Spain) and the coldest (Sweden). The germination months were defined as February, March and April; the flowering months were defined as May, June and July. Gridded climate data were taken from the CRU TS v.3.23 dataset (Harris, Jones, Osborn, & Lister, 2014) at 0.5 degree resolution and I used monthly data from 2011-2014 for the whole of Europe.

I compared germination and growth traits in temperature treatments that represented the cold and warm range edges of *I. amara*. The cold treatment cycled from a night temperature of 3°C to a day temperature 12°C, the warm at 6 to 17°C. Light was cycled 12/12h in both cases. Six weeks after germination of the first seeds the cold incubator was increased to 8 to 18°C, and the warm to 15 to 25°C.

I calculated the incubation temperatures as the 10th and 90th percentile of the monthly minimum, maximum and mean temperatures (Tmin, Tmax and Tmp respectively) during germination and flowering months. These temperatures therefore represent the upper and lower extremes of the temperature conditions *I. amara* faces in Europe. These temperatures also approximately match monthly temperatures from northern Spain and southern Sweden during germination and flowering months.

Fifty seeds were sterilised from each population in a minor disinfectant and placed on agar jelly in petri dishes and placed in their respective incubators. The plates were checked every other day for germination, defined as extension of the emerging radicle longer than one millimetre. The germinating seed was then placed on water-saturated builder's sand and fed with excess Hoagland's solution three times a week (Hendry & Grime, 1993)

5.2.3 Plant Measurements

I measured germination rate, growth rate, plant height, total biomass and root/shoot ratio across all populations.

Date of germination was recorded at the point the radicle extended from the seed by at least one millimetre. At periods 7 and 21 days after germination I recorded the height and the number of leaves in situ. At 7 and 21 days, one in every three plants from each population was also destructively sampled for ex situ measurements. I recorded the size of the largest leaf, the fresh weight of root and shoot sections. Following this I desiccated plants for 48 hours at 80°C in an oven and then took dry weight measurements of root and shoot sections. I intended to measure flowering attributes, but no individual flowered during the course of the experiment. At 100 days all remaining plants were removed for fresh and dry weight measurements.

Using biomass measurements from 7, 21 and 100 days I calculated growth rate as the natural log of mass gained per day since germination (ln(g) per day).

5.2.4 Statistical Analysis

For all analyses I used R 3.3.1 (R Team Core, 2016)

Growth rate was compared across populations and temperature treatments using a Kruskall-Wallis test, followed by a post-hoc Dunn test with Bonferroni correction for pair-wise comparisons.

To analyse plant height between populations and treatments I performed a linear mixed effects analysis using lme4 (Bates, Maechler, Bolker, & Walker, 2014). Plant height was squared for normality. I included source population, time since germination, and temperature treatment as fixed effects. I also included plant ID as a random effect, as most individuals were measured at multiple time points. Model selection was carried out by dropping each interaction or parameter in turn and using a likelihood ratio test to eliminate parameters that did not contribute to the model power. Visual inspection of residual plots from the final model did not reveal any obvious deviations from homoscedasticity or normality. p-values were obtained by likelihood ratio tests of the full model containing the effect in question against the model with that effect removed.

To analyse root:shoot ratio and dry mass I used linear models, where root:shoot ratio was logged for normality. I included temperature treatment as a categorical effect, and days since germination as both a linear and a quadratic fixed effect. Model selection was carried out by dropping each interaction or parameter in turn and using a likelihood ratio test to eliminate parameters that significantly alter the model if removed. Visual inspection of residual plots from the final model did not reveal any obvious deviations from homoscedasticity or normality.

5.3 Results

5.3.1 Germination rate

In total 60 seeds germinated in the cold treatment, and 63 seeds germinated in the warm treatment.

Seeds from Sweden had the highest germination proportion in both the warm and cold conditions out of any of the three populations, and germinated earliest of all populations in the warm treatment. Seeds from the UK had a higher germination proportion in the warm conditions than under cold conditions, but did not germinate any earlier in the warm treatment. Spanish seeds germinated later and had the lowest germination proportion of any population in both treatments. No Spanish seeds germinated in the cold treatment (Fig. 5.2)

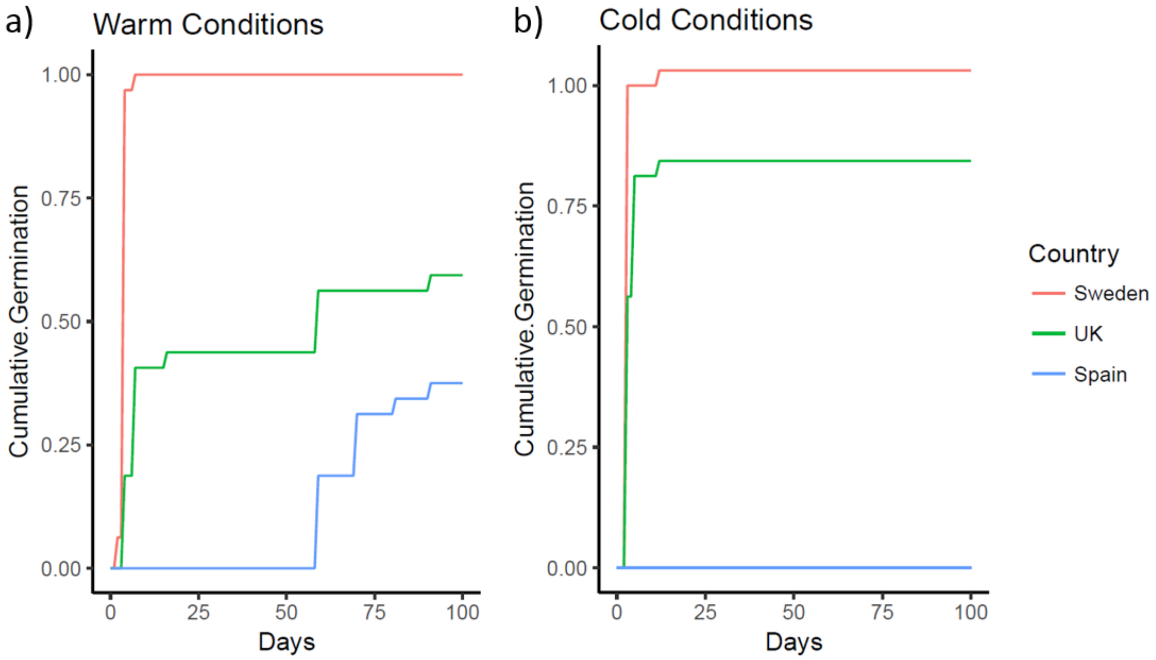


Figure 5.2: Cumulative germination success of all three populations in a) warm and b) cold conditions

5.3.2 Growth rate and biomass

In total 78 plants were measured during the course of the experiment (41 in the warm treatment, 37 in the cold).

Growth rate of all populations was significantly lower in cold conditions, with no significant variation between populations (Fig. 5.3: Kruskall-Wallis test, χ^2 =61.16, df=4, p<0.001, pairwise comparisons carried out using Dunn test with Bonferroni correction).

Total biomass was significantly lower in all populations in the cold treatment and did not vary between populations, once time since germination was taken into account (Table 5.1a).

5.3.3 Plant height

Plant height was significantly different across populations. Plants from Spain were always taller per gram of mass, and height was not significantly different between temperature conditions. (Table 5.1b; Fig. 5). However, plant height did not differ under different temperature regimes and temperature was not retained in the final model.

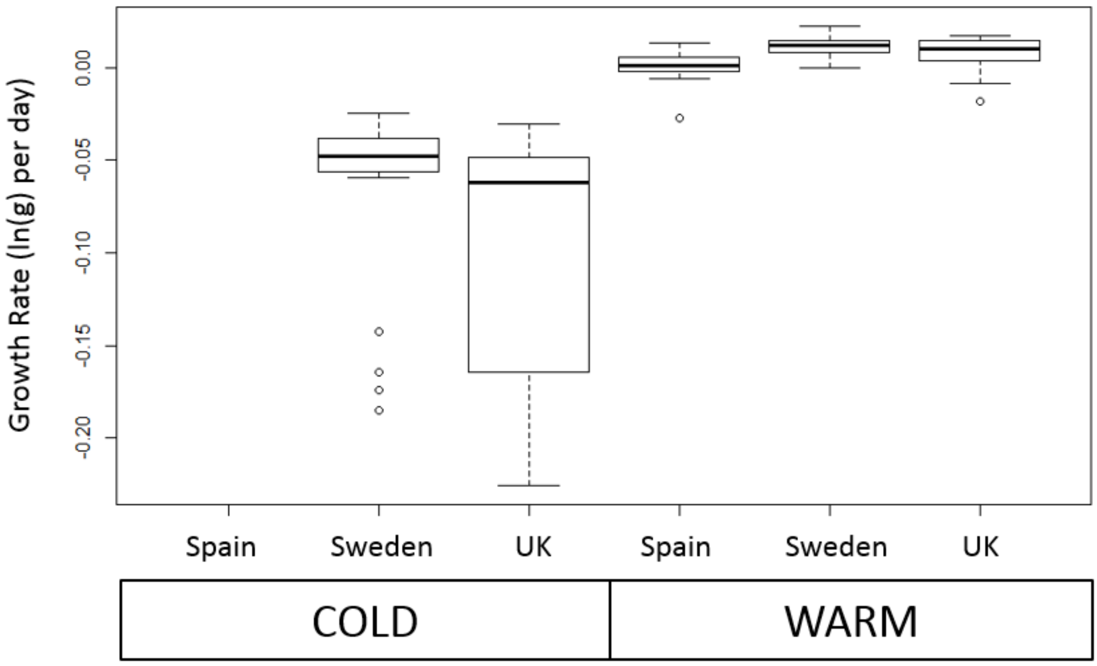


Figure 5.3: Growth rate (ln(g) per day) of all three populations in warm and cold conditions

5.3.4 Root/Shoot ratio

Root/shoot ratio did not vary across populations but was significantly higher in the warm treatment (more shoot proportional to root mass Table 1c, Fig 4).

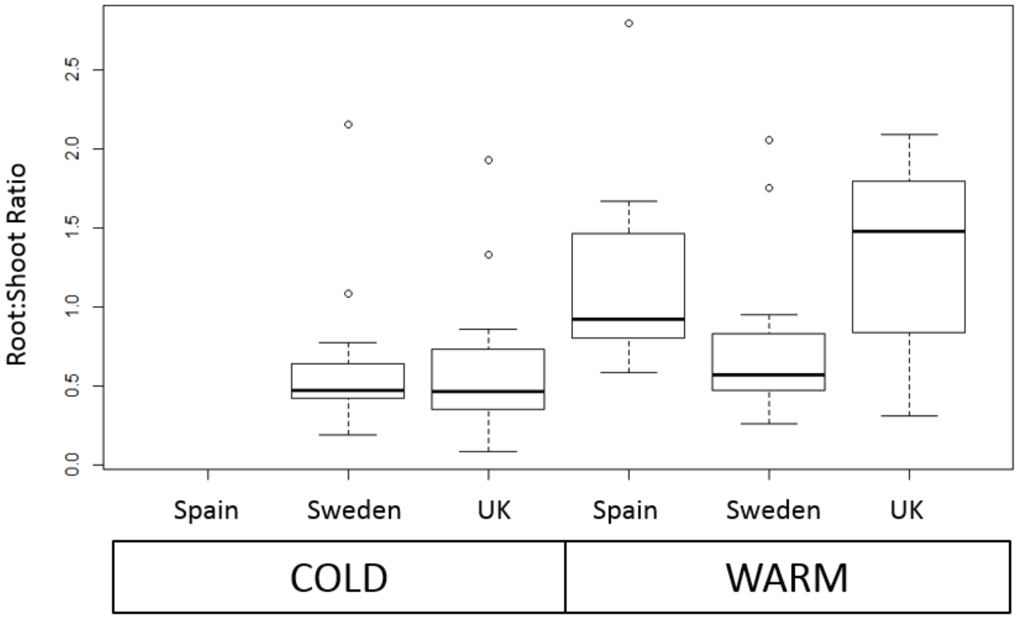


Figure 5.4: Root:shoot ratio of all three populations in warm and cold conditions

5.4 Discussion

Climatic niche models assume that species' climatic niches are stable, and that a species range margin approximately corresponds to the edge of its climatic tolerance. In this experiment, I wished to test if species' responses to temperature were consistent between several different range margin populations of *I. amara,* and whether there is evidence of temperature acting as a range limitation. I found that species' responses to climate were not consistent, and found evidence of differences between populations in several different traits. Out of all the traits tested, germination rate and plant height varied between populations. Growth rate, total biomass and root:shoot ratio did not vary between populations, but did vary between the two temperature conditions. No plants flowered during the experiment, which unfortunately meant reproductive traits could not be measured.

If it can be established that the observed differences are due to local adaptation, then it would provide evidence that climate is acting as a range limit on multiple species ranges. In order to distinguish whether inter-population variation in traits is due to genetic drift, maternal effects or local adaptation, the key is to establish whether the observed differences in traits that are adaptive.

Before considering if the observed differences in traits are adaptive, it is worth also considering whether populations of *I. amara* are able to locally adapt. Local adaptation occurs when there is strong selection pressure, but this is not the only factor that affects the development of local adaptation. A number of different conditions can either help or hinder the development of local adaptations. Spatially varying selection can lead to local adaptation and eventually to genetic differentiation (Leimu & Fischer, 2008). Temporally varying selection can hinder local adaptation, as can a high rate of extinction and recolonisation of local populations. A medium rate of gene flow, habitat specificity, and sufficient standing genetic variation can promote local adaptation (Kawecki & Ebert, 2004; Savolainen et al., 2013). If populations of *I. amara* do not meet at least some of these characteristics, then it suggests that the observed phenotypic differences are not due to local adaptation as it is unlikely populations can adapt at all.

Table 5.1: Results of linear models with explanatory factors retained in final models. “Temp” represents temperature treatment as a categorical effect, “time” is time since germination in days, “CI” represents 2.5% and 97.5% estimates of parameter. a) biomass (natural logged) as predicted by temperature, time and time squared. Positive estimates indicate increasing biomass. b) plant height (square rooted) as predicted by population, time since germination and the random effect of plant ID. Positive estimates indicate increasing plant height c) root:shoot ratio (natural logged) as predicted by temperature, time since germination, and time squared. Positive estimates indicate more biomass has been invested in root development.

a) ln(biomass) ~ Temp + Time + Time^2

Fixed Effects	Estimate (2.5%, 97.5% CI)	t value	SE	p value
Intercept	-6.14 (-7.04, -5.24)	-13.80	0.44	
Temp:Hot	1.79 (1.36, 2.21)	8.32	0.21	p<0.001
Time	0.10 (0.07, 0.13)	7.12	0.014	p<0.001
Time^2	-0.0004 (-0.0006, -0.0003)	-5.11	0.00008	p<0.001

b) √ height ~ Population + Time + (1\|ID)

Fixed Effects	Estimate (2.5%, 97.5% CI)	t value	SE	p value
Intercept	1.54 (1.33,1.73)	14.93	0.10	
Pop:Sweden	-0.70 (-0.90,-0.50)	-6.76	0.10	p<0.001
Pop:UK	-0.92 (-1.14,-0.71)	-8.62	0.10	p<0.001
Time	0.015 (0.014,0.016)	26.03	<0.001	p<0.001
Random Effects	**Variance**	**% of total variance**	**SD**	**p value**
Plant ID	0.016	16.6%	0.13	p<0.001

c) ln(Root:Shoot) ~ Temp + Time + Time^2

Fixed Effects	Estimate (2.5%, 97.5% CI)	t value	SE	p value
Intercept	-1.52 (-2.37, -0.67)	-3.57	0.43	<0.001
Temp:Hot	0.75 (0.34, 1.16)	3.67	0.21	<0.001
Time	0.031 (0.003, 0.058)	2.26	0.01	0.03
Time^2	-0.00024 (-0.0004, -0.00007)	-2.81	<0.001	0.006

There is considerable spatially varying selection across *I. amara*’s range in Europe. The physiological challenges encountered during the germination and flowering period in the summer heat in Spain are drastically different to those in Spring and Autumn in Sweden (*I. amara* is an annual, so adult plants will not encounter winter temperatures). It is not known how selection pressure varies year to year at the sampling sites, but this can be assessed by looking for evidence of extinction and recolonisation events in *I. amara* populations. The sampled populations of *I. amara* have been sporadically recorded for at least thirty years in all cases, and so do not appear prone to local extinctions (Anthos, 2016; Artportalen, 2016; Font et al., 2010; Stroh & Pearman, 2016).

I. amara populations are usually very localised, and typically do not disperse from established sites (Stroh & Pearman, 2016). High gene flow is therefore not likely to swamp local adaptation in *I. amara,* but low gene flow may hinder local adaptation as complete isolation can lead to a lack of standing genetic variation in small populations (Savolainen et al., 2013). A lack of standing genetic variation is less of a problem in cases where range margin populations are large (Leimu & Fischer, 2008). While *I. amara* tends to have quite isolated populations, large populations may still have enough genetic variation to promote local adaptation. The population sampled in Gotland comprised of many thousand individuals, so is large enough to maintain considerable genetic diversity (Vander Mijnsbrugge, Bischoff, & Smith, 2010). Overall, populations of *I. amara* are under strong spatially varying selection, have high site specificity, and are frequently large and isolated. These characteristics suggest local adaptation can arise in *I. amara* and it is plausible that adaptive differences between populations may be due to local adaptation.

Germination was always lowest in the Spanish population, which only germinated in the warm treatment. Seeds from the Swedish population germinated most quickly and with the highest success rate (Fig. 5.2).

There are a few circumstances in which low germination rate can be adaptive for a population in the medium to long term. Dormancy in non-ideal conditions can be adaptive over the long term if seeds can remain as part of a seed-bank (Estrada et al., 2015; Van der Veken, Bellemare, Verheyen, & Hermy, 2007). It is possible Spanish plants are more prone to forming a seed bank, which *I. amara* is known to do occasionally (Stroh & Pearman, 2016), and will wait for optimum conditions before germinating. However, there is no existing evidence that *I. amara* is more likely to form seed banks in some parts of its range than other, and in general a higher germination proportion is considered adaptive (Donohue, Rubio de Casas, Burghardt, Kovach, & Willis, 2010). Previous examples of local adaptation in germination traits have found that seeds germinate best in their local conditions (Bischoff et al., 2006; Hämälä, Mattila, Leinonen, Kuittinen, & Savolainen, 2017; Jiménez-Alfaro, Silveira, Fidelis, Poschlod, & Commander, 2016), and examples of adaptive dormancy are rarer

(Donohue et al., 2010). This suggests that the observed differences in germination traits are not due to local adaptation.

Although growth rate, total biomass and root:shoot ratio did not vary between populations, Spanish plants were consistently taller than plants from any other population at any given age (Table 5.1a). It is unknown whether this is unique to the Spanish population, or whether populations at the centre of *I. amara*’s range have a similar growth pattern. It is therefore unknown if taller, more upright growth is an advantage to the Spanish population, or a neutral trait. Similarly, it is uncertain if the growth pattern of UK and Swedish are adaptive to local conditions or neutral.

In the first case, and greater height is adaptive in the Spanish population, greater height may be an advantage as it is strongly linked to competitive ability (Violle et al., 2009; Westoby, Falster, Moles, Vesk, & Wright, 2002), especially when the main limiting resource is light. Thus, the increased height of individuals in Spain may be due to selection for competitive ability. A common garden experiment that included competitors could establish if this is the case. Species can display adaptation to local competitors (Losos & Ricklefs, 2009; Peterson, Rice, & Sexton, 2013), and this has been suggested to occur more frequently on the equator-ward range boundary (Vergeer & Kunin, 2013). However, it may also be the case that the shorter, more rosette-like growth of UK and Swedish populations is adaptive. Increased investment in height and vegetative growth can be adaptive in productive environments, but can be maladaptive and result in lower reproductive success when the growing season is restricted in colder environments (Colautti & Barrett, 2013). As such, the shorter, more compact growth-form may reflect a shorter life-cycle and earlier flowering time, though that could not be confirmed in the experiment. Further comparisons between populations, especially between flowering times and seed mass production, would be needed to clarify whether one, both or none of the populations’ growth-forms are adaptive.

There are several processes that lead to differences between populations other than local adaptation, so simply detecting differences between populations does not directly provide evidence of local adaptation. Differences between populations can arise from local adaptation, maternal effects, plasticity or genetic drift (Kawecki & Ebert, 2004). If it is possible to rule explanations out other than local adaptation, then it can provide strong support that the observed phenotypic differences are due to local adaptation.

One possible artefact caused by the handling of the seeds may have lowered germination potential in the Spanish seeds. Germination potential can be affected by cold storage, and the Spanish seeds were older than the other seeds by at least a year. However, this can be ruled out. Cold storage is not likely the cause of lower germination potential as *I. amara* has not previously shown a significant drop in germination potential even after several years in cold storage (Royal Botanic Gardens Kew, 2019).

Germination potential and seedling survival rate can be affected by parental condition, and while later life-history traits can be affected by parental effects, it occurs to a lesser degree (Blödner, Goebel, Feussner, Gatz, & Polle, 2007; Donohue, 2009). When adult plants are stressed, it can lead to a lack of maternal investment in seed set that can lower germination potential in offspring (Donohue, 2009). The lower germination potential in Spanish seeds could be explained by parental condition. Spanish adults could be in poorer condition than individuals from other populations, whether because of thermal or drought stress. Typically, with repeated experimentation over multiple generations, the effects of plasticity or maternal effects can be measured and separated from genetic drift and local adaptation (Kawecki & Ebert, 2004). Unfortunately, no individuals in this experiment flowered so it was not possible to definitively rule out maternal effects and plasticity.

If seeds are in a poor condition then germination potential is lowered, and subsequent fitness later in life will be likewise lowered (Blödner et al., 2007). Therefore, if traits such as total biomass, or growth rate can lower in the Spanish population, it suggests that the germination trait differences are due to poor seed condition. However, while individuals from Spanish populations germinated much later than individuals from other populations, they displayed a similar growth rate. This suggests that Spanish seeds were not in poor condition but instead did not germinate due to non-ideal conditions as part of a plastic response (Donohue et al., 2010).

There are several shortcomings to the experimental design that limit what we can infer about local adaptation in *I. amara*. *I. amara* grows in localised populations, and while multiple sites were investigated based on botanical records, few sites had viable populations of *I.amara*. In Sweden only one site was sampled, though this did encompass several square kilometres of beach. In the UK nearly all of the permanent populations grow in and around the Chilterns, and even though samples were collected from several of these, the genetic and physiological similarity of different UK populations is not known. Sampling of Spanish populations was similar, and individuals were collected from several small populations within a few square kilometres. In addition, the experiment was initially designed as a comparison between edge and central population of *I. amara.* Several populations of *I. amara* were sourced from central Europe, but in most cases the provenance of these seeds was unknown. Due to time constraints the experiment was not replicated across as many populations as would be desirable. It is therefore uncertain which populations discussed here are similar to central populations, and which are distinct. It is also not known whether distinct traits are shared by multiple populations at a particular range edge. Evidence of traits shared by multiple range edge populations, that are distinct from central populations, would have provided stronger evidence of local adaptation.

Despite inconclusive proof that populations of *I. amara* are locally adapted to temperature*,* there are clear differences in traits between populations. Variation in response to climate between populations can create several complications for predicting future ranges. Typically, climatic niche models are based on the entirety of a species' current range, and assume that this describes the species overall climatic tolerance. Climatic niche models also assume that the species response to climate is uniform across all populations. In the case of invasive species, it is assumed that a species potential range will match the climatic conditions of its entire native range. However, since introductions typically comprise of individuals from one or a few native populations, the potential range may be smaller than it would be for the total population.

Predictions of climate-induced range shifts face a similar problem, as if responses to climate vary from population to population, range shift predictions based on the entire range may be inaccurate. While examples of genetic drift do not provide evidence that climate sets species range margins, it still has consequences for climatic niche modelling. Climatic niche modelling assumes that species' climatic niche is the same across their range, and that species will respond in the same manner to climatic change regardless of which population they are from. Even the seemingly small differences observed between populations in this study reflect the ability of populations to have different responses to climate.

If *I. amara* has not filled all climatically suitable areas in Europe, perhaps due to dispersal limitations, then its true climatic tolerance is not known, and its potential range after introduction or climate change is likewise unknown. *I. amara* has within the last one hundred years colonised northern Europe and Scandinavia (Fig. 5.1). This expansion may be as a result of an expansion of *I. amara*'s climatic niche, and the species is now able to colonise new areas. Alternatively, Scandinavia was always climatically suitable, but *I. amara* was unable to colonise these areas due to non-climatic limitations, most likely dispersal. There is little evidence of a novel adaptation in *I. amara* populations in Sweden, so I would suggest that the recent range expansion was not caused by an expansion of *I. amara'*s climatic niche. Given the fact that *I. amara* has a low dispersal ability, and the fact it is occasionally transported as a horticultural species, I would suggest that the observed range expansion has been due to assisted dispersal by humans.

Changes in species climatic niches, whether it is through local adaptation or genetic drift, have consequences for climatic niche modelling. Climatic niche models assume that species' climate niches are stable, and do not change over a species range or through time. If a species' climatic niche can change, then species' potential ranges can also change. This jeopardises predictions of climate-change induced range shifts, as species may be able to adapt to local conditions rather than shift their range (Valladares et al., 2014). Several species have already adapted to changing climate (Anderson, Panetta, & Mitchell-Olds, 2012; Valladares et al., 2014), but for most species it is unclear how adaptable species' climatic niches are in order to mitigate the impacts of climate change (Hoffmann & Sgrò, 2011). Predictions of invasive species spread are also less reliable if species climatic niches are malleable. Predictions of species invasion will identify climatically suitable areas for an invasive species, but if a species' climatic niche can vary then such predictions become very difficult. There is evidence that species can change their climatic niche in their non-native range, for example through the development of novel adaptations, which results in species spreading much further than initial models predicted (Moran & Alexander, 2014; Prentis, Wilson, Dormontt, Richardson, & Lowe, 2008).

I wished to answer three questions in relation to the range margins *I. amara.* Firstly, is there evidence of local adaptation to temperature, which would indicate temperature acts as a range limitation. It is not certain if the observed differences in germination traits and plant height are adaptive or not, so there is no direct evidence that populations are locally adapted to temperature.

Secondly, with or without local adaptation, do populations have difference climatic tolerances at different range edges. Overall, the fitness of *I. amara,* as judged by several traits, was lower at cold temperatures. Germination rate, growth rate, and total biomass were all lower in cold temperatures. This suggests *I. amara* is nearing the edge of conditions it can persist in on its cold range edge, as presumably fitness would be lower the further north it spreads. On the other hand, *I. amara* seemed to germinate well, and grow well under warm conditions. *I. amara's* range limit in southern Europe therefore is more likely set by factors other than temperature. The Spanish population was consistently taller than other populations, which may or may not be an adaptive trait. It could potentially be a result of selection for greater competitive ability at *I. amara*'s southern range edge (Violle et al., 2009; Westoby et al., 2002), or an adaptive change in growth-form in more northern populations.

Thirdly, I wished to address whether there is evidence *I. amara* has expanded its range in Europe with the assistance of adaptation to cold conditions. I found seeds from the Swedish population germinated more successfully in cold conditions, but this may be due to maternal effects rather than local adaptation. Given *I. amara'*s low dispersal ability, and the lack of evidence for local adaptation, I suggest that the recent range expansion is not due to a change in climatic niche. Instead it seems more likely that the previous native range *I. amara* did not matched its climatic tolerances, and human-assisted dispersal has allowed it to colonise new areas.

Chapter 6: General discussion

6.1 Introduction

The study of species range edges has a long history of academic interest, but has recently become especially relevant due to the large scale range shifts induced by anthropogenic climate change, and the large number of species introductions to new areas of the world. There is a need to predict changes to species ranges in the future, and in order to do this we need to understand what factors set species range edges currently. Climate has long been assumed to be the primary factor that sets species range edges, and species ranges have generally been assumed to correlate with a species' climatic tolerance (Araújo & Pearson, 2005; Pearson & Dawson, 2003). Recent work has challenged this paradigm, and emphasised the potential role of non-climatic factors such as dispersal, biotic interactions and gene flow in limiting species ranges (Early & Keith, 2019; Louthan, Doak, & Angert, 2015; Wisz et al., 2013). However, it is still not clear how frequently a species' range edge coincides with the limit of its physiological tolerance, or the factors that can help or hinder species spreading to their climatic limits. I investigated the role of climatic and non-climatic factors on species range margins, using a number of different systems. Firstly, I considered under what circumstances do naturalised species not achieve their native climatic limits. Secondly, I considered under what circumstances do species exceed their native climate limits in their naturalised range. Thirdly, I looked for evidence of local adaptation to climate in populations of *Iberis amara* at multiple range edges.

In this discussion I will briefly summarise the findings from each chapter, what this tells us about the role of climatic versus non-climatic factors on species ranges, and the wider ramifications for studies of species range margins going forward.

6.2 Summary of chapter results

In chapter two, I asked what areas are most under threat by spreading non-native species, if we assume climate and time for dispersal are the only factors that limit species ranges. I compiled range information of non-native birds, mammals and plants to create a large, multi-taxonomic database of species' native and naturalised occurrences. For each species I estimated the area of the naturalised range that is climatically suitable and overlaid all potential ranges of species to produce a map of global colonisation threat. I then overlaid a global measure of national capacity (Early et al., 2016), to create a threat map that highlights areas with the highest potential impact of non-native species, and the lowest capacity to mitigate those impacts. Particular areas of risk were found in China, central Africa and South America.

Non-native species can have severe impacts on local ecosystems, agriculture and human infrastructure, even if they are not currently classified as invasive. Many species only become classified as invasive after they have a large range size (Hawkins et al., 2015), so it is important to identify potential invasive species before they become invasive. The impact of non-native species is also not necessarily additive, invasional meltdown can lead to multiplicative effects where non-native species facilitate each other and lead to much higher impact than they would individually (Braga et al., 2018; Simberloff & Von Holle, 1999). Recognising the potential range of species, and recognising where multiple species are likely to invade, is one way to estimate the potential threat.

In chapter three, I asked what can help or hinder non-native species to colonise climatically suitable areas. Species may be slowed from spreading by a number of non-climatic factors, or may be stopped from spreading entirely. I used a hierarchical Bayesian approach to investigate factors that contribute to species spreading successfully, with features from species' introduction history, species traits, the spatial distribution of suitable areas and interactions between the invader and native landscape. The results showed that non-native species spread was correlated to time since introduction, dispersal, fragmentation of habitat, and the region of introduction. How successfully species can colonise climatically suitable areas is tied to time since introduction and land-scape scale factors rather than species traits.

In chapter four I looked at a different aspect of naturalised ranges. Rather than ask why naturalised species fill less of their potential range than expected, I asked how and why might species fill more of their potential range than expected. In particular I asked how commonly do species exceed the climatic limits observed in their native range? Could this be because of non-climatic limits acting on their native range? I compared native and naturalised niches and looked for evidence of naturalised species colonising new types of climate (known as "niche expansion"). I investigated if expansion was equally likely to occur in any climatic direction, or whether species expand their niches more frequently towards hotter, colder, wetter or drier climate. I found that species expand their niche expansions most frequently towards wetter climate than that found in their native range. Species also expanded their niche towards drier climate, but to a much lesser degree. Niche expansions towards hotter or colder climate were rare.

In chapter 5 I compared populations from several range margins in *Iberis amara* (L.). If climate, and in particular temperature, act as a range limitation then there may be evidence of local adaptation to increase fitness to local temperature regimes. I therefore asked do range margin populations vary in response to temperature? Is this a sign of local adaptation and selection pressure at range margins? I carried out a common garden experiment using seed samples from multiple range margin populations of a study species, *Iberis amara.* Seeds from populations in Spain, the UK and Sweden were germinated and grown in two temperature treatments. Firstly in a cold treatment, where temperature conditions matched the coldest part of its climatic niche (which matched the conditions at the northern-most range margin). Secondly in a warm treatment, where temperature conditions matched the warmest part of its climate niche (which matched the conditions at the southern-most range margin). I looked for evidence of local adaptation to local thermal conditions across multiple life-history traits, from germination success rate to total biomass at the end of the experiment.

I found that several traits vary between populations, specifically germination traits and plant height. Seeds from the Swedish population germinated the most quickly and with the highest success rate in both temperature treatments. All populations germinated more successfully and grew more quickly in the warm temperature treatment, and seeds from the Spanish population did not germinate at all in the cold treatment. All populations had a similar growth rate in the warm treatment, but individuals from the Spanish population grew proportionally taller for every gram of biomass.

6.3 Niche expansion is the norm, not the exception

The results presented here are robust, and account for analogue climate and for availability of climate in the native and naturalised regions. Species expand their naturalised niche into climate that is available in their native region, but is not colonised. It seems likely non-climatic factors are preventing species from colonising all climatically suitable areas in their native region.

The frequency of niche expansions (45% of native versus naturalised expansions overall) provides evidence that native species quite frequently do not fill their climatic niche. As such, we should not assume climate constrains species distribution. Climate certainly can set species range edges, but it is not a given.

This is especially true in the case of precipitation, as species frequently show expansions into new precipitation regimes. This suggests native range edges do not correlate to their physiological limits of moisture. This pattern is consistent regardless of which region species are from (i.e. where they are native) or where they are introduced to (i.e. where they are naturalised). Temperature appears to more commonly set range limits, as species only rarely show niche expansions into hotter or colder climate.

6.4 Climate niches are malleable

If temperature sets multiple range edges, then there should be selection pressure for populations to increase their fitness to local temperature conditions. However, populations can have phenotypic differences through processes other than local adaptation, such as genetic drift (Sexton et al., 2009). In order to distinguish between local adaptation and other processes I looked for evidence the observed differences in traits were adaptive.

While I could not prove for certain the observed differences in traits between populations are due to local adaptation, there is certainly evidence that responses to temperature varies among populations. Climatic niche models assume that a species distribution represents its full range of climatic tolerances and that the response to climate is consistent between populations. Differences in response to temperature between populations, whether they are due to local adaptation or other processes, create a problem for climatic niche models in several ways. Firstly, different populations may respond differently to the same climate conditions. Models of range shift caused by climate change assume that different populations have similar climatic tolerances, and their range will consistently coincide with a certain set of climatic limits. If species' thermal tolerances are different, then this would clearly demonstrate that species' climatic niches are not stable across population in the current species range. Secondly, species responses can change dependent on local conditions. Even minor differences in species traits may affect species' response to climate change, or the likelihood of success in an introduced area. If species change their response to climate, especially adaptively, then predictions based on current climatic tolerance are not reliable. Introduced species may be particularly prone to this if they are removed from maladaptive gene flow (Alexander & Edwards, 2010) or have several source populations hybridise to form novel genotypes (Moran & Alexander, 2014; Schierenbeck & Ellstrand, 2009).

6.5 Species traits are not that useful at predicting species range limits

None of the wide variety of species traits considered helped predict introduced species success. This suggests that overall, species traits are a poor way to predict introduced species success. Several previous studies have found species traits can promote invasiveness (Moravcová, Pyšek, Jarošík, & Pergl, 2015; van Kleunen, Weber, & Fischer, 2010), and non-native species establishment success (Blackburn & Duncan, 2001; Capellini, Baker, Allen, Street, & Venditti, 2015; van Kleunen, Dawson, & Maurel, 2015). Traits that were found to significantly predict success in one taxonomic group commonly are not significant in another taxonomic group, and traits associated with success can be very different from one taxonomic group to another.

Previous studies of non-native species spread also typically measure success as species range size, which does not account for the total climatically suitable area or how climate may limit a species range irrespective of species traits.

My results suggest that no set of traits is important to species success across multiple taxonomic groups. The results presented in this thesis suggest the success of an introduced species has more to do with the region that is being invaded and its interaction with the introduced species. Factors such as habitat fragmentation, human-assisted dispersal, and potential biotic resistance may be more important to non-native species success than previously recognised. More work is needed to understand how these factors can limit the spread of non-native species, and how human action can manage non-native species effectively.

6.6 Shortcomings

While I believe the conclusions presented in this thesis are robust, there are a number of shortcomings and improvements that should be kept in mind.

The analyses in chapters two, three and four all used coarse distribution data. For each ten-minute grid-cell a species could either be present or absent, and the climate of each grid-cell was an overall average. The role of microclimate can be very important for species distribution, in particular microrefugia where species occur in specific areas that are climatically suitable (Hannah et al., 2014; Kearney et al., 2014). As such, coarse distribution data may over estimate a species climatic niche. While this is a potential shortcoming, the nature of the analysis justifies the use of coarse data to some extent. I compared native and naturalised species on a global scale, and many species records are not geolocated to a high degree of accuracy. Using such data in conjunction with fine-scale fine-scale gridded climate may misrepresent a species' climate niche. In addition, climate has often been stated to be the most important factor at broad spatial scales (Araújo & Guisan, 2006; Pearson & Dawson, 2003), and since one of the primary goals of this thesis was to verify this theory, it was logical to use coarse -scale data.

Comparing native and naturalised ranges is a useful study system to consider species ranges, but is not without reservations. Its advantages are it allows comparison of species niche with two independent sets of non-climatic factors, in particular many naturalised populations have fewer predators and competitors in their naturalised range (Heger & Jeschke, 2014). This comparison is a powerful way to investigate the role of non-climatic factors in structuring species ranges, as well as species niches. The disadvantages arise from the stochastic nature of species introductions. In my analysis of species spread, I included a variety of factors that could influence species spread to climatically suitable areas, but there were a number of influential factors that were not included as the information is often not known. Propagule pressure was unknown for many species, including the number of individuals introduced, the number of repeated introductions and the genetic makeup of individuals introduced. These factors can have a drastic impact of species establishment and post-establishment success (Simberloff, 2009). In addition, species that are introduced are not selected at random from all available species on Earth. Most introductions are escapees from horticulture or the pet trade (Early et al., 2016; Hulme, 2009), or are agricultural pests (Chytrý et al., 2009), and species associated with these trade links are likely to have a species set of traits (Early & Sax, 2014). In particular taxa that are able to establish and spread successfully tend to have large native ranges (Li et al., 2014), and have a broad climatic niche (Higgins & Richardson, 2014). While I tried to compensate for this by using as a broad range of plant, bird and mammal species as possible with a wide variety of life traits, non-native species are still a subset of all species. Any conclusions about climate niches for naturalised species therefore have a potential bias in the type of species studied.

In chapter four I found that species frequently expand their climatic niche towards wetter or drier environments. One possible interpretation of this is that the measure of precipitation I used, total annual precipitation (TAP), is an inappropriate measure of moisture that does not relate to species' physiological stress, and therefore does not limit species ranges. More specific measures of precipitation, such as seasonality or precipitation in the driest quarter of the year, may be a more informative measure of species' climatic tolerance. As such, the estimates of a species' potential range in chapters two, three and four may not be accurate. However, if TAP is not an ecologically relevant factor, this is in itself an interesting conclusion. TAP is used widely in models that assume climate matching between native and naturalised niches, as TAP is a simple, widely available measure of precipitation, and used as a basic measure of species precipitation tolerance (Early & Sax, 2014). The frequency of niche expansion towards drier or wetter climate therefore highlights that TAP does not set range limits in the native range. Any models that wish to consider species' climatic tolerance should therefore avoid using TAP in the species range as a proxy.

6.7 The potential role of non-climatic factors in limiting species ranges

There is evidence that species native ranges are frequently constrained by non-climatic factors, especially in the wettest part of their range. There are several factors that may constrain species ranges, such as dispersal, biotic interactions, gene flow, and physical barriers. I presented an argument in chapter four that the most likely explanation, given the pattern of niche expansion, is that biotic interactions are constraining native species ranges on the wettest edge of their niche. If biotic interactions are the correct explanation, there are multiple mechanisms such as competition, predation, parasitism, disease transferral (Early & Keith, 2019; Wisz et al., 2013) that may contribute to limiting a species range. However, it is not currently known which factor is causing a range limit on species native ranges, whether it is a biotic interaction, or what type of biotic interaction is constraining species. This is a huge gap in knowledge if we want to make accurate predictions, and it is a difficult gap to fill with only correlational studies.

6.8 New techniques and future work

There is certainly a need to gather more data on species traits, species distributions, and correct some of the data bias globally (Meyer, Kreft, Guralnick, & Jetz, 2015). There is also a need for modern theory to incorporate biotic interactions and other non-climatic factors into models of species range margins (Early & Keith, 2019; Wisz et al., 2013), and to recognise their importance in invasion models. Modern statistical techniques can extrapolate biotic interactions from co-occurrence, and use this information in a species distribution model (Pollock et al., 2014). Such models require a large amount of occurrence information and information regarding likely candidate interacting species, but have successfully derived biotic interactions’ effect on species ranges (Early & Keith, 2019; Staniczenko, Sivasubramaniam, Suttle, & Pearson, 2017). In cases where there is not a large amount of extant data on species occurrences or physiological tolerances, phylogenetic studies have estimated species physiological tolerances and fundamental climatic niches with some success (Cooper, Jetz, & Freckleton, 2010; Crisp & Cook, 2012).

Future work could focus on potential new modelling techniques that incorporate biotic interactions. However, this might not be necessary for every species. In many species, range edges consistently correlated with climatic conditions, especially temperature factors, so for many species standard climatic niche models may still be valid. The key problem is identifying which species are constrained by non-climatic factors and which are not.

At the moment there is no systematic way to identify these factors, but a case-by-case process can inform future models. For example, if a study wishes to predict how a species range will respond to climate they would need to establish several points: 1) does a species' current range match its climatic tolerance? This can be established through one of the methods discussed above, by consulting historical records, physiological studies, evidence of stress caused by climatic conditions at range margins, or extrapolating the climatic niche from a phylogenetically related species. If a species does not match its climatic niche, then the non-climatic factor that is limiting a species range needs to be identified. 2) What climatic factors may change under climate change? As shown in this thesis, range limits set by temperature are more likely to be conserved. Any temperature changes across the species are more likely to drive a species range shift. If there are associated precipitation changes, then a species' response will become harder to predict. Identifying a species' vulnerability to precipitation change would need to be established on a per species basis, rather than assuming species' will shift their range to track changes in precipitation. Vulnerability to precipitation change may be set by a minimum precipitation threshold or another limiting moisture factor. 3) Is there any evidence of non-climatic factors acting as a range limit? This may involve collating information on species' dispersal abilities, competitors, predators, local population differences or other candidate factors. There have been recent calls to collate information on biotic interactions into online databases, some of which have been published or are in the process of being built. For example, parasite-host interactions are now publicly available and can be used to check common associations between species.

The field of macroecology has to some extent moved past the point where one factor, climate, is thought to completely structure species range, but how and where non-climatic factors can structure species ranges is still poorly understood. Identifying broad macroecological patterns to infer how species ranges may be structured is one step to understanding how climatic and non-climatic factors can interact but it is only one step of many. Testing broad macroecological principles robustly requires a mechanistic understanding of what factors can structure a species range and how they can vary across and between species. Collation of information of previous experiments and studies of non-climatic factors could be the first step to testing whether some range limiting factors are more common, or act more strongly, in certain circumstances or for certain types of species. In addition, physiological data on species tolerance could be included to estimate a species' climatic niche, rather than deriving it through correlation with species ranges. Mechanistic niche models require validation with physiological data but are a very reliable way to compare a species realised climatic niche with their fundamental niche. Species that are known not to fill their climatic niche could then be investigated either in the field or in the laboratory in classical exclusion or transplant experiments. Unfortunately, we currently lack strong empirical evidence of the underlying processes structuring species ranges for all but a few species, which often makes our understanding of the mechanisms behind species range edges anecdotal rather than systematic.

Ultimately there is a need for more experimentation and general testing of species range edges. There is a severe lack of experiments that test the mechanisms controlling a species range edge at multiple range edges (though see Vergeer & Kunin, 2013). This needs to include more than verifying (for example) that a predator can lower a species' fitness locally, but explicitly test that a species' range edge is at least partially set by the predator's presence.

Experiments such as transplant experiments, exclusion experiments, common garden experiments can all be used to test between several possible mechanisms of range limitation. For example, a transplant experiment over a species range edge can verify 1) whether species grow up to their physiological limit (i.e. they are climatically limited) 2) whether they are capable of surviving past their current range margin (i.e. they are dispersal limited), or 3) whether they can survive past their current range margin but only if competitors/predators are excluded (i.e. they are limited by biotic interactions). Populations from different range edges can also be compared to test if species are able to adapt and change their responses to varying climate and species interactions, and provide more information on how flexible species niches can be. In addition, collation and testing of experimental information can inform us of what factors are more likely to act on specific range edges, and whether these form broad trends over different areas and different species.

6.9 Conclusion

I asked whether climate is the dominant factor that sets species range edges. I find, using several lines of evidence, climate is important, but it is by no means the only factor that sets species ranges. Habitat fragmentation, dispersal ability and the region of introduction correlate to how effectively naturalised species colonise climatically suitable areas. Species' niches have consistent temperature limits across parts of their range, and rarely display expansions into new thermal regimes. By contrast precipitation does not seem to set species range edges in the native range, suggesting a role for non-climatic factors that prevent species spreading to all climatically suitable areas in the native range. I also find evidence that species have different germination and growth responses to local thermal conditions, further supporting a malleable climate niche that can change across native and non-native populations, and even within contiguous populations.

Supplementary Materials

Table S1: List of all plant species used in this thesis.

Abies concolor
Abies lasiocarpa
Abutilon theophrasti
Acacia dealbata
Acacia mearnsii
Acacia melanoxylon
Acer ginnala
Acer negundo
Acer platanoides
Acer pseudoplatanus
Acer saccharinum
Achillea millefolium
Acroptilon repens
Adenanthera pavonina
Aegilops cylindrica
Aegopodium podagraria
Agropyron cristatum
Agrostis capillaris
Agrostis gigantea
Agrostis scabra
Ailanthus altissima
Akebia quinata
Albizia julibrissin
Albizia lebbeck
Alhagi maurorum
Alliaria petiolata
Allium vineale
Alnus glutinosa
Aloe arborescens
Aloe maculata
Alopecurus geniculatus
Alopecurus myosuroides
Alopecurus pratensis
Alternanthera philoxeroides
Alyssum alyssoides
Alyssum desertorum
Amaranthus albus
Amaranthus blitoides
Ambrosia artemisiifolia
Epilobium hirsutum
Epilobium parviflorum
Epiphyllum phyllanthus
Equisetum arvense
Eragrostis cilianensis
Eragrostis curvula
Eragrostis echinochloidea
Eremopyrum triticeum
Erigeron speciosus
Erodium cicutarium
Eruca vesicaria
Erysimum repandum
Eucalyptus camaldulensis
Eugenia uniflora
Euonymus fortunei
Euphorbia cyparissias
Euphorbia dendroides
Euphorbia esula
Euphorbia mellifera
Euphorbia myrsinites
Euphorbia tirucalli
Euryops multifidus
Festuca arundinacea
Festuca ovina
Festuca trachyphylla
Flacourtia indica
Foeniculum vulgare
Fragaria vesca
Fragaria virginiana
Frangula alnus
Fraxinus americana
Fraxinus pennsylvanica
Gaillardia aristata
Galanthus elwesii
Galanthus nivalis
Galeopsis tetrahit
Geranium molle
Geranium pusillum
Geum macrophyllum
Pastinaca sativa
Paulownia tomentosa
Peganum harmala
Pennisetum ciliare
Pennisetum purpureum
Pennisetum setaceum
Phalaris arundinacea
Phalaris minor
Phleum pratense
Phlox paniculata
Phoenix canariensis
Phoenix dactylifera
Physalis virginiana
Picea abies
Picea engelmannii
Picea pungens
Pinus contorta
Pinus ponderosa
Pinus sylvestris
Pistacia vera
Pistia stratiotes
Plantago lanceolata
Plantago major
Poa annua
Poa bulbosa
Poa compressa
Poa nemoralis
Poa palustris
Poa pratensis
Poa trivialis
Podalyria sericea
Polygonum arenastrum
Polygonum caespitosum
Polygonum perfoliatum
Polygonum persicaria
Polypogon monspeliensis
Polypogon viridis
Poncirus trifoliata
Pontederia cordata

Ambrosia trifida
Amelanchier alnifolia
Amorpha fruticosa
Ampelopsis brevipedunculata
Amsinckia menziesii
Anthemis arvensis
Anthemis cotula
Anthoxanthum odoratum
Anthriscus caucalis
Anthriscus sylvestris
Antigonon leptopus
Apium graveolens
Aquilegia vulgaris
Aralia chinensis
Araucaria araucana
Arctium minus
Ardisia crenata
Ardisia elliptica
Armeniaca vulgaris
Arnica chamissonis
Arrhenatherum elatius
Artemisia absinthium
Artemisia campestris
Artemisia dracunculus
Artemisia vulgaris
Arundo donax
Asparagus officinalis
Asphodelus fistulosus
Asystasia gangetica
Avena barbata
Avena fatua
Azolla caroliniana
Azolla filiculoides
Azolla pinnata
Babiana angustifolia
Babiana stricta
Barbarea vulgaris
Bauhinia variegata
Begonia cucullata
Berberis thunbergii
Berberis vulgaris
Berteroa incana
Beta macrocarpa
Glaucium flavum
Glechoma hederacea
Gleditsia triacanthos
Glossostigma cleistanthum
Glyceria maxima
Glyceria striata
Grevillea robusta
Grindelia squarrosa
Gypsophila paniculata
Harrisia martinii
Harrisia tortuosa
Hedera helix
Hemarthria altissima
Hemerocallis fulva
Hesperis matronalis
Hibiscus syriacus
Hiptage benghalensis
Holcus lanatus
Hordeum jubatum
Hordeum marinum
Hordeum murinum
Hydrilla verticillata
Hydrocharis morsus-ranae
Hydrocleys nymphoides
Hylocereus undatus
Hymenachne amplexicaulis
Hyoscyamus niger
Hypericum perforatum
Hypochaeris radicata
Impatiens capensis
Imperata cylindrica
Ipomoea aquatica
Ipomoea purpurea
Iris pseudacorus
Isatis tinctoria
Jacaranda mimosifolia
Juglans nigra
Juglans regia
Juncus bufonius
Juncus compressus
Juncus ensifolius
Juncus gerardii
Juncus inflexus
Populus alba
Populus deltoides
Populus nigra
Portulacaria afra
Potamogeton crispus
Potentilla argentea
Potentilla pensylvanica
Potentilla recta
Potentilla rivalis
Prunus lusitanica
Prunus serotina
Prunus virginiana
Pseudotsuga menziesii
Psidium cattleianum
Psidium guajava
Pteris vittata
Pterocarpus indicus
Puccinellia distans
Pyracantha koidzumii
Pyrostegia venusta
Pyrus calleryana
Ranunculus cymbalaria
Ranunculus ficaria
Ranunculus repens
Ranunculus sceleratus
Rapistrum rugosum
Rhamnus cathartica
Rhus glabra
Ribes aureum
Robinia pseudoacacia
Rorippa amphibia
Rorippa nasturtium-aquaticum
Rorippa palustris
Rorippa sylvestris
Rosa multiflora
Rosa rugosa
Rotala rotundifolia
Rubus allegheniensis
Rubus idaeus
Rubus parviflorus
Rubus phoenicolasius
Rumex acetosa
Rumex acetosella

Betula pendula
Bidens pilosa
Brassica nigra
Brassica tournefortii
Briza maxima
Bromus arvensis
Bromus carinatus
Bromus catharticus
Bromus hordeaceus
Bromus inermis
Bromus japonicus
Bromus racemosus
Bromus secalinus
Bromus tectorum
Broussonetia papyrifera
Butomus umbellatus
Cabomba caroliniana
Caesalpinia gilliesii
Callitriche stagnalis
Camelina microcarpa
Campanula rapunculoides
Capsella bursa-pastoris
Cardamine impatiens
Cardaria draba
Cardaria pubescens
Carduus acanthoides
Carduus crispus
Carduus nutans
Carduus pycnocephalus
Carduus tenuiflorus
Carex disticha
Carex flacca
Carum carvi
Casuarina cunninghamiana
Casuarina equisetifolia
Cedrela odorata
Celastrus orbiculatus
Cenchrus longispinus
Centaurea calcitrapa
Centaurea cyanus
Centaurea diffusa
Centaurea jacea
Centaurea melitensis
Juncus tenuis
Juniperus virginiana
Kalanchoe pinnata
Khaya senegalensis
Kochia scoparia
Koeleria macrantha
Lactuca serriola
Lamium amplexicaule
Lampranthus glaucus
Lantana camara
Lathyrus latifolius
Leonurus cardiaca
Lepidium densiflorum
Lepidium latifolium
Lepidium perfoliatum
Lepidium virginicum
Lespedeza cuneata
Leucaena leucocephala
Leucanthemum vulgare
Leymus arenarius
Ligustrum japonicum
Ligustrum lucidum
Ligustrum ovalifolium
Ligustrum sinense
Ligustrum vulgare
Limnobium laevigatum
Linaria vulgaris
Linum perenne
Lolium multiflorum
Lolium perenne
Lonicera involucrata
Lonicera japonica
Lonicera maackii
Lonicera tatarica
Lonicera xylosteum
Lotus corniculatus
Ludwigia grandiflora
Ludwigia peploides
Ludwigia peruviana
Lupinus polyphyllus
Luzula luzuloides
Lycopus europaeus
Lygodium japonicum
Rumex crispus
Rumex longifolius
Rumex obtusifolius
Saccharum ravennae
Sagina procumbens
Sagittaria graminea
Sagittaria montevidensis
Sagittaria rigida
Salix alba
Salix purpurea
Salsola kali
Salvia aethiopis
Salvinia minima
Sambucus racemosa
Sanguisorba minor
Saponaria officinalis
Sarracenia purpurea
Schefflera actinophylla
Schinus terebinthifolius
Schismus barbatus
Sedum acre
Senecio jacobaea
Senecio sylvaticus
Senecio vulgaris
Senna pendula
Sequoia sempervirens
Sequoiadendron giganteum
Sesbania punicea
Setaria faberi
Setaria viridis
Silene antirrhina
Silene noctiflora
Silene vulgaris
Silphium perfoliatum
Silybum marianum
Sinapis arvensis
Sisymbrium altissimum
Sisymbrium irio
Sisymbrium loeselii
Sisymbrium officinale
Sisyrinchium angustifolium
Sisyrinchium montanum
Solanum carolinense

Centaurea solstitialis	*Lygodium microphyllum*	*Solanum dulcamara*
Cerastium arvense	*Lysimachia nummularia*	*Solanum nigrum*
Cerastium fontanum	*Lysimachia vulgaris*	*Solanum torvum*
Ceratocephala testiculata	*Lythrum salicaria*	*Solanum triflorum*
Cereus hildmannianus	*Macfadyena unguis-cati*	*Solanum viarum*
Chamaecyparis lawsoniana	*Maclura pomifera*	*Solidago canadensis*
Chelidonium majus	*Maianthemum stellatum*	*Solidago gigantea*
Chenopodium album	*Malcolmia africana*	*Solidago sempervirens*
Chenopodium opulifolium	*Malva neglecta*	*Sonchus arvensis*
Chondrilla juncea	*Malva parviflora*	*Sonchus asper*
Chorispora tenella	*Marrubium vulgare*	*Sonchus oleraceus*
Cichorium intybus	*Marsilea quadrifolia*	*Sorghum bicolor*
Cinnamomum camphora	*Medicago lupulina*	*Sorghum halepense*
Cirsium arvense	*Medicago minima*	*Sparaxis tricolor*
Cirsium palustre	*Medicago polymorpha*	*Spartina alterniflora*
Cirsium vulgare	*Medicago sativa*	*Spartina anglica*
Clematis orientalis	*Melaleuca quinquenervia*	*Spartina densiflora*
Clematis terniflora	*Melia azedarach*	*Spartina patens*
Coleonema pulchrum	*Melilotus indicus*	*Spathoglottis plicata*
Collomia grandiflora	*Melilotus officinalis*	*Sphagneticola trilobata*
Collomia linearis	*Melinis minutiflora*	*Spiraea japonica*
Colocasia esculenta	*Mentha aquatica*	*Spirodela punctata*
Commelina diffusa	*Mentha pulegium*	*Sporobolus cryptandrus*
Conium maculatum	*Mentha spicata*	*Sporobolus vaginiflorus*
Conringia orientalis	*Merremia tuberosa*	*Stellaria media*
Convolvulus arvensis	*Mesembryanthemum crystallinum*	*Stenocereus griseus*
Conyza canadensis	*Mesembryanthemum nodiflorum*	*Stuckenia vaginata*
Cornus sericea	*Microstegium vimineum*	*Swietenia macrophylla*
Coronilla varia	*Miscanthus sacchariflorus*	*Symphoricarpos albus*
Cortaderia selloana	*Miscanthus sinensis*	*Syringa vulgaris*
Cotula coronopifolia	*Monarda didyma*	*Syzygium cumini*
Crepis capillaris	*Monochoria vaginalis*	*Syzygium jambos*
Cupaniopsis anacardioides	*Morus alba*	*Taeniatherum caput-medusae*
Cupressus macrocarpa	*Murdannia keisak*	*Tamarix gallica*
Cyathea cooperi	*Myosotis arvensis*	*Tanacetum vulgare*
Cycas revoluta	*Myosotis scorpioides*	*Taxus cuspidata*
Cyclamen coum	*Myosotis sylvatica*	*Tecoma stans*
Cyclamen hederifolium	*Myosoton aquaticum*	*Thlaspi arvense*
Cyclamen repandum	*Myriophyllum aquaticum*	*Torilis japonica*
Cylindropuntia imbricata	*Myriophyllum heterophyllum*	*Tradescantia fluminensis*
Cylindropuntia kleiniae	*Myriophyllum spicatum*	*Tradescantia spathacea*

Cylindropuntia spinosior
Cylindropuntia tunicata
Cynara cardunculus
Cynodon dactylon
Cynoglossum officinale
Cyperus difformis
Cyperus prolifer
Cyperus rotundus
Cytisus scoparius
Dactylis glomerata
Dalbergia sissoo
Datura stramonium
Datura wrightii
Daucus carota
Delonix regia
Descurainia pinnata
Descurainia sophia
Dianthus armeria
Dietes bicolor
Digitalis grandiflora
Digitalis lutea
Digitalis purpurea
Digitaria sanguinalis
Dioscorea bulbifera
Dipsacus fullonum
Dipsacus laciniatus
Dracocephalum parviflorum
Duchesnea indica
Echinochloa colona
Echinochloa crus-galli
Echium plantagineum
Egeria densa
Eichhornia crassipes
Elaeagnus angustifolia
Elaeagnus pungens
Elaeagnus umbellata
Elsholtzia ciliata
Elymus canadensis
Epilobium brachycarpum
Epilobium ciliatum
Najas graminea
Najas minor
Narcissus pseudonarcissus
Nasturtium officinale
Nelumbo nucifera
Nemesia strumosa
Nepeta cataria
Nerium oleander
Nicotiana glauca
Nymphaea ampla
Nymphaea lotus
Nymphaea odorata
Nymphoides peltata
Oeceoclades maculata
Oenothera biennis
Onopordum acanthium
Opuntia aurantiaca
Opuntia elata
Opuntia humifusa
Opuntia leucotricha
Opuntia microdasys
Opuntia monacantha
Opuntia phaeacantha
Opuntia polyacantha
Opuntia puberula
Opuntia robusta
Opuntia streptacantha
Opuntia stricta
Opuntia tomentosa
Ornithogalum umbellatum
Ottelia alismoides
Oxalis stricta
Pachysandra terminalis
Paederia foetida
Panicum antidotale
Panicum repens
Parthenocissus quinquefolia
Paspalum notatum
Paspalum urvillei
Passiflora foetida
Tragopogon porrifolius
Tragopogon pratensis
Trapa natans
Triadica sebifera
Tribulus terrestris
Trifolium arvense
Trifolium campestre
Trifolium dubium
Trifolium hybridum
Trifolium pratense
Trifolium repens
Tussilago farfara
Typha latifolia
Ulex europaeus
Ulmus pumila
Urtica dioica
Utricularia gibba
Valeriana officinalis
Verbascum blattaria
Verbascum thapsus
Verbascum virgatum
Verbena bonariensis
Veronica anagallis-aquatica
Veronica arvensis
Veronica beccabunga
Veronica peregrina
Vicia cracca
Vicia sativa
Vicia villosa
Vinca major
Vinca minor
Vincetoxicum nigrum
Vulpia bromoides
Wisteria sinensis
Woodwardia radicans
Xanthium strumarium
Zeuxine strateumatica
Zizania aquatica

Table S2: List of all bird species used in this thesis.

- *Acridotheres cristatellus*
- *Acridotheres fuscus*
- *Acridotheres ginginianus*
- *Acridotheres grandis*
- *Acridotheres javanicus*
- *Acridotheres tristis*
- *Agapornis fischeri*
- *Agapornis personatus*
- *Agapornis roseicollis*
- *Alectoris barbara*
- *Alectoris graeca*
- *Amandava amandava*
- *Amazona albifrons*
- *Amazona amazonica*
- *Amazona autumnalis*
- *Amazona finschi*
- *Amazona oratrix*
- *Amazona viridigenalis*
- *Aplonis panayensis*
- *Ara ararauna*
- *Ara severus*
- *Aratinga erythrogenys*
- *Aratinga holochlora*
- *Aratinga mitrata*
- *Aratinga nana*
- *Athene noctua*
- *Bambusicola thoracicus*
- *Bonasa umbellus*
- *Brotogeris chiriri*
- *Brotogeris versicolurus*
- *Cacatua galerita*
- *Cacatua sanguinea*
- *Callipepla californica*
- *Callipepla gambelii*
- *Cardinalis cardinalis*
- *Cereopsis novaehollandiae*
- *Chloebia gouldiae*
- *Chloephaga picta*
- *Chrysolophus amherstiae*
- *Chrysolophus pictus*
- *Colinus virginianus*
- *Copsychus malabaricus*
- *Copsychus saularis*
- *Corvus splendens*
- *Coturnix ypsilophora*
- *Crotophaga ani*
- *Cygnus atratus*
- *Dacelo novaeguineae*
- *Estrilda astrild*
- *Estrilda caerulescens*
- *Estrilda melpoda*
- *Estrilda troglodytes*
- *Euplectes afer*
- *Euplectes franciscanus*
- *Forpus passerinus*
- *Foudia madagascariensis*
- *Francolinus erckelii*
- *Francolinus francolinus*
- *Francolinus pondicerianus*
- *Garrulax canorus*
- *Geopelia striata*
- *Gracula religiosa*
- *Gymnorhina tibicen*
- *Leiothrix lutea*
- *Lonchura atricapilla*
- *Lonchura cantans*
- *Lonchura castaneothorax*
- *Lonchura malabarica*
- *Lonchura malacca*
- *Lonchura punctulata*
- *Lophura ignita*
- *Lophura leucomelanos*
- *Lophura nycthemera*
- *Lyrurus tetrix*
- *Meleagris gallopavo*
- *Menura novaehollandiae*
- *Molothrus bonariensis*
- *Mycteria leucocephala*
- *Myiopsitta monachus*
- *Nandayus nenday*
- *Neochmia temporalis*
- *Nesoenas picturata*
- *Numida meleagris*
- *Nymphicus hollandicus*
- *Padda oryzivora*
- *Paroaria capitata*
- *Paroaria coronata*
- *Pavo cristatus*
- *Phasianus colchicus*
- *Pica pica*
- *Platycercus eximius*
- *Ploceus cucullatus*
- *Ploceus manyar*
- *Ploceus melanocephalus*
- *Poicephalus senegalus*
- *Porphyrio porphyrio*
- *Psittacula cyanocephala*
- *Psittacula eupatria*
- *Psittacula krameri*
- *Pterocles exustus*
- *Pycnonotus aurigaster*
- *Pycnonotus cafer*
- *Pycnonotus jocosus*
- *Serinus canaria*
- *Serinus mozambicus*
- *Sicalis flaveola*
- *Streptopelia chinensis*
- *Streptopelia decaocto*
- *Streptopelia senegalensis*
- *Streptopelia tranquebarica*
- *Struthio camelus*
- *Syrmaticus reevesii*
- *Taeniopygia guttata*
- *Vidua macroura*

Table S3: List of all mammal species used in this thesis.

Aepyceros melampus	*Macropus rufogriseus*	*Pseudocheirus peregrinus*
Ammotragus lervia	*Martes martes*	*Rattus argentiventer*
Antilope cervicapra	*Microtus arvalis*	*Rattus exulans*
Atelerix algirus	*Muntiacus reevesi*	*Rattus nitidus*
Axis axis	*Mus musculus*	*Rattus norvegicus*
Bandicota indica	*Mustela erminea*	*Rattus praetor*
Boselaphus tragocamelus	*Mustela nivalis*	*Rattus rattus*
Cervus elaphus	*Mustela putorius*	*Rattus tanezumi*
Cervus nippon	*Mustela sibirica*	*Rupicapra rupicapra*
Crocidura russula	*Myocastor coypus*	*Rusa unicolor*
Crocidura suaveolens	*Myodes glareolus*	*Sciurus carolinensis*
Dama dama	*Neovison vison*	*Sciurus niger*
Didelphis marsupialis	*Nyctereutes procyonoides*	*Sciurus vulgaris*
Erinaceus europaeus	*Odocoileus virginianus*	*Spilocuscus maculatus*
Genetta genetta	*Ondatra zibethicus*	*Suncus murinus*
Glis glis	*Oreamnos americanus*	*Sus scrofa*
Herpestes ichneumon	*Oryctolagus cuniculus*	*Sylvilagus floridanus*
Herpestes javanicus	*Ovibos moschatus*	*Tamias sibiricus*
Hydropotes inermis	*Paguma larvata*	*Tamiasciurus hudsonicus*
Hystrix cristata	*Petaurus breviceps*	*Vulpes lagopus*
Lepus europaeus	*Phascolarctos cinereus*	*Vulpes vulpes*
Lepus timidus	*Procyon lotor*	

Table S4: List of sources used to classify populations as native or naturalised. Unless otherwise stated plant sources were accessed June 2017, bird and mammal sources were accessed September 2017.

Taxon	**Citation**
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MAMMALS	IUCN (2019). The IUCN Red List of Threatened Species. Version 2019-1. http://www.iucnredlist.org.

Table S5: List of sources that provided either first introduction date or first observed record of introduced species. Taxa indicates which taxonomic group the source covered. All sources accessed March 2018.

Citation	**Taxa**
Atlas of Living Australia website (2019) at http://www.ala.org.au.	plant
Dyer, E. E., Redding, D. W., & Blackburn, T. M. (2017). The global avian invasions atlas, a database of alien bird distributions worldwide. Scientific data, 4, 170041.	birds
Early, R., & Sax, D. F. (2014). Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. Global ecology and biogeography, 23(12), 1356-1365.	plant
European Commission - Joint Research Centre (2019). European Alien Species Information Network (EASIN) https://easin.jrc.ec.europa.eu/	plant
Long, J. (2003). Introduced Mammals of the World.,(CSIRO Publishing: Melbourne.).	mammals
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Table S6: Copy of plant dispersal category definition table, as presented in Vittoz & Engler (2007). Dispersal is defined as a ranked category, estimated as the upper limits of the distances within which 50% and 99% of the seeds of a plant population are dispersed. Dispersal category is determined by a species' associated life history traits, which can include its dispersal vectors, its height its main habitat and its taxonomic group.

Dispersal category	**Dispersal distances (m)**		**Associated life history traits**
	50%	**99%**	
1	0.1	1	Blastochory (autochory)
			Boleochory (anemochory) for species < 30 cm
			Ombrochory (hydrochory)
2	1	5	Ballochory (autochory)
			Cystometeorochory (anemochory)
			Chamaechory (anemochory) for fruits in grassland
			Boleochory (anemochory) for species > 30 cm
3	2	15	Pterometeorochory (anemochory) for herbs
			Myrmecochory (zoochory)
			Cystometeorochory (anemochory) ferns, Orchidaceae, Pyrolaceae, Orobanchaceae in forest

			Trichometeorochory (anemochory) in forest or little efficient plumes
			Epizoochory (zoochory) for small mammals
4	40	150	Chamaechory (anemochory) for seeds on snow or dry inflorescence
			Pterometeorochory (anemochory) for trees
			Dyszoochory (zoochory) for seeds not stocked and dispersed by small animals
5	10	500	Trichometeorochory (anemochory) in openland with efficient plumes
			Cystometeorochory (anemochory) ferns, Orchidaceae, Pyrolaceae, Orobanchaceae in openland
6	400	1500	Dyszoochory (zoochory) for seeds stocked by large animals
			Endozoochory (zoochory) for seeds eaten by birds and large vertebrates
			Epizoochory (zoochory) by large mammals
7	500	5000	Agochory (anthropochory)

Table S7: All plant growth forms used in this analysis. This is a simplified form of the IUCN classification scheme (available from https://www.iucnredlist.org/resources/classification-schemes), and includes the following forms:

Form	**Definition**
annual	An annual plant, also termed a Therophyte
herbaceous perennial	Biennial or perennial herbacaeous plant, also termed a Hemicryptophyte
shrub	Perennial shrub (any size), also termed a Phanerophyte if >1m or a Chamaephyte if <1 m
tree	Tree (any size), also termed a Phanerophyte (>1 m)
grass	Grasses, sedges, restios
succulent	Succulent (leaves, stems, etc.) of any form
climber	Vines, lianas and creepers
fern	Ferns and fern-allies

Table S8: An example Bayesian model based on a beta distribution with a logit link written in JAGs. This model contains one continuous parameter (beta1), and one hierarchical effect (cat1). N is the total sample size, N_cat1 is the total number of levels of cat1, y is the response variable, x1 is the continuous predictor variable (scaled to have a mean of 0 and a standard deviation of 2).

```
model
{
### MODEL section
  for (t in 1:N) {
   #define a beta distribution
    y[t] ~ dbeta(a[t], b[t])
   #create a parameter for a post-predictive check
    y_pred[t] ~ dbeta(a[t], b[t])

    #extract loglikelihood (needed for WAIC)
    LogLik[t] <- log(dbeta(y[t], a[t], b[t]))

   #define a and b terms for beta distribution
    a[t] <- mu[t] * phi
    b[t] <- (1 - mu[t]) * phi

   #define logit link.  Equation is a simple linear a+bx with a hierarchical effect on b
    logit(mu[t]) <- alpha[cat1[t]] +
                        beta1[cat1[t]] * x1[t]
  }

### PRIOR section
  # Priors will loop across all levels of hierarchical effect.
  for(j in 1:N_cat1){
       alpha[j] ~ dnorm(mu_alpha, sigma_alpha^-2)
       beta1[j] ~ dnorm(mu_beta1, sigma_beta1^-2)
  }

  # Priors for continuous parameter. Intercept varies around -1, continuous parameter
varies around 0
  mu_alpha ~ dnorm(-1, 2^-2)
  mu_beta1 ~ dnorm(0, 1^-2)

  #specify hierarchical priors as a half-Cauchy distribution with a long tail.
  sigma_alpha ~ dt(0,5,1)T(0,)
  sigma_beta1 ~ dt(0,5,1)T(0,)

  #define prior for dispersion of the model
  phi ~ dunif(0, 10)
}
```

Table S9: Correlates of range filling for plants, and model verification, for use in sensitivity analysis. This table presents results for the same model as in Table 3.2, but with a threshold of 20 grid-cells with naturalised occurrences, instead of 5. Estimates for parameters retained in the final model are given as the mean estimate of all posterior draws, with the 5% and 95% estimates as confidence intervals in parentheses. Parameter estimates are given as the linear slope of the logit link equation. When parameter estimates vary across realms, this is indicated by providing the names of the realms in which it varies (Aus = Australian, Nea = Nearctic, Neo=Neotropical). Model verification data are given for the final models, including sample size, Widely Applicable Information Criterion (WAIC) of the model, the effective number of parameters (pD), and correlation of the linear predictor against the link transformed response given as a pseudo R-squared.

	Model Parameter	**Estimate**	**95% CI**	**Differences between realms?**	**Model Verification**	**Estimate**
Plants	Intercept	-1.98	(-1.25, -2.71)	Aus	Sample Size	411
	Years since Introduction	0.27	(0.45, 0.11)		DIC	-738.13
	Days till Flowering (logged)	-0.16	(0.03, -0.31)	Aus, Nea	pD	16.13
	Local sampling effort	-0.21	(0.53, -0.74)	Aus	Pseudo R-Squared	0.31

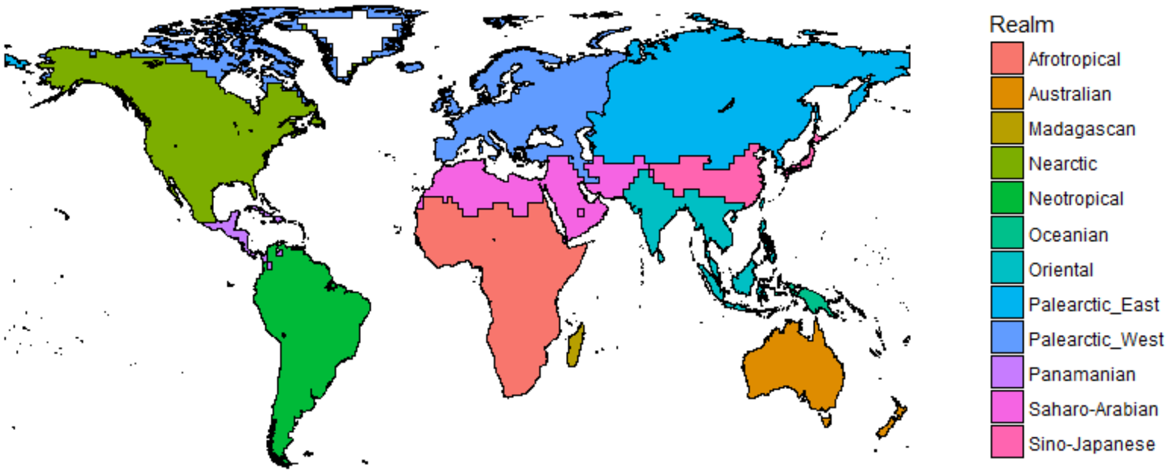


Figure S1: Biogeographic realms as defined by Holt et al (2013). Note the line between the western and eastern Palearctic has been added along the Ural mountains and is not a distinction in the original study.

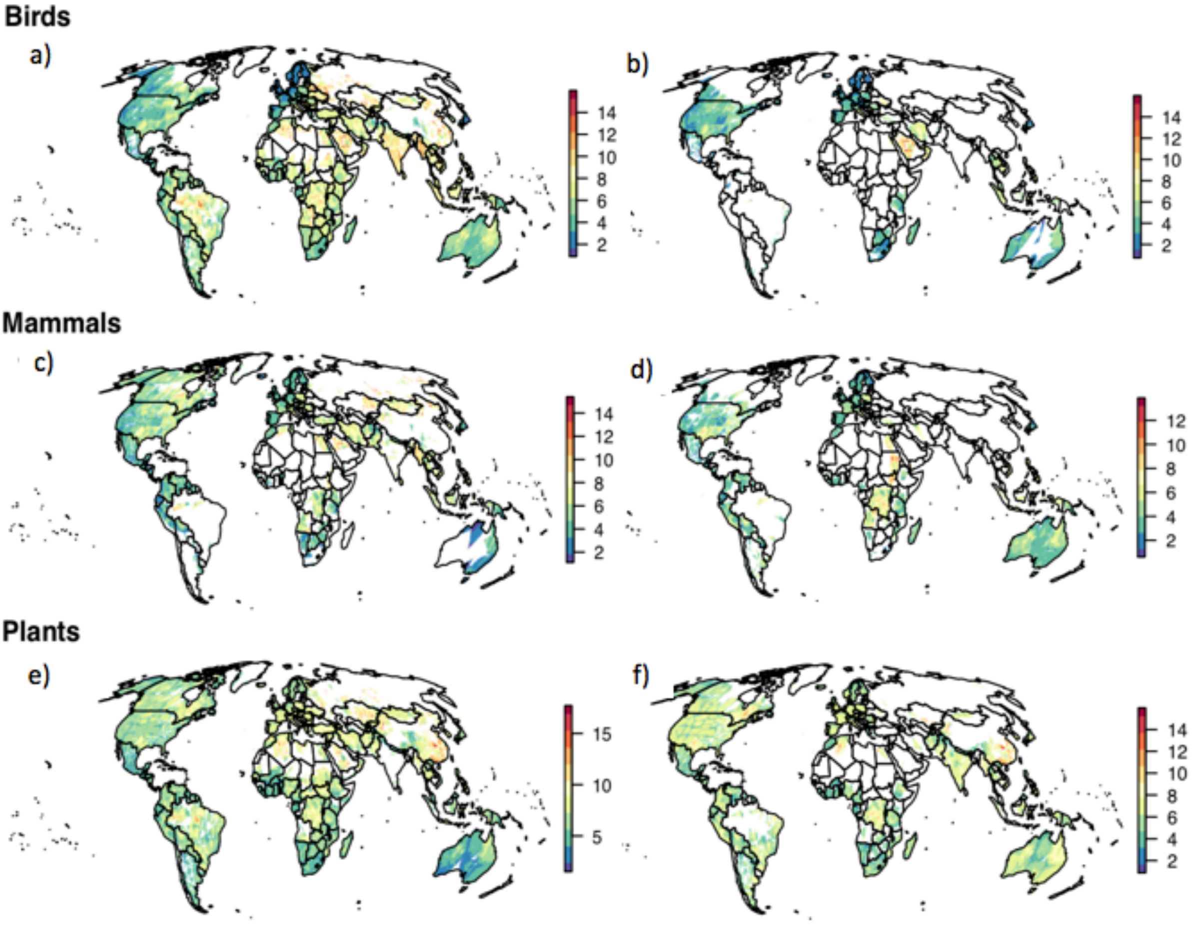
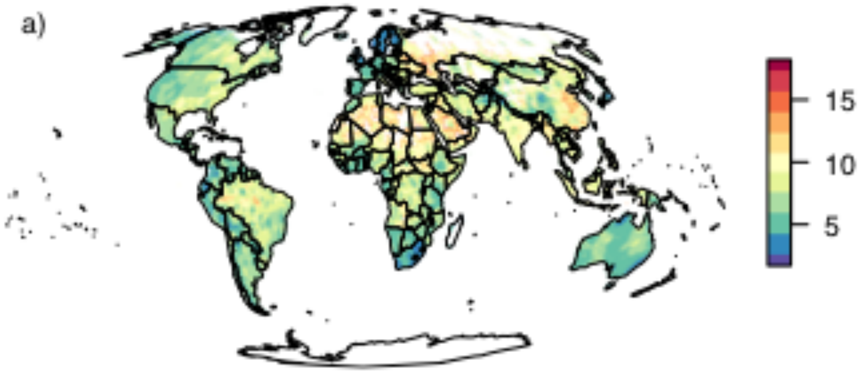


Figure S2: Number of native species (a,c,e) and naturalised species (b, d, f) globally in collated dataset. Native and naturalised range polygons are overlaid to give total number of species present for birds (a,b), mammals (c,d) and plants (e,f). The number of species is then offset by estimate of logged reporting effort, scale is therefore number of species multiplied by the inverse of the detection probability

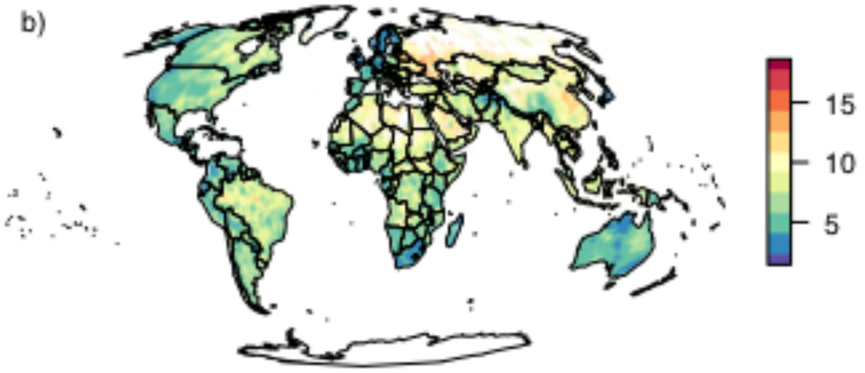
Birds

a)



Mammals

b)



Plants

c)

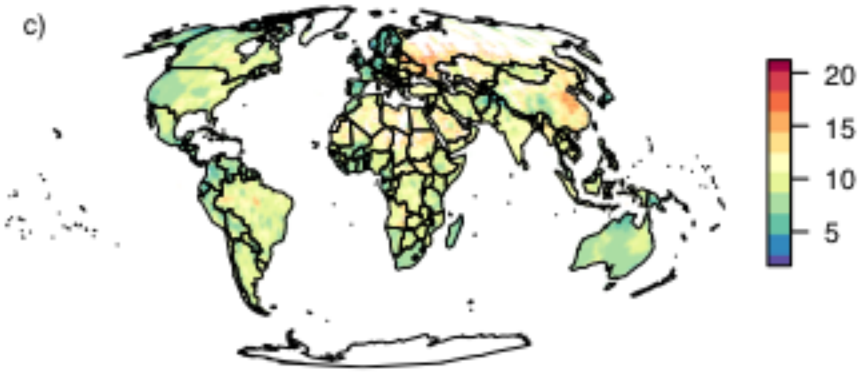


Figure S3: Threat of invasion globally. For each naturalised species I calculated all climatically suitable area within the naturalised region (black borders in figure) and then overlaid them. The number of species that could potentially colonise each geographic grid-cell is offset by estimate of reporting effort. The scale is therefore number of species multiplied by the inverse of the detection probability.

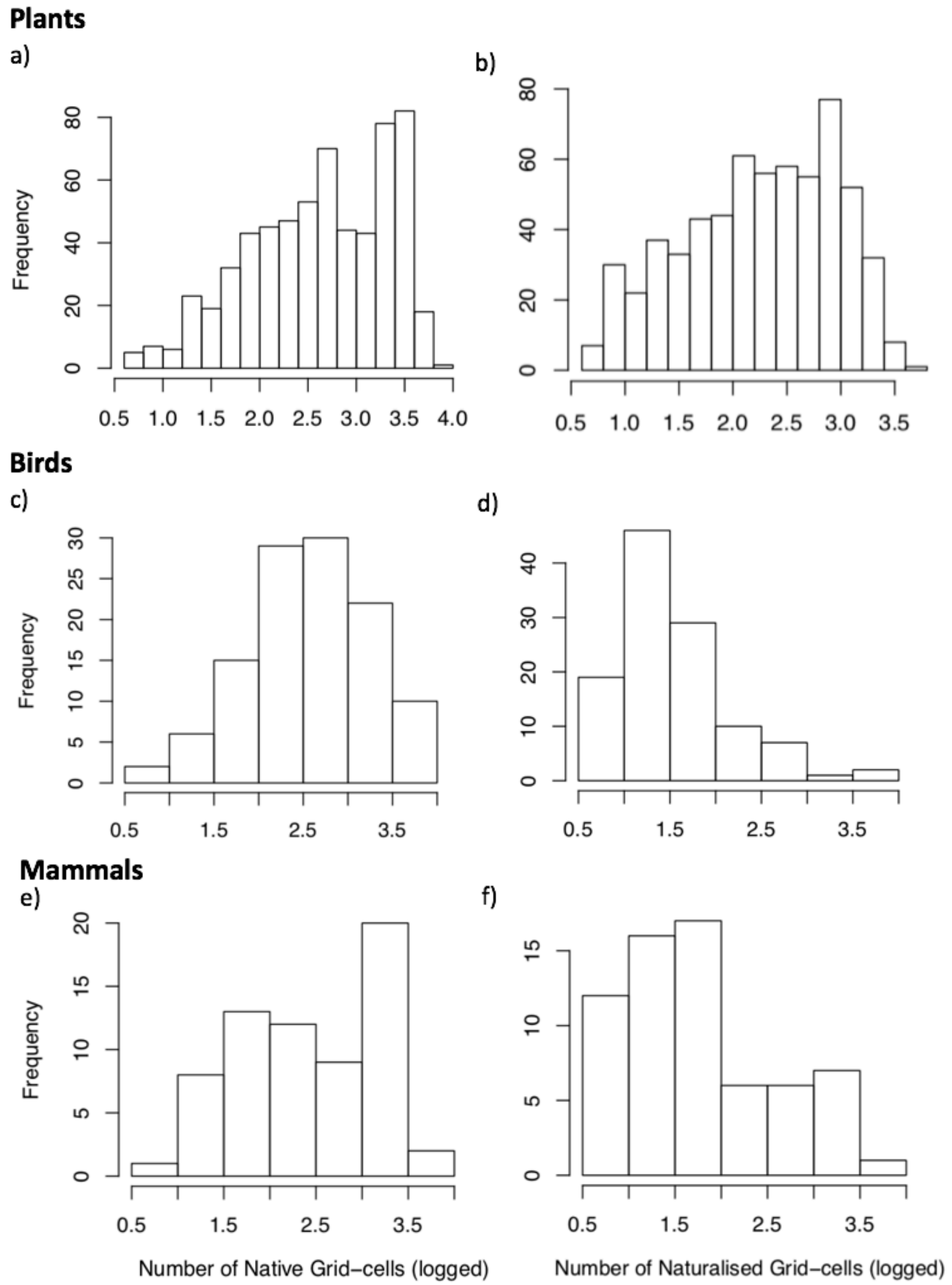


Figure S4: Summary of number of grid-cells occupied by each species in their native and naturalised ranges. Total number of grid-cells has been logged for all taxonomic groups. Number of grid-cells is shown for all native plant (a), bird (c) and mammal species (e), and all naturalised plant (b), bird (d) and mammal species (f) in the final global database.

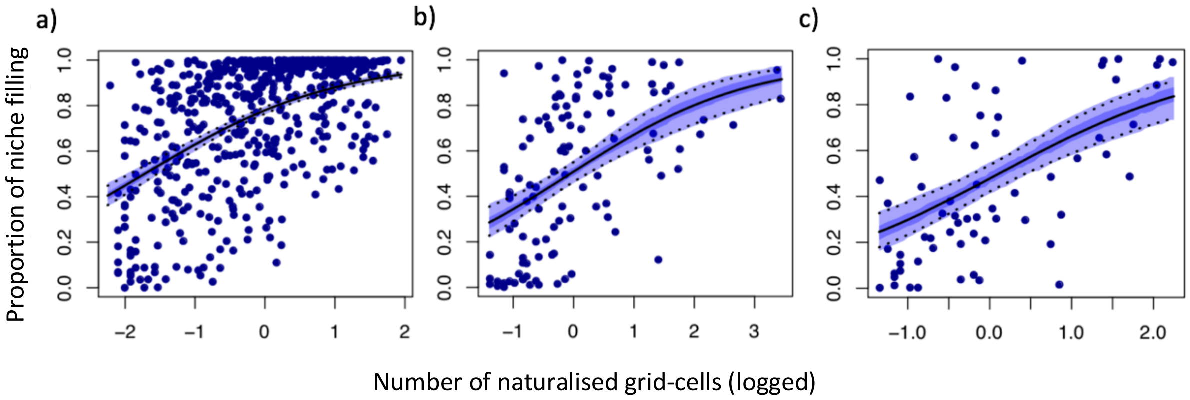


Figure S5: Correlation of number of naturalised grid-cells with proportion of niche filling for plants (a) birds (b) and mammals (c). A solid line signifies the estimate was consistently above or below 0 in >95% of simulations (and therefore judged as significant), a dashed line means it was not. The lighter shaded area shows the 95% probability density interval for the parameter estimate, and the darker shows the 50% interval.

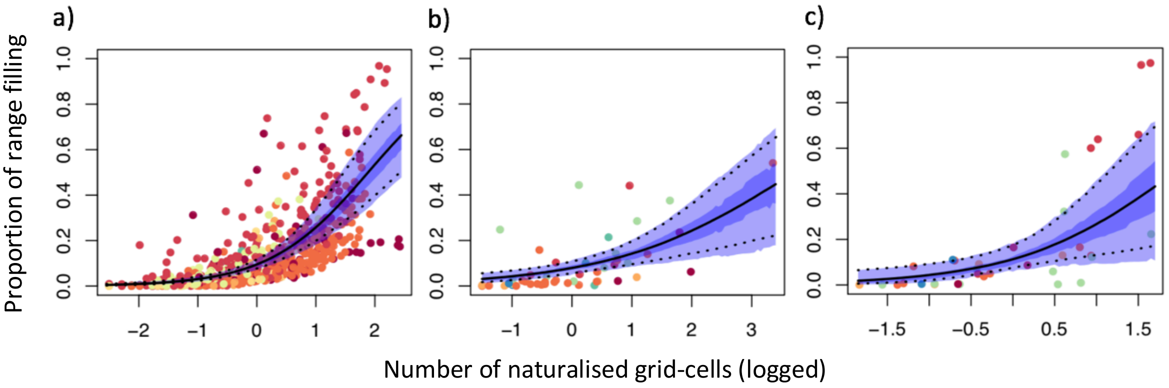


Figure S6: Correlation of number of naturalised grid-cells with proportion of range filling for plants (a) birds (b) and mammals (c). A solid line signifies the estimate was consistently above or below 0 in >95% of simulations (and therefore judged as significant), a dashed line means it was not. The lighter shaded area shows the 95% probability density interval for the parameter estimate, and the darker shows the 50% interval. Point colour represents region, but as parameter estimates did not vary between region, only the global regression line is shown.

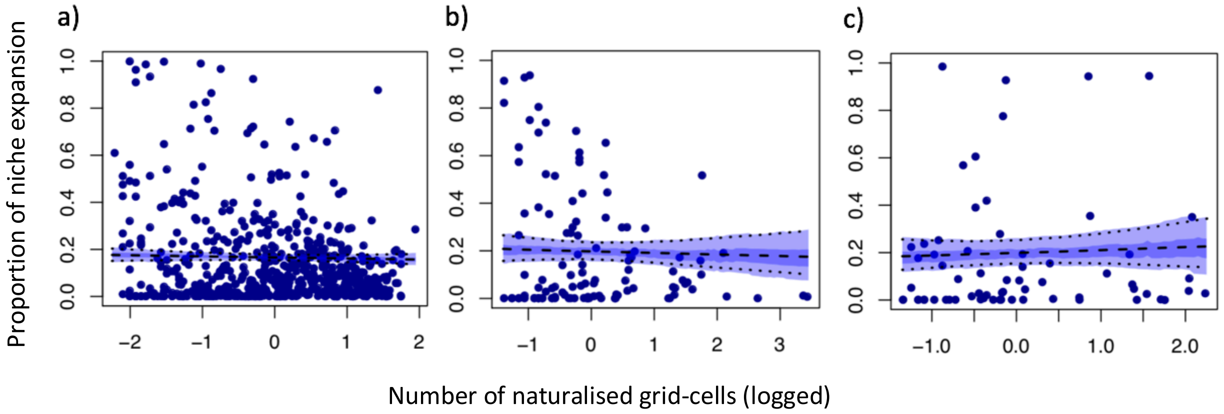


Figure S7: Correlation of number of naturalised grid-cells with proportion of niche expansion for plants (a) birds (b) and mammals (c). A solid line signifies the estimate was consistently above or below 0 in >95% of simulations (and therefore judged as significant), a dashed line means it was not. The lighter shaded area shows the 95% probability density interval for the parameter estimate, and the darker shows the 50% interval.

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