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The impacts of climate change and biotic interactions on non-native plants in Norway

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2022

Submitted for the degree of Doctor of Philosophy

Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other university. The research reported within this thesis has been conducted by the author unless indicated otherwise.

Katy Ivison

2022

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Abstract

Invasive species are considered one of the greatest threats to biodiversity today, causing huge ecological and economic impacts globally. Understanding the factors which may contribute to their success is therefore of paramount importance, particularly in a changing climate. Global warming is predicted to benefit invasive plants by increasing their potential range sizes, causing expansion into higher latitudes, and may result in increased plant performance due to the phenotypic plasticity traits shared by many invasive plants which facilitate their rapid response to change. In addition, biotic interactions, particularly in the form of herbivory, can largely impact the performance of invasive species. The enemy release hypothesis is a leading hypothesis to explain why invasive plants become successful in their invaded ranges, positing that their success is in part due to release from natural enemies. Other biotic interactions which might influence invasive plants include competition with native plants, which may limit the performance of invasive plants or even completely suppress their growth. Research into factors which may limit or facilitate invasive plants is even more important in high-latitude regions such as Norway where climate change is occurring at a faster rate. Norway is already home to over 2,000 non-native species and research into the effects of climate change or biotic interactions on non-native plants in Norway is lacking. In this thesis, I address climate change in terms of future temperature and precipitation changes, and I use latitude as a proxy to represent future climatic warming. I investigate biotic interactions mostly in terms of insect herbivory, but with some focus on competition with native plants. The majority of this work focuses on a variety of different non-native plant species in Norway, but I also include a study across Central and Northern Europe with a Norwegian focus. More specifically, I identified a set of high-risk species which are not yet present in Norway but could become naturalised or invasive if introduced, and investigated the areas of Norway most suitable to these species. I then investigated the enemy release hypothesis and how this changes across latitude, to predict changes in biotic interactions under climate change, using herbarium specimens and botanical garden survey data. Finally, I carried out a common-garden experiment in Norway to determine the effects of artificial warming, herbivore exclusion and native plant competition on the performance of a set of non-native species. From this research, I first found that Norway is already suitable to a large number of non-native species and that its suitability increases under climate change. I then found evidence both contradicting and supporting the enemy release hypothesis, and found that in some contexts herbivory levels are reduced at higher latitudes but in others herbivory does not differ across a latitudinal gradient. Finally, I found that artificial warming increases the performance of non-native species and that presence of herbivores and competition with native plants can limit non-native species performance. These results suggest that in Norway, climate change is likely to benefit non-native species either by causing Norway’s climate to be more hospitable and easier to invade, or by facilitating faster growth of non-native plants. Not all non-native plants benefit from enemy release and climate change may result in greater levels of herbivory in some contexts. Finally, non-native plants in Norway may be limited by native biota. These results, particularly in terms of enemy release, show how ecological trends can vary, and therefore highlight how generalisations within invasion science must be avoided and the importance of system-specific research. This research has implications for invasive species management in Norway, by demonstrating which factors may limit non-native plants in Norway and how they might respond to climate change, and should inform biosecurity decisions about which species’ import should be regulated.

Contents

Chapter 1

Introduction

1.1 Invasive species

Increasing anthropogenic activity has resulted in a huge upsurge of human-mediated dispersal of non-native plants around the world (Blackburn et al., 2011; van Kleunen et al., 2015), and many of these species have subsequently become established and have spread in their introduced range. Introductions can be intentional, such as the trade of plants for horticulture, forestry or agriculture (Reichard & White, 2001; Richardson, 1998), or unintentional, such as the contamination of shipped goods or luggage with seeds (Rahman et al., 2003; Ware et al., 2012). Invasion science is therefore an increasingly prevalent field of research that aims to develop understanding of the mechanisms by which species become invasive and how this can be prevented.

According to the Convention of Biological Diversity, invasive species are non-native species which have negative environmental or economic impacts on their invaded ecosystems (CBD, 2006) and are considered to be one of the greatest risks to biodiversity today (Chornesky & Randall, 2003). However, not all non-native species become invasive; a species which has simply been moved to an ecosystem outside its native range is known as 'introduced', and one which has established a self-sustaining population and is able to disperse within its non-native range is known as 'naturalised' (Richardson et al., 2000). A recent study has suggested that there are more than 13,000 plant species worldwide which have become naturalised in non-native ecosystems (van Kleunen et al., 2018). Because I will be investigating a range of different species in this thesis, herein I will use the phrase 'non-native' to refer to a species found outside its native range, regardless of its naturalisation status or negative impacts on the native ecosystem.

Numerous frameworks have been devised to explain biological invasions, the most common two proposed by Williamson in 1996 and Richardson et al. in 2000. These frameworks are mostly adopted by animal ecologists and plant ecologists respectively; however, a combination of these frameworks has since been proposed by Blackburn et al. (2011) which aims to address invasion ecology of all organisms. This revised framework takes into account stages of invasion and the barriers facing species at each stage (Figure 1**).** The specific characteristics of an organism that facilitate invasion success have been addressed in a further framework by Foxcroft et al. (2011), which comprises both species traits and traits relating to the invasibility of the new habitat. In addition, Foxcroft et al. (2011) discuss the importance of 'system context', which looks at the way in which organisms are transported, including the arrangement of habitats within a landscape and how these habitats interact. Figure 1 combines the frameworks of Blackburn et al. (2011) and Foxcroft et al. (2011), providing a comprehensive framework of invasion ecology. In this combined framework, each stage has been linked to a barrier which has the potential to prevent the organisms moving to the next stage as discussed by Blackburn et al. (2011). Each barrier has then been linked with contributors discussed by Foxcroft et al. (2011), which play an important role in how the barrier is overcome.

More generally, several ecological theories exist which were developed to understand the drivers behind invasions and the subsequent structure of invaded communities. One such theory is the community assembly theory, which suggests that the composition and species abundance of a community is determined by a series of barriers which new individuals must overcome. Some barriers are due to extrinsic processes such as dispersal, which determine which individuals can arrive to a particular community. Further barriers are associated with intrinsic processes such as abiotic or biotic factors, which act upon individuals which have successfully overcome extrinsic processes and drive the resultant composition and species abundance of the community (Pearson et al., 2018). Similarly to the framework outlined in Figure 1, community assembly theory takes both anthropogenic and biogeographic factors into account. Another theory states that community composition is driven partly by metacommunities, sets of local communities each containing species which may interact via dispersal (Wilson, 1992). In the context of invasion ecology, metacommunity theory can be used to investigate the interactions between local conditions and dispersal factors, such as propagule pressure, to explain the spread of invasive species within a metacommunity (Brown & Barney, 2021).

There are several characteristics of non-native plants which contribute to survival and establishment within a new community, including mode of dispersal, competitive ability and defence mechanisms. Low seed mass and rapid growth to reproductive age are particularly important factors to help plants increase their population size, as well as large native geographic range and climatic tolerance (Hellmann et al., 2008). These traits are often specifically selected for in trades such as horticulture to allow garden plants to grow in a range of countries and in different environmental conditions (Haeuser et al., 2019), and garden plants are a major source of exotic plants (van der Veken et al., 2008).

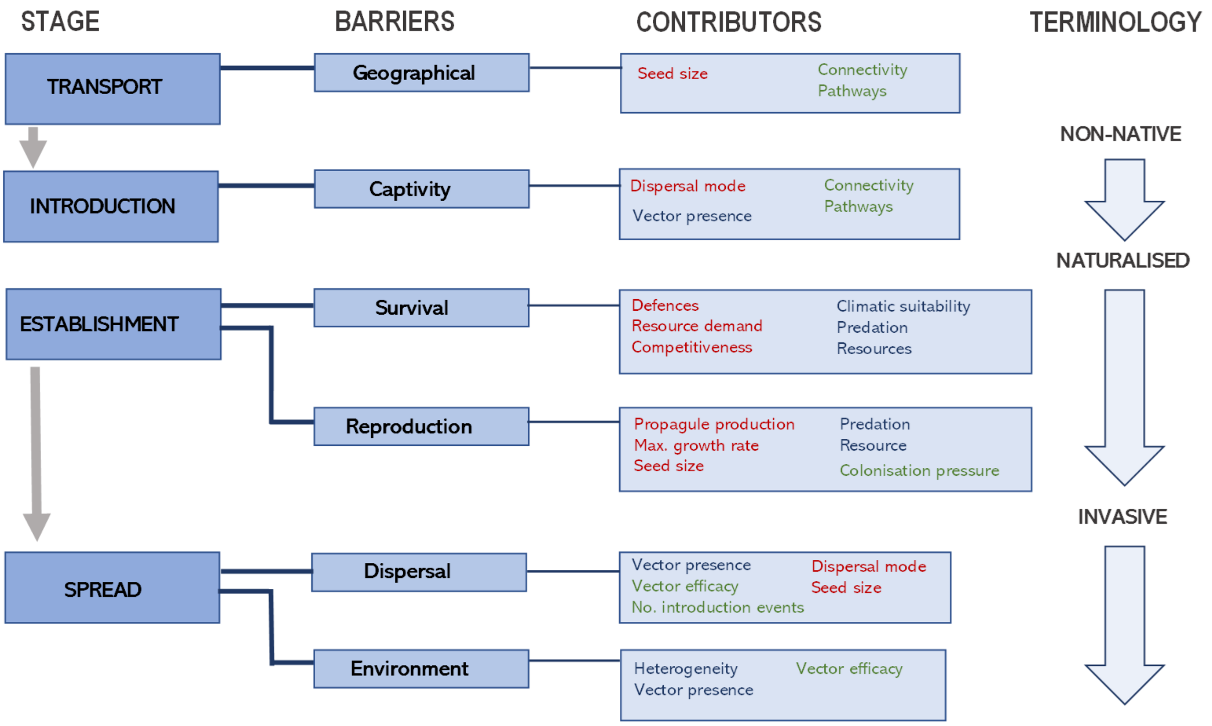


Figure 1: An invasion framework combining frameworks proposed by Blackburn et al. (2011) and Foxcroft et al. (2011). Red text in 'Contributors' section refers to species traits which influence invasion success. Green text refers to system characteristics which affect invasion success. Blue text refers to habitat factors which affect invasion success.

1.2 Impacts of non-native species

1.2.1 Ecological

Non-native plants can have huge and varied ecological impacts on recipient ecosystems. In a broad analysis of plant invasions within the literature, it was found that overall, non-native plants have a larger impact on native plants within the invaded ecosystem than on native animals or soil organisms (Pyšek et al., 2012). Impacts on plants include the competitive exclusion of native plants (Bezemer et al., 2014), resulting in reduced species richness (Hejda et al., 2009), and suppression of native plant growth (Chornesky and Randall, 2003). Other effects include altering soil chemistry (Weidenhamer & Callaway, 2010), causing changes in insect populations (Litt et al., 2014), hybridization of plant species and changes to pollination services (Pyšek et al., 2012).

1.2.2 Socioeconomic

Non-native species can be associated with huge economic costs and social impacts. One of the main industries affected by non-native species is agriculture, losing crop yields due to introduced weeds and losing livestock due to toxic introduced plants growing in pasture ground (Pimentel et al., 2001). Further impacts include reduced water supply due to plant growth in water sources, which can block the flow of water through infrastructure to human settlements, and increased risk of wildfires due to displacement of native plant species (Pimentel et al., 2001). In order to understand the economic costs of non-native species, the project InvaCost was established in 2014 to construct a database of all known economic costs associated with non-native species worldwide (Diagne et al., 2020). In addition to this database, InvaCost is associated with a number of publications highlighting the economic costs of non-native species to specific countries or taxa. For example, the annual costs (in US dollars) of managing the damaging effects of non-native species is around $21 billion in the US (Fantle-Lepczyk et al., 2022), around $20 billion in Australia (Bradshaw et al., 2021) and around $157 million in the UK (Cuthbert et al., 2021). Examples of individual species and their effects include *Hydrilla verticillata,* which grows in lakes and prevents their recreational use (Pimentel et al., 2005); Japanese knotweed *Fallopia japonica*, which can cause structural damage to buildings and affect water quality and flow rate when found along riverbanks (Metličar et al., 2019); and *Rhododendron ponticum* which invades forest sites in the UK and affects forest management (Edwards et al., 2000).

1.3 Factors which affect non-native species success

1.3.1 Climate change

Global surface temperatures have increased by an average of 0.78 °C since the mid 19th century, accompanied by loss of ice sheets and rising sea levels. Precipitation levels are changing and there has been an increase in the frequency of extreme weather events (IPCC, 2014). Understanding the performance of non-native plants under climate change is key in predicting their future impacts on ecosystems worldwide. Invasive plants tend to have a broader climatic niche and higher phenotypic plasticity than non-invasive plants (Davidson et al., 2011; Liu et al., 2017), traits which could help them perform better under climate change. A recent meta-analysis by Liu et al. (2017), where data concerning 74 non-native plant species and 117 native plant species was collected, showed that non-native species tended to perform better under increased temperature and CO_2 (Figure 2). As well as being able to adapt better than their native counterparts, non-native plants may benefit in other ways under climate change. Global warming is likely to lengthen the suitable seasons during which an introduction could happen and extend the range in which a non-native plant could survive. Longer warm periods also mean non-native plants may be able to produce fruit and reproduce within the growing season in areas with climates which, in the past, would not have supported such quick growth (Liu et al., 2017).

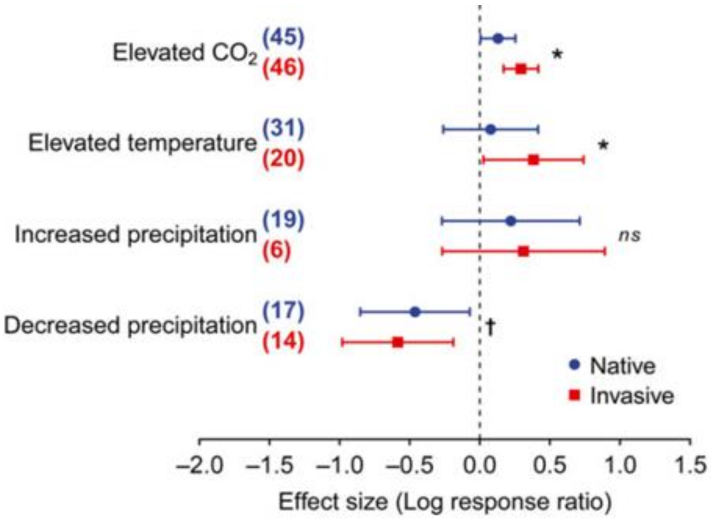


Figure 2: Performance of invasive and native plant species, using data from a meta-analysis. * indicates significant difference ($P<0.05$), *ns* indicates no significant difference, † indicates marginally significant difference ($P<0.1$). Edited from Liu et al. (2017).

One significant impact of climate change on both non-native and native plants is that warming enables plants to move to higher latitudes (Schweiger et al., 2010; van der Putten et al., 2010; Walther et al., 2009). In addition, changes in invasion success, such as increased performance and longer growing seasons, are likely to be more obvious at higher latitudes and altitudes (Walther et al., 2009). This has implications for species native to higher latitude areas which, as well as potentially facing competition from non-native plants in the future, have a slower growth rate than plants in warmer climates (Tolvanen & Kangas, 2016). It is therefore possible that under climate change, non-native plants may displace native species at high latitude and elevations.

1.3.2 Biotic interactions

The interactions, or lack of interactions, with native biota can have a significant effect on a non-native plant's ability to establish, reproduce and spread its range. Of these, herbivory is perhaps the most widely researched. Herbivory often determines the success of non-native plant populations (Huang et al., 2012) and can limit the range a species can expand to (van der Putten et al., 2010). However, herbivore species often differ between the native and invaded range of a non-native plant. One of the most widely researched hypotheses in invasion ecology is the enemy release hypothesis, which states that the success of non-native species could be due to their release from the natural enemies found in their native ecosystems. Darwin (1859) was arguably the first to posit that enemy release could be the reason why many non-native populations seem more successful than native populations (Mitchell et al., 2006). However, this hypothesis has been widely debated, with ambiguous results across studies (e.g. Colautti et al., 2004; Liu & Stiling, 2006; Meijer et al., 2016; Schultheis et al., 2015), and it relies on three main assumptions: first that the specialist enemies of the non-native plant are not present in the invaded range, second that specialist native herbivores will not switch hosts to non-native plants, and third that generalists will have a greater impact on native than non-native plants (Keane & Crawley, 2002).

Wolfe (2002) investigated herbivory of *Silene latifolia*, a plant native to Europe which has recently become invasive in North America. In native European populations of *S. latifolia*, 84% of studied plants showed damage from herbivory, whereas in non-native populations in America only 40% showed damage. European populations were attacked by up to 4 types of herbivore (sucking, chewing etc.), significantly higher than American populations. Finally, it was found that two specialist herbivores which feed on *S. latifolia* in Europe, a fungus and a seed predator, were absent in America. *S. latifolia* therefore escaped predation in its non-native habitat (Wolfe, 2002). Further studies include Castells et al. (2013) who found reduced seed predation of *Senecio pterophorus* in its introduced range and Xu et al. (2021) who carried out a meta-analysis of the literature and found lower levels of herbivory on non-native than native plant species. Other research has found links between enemy release and plant success in support of the enemy release hypothesis. The Scotch broom *Cytisus scoparius* has a lifespan of around 10 years in its native Europe; non-native *C. scoparius* in the US, however, have been found to live up to 20 years (Rees & Paynter, 1997). Prior to this, Waloff & Richards (1977) discovered that significantly more *C. scoparius* trees survived to 10 years when protected from herbivory in a plot experiment in the UK. This suggests that the extra longevity occurring in the non-native *C.*

scoparius populations in the US is at least in part due to a lack of native herbivores (Maron & Vila, 2001). Other studies include that of DeWalt et al. (2004) who found that the plant *Clidemia hirta* grows well in forested areas of its non-native range in Hawaii, but does not grow in forests in its native Costa Rica unless treated with insecticides. In addition, untreated plants suffered up to five times more leaf area damage in the native range than in Hawaii, suggesting that herbivory is far more abundant in the native range. In this case study, it seems that presence of natural enemies is preventing *C. hirta* from growing in native forests, but a lack of these enemies in Hawaii allows the plant to expand its range (DeWalt et al., 2004). Finally, in a study by Lakeman-Fraser & Ewers (2013) it was found that the shrub *Macropiper excelsium* was able to spread more outside its natural range due to absence of its main herbivore, the moth *Cleora scriptaria*.

There is some debate as to how much enemy release influences non-native plant success, as many plants thrive in their native communities despite an abundance of native herbivores. A meta-analysis by Colautti et al. (2004) found that only around half of the reviewed studies of non-native plants support the enemy release hypothesis, and of these fewer linked enemy release to significant increase in plant success. Another meta-analysis by Chun et al. (2010) found that non-native plants did not have lower levels of herbivory compared to natives, and that their performance was not reduced in the presence of enemies. However, they did find that non-native plant performance was lower than native plant performance in the presence of enemies, suggesting that non-native plants were less tolerant to herbivory than native species (Chun et al., 2010) . The enemy release hypothesis is thought to rely on whether more damage is done to a plant by a specialised native enemy, in which case escaping its native habitat would benefit the non-native species, or by a generalist enemy in the introduced range (Maron and Vilà, 2001). The latter, if true, would then support the opposing hypothesis of biotic resistance, originally suggested by Elton (1958).

The biotic resistance hypothesis states that interacting with native biota, such as competing with plant species or suffering from herbivory, hinders the ability of a non-native plant to establish and spread (Elton, 1958; Maron & Vila, 2001). For example, one study found that three species of tree were once introduced to tropical areas for use in forestry and none was able to become naturalised due to such high herbivory levels (Mack, 1996). Another study found that introduced species can accumulate herbivores rapidly; in Florida, the introduced oak *Quercus acutissima* was found to have acquired just as many leaf-miners as the native oak species in under 20 years since its introduction (Auerbach & Simberloff, 1988).

The range of studies both supporting and opposing the enemy release hypothesis demonstrate how the interactions between native herbivores and non-native plants can vary depending on ecosystem and context. It is therefore difficult to make assumptions about the factors which affect non-native species in a system which has not been studied before, and including herbivory in invasion ecology research is important to fully understand the limitations faced by non-native species.

1.3.3 Climate change and biotic interactions

The interactions between non-native plants and their surrounding biota make predicting their response to climate change more difficult (van der Putten et al., 2010), and range-shifting of non-native species due to climate change means there will be ever more novel interactions between the plants and organisms in their new environment (Schweiger et al, 2010).

Latitudinal studies are an effective way of observing how non-native plants interact with other biota under different climatic conditions, particularly across temperature gradients (Frenne et al., 2013). One such latitudinal study used a line transect from Louisiana (USA) to Quebec (Canada) to compare herbivory rates of native and non-native genotypes of the common reed *Phragmites australis*. *Phragmites australis* is native to both North America and Europe, but European genotypes were introduced to North America and have since become widespread and invasive. It was found that herbivory of the native genotype decreased as latitude increased; however, non-native genotypes did not exhibit any gradient of herbivory and generally showed much lower levels of herbivory than their native counterparts. These results show support for the enemy release hypothesis in that the non-native *P. australis* left its natural enemies behind when it became introduced to North America. At lower latitudes the non-native *P. australis* may therefore show greater invasion success as it suffers less from herbivory than the native species. However, lower herbivory levels of the native genotype at higher latitudes are likely due to fewer native herbivores, and therefore mean that non-native genotypes' competitive advantage over native genotypes is likely to be lessened. In the future, climate warming may mean that natural enemies shift their range to higher latitudes, resulting in greater herbivory of native *P. australis* and benefitting the non-native genotype as observed at lower latitudes today (Cronin et al., 2015). Figure 3 demonstrates how herbivory might change across latitudes, showing lower levels at higher latitudes for native plants and remaining constant for non-native plants.

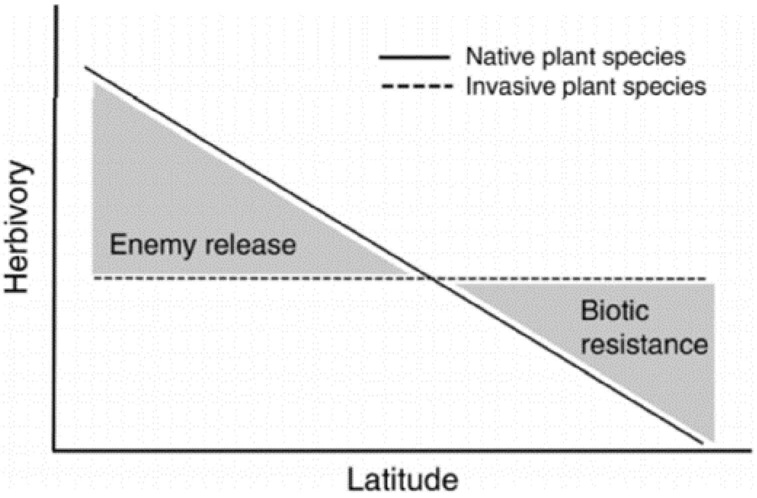


Figure 3: Representation of how herbivory levels differ between native and invasive plant species across a latitudinal gradient. Herbivory decreases as latitude increases for native species but non-native species herbivory remains at a low, constant level. At lower latitudes, native species undergo high levels of herbivory and non-native species escape from herbivory. At higher latitudes, there is less herbivory of native species which can then compete with non-native species. Adapted from Cronin et al. (2015).

Another latitudinal study by Lu et al. (2013) investigated the relationship between the non-native plant *Alternanthera philoxeroides* and the beetle used as a biocontrol, *Agasicles hygrophila. Alternanthera philoxeroides*, invasive to China, has been moving further north, with a corresponding decrease in abundance of its biocontrol *A. hygrophila*; *A. philoxeroides* is therefore released from this enemy at higher latitudes. The biocontrol species is likely to move further north under climate warming and will begin to control populations of *A. philoxeroides* at their current latitude, but it is also probable that *A. philoxeroides* will move further north still and escape its enemies again. In this case, the interactions between the non-native plant and its natural enemy are critical in determining the future for higher-latitude ecosystems in China (Lu et al., 2013).

Both aforementioned case studies investigating how herbivory changes across a latitudinal gradient (Cronin et al., 2015; Lu et al., 2013) highlight a further ecological concept; the latitudinal biotic interactions hypothesis. This hypothesis states that biotic interactions, such as herbivory, become less prevalent at higher latitudes due to lower species diversity and less tolerable climates (Schemske et al., 2009). This trend is observed in the above studies and further evidence has been found by Kambo & Kotanen (2014), who found that herbivory of lesser burdock *Arctium minus* decrease with latitude in Ontario, and Moreira et al. (2018) who found the same trend for English oak *Quercus robur* across a latitudinal gradient from Spain to the Netherlands. However, there are several studies which found no evidence supporting the latitudinal biotic interactions hypothesis (Cronin et al., 2015; Moles et al., 2011; Xu et al., 2021). By investigating this hypothesis, it is possible to infer how herbivory levels might change with latitude and therefore might be affected by a warming climate, as interactions currently observed at lower latitudes can be used to predict how interactions at higher latitudes might develop under climate change (Frenne et al., 2013).

1.3.3.1 Phenology

Many key interactions between plants and other biota rely on phenological events, such as germination or reproduction. Plants often respond to climate change with shifts in their phenology (Hellmann et al., 2008; Van der Putten et al., 2010), whereas the phenology of interacting biota does not always change in the same way. This can result in greatly varying consequences for the plant. For example, Liu et al. (2011) observed a phenological advance of flowering by one week in *Gentiana formosa* under experimental warming of 1.5 °C. This resulted in a much higher herbivory rate due to earlier flowering, and reproductive success declined. In contrast, when St John's wort *Hypericum perforatum* developed earlier in the year in response to warming, it was exposed to fewer herbivores and reproductive success increased (Fox et al., 1999). However, little research has been carried out about the effects of phenological change on the interactions of non-native plants with native biota.

1.4 Non-native species in Norway

The most recent inventory of non-native species in Norway was published in 2019. 2,496 non-native species were identified, with 1,039 of these naturalised, making up 3% of all reproducing species in Norway. Plants made up the largest percentage of naturalised species (71%; Figure 4a), representing 22 families, the most abundant of which was Rosaceae followed by Asteraceae. Norway was found to have the most naturalised plant species of all European countries except the UK (Sandvik et al., 2019). The number of naturalised species in Norway is lower in higher-latitude counties (Figure 4b), and in the high Arctic, although species have been introduced, none of these had been classed as invasive in 2015 (Alsos et al., 2015). However, a higher rate of human-mediated dispersal and increasing suitability of climate for non-native species under climate change means that the number of non-native species found at higher latitudes has increased, with more successfully naturalising (Alsos et al., 2015). An example of a widespread non-native plant in the Norwegian Arctic is *Heracleum persicum* (Persian hogweed). This species is extremely common throughout Norway, found as far north as the Troms and Finnmark regions (the two most northern counties in Figure 4b). It has become so well-known that it has been given the nickname *tromsøpalme* and is an unofficial emblem of the city Tromsø. It is now very well-established and is detrimental to local flora (Alm, 2013).

It is not just mainland Norway currently at risk. In recent decades Svalbard, a Norwegian archipelago in the Arctic Ocean, has seen an increase in tourism by 225%, coupled with an increase in scientific research (Ware et al., 2012). These trips often result in inadvertent introduction of non-native species; one study found that of a set of tourists travelling to Svalbard, 75% were wearing shoes capable of carrying substantial amounts of soil, and 40% of tourists' shoes actually carried seeds; one tourist was even found to be carrying 117 seeds on their shoes. Of the seeds removed from shoes, 26% successfully germinated when grown experimentally under simulated Svalbard conditions (Ware et al., 2012).

1.4.1 The Norwegian climate

Norway has a diverse range of ecosystems and climates, with higher temperatures around the southern and western coasts and average annual temperatures ranging from below -8° Celsius (C) to above 8° C. Rainfall is heaviest along the southwest coast of Norway, with annual precipitation levels ranging from less than 500 mm to more than 6,000 mm (Norwegian Climate Service Centre, 2021). According to the bioregions presented by One Earth, defined as major subdivisions of the earth's biomes, Norway contains two bioregions: Ural Mountains & West Eurasian taiga forests, and Scandinavian birch & coastal conifer forests. Within these bioregions, more specific classifications of 'ecoregions' include Scandinavian coastal conifer forests, which contain areas of boreal rainforest, Scandinavian montane birch forests & grasslands, which contain high altitude plateaus, and Scandinavian & Russian taiga, the largest ecoregion in Europe spanning Scandinavia and northern Russia (One Earth, 2022).

High latitude countries such as Norway are predicted to undergo a faster rate of warming than lower latitudes (IPCC, 2014). More specifically, Norway's temperatures are predicted to increase by an average of 4.5° C by 2100 under the most severe climate change scenario, with the largest warming effect seen in winter and in the north of Norway (Hanssen-Bauer et al., 2017), compared to the global mean predicted temperature increase of 2° C by 2100 under the same climate change scenario (IPCC, 2014). This is likely to increase the climatic suitability of Norway to non-native species, as some non-native species are currently prevented from naturalising within Norway due to its inhospitable climate (Gjershaug et al., 2009). However, apart from suggesting an increase in the number of non-native species under climate change (Alsos et al., 2015; Gjershaug et al., 2009; Ware et al., 2012), we lack studies that address how climate change may affect the performance of non-native plants in Norway and their biotic interactions.

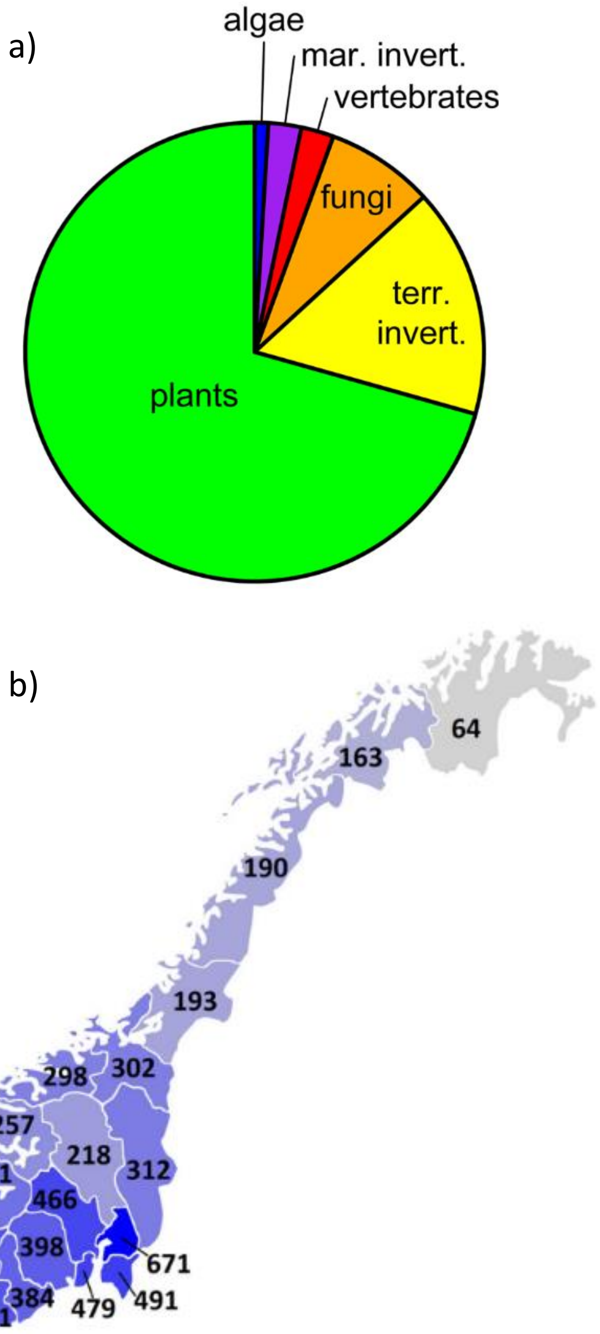


Figure 4: The proportion of naturalised non-native species in Norway in each taxonomic group (a) and the number of naturalised non-native species found in each Norwegian county (b). Adapted from Sandvik et al. (2019).

1.5 Knowledge gaps & project aims

The studies discussed in this review demonstrate the large amount of research which has been carried out to understand the biotic interactions experienced by non-native plants and their response to climate change. For the enemy release hypothesis and the latitudinal biotic interactions hypothesis, support has been found in some studies and not in others. Predicting the effects of biotic interactions and climate change on non-native species in an ecosystem is therefore likely to be difficult.

Non-native plant research throughout the literature is highly skewed, with only 21 species making up 50% of all studies investigating the impact of non-native plants in 2012 (Pyšek et al., 2012), although this may have since changed. Many experiments take place in North America (Carroll et al., 1997; Cronin et al., 2015; Parker & Hay, 2005) and Asia (Fan et al., 2016; Lu et al., 2013), and studies in Norway have been scarce. There are also many studies investigating the interplay between non-native plants and biotic interactions (e.g. Auerbach and Simberloff, 1988), or the response of non-native plants to climate (e.g. Schweiger et al., 2010), but there are fewer studies which take both variables into account. Understanding how these factors influence non-native plants is particularly important in a country such as Norway which will undergo faster rates of warming than lower latitude regions (IPCC, 2014). This suggests a large knowledge gap which I will address in this thesis. Specifically, I aim to answer the following questions: 1) How climatically suitable is Norway to non-native plants and how might this change under climate warming? 2) How do non-native plants in Norway interact with native herbivores and will this change under climate change? 3) How do biotic interactions (insect herbivory and native plant competition) and climate change interact to affect non-native plant success in Norway? I carried out the following research to investigate these questions, the answers to which may help in informing biosecurity efforts and in making decisions about non-native plant management.

Chapter 2: Horizon scanning of potentially invasive plant species in Norway under a changing climate

It is important to prevent the further introduction of non-native species to Norway, so here I carried out a horizon scanning study to identify a list of high-risk species not yet established in Norway but which could become naturalised or invasive if introduced. These species were chosen based on their current ability to invade non-native regions, whether they could survive in Norway if introduced based on the climatic suitability of Norway, whether they are likely to be introduced due to economic use, and whether they could become invasive based on their known ecological impacts. I investigated on a country-wide scale how the climate suitability of mainland Norway might alter under climate change for these potentially invasive plants.

Chapter 3: Predicting the distribution of potentially invasive plant species in Norway under a changing climate

Having identified a set of potentially high-risk species to Norway in Chapter 2, I used species distribution modelling to determine which areas of Norway are most suitable for these species and how climate change affects species' suitable range and northern limits. This enabled me to identify 'hotspots' which are climatically suitable for a large number of high-risk species and to further understand how these species' distributions may be affected by climate change.

Chapter 4: Testing the enemy release hypothesis across time and space in Norway using herbarium specimens

To investigate the enemy release hypothesis and the latitudinal biotic interactions hypothesis, I carried out a study to compare herbivory of non-native and native plants at different locations. I utilised historical herbarium records from Norway to investigate how herbivory differs between closely-related groups of non-native and native species, and how herbivory changes along a latitudinal gradient and over time. This enabled me to determine whether the herbivore release of non-native plants is transient or remains constant over time, and how herbivory may be affected by climate change.

Chapter 5: Investigating enemy release of non-native plants in botanical gardens across a European latitudinal gradient

To further investigate enemy release across a larger latitudinal gradient, I combined data taken in 2007-2009 from botanical gardens across Europe with new data collected by myself and collaborators in 2021 from the UK and Norway to compare herbivory levels of a large number of non-native (non-naturalised and naturalised) and native plants (2,752 species in total). I carried out a meta-analysis of results from all gardens to determine whether there is an overall trend of enemy release, whether this is affected by the naturalised status of non-native plants and whether differences vary with latitude to test the latitudinal biotic interactions hypothesis on a broader scale than in Chapter 4.

Chapter 6: Investigating the effects of warming and biotic interactions on invasive plant success in Norway

To investigate how herbivory, native plant competition and climate change might impact non-native plant success, I set up an experiment at the Ringve Botanic Garden in Trondheim, Norway. This experiment contained artificial warming and herbivore exclusion treatments, and non-native plants were grown alone and with native plant competition. This enabled me to investigate how these three factors might impact non-native plant performance, and how they may interact, to give a deeper understanding of the limitations faced by non-native plants in Norway.

1.6 A note on supplementary material

Supplementary material in this thesis can be found either in the Appendices at the end of the thesis or in the directory linked below, where material is separated by chapter. The Appendices contain figures or tables relevant to the text and are referred to as ‘Figure/Table A-‘. The directory contains files which are too large to include in this thesis and are referred to as ‘File S-‘. Additional figures or tables which are too large to include in this thesis or are less relevant to the text are numbered ‘Figure/Table S-‘ and the supplementary file which contains these figures or tables will be referred to as ‘File S-‘.

https://figshare.com/s/fa407b3d48532c0b171b

Chapter 2

Horizon scanning of potentially invasive plant species in Norway under a changing climate

2.1 Abstract

Invasive plant species can cause considerable ecological, economic, and social impacts, and the number of impactful species will likely increase with globalisation and anthropogenic climate change. High-latitude countries such as Norway are likely to experience marked increases in temperatures, and increased numbers of introduced and naturalizing plant species. Preventing potentially invasive plant species from becoming introduced is the most cost-effective way to protect Norway's ecosystems from future invasions. Here, I carried out a horizon scanning study to identify high-risk potentially invasive plant species which are not yet present in Norway but could be introduced and become naturalized in the future. I first investigated the climate suitability of Norway for a starting pool of over 10,000 species known to be naturalized somewhere globally. To do this I used hypervolumes to calculate the overlap between each species' climatic niche and the climate of Norway under both current and predicted future climate scenarios. I then investigated the latitudinal and climatic characteristics of species and how this influenced their climate overlap with Norway. Of the species with climate overlap above zero, I used economic use and environmental impact data to determine which were likely to be introduced to Norway and, of these, whether they would potentially harm native biota once established. A total of 284 plant species were identified as posing a high potential invasion risk to Norway, fulfilling every criterion in the horizon scanning study. Under the current climate high-risk species mostly had climate overlap with the southeast counties of Norway, and under future climate scenarios a greater number of high-risk species had overlap with counties further north. In this study I have developed a novel method of horizon scanning with particular focus on climate matching between species and the area of interest. I strongly recommend that the import into Norway of species identified in this study should be closely monitored and/or restricted to reduce the risk of species invasions and to safeguard Norway's native biodiversity. Further work is needed to identify the specific areas within Norway at risk from these species and how this is affected by climate change.

2.2 Introduction

Invasive species are known to be a major component of local and global environmental change, with a wide range of impacts on biodiversity, ecosystems, and economies (Chornesky & Randall, 2003; Dueñas et al., 2018; Essl et al., 2011; Welch & Leppanen, 2017). Among invasive species, plants are typically the most numerous, and they can transform ecosystems through, for example, changes in vegetation structure, pollinator populations, nutrient cycling and hydrology (Bezemer et al., 2014; Pyšek et al., 2012; Weidenhamer & Callaway, 2010; Weidlich et al., 2020). Plants can be intentionally or unintentionally introduced via many different pathways, but especially through trade in ornamental plants (Reichard & White, 2001). Other key industries (forestry and agriculture) may be responsible for introductions of fewer species globally but involve planting species in high numbers and in multiple locations, across large areas of landscape (Richardson, 1998). Furthermore, it is predicted that recent increases in global trade will result in greater levels of plant naturalization in the future due to a lag between trading activity and non-native species accumulation (Seebens et al., 2015). Unintentional introductions can also occur through transportation of habitat material (e.g. soil), contamination of shipped goods, vehicles, luggage or packaging (Rahman et al., 2003; Ware et al., 2012). The most-cost effective way to prevent future invasions is to identify those species that pose a high risk of invasion to a recipient region, and to prevent their introduction (CBD, 2010; Essl et al., 2011; Shine et al., 2010). Identification and prevention of introduction of high-risk plant species is easier to achieve for intentionally introduced species, e.g., through creation of legislation and enforcement that would ban imports for established economic use.

The impacts of invasive plants are likely to be exacerbated globally under climate change, which is predicted to increase invasive species' ability to invade new areas while simultaneously decreasing native species' ability to resist invasions (Thuiller et al., 2007). More specifically, climate-change induced warming enables plants to move to higher latitudes (Schweiger et al., 2010; van der Putten et al., 2010; Walther et al., 2009) and elevations (Walther et al., 2009) where increased performance and longer growing seasons are likely to enhance invasion success. High-latitude countries such as Norway are therefore likely to become more vulnerable to plant invasions in the future because rates of temperature increase are higher towards the poles (IPCC, 2014). Norway is already home to over 2,000 non-native plant species (Sandvik et al., 2019; Norwegian Biodiversity Information Centre, 2020), and according to a recent inventory, 3% of all stably reproducing species in Norway are non-native, and of these, 71% are plants (Sandvik et al., 2019).

While a wide range of evidence-based weed risk assessment and risk analysis systems have been developed (outlined below) and implemented to evaluate invasion risks and inform biosecurity legislation, the sheer number of plant species that could be introduced to a country and become invasive now or in the future demands a more rapid approach. Recently, several horizon-scanning approaches have been developed and tested to rapidly identify high-risk invasive plant species, which either involve consensus-building methods (e.g. Gallardo et al., 2016; Peyton et al., 2019; Roy et al., 2014; Sutherland et al., 2008), or decision trees that consider suitability, such as the notable example of the Australian Weed Risk Assessment (WRA) proposed by Pheloung et al. (1999) which has been used to identify high-risk species to Spain (Bayón & Vilà, 2019) and to determine 'weediness' (invasive potential) of species in South Africa (Cheek et al., 2021). However, the suitability of climate for a species in the location in question has not been assessed with great accuracy in horizon scanning studies and methods used in the literature have been varied. Bayón & Vilà (2019) compared the temperature tolerances of each species with the climatic extremes of Spain to assess species' survivability. Matthews et al. (2017) recommended the Köppen−Geiger Climate Classification, whereby the world is split into broad climatic zones which are used to determine where a plant could survive based on its known distributions (Rubel & Kottek, 2010). Finally, Sandvik (2020) used data on species' biogeography according to Plants of the World (POWO, 2022) to predict species' climatic tolerances. These approaches do not consider the specific climatic niche of each species individually or how climate suitability may change in future, and how these changes will affect whether and where introduced plant species could pose a higher invasion risk.

In this study, I developed and applied a novel method of horizon scanning to identify which species could pose a threat to Norway. I considered the economic use and environmental impact of a large starting pool of species, with particular focus on the climatic suitability of Norway for each species, and carried out validation analyses on this method of determining climate suitability, Finally, I investigated how climate suitability for these species will likely change in the future and which areas of Norway are most at risk under current and predicted future climate scenarios.

2.3 Methods

I first established a set of criteria and used these to assess an initial list of 16,866 plant species to determine which could pose a risk to mainland Norway (Figure 1). These assessment criteria were chosen to determine whether a plant could survive in Norway if introduced (climatic suitability), if it was likely to become introduced (economic use), and if it was likely to harm Norwegian ecosystems if established (environmental impact). Here I describe the different stages of the framework used to assess which species could pose a risk to Norwegian ecosystems if they were to become established. This framework and the key questions explored are summarised in Figure 1, and the following methods outline how each key question was addressed.

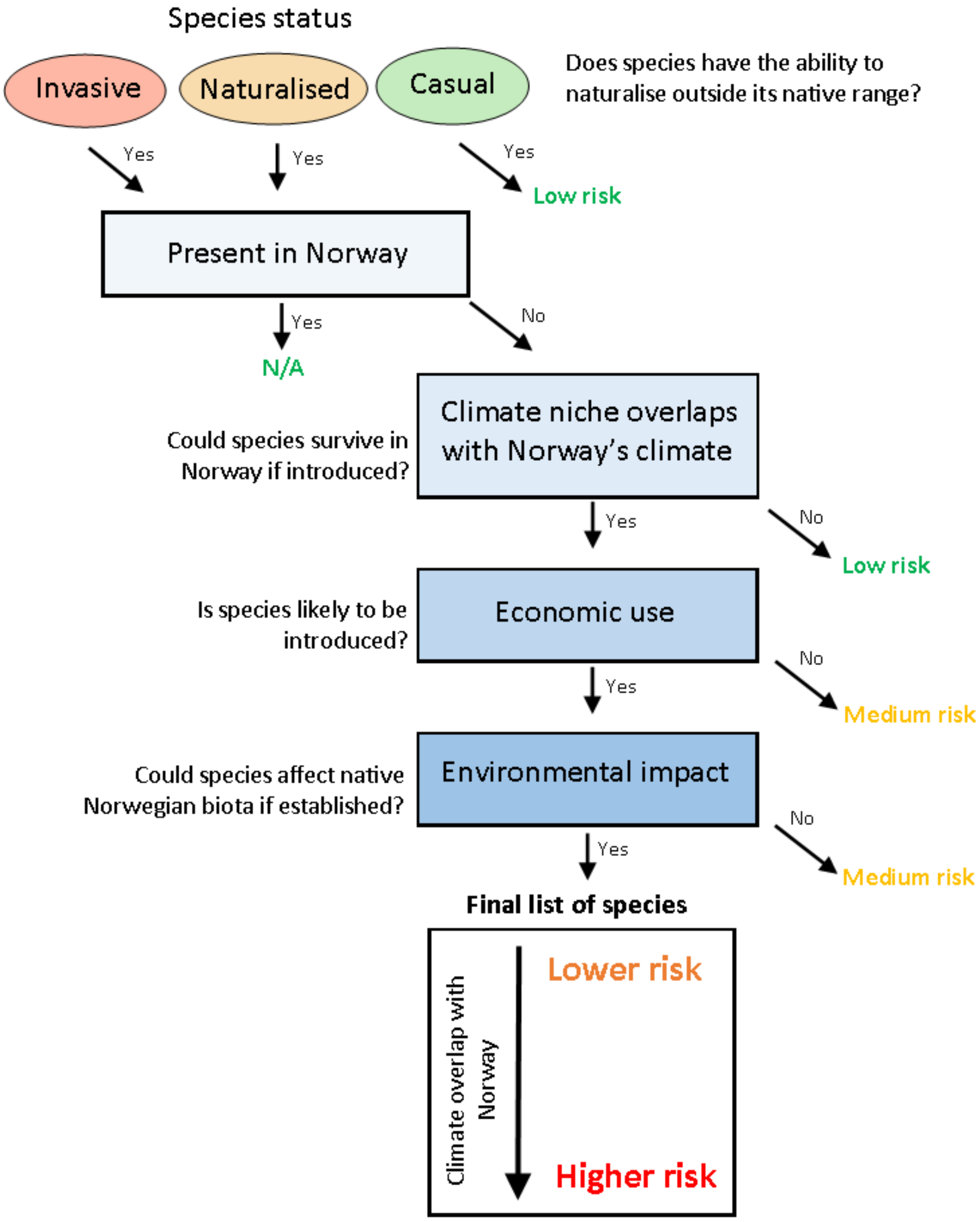


Figure 1: Framework used to assess species to determine which could pose a risk to Norway. Key questions are in bold and are addressed in each methods section below. Blue boxes represent how questions were addressed.

2.3.1 Does species have the ability to naturalise outside its native range?

A list of global, currently-known non-native vascular plants was downloaded from the GloNAF (Global Naturalized & Alien Flora) database (van Kleunen et al., 2019) in December 2019 as the initial pool of species. The downloaded dataset of 16,866 species included species binomials (names both from the original data source and accepted names checked against The Plant List (2010)), regional code of occurrence, and status (alien, casual, naturalised, invasive). Of these, only naturalised or invasive non-native plants were selected for analysis, as these species are already known to be capable of establishing outside their native range. Non-native species which were listed as already present in Norway were removed. Norwegian plant species were also removed from the list using native species lists obtained from the Germplasm Resources Information Network (GRIN; USDA Agricultural Research Service, 2015) and the Norwegian Biodiversity Information Centre (2020), standardised according to The Plant List (2010) using the 'Taxonstand' package (Cayuela et al., 2012). This resulted in a final list of species that excluded all species naturalised or native to Norway. The resulting list contained a total of 13,026 species. All data handling in this and the following sections was completed in R version 3.6.1 (R Core Team, 2019).

2.3.1.1 Occurrence data

Occurrence data were downloaded for all species, obtained from the Global Biodiversity Information Facility (GBIF, 2022). The R package 'rgbif' (Chamberlain et al., 2020) was used to access and download these data for all selected species and coordinates of 0,0 (longitude, latitude) or N/A were removed. Occurrence data for 10,548 species were successfully downloaded from GBIF and there were 2,478 species with either no existing occurrence records, or no records with coordinates. These species were no longer considered in the analysis. Species' occurrences were included whether they were in the native or non-native range (Bocsi et al., 2016).

2.3.1.2 Removing species in Norway

To check if any of the species in fact had records of occurrence in Norway, occurrence records were plotted for all species. Several occurrence records were plotted within Norway, indicating that there were still species present in the GloNAF species list which should have been removed. This was rectified by downloading the polygon shape of Norway using the R package 'raster' (Hijmans & van Etten, 2012) and plotting this against the coordinates for all species using the package 'sp' (Pebesma & Bivand, 2005). If there was overlap, that species was removed from the overall list. 197 species had occurrence records in Norway and were later used for creating binomial GLMs to validate the use of climate variables (see *2.3.2.2.2 Validating the use of bioclimatic variables*).

2.3.2 Could species survive in Norway if introduced?

There are several possible methods to assess climate matching. Bayón & Vilà (2019) used the temperature tolerances of each species compared with the climatic extremes of Spain to assess species' survivability, whereas Matthews et al. (2017) used the Köppen–Geiger Climate Classification (Rubel & Kottek, 2010) to assess climatic niches based on species' current distribution. However, there are other methods to determine climate matching which, as far as I am aware, have never been used in horizon scanning studies before. Hypervolumes are a set of points representing biologically-relevant variables represented in an *n*-dimensional space (Hutchinson, 1957), and it is possible to quantify the size and overlap of these hypervolumes. Comparing hypervolumes of Norway's climate and a species' climatic niche is a potentially useful way of assessing Norway's habitat suitability for each species, allowing for a range of climatic variables to be considered.

2.3.2.1 Climate data

Global current climate data at 5-minute resolution were downloaded from WorldClim version 1.0 (Fick & Hijmans, 2020) for all of the 19 bioclimatic variables described on WorldClim using the R package 'raster' (Hijmans & van Etten, 2012). 'Current' refers to near-current climate data from the years 1970-2000. A Principal Component Analysis (PCA) was applied to all 19 variables within Norway, which was isolated by cropping the shapefile of Norway, downloaded using the 'raster' package, from the global raster of climatic variables, to select the bioclimatic variables that best explained total variation in Norway's climate. The first axis (62.7% of total variance) was correlated with precipitation and temperature variables. The second axis (16.3%) was correlated with mostly temperature variables and the third axis (8.3%) correlated with precipitation seasonality. These variables together explained 87.5% of the total bioclimatic variation across Norway. For each principal component, a variable was chosen that was strongly correlated with each PC axis. The resulting three variables were annual precipitation (mm; AP), mean temperature of the warmest quarter (° Celsius; TWQ) and precipitation seasonality (coefficient of variation (CV); PS) respectively (Figures A1-A3). These variables were also chosen to represent the Norwegian climate in a study by Speed & Austrheim (2017) who employed a similar technique.

To predict species' future climate suitability across Norway, CMIP6 (Coupled Model Intercomparison Project Phase 6) climate predictions were acquired from WorldClim (Eyring et al., 2016, Fick & Hijmans, 2020). Bioclimatic variable data at 5-minute resolution were downloaded for shared socioeconomic pathways SSP2-45 and SSP5-85 for eight different General Circulation Models (GCMs) for the years 2061-2080. This time period was selected to represent the climate 50 years from now. Shared socioeconomic pathways (SSPs) represent a series of scenarios (SSP1-5) each describing the potential development of society, demographics and the economy (Riahi et al., 2017), which have been combined with representative concentration pathways (RCPs) describing emission scenarios (2.6, 4.5, 6.0 and 8.5; van Vuuren et al., 2011). SSP2-45 and SSP5-85 therefore represent intermediate and high-end climate change scenarios. Which scenario is the more likely remains a matter of debate and is dependent on climate policy and how it evolves (Hausfather & Peters, 2020; Schwalm et al., 2020). Correlation analysis showed pairwise correlations between the corresponding climatic variables within each GCM of above 0.95. For each cell in the 5-minute resolution map of Norway, a mean value was therefore calculated across all of the available GCMs.

2.3.2.2 Climate overlap

There were two methods chosen to create hypervolumes which calculated overlap between a species' climatic niche and the climate of Norway; the 'hypervolume' R package (Blonder et al., 2014) and the 'dynRB' R package (Junker et al., 2016). Two methods were used, rather than selecting just one method, as a form of validation to determine whether both methods of calculating hypervolumes yielded similar results. To create species' climatic niches, data for bioclimatic variables TWQ, AP and PS were extracted from each occurrence record downloaded from GBIF for each species (see *2.3.1.1 Occurrence data*). Climatic niches therefore included both native and non-native ranges. Each species' climatic niche hypervolume was compared against the climatic hypervolumes of Norway for current and future (SSP2-45 and SSP5-85) climate scenarios. Climate overlap values were successfully calculated for 9,544 of the 10,548 species using the package 'hypervolumes' and were successfully calculated for 10,534 species using 'dynRB'.

To determine if both methods of calculating climate overlap – 'hypervolume' or 'dynRB' packages – were producing similar results, a correlation analysis was carried out for the overlap values created by each package using species' overlap with Norway's current climate. Analysis was only carried out on species which had successfully calculated overlap values from both methods. There was high Pearson's correlation (0.85) between the overlap metrics of Sorensen similarity from 'hypervolumes' (2 x (volume of intersection of hypervolume 1 (e.g. Norway's climate) + volume of intersection of hypervolume 2 (e.g. species' climatic niche)) / (volume of hypervolume 1 + volume of hypervolume 2)) and 'Gmean' from 'dynRB' (geometric mean overlap of the dimensions), suggesting that both methods used are comparable. A greater number of species' climate overlap values were successfully calculated using the 'dynRB' package than the 'hypervolume' package so this method was chosen of the two.

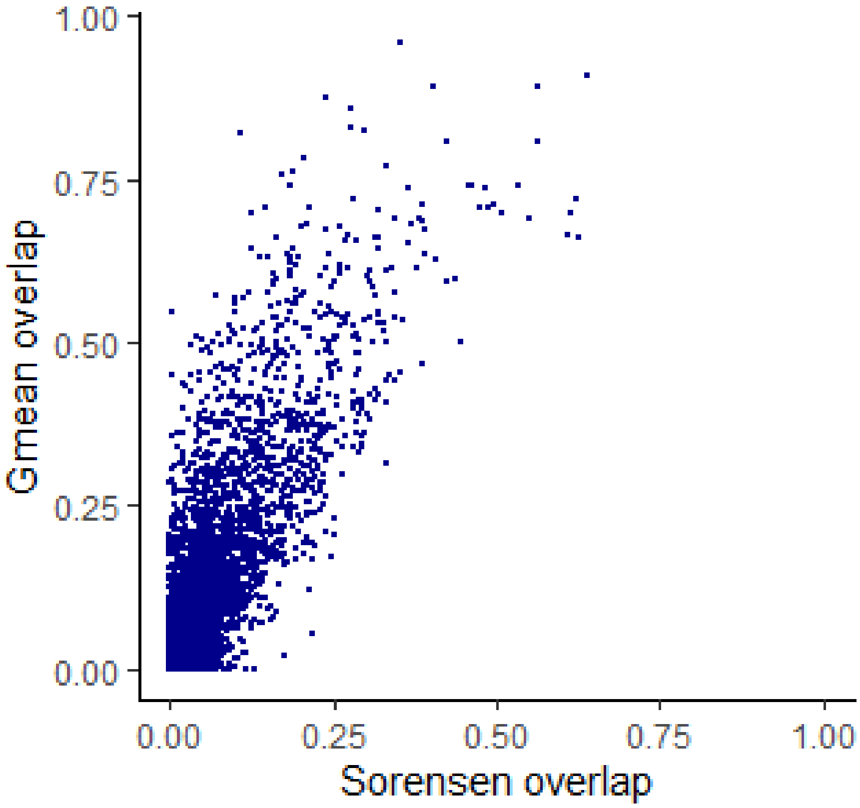


Figure 2: Comparison between Gmean overlap (produced by 'dynRB' package (Junker et al. , 2016)) and Sorenson similarity overlap (produced by 'hypervolume' package (Blonder et al., 2014)) calculated for 9,544 species to investigate the overlap between their climatic niche and the current climate of Norway.

2.3.2.2.1 Threshold for species occurrence records

The number of species' occurrence records may affect the resulting overlap value between the species' and Norway's climate volumes, as fewer data points might mean that the true niche of a species is not represented by the occurrence data on GBIF. It was important to determine the minimum number of occurrence data points required for each species to give accurate climate overlap values. To do this, the test species *Betula pubescens* was used as it is prevalent throughout Norway and the northern hemisphere. This species is well documented so there was an abundance of occurrence data on GBIF which was likely to represent the true niche of *B. pubescens* within Norway.

Firstly, 74,000 occurrence records were downloaded from GBIF using the package 'rgbif' (Chamberlain et al., 2020). Climatic data for these coordinates for bioclimatic variables TWQ, AP and PS were extracted from a WorldClim (Fick and Hijmans, 2017) world raster at 5-minute resolution. Using the 'dynRB' package, the overlap between the climatic niche for *B. pubescens* and the current climate of Norway was calculated to be 0.63. To determine if the number of coordinate points used to create the hypervolume made a difference to the overlap output, samples of 4000, 2000, 1000, 500, 200, 100 and 50 were randomly taken from the extracted climatic data for *B. pubescens*. These samples were each used to calculate hypervolume overlap, and this process was repeated 100 times for each sample size. The results showed that as the sample size decreased, the variation between overlap values increased (Figure 3). Based on this analysis, 100 data points was chosen as the minimum number of occurrence records required, as a compromise between overlap variation and reducing the number of species which were discounted going forward for analysis.

2.3.2.2.2 Validating the use of bioclimatic variables

The next step was to determine if the overlap between the bioclimatic variables of a species' current distribution and the bioclimatic variables of Norway was an accurate predictor of whether or not a species could naturalise in Norway. To do this, binomial Generalised Linear Models (GLMs) were run using the climate overlap values as the explanatory variable for a series of species. For the first GLM, a set of species known to have established in Norway before the year 1800 was compared with a group of 'door knocker' species, defined as "an alien species that is not currently established in Norway, but that can be expected to become established in Norway within 50 years" according to Sandvik et al. (2017). These species were taken from the Norwegian Biodiversity Information Centre's database. There were 35 naturalised species and 72 door knocking species, of which 35 were randomly sampled for use in the GLM. For each species, occurrence data were downloaded from GBIF using the package 'rgbif' (Chamberlain et al., 2020) and climate overlap values between each species' climatic niche and the current climatic niche of Norway calculated using the 'dynRB' package (Junker et al., 2016). For the binary response variable, 'successful' species which had established in Norway before 1800 were given the value of 1, and 'unsuccessful' door knocking species which have not yet naturalised were given the value of 0 (Figure 4a).

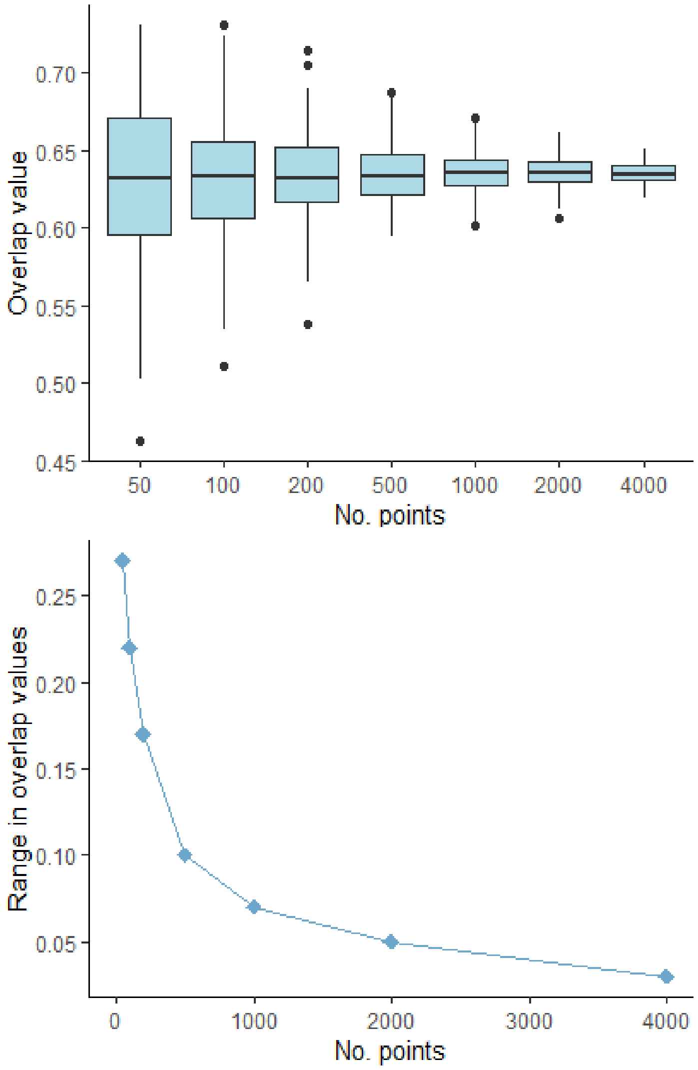


Figure 3: Variation in climate overlap calculated when using different occurrence record sample sizes of *Betula pubescens*: **a**) range of overlap values produced for 50-4000 occurrence record samples; **b**) range between lowest and highest overlap values produced.

A second binomial GLM was built to analyse a second set of species downloaded from the GloNAF database (van Kleunen et al., 2019). For the second set, the naturalised 'successful' species (given the value of 1) were species that were recorded as being naturalised in Norway according to GloNAF. The non-naturalised 'unsuccessful' species (given the value of 0) were those which had naturalised across Europe but not in Norway. There were 600 species naturalised to Norway and 7,189 naturalised to Europe, of which 600 were randomly sampled for use in the GLM. Overlap values were calculated for each species and a binomial GLM produced (Figure 4b). A third binomial GLM compared the climate overlap of 197 species from GloNAF with occurrence records in Norway (see *2.3.1.2 Removing species in Norway*) and a random sample of 197 species from the rest of the GloNAF database (Figure 4c). Species with occurrence records in Norway were classed as ‘successful’ and given the value of 1, and the species from elsewhere were classed as ‘unsuccessful’ and given a value of 0.

To test the predictive accuracy of these three models, Receiver Operator Characteristic (ROC) curves were produced (Figure 4). The ROC curves visualise the predictive power of a binary model and show the relationship between the true positive rate (TPR) and false positive rate (FPR). The TPR is the proportion of observations that are correctly predicted to be positive of all the predicted positive observations (observations which predict a value of 1 rather than 0). The FPR is the proportion of observation incorrectly predicted to be positive of all the negative observations (observations which predict a value of 0 rather than 1) (Fawcett, 2006). The steeper the curve, the larger the area under the curve (AUC) and the greater the predictive power. An AUC of 0.5 suggests that the model shows predictive abilities no better than chance, and the higher the AUC above 0.5, the better the predictive capabilities of the model. For the model using species from Norwegian Biodiversity Information Centre (naturalised vs door knockers in Norway), the AUC was 0.73 (Figure 4a). For the second model, using species taken from GloNAF (species naturalised in Norway vs naturalised within the rest of Europe), the AUC was 0.84 (Figure 4b), and for the third model (species naturalised in Norway vs naturalised across the rest of the world) the AUC was 0.91 (Figure 4c). These models therefore showed that the climate overlap value of a species could be used as a fair predictor of a species’ ability to naturalise.

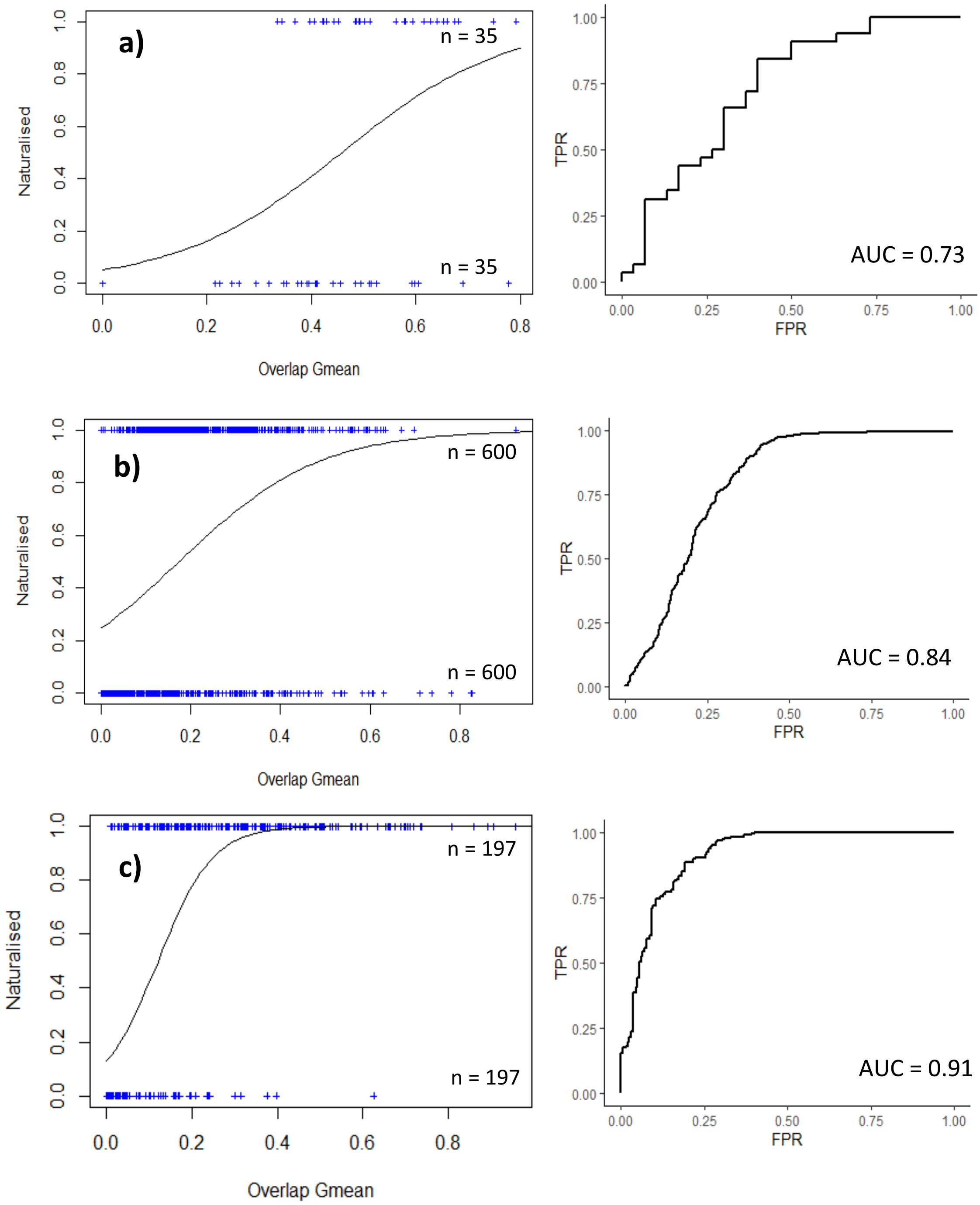


Figure 4: Generalised Linear Models (GLMs) and ROC curves of the climate overlaps between the climatic niche of Norway and the climatic niche hypervolumes of (a) First model: species naturalised in Norway vs species not naturalised to Norway according to the Norwegian Biodiversity Information Centre (2020); (b) Second model: species naturalised to Norway vs species which are naturalised elsewhere in Europe; (c) Third model: naturalised species from GloNAF with occurrence records in Norway vs species naturalised around the world.

To summarise the above analyses, climate overlap was shown to be a fair predictor of a species' ability to naturalise and was successfully calculated for 10,534 species comparing their climatic niche to the current and predicted future (SSP2-45 and SSP5-85) climates of Norway using the package 'dynRB' (Junker et al., 2016). Of these, 6,778 species had over 100 documented occurrence records and some overlap with Norway's current climate and were therefore shortlisted for further analysis in the horizon scanning study.

2.3.2.3 Current and future climate overlaps

More in-depth analysis of was carried out to investigate how species' current niches affect their response to climate change within Norway. Predicted future climate data were limited to SSP2-45 for simplicity. Species used in this section were all those with over 100 documented occurrence records (7,819 total; see *2.3.2.2.1 Threshold for species occurrence records*) and included species with a climate overlap of zero, even though these species were later discarded for this horizon scanning study.

To investigate how species' current distributions affected their change in overlap between Norway's current and future climates, each species' median latitude of occurrence was calculated using occurrence data from GBIF. The species were split into three categories of median latitude: 0-25°, 25-50°, and above 50°, irrespective of northern or southern hemispheres. Overlap values between species' climatic niche and Norway's current climate were then binned into 0, 0-0.2, 0.2-0.4, 0.4-0.6, 0.6-0.8 and 0.8-1. For each median latitude's group of species, the number of species with current climate overlap in each overlap bin was first determined, and of these the number of species whose overlaps increased or decreased in overlap bin under the future climate were recorded.

Species that had greater climate overlaps under climate change were separated from those whose overlaps decreased. For each of these two groups, the bioclimatic variables associated with each species' occurrence records were plotted in pairs: TWQ and AP; TWQ and PS; AP and PS. Plotting was achieved by creating three presence/absence rasters for each species with each pair of bioclimatic variables as axes using the R package 'raster' (Hijmans & van Etten, 2012). The sum of the rasters produced for each pairwise comparison of each species group (those with increasing or those with decreasing overlap) was calculated to determine how many species had occurrences in each climatic variable raster cell. This technique allowed visualisation of the climatic space currently occupied by each group of species.

Finally, the difference in climate overlap between Norway's current and predicted future climates was calculated for each species and plotted against the mean variable of TWQ, AP and PS for each species' current climatic niche.

2.3.3 Is the species likely to be introduced?

To continue the horizon scanning framework, plants are often introduced to non-native areas for economic purposes and economic use was therefore chosen as a proxy for introduction pathway. Data describing the economic uses of plant species were obtained from the World Economic Plants database, accessed via the Germplasm Resource Information Network (USDA Agricultural Research Service, 2015) of the US National Plant Germplasm System and downloaded in June 2020. This database contains information on the economic uses of almost 17,000 species. A total of 3,974 species from the original GloNAF list of naturalised species had recorded economic uses in this database. As different countries will tend to import plants for different economic uses, the key economic uses were identified that are important for introduced plants in Norway. To achieve this, data concerning 129 plant species already in Norway and deemed high or very high risk (*Norwegian Biodiversity Information Centre*, 2020) were used, which contained information about the reason for their introduction to Norway. Ornamental (82 species), forestry (6 species) and livestock fodder (6 species) were identified as the top economic uses. These corresponded with ‘Environmental – ornamental’, ‘Materials – wood’ and ‘Animal food’ in the World Economic Plants database, and plants with at least one of these three economic uses were listed as those which could be intentionally introduced to Norway.

2.3.4 Could the species negatively impact Norwegian native biota if established?

An invasive non-native plant is generally defined as a plant which harms organisms in its invaded range (Hellmann et al., 2008), so this factor was therefore important to include in this horizon scanning study. The Global Register of Introduced and Invasive Species (GRIIS) database contains information about whether or not a species has a documented ecological impact and in which country this impact has occurred (Pagad et al., 2018). Data from the GRIIS database were downloaded in June 2020. Species names were standardised using the R package ‘Taxonstand’ (Cayuela et al., 2012), according to The Plant List. A total of 1,215 species from the original GloNAF list had recorded ecological impacts in the GRIIS database. To determine whether these environmental impacts occurred in places with a similar climate to Norway, spatial polygon data were downloaded for all of the countries listed in the GRIIS database where the listed species had an impact using the ‘raster’ package (Hijmans & van Etten, 2012). Each country’s polygon shapefile was cropped from the world dataset of TWQ, AP, and PS variables and the data points within it were saved. Overlap between each country’s climate and Norway’s climate was calculated using the ‘dynRB’ package (Junker et al., 2016). Countries with a climate overlap of more than zero shared some climatic characteristics with Norway. Only species which had a known ecological impact in countries with some climatic overlap with Norway were selected.

2.3.5 High risk species

In summary, the final shortlist of species considered to pose a high invasion risk to Norway included species that: i) have a known global occurrence distribution that has non-zero overlap with Norway's current climate, ii) have at least one of the three top economic uses important to Norway, and iii) have known impacts in other regions with a similar climate to Norway. A total of 284 species met these criteria and were ranked according to the level of climate overlap with Norway's current climate (using the geometric mean of hypervolume overlap already calculated; File S1).

2.3.5.1 Regional climatic niches

Finally, the areas of Norway that these shortlisted species are more likely to survive and naturalise in were determined. A spatial polygon of Norway containing the 1770-2017 regional borders for 19 counties was downloaded using the R package 'raster' (Hijmans and van Etten, 2012). From January 2020, several of these regions were combined to form a total of just 11 counties (Kartverket, 2021), many of them much larger than the previous regions. The 1770-2017 regional borders were chosen for this analysis as they represent finer-grained areas than the 2020 county borders. However, counties were chosen as opposed to the 350 smaller municipalities within Norway because of time constraints. Each region of this shapefile was separated and the climate data for each taken from WorldClim (Fick and Hijmans, 2017) for the bioclimatic variables TWQ, AP and PS for Norway's current and predicted future climate. Again, only SSP2-45 of the predicted future climates was used here for simplicity. The climate data for each region was compared to climate data extracted from the occurrence records downloaded from GBIF for every species. The package 'dynRB' was used to calculate the climate overlap between each region's climate and species' climatic niche. The number of species with ae climate overlap of more than zero for both the current and predicted future climate of Norway were recorded for each region.

2.3.5.2 Climate overlap sensitivity analysis for high-risk species

Climatic variables associated with occurrence records may not be accurate in areas where there is high climatic variation within a single grid cell, such as within mountainous regions, and may misrepresent the true climatic niche of a species. Outlying species' climatic variables may therefore be inaccurate and may influence a species' climate overlap with Norway. Plotting the climatic range of the top five high-risk species (*A. decurrens, G. tinctoria, S. multiglandulosa, P. pyrenaicus* and *A. melanoxylon*; Table 1) showed that the climatic variable which had the least similarity with Norway's current climate was the temperature variable TWQ (Figures S1-S5 in File S2). This suggested that this climatic variable may be the most limiting on species' climate overlaps. To investigate whether removing outliers affected species' climate overlap with

Norway, TWQ variables outside the 1.5 interquartile range (IQR; third quartile plus 1.5 x the IQR and first quartile minus 1.5 x IQR) were removed and climate overlap calculations were repeated for these five species (File S2).

2.4 Results

In the results section, ‘all species’ refers to naturalised species with over 100 occurrence records on GBIF (7,819 in total; Figure 5).

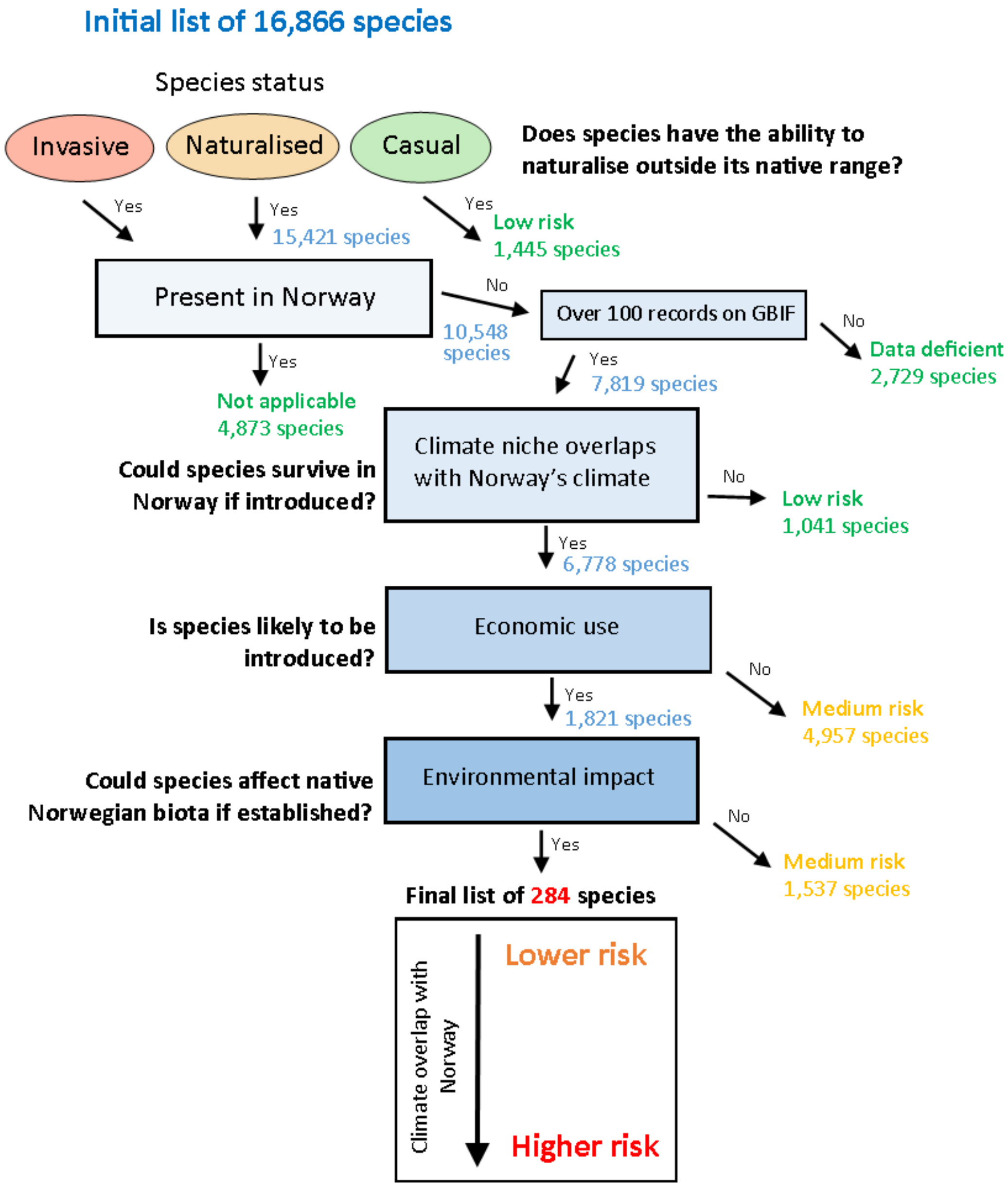


Figure 5: Framework used to assess species to determine which could pose a risk to Norway. Key questions are in bold and are addressed in each methods section below. Blue boxes represent how questions were addressed. Numbers indicate how many species fulfil each category and how many were discarded at each stage. Low risk (green) species are very unlikely to become a risk to Norway due to their inability to naturalise outside their native ranges and the climatic unsuitability of Norway. Medium risk (yellow) species are unlikely to become a risk to Norway as they are not used in industries prevalent in Norway, so are unlikely to be introduced, and have no known environmental impacts so are unlikely to harm Norwegian biota if introduced.

2.4.1 Climate overlap

The majority of species (7,329) showed an increase in climate overlap under climate change (Figure 6). Most species' climate overlaps lie between 0 and 0.25 under both current and future climate scenarios. The mean difference between climate overlap under SSP2-45 and current conditions was 0.06 and the median difference was 0.04.

2.4.1.1 Change in climate overlap based on species' latitude

The change in climate overlap between current and future Norway was plotted for species with median latitudes in three groups (Figure 7). There were 2,694 species with a median latitude of 0-25° (Figure 7a). Species in this group generally had the lowest climate overlaps of the three categories. 0-0.2 was the most common overlap bin for both current and future Norway. Only 7 species had a decrease in climate overlap large enough to move down in overlap bin, and most species remained in the same overlap bin in both climate scenarios.

There were 4,970 species with a median latitude of 25-50° (Figure 7b). The overlap bin with the most species was 0-0.2 in both current and future scenarios. A total of 1,131 species had an increase in climate overlap which moved them into the next overlap bin. Only 68 species had decreased overlap and moved down a bin.

The final group of above 50° median latitude contained 335 species (Figure 7c). Just 4 species (under 2%) had no overlap with Norway's current climate. 213 species had a current overlap of 0-0.2, 139 of which increased to a future overlap of 0.2-0.4. This latitude group had the greatest proportion of species with overlaps of above 0.2; 76% compared with 4% in the latitude group 0-25° and 23% in the latitude group 25-50°.

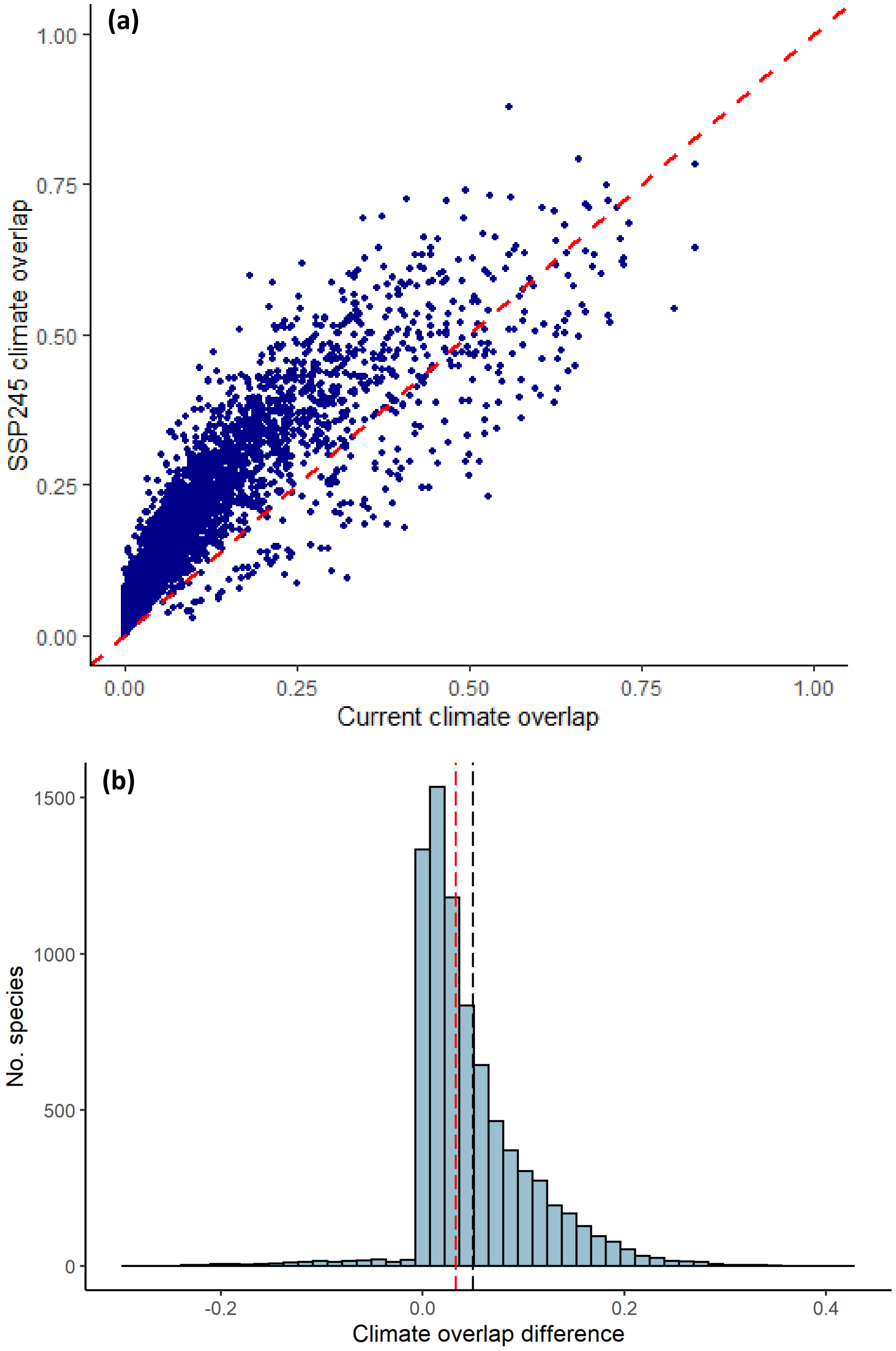


Figure 6: (a) Comparison between species' climate overlaps with Norway's current climate and predicted future climate for the SSP2-45 pathway representing intermediate emissions. Red dotted line depicts perfect positive correlation. (b) Difference between climate overlap under SSP2-45 and Norway's current climate. Black dotted line = mean difference. Red dotted line = median difference.

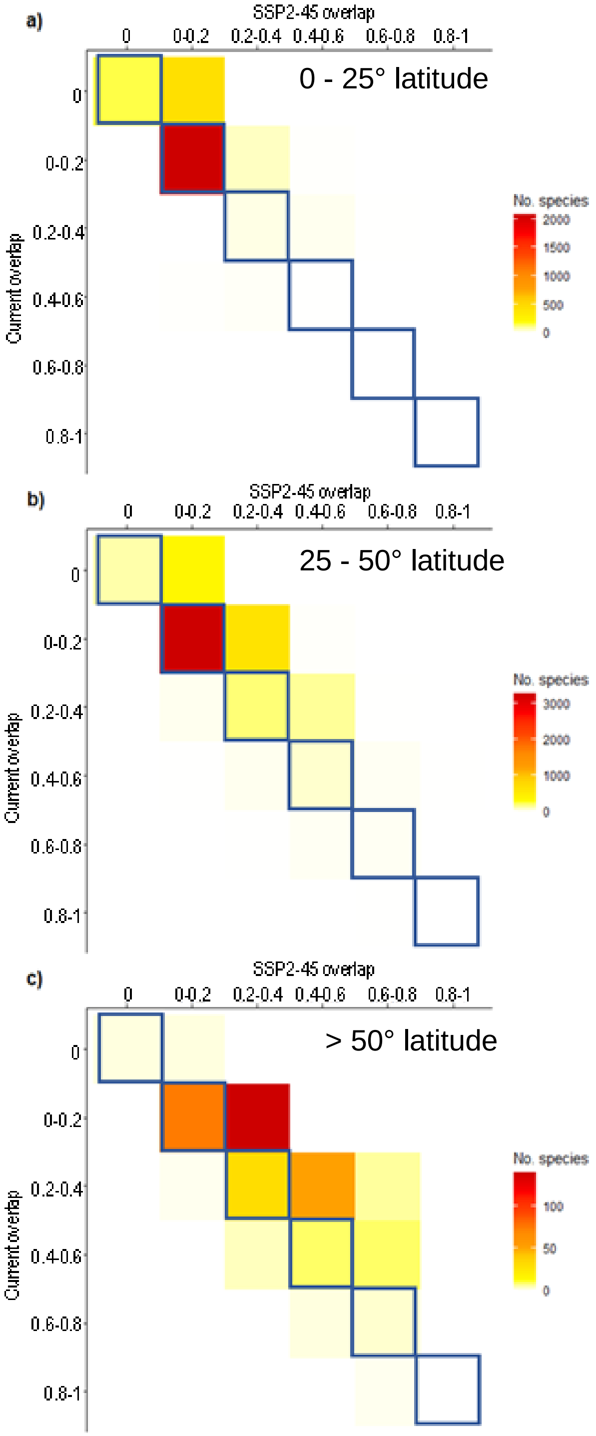


Figure 7: The climate overlap between species' niches and Norway's current and future (SSP2-45) climate organised into 0.2 bins from 0 to 1 for **a**) Species occurring in areas with a median latitude of 0-25°; **b**) Species occurring in areas with a median latitude of 25-50°; **c**) Species occurring in areas with a median latitude of above 50°. Diagonal cells within blue squares represent species with no change in climate overlap bin; cells in the bottom left, below diagonal cells, are species with decreasing overlap under climate change (species which fall into lower bins in the future), while cells in the top right, above diagonal cells, are species with increasing overlap under climate change (species which fall in higher bins in the future).

2.4.1.2 Climatic niches of species with increasing and decreasing climate overlap

Species with climate overlap that increased under projected climate change were generally distributed in warmer locations (with TWQ centred approximately 22° Celsius) compared to species whose climate overlap decreased (with TWQ centred around 15°C). PS also varied; species with increasing overlaps occurred in areas with varying precipitation seasonality, whereas those with decreasing overlaps mostly occurred in areas with low precipitation seasonality. AP values did not differ greatly between the two groups of species, all of which occurred mainly in areas with 800-1100 mm of rainfall annually (Figure 8).

2.4.1.3 Change in climate overlap in relation to bioclimatic variables

A decrease in climate overlap under climate change was seen mostly in species whose niche had a mean TWQ of 7-15°C. Species whose niche had a mean of 15-17°C experienced the greatest increase in climate overlap under climate change, and as the average TWQ of species' niches increased, the species which inhabit these areas experienced a lesser increase in climate overlap under climate change (Figure 9a). Species whose niche had a mean AP of 500-1200 mm had the greatest increase in climate overlap under climate change (Figure 9b). This range strongly overlapped the range of Norway's mean (± SD) rainfall, both current and future. Species in areas with greater AP did not have such an increase in climate overlap. For PS, species with seasonality below around 20 coefficient of variation (CV) units showed decreased overlap under climate change (Figure 9c). Species above 20 CV had the greatest increase in climate overlap in the future, and as seasonality increased the amount of increase in climate overlap decreased.

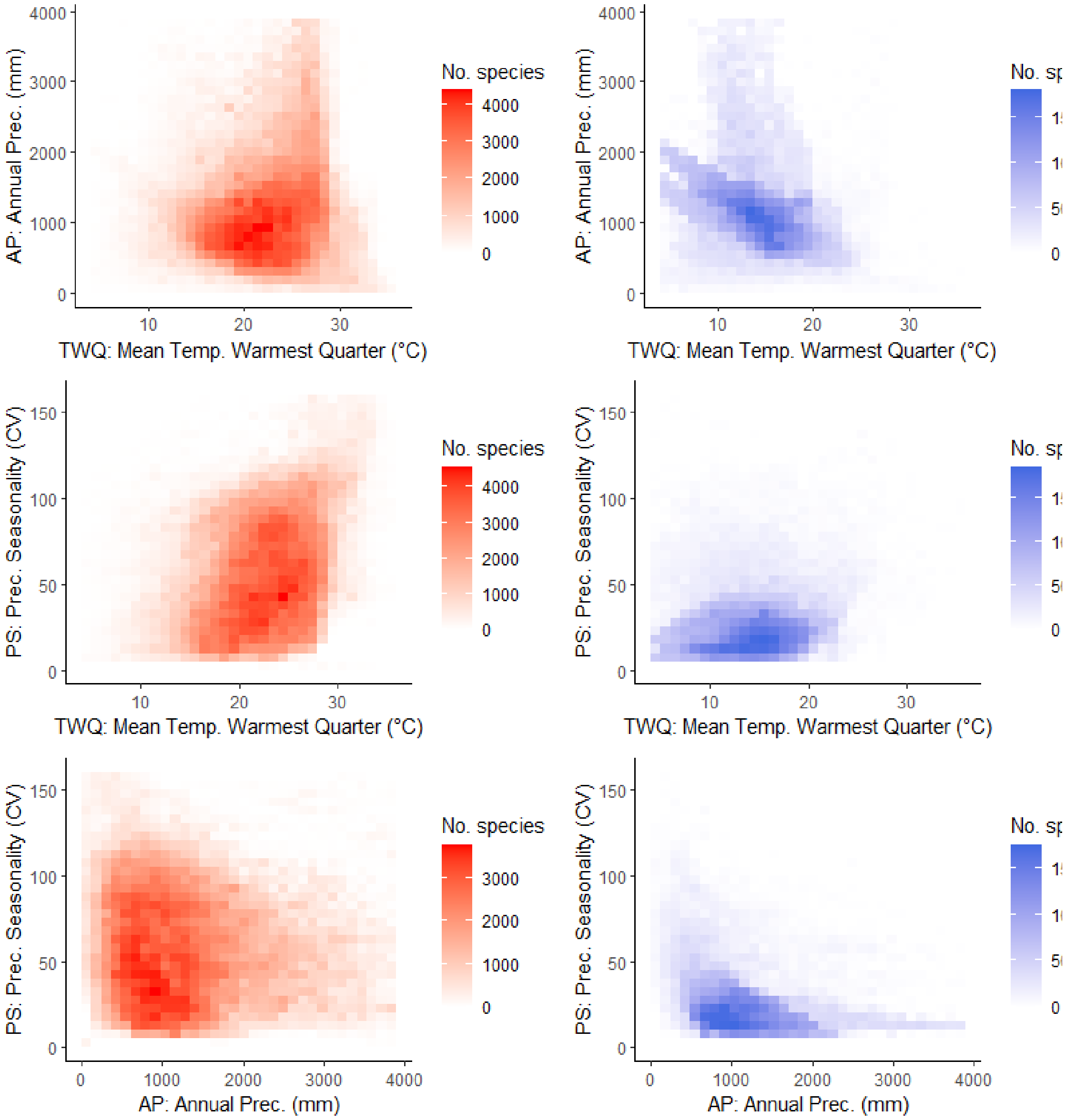


Figure 8: Climate space taken up by species known to be naturalised somewhere in the world and with over 100 relevant occurrence records on GBIF. No. species refers to number of species with occurrence records in areas with climatic variables represented in each cell; a single species will therefore be present in multiple cells which represent its climatic range. Red plots are species with increasing climate overlap from Norway's current to future (SSP2-45) climate. Blue plots are species with decreasing climate overlaps.

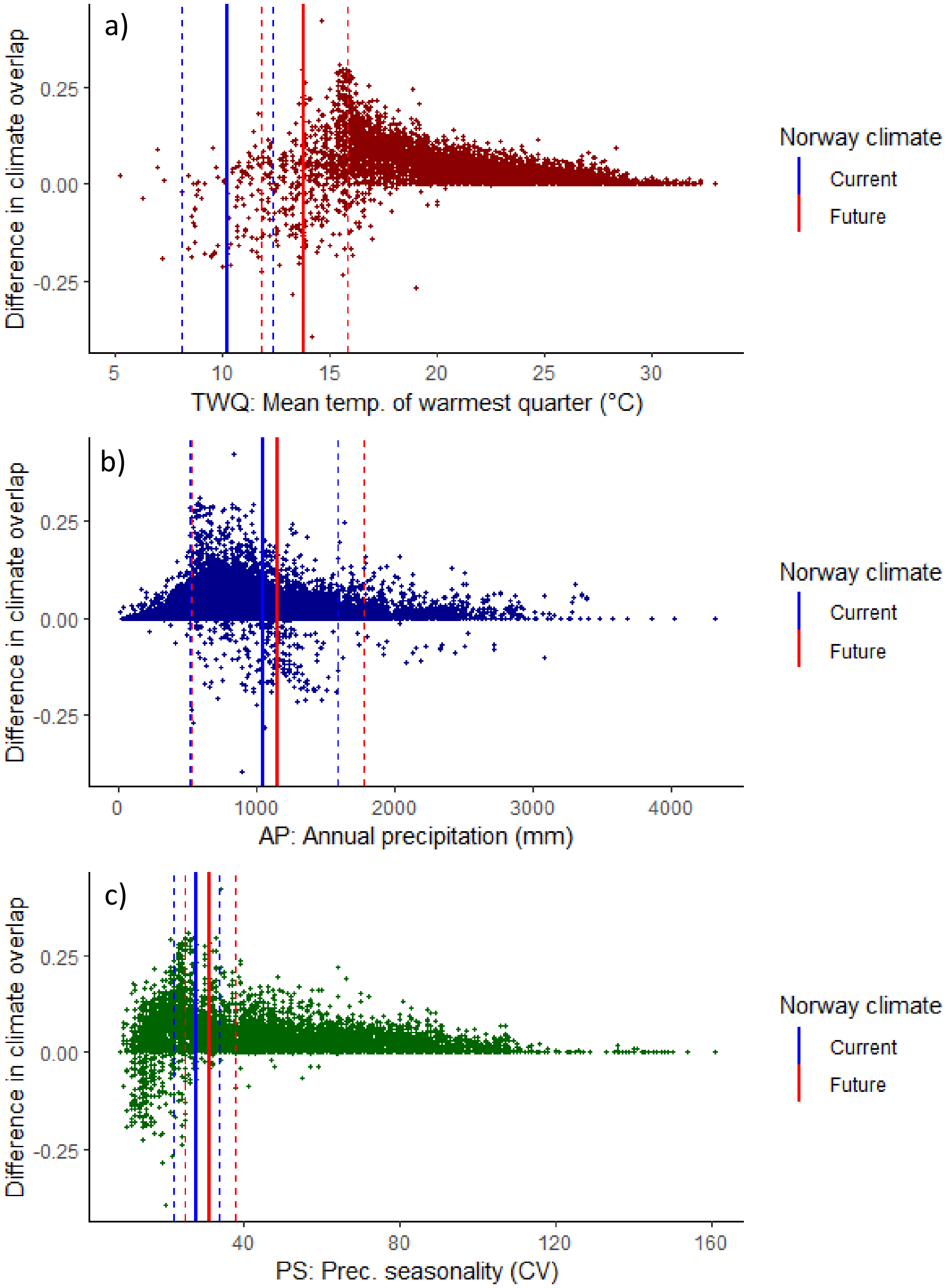


Figure 9: Difference in climate overlap between Norway's current and future (SSP2-45) climate compared with the mean climatic variable of each species known to be naturalised somewhere in the world and with over 100 occurrence records on GBIF. Each dot represents one species. Solid lines represent mean of Norway's current and future climatic variables, and dotted lines represent ± SD for Norway's current and future climatic variables.

2.4.2 High risk species

A total of 284 species were identified as high-risk to Norway based on climate overlap, economic use, and ecological impact (Table 1; File S1). These species are currently mostly distributed across western Europe, central America, South Africa and southern Australasia (Figure 10) . The high-risk species belonged to 77 families, the most common being Fabaceae with 38 species, followed by Poacae with 28 species and Asteraceae with 18 species (Figure 11). A total of 250 species are used as ornamental plants, 42 for timber and 36 as animal fodder (note that some species have multiple uses). Climate overlap of high-risk species ranged from <0.01 to 0.38 with a mean of 0.04 (0.01 lower quartile (LQ) to 0.08 upper quartile (UQ)) under current climate conditions. Climate overlap increased significantly both from the current climate to SSP2-45 with a mean of 0.11 (0.03 LQ to 0.12 UQ), current climate to SSP5-85 with a mean of 0.14 (0.06 LQ to 0.20 UQ), and between SSP2-45 and SSP5-85 (Figure 12a & b). Species which had a greater overlap with Norway's current climate showed the greatest increase in overlap under climate change (Figure 12c). The species with the highest climate overlap in all climate scenarios was *Acacia decurrens*, the green wattle, native to Australia.

2.4.2.1 Regional climate suitability in Norway – current and future

The climate overlap between each of the 284 high-risk species and each of Norway's 19 former counties were calculated (Figures 13 & 14). A greater number of species had climate overlap with regions at lower latitudes under Norway's current climate, particularly in the east. There were five eastern counties which had climate overlap with 280 species; Hedmark, Buskerud, Akerhus, Oslo and Østfold. The number of species with climate overlap decreased as latitude increased, the lowest number of species occurring in the northernmost regions. There were also fewer species with overlap in the west.

When comparing species' niches to the predicted future climate of Norway, however, the number of species with overlap increased in every region (Figure 13). In 13 of the 19 regions, all 284 species had some overlap. There were only two regions with fewer than 270 species, the lowest numbers again seen in the northern regions. These two regions also had the greatest increase in species, suggesting that there may be a more dramatic change in climate at higher latitudes. Southeast regions had the lowest increase in species. The increase in number of species with overlap corresponded to an overall increase in climate overlap values in the future. The median climate overlap value and the upper range of climate overlap values increase in each region under climate change (Figure 14).

Table 1: Top 10 species identified in the horizon scanning study ranked according to climate overlap between species' climatic niche and Norway's current climate using hypervolumes. For predicted distribution of these across Norway see Figure A4.

Species	**Family**	**Current overlap**	**SSP2-45 overlap**	**SSP5-85 overlap**	**Economic use**	**Where is it native?**	**Where is it invasive?**
Acacia decurrens	Fabaceae	0.37	0.70	0.69	Ornamental	Australia	S Australasia, Asia, Africa, N & S America, Europe
Gunnera tinctoria	Gunneraceae	0.33	0.60	0.68	Ornamental	South America	NW Europe, S Australasia, N Am
Senna multiglandulosa	Fabaceae	0.29	0.38	0.41	Ornamental	Central and South America	S Asia, S Australasia, Africa, N America
Petasites pyrenaicus	Asteraceae	0.28	0.45	0.51	Ornamental	Mediterranean Europe	NW & S Europe,S Australasia, N America
Acacia melanoxylon	Fabaceae	0.24	0.43	0.57	Ornamental, forestry	Australasia	S Europe, S Asia, Africa, N & S America
Acacia dealbata	Fabaceae	0.23	0.41	0.53	Ornamental	Australasia	NW & S Europe, E Asia, S Australasia, Africa, N & S America
Erica lusitanica	Ericaceae	0.22	0.48	0.59	Ornamental	Southwest Europe	NW Europe, S Australasia
Pinus radiata	Pinaceae	0.22	0.51	0.60	Ornamental, forestry	North and Central America	S Australasia, S America, Africa
Eucalyptus globulus	Myrtaceae	0.21	0.39	0.46	Ornamental, forestry	South America	S Asia, S Australasia, Africa, N & S America
Prunus lusitanica	Rosaceae	0.21	0.39	0.45	Ornamental	Southwest Europe	NW & E Europe, S Australasia, N America

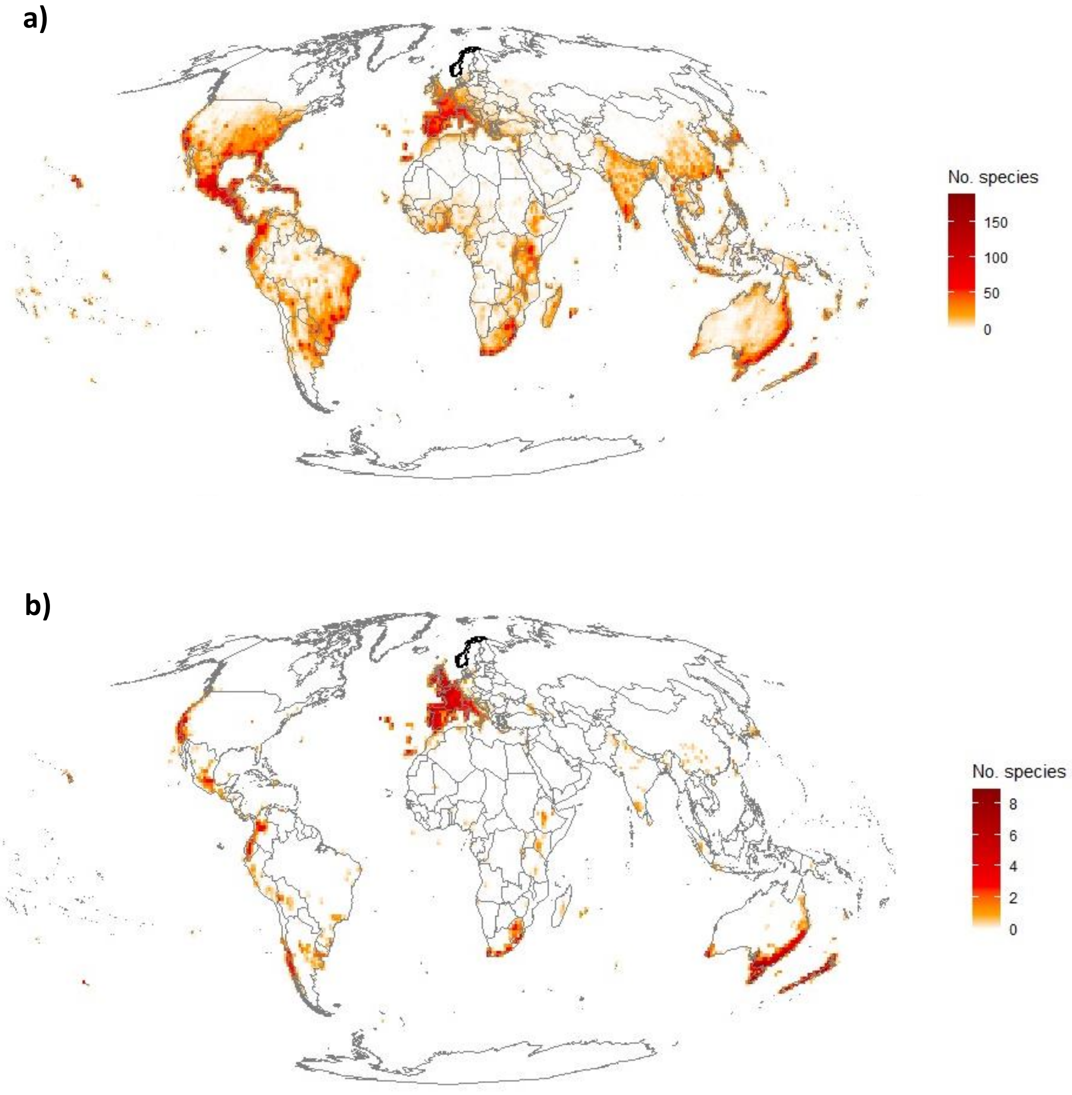


Figure 10: The current known distributions (both native and non-native) of **(a)** all 284 high-risk species identified in this horizon scanning study and **(b)** the top 10 high-risk species based on climate overlap with Norway's current climate. Norway is highlighted in bold. Occurrence data downloaded from GBIF (2020).

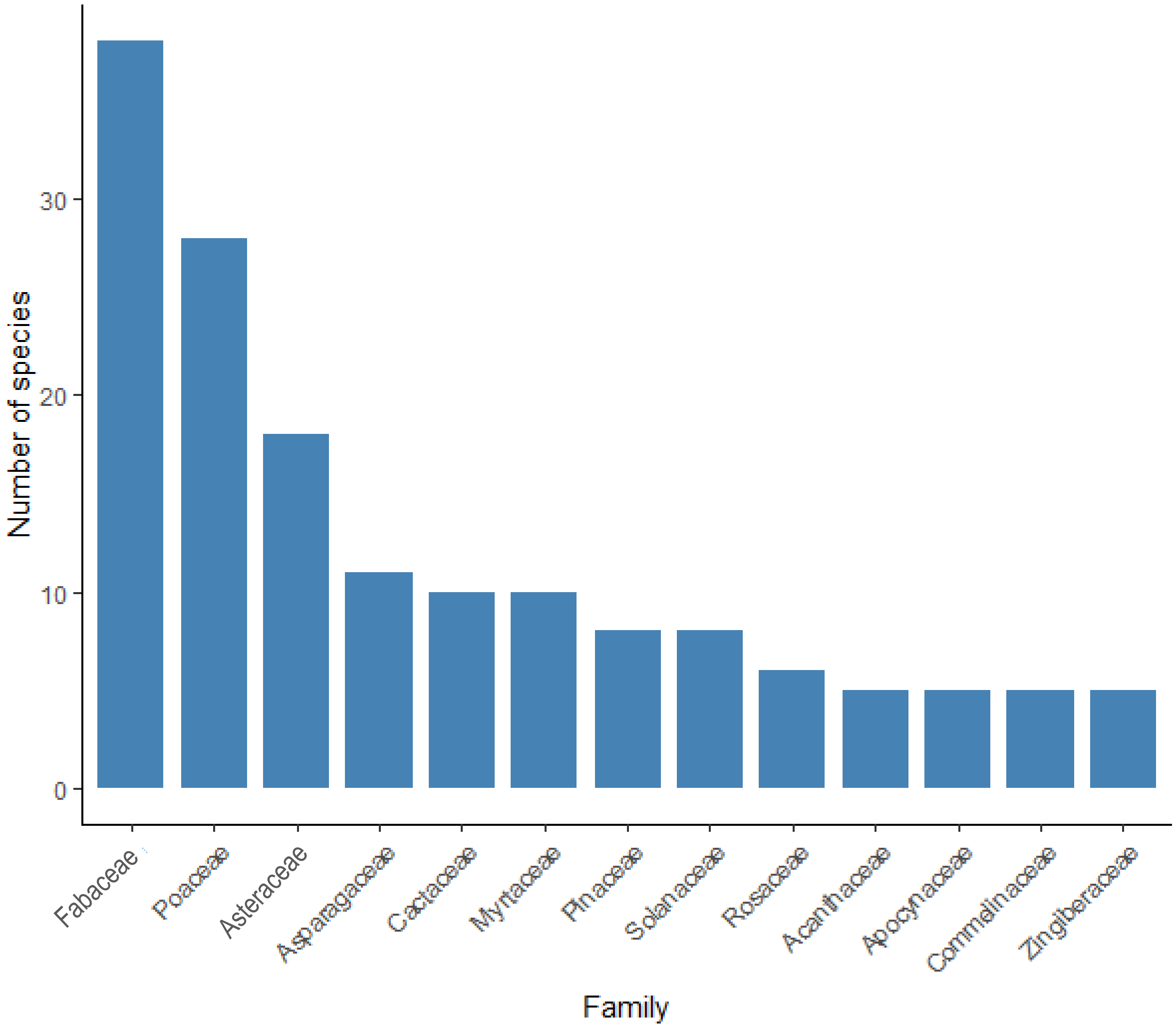
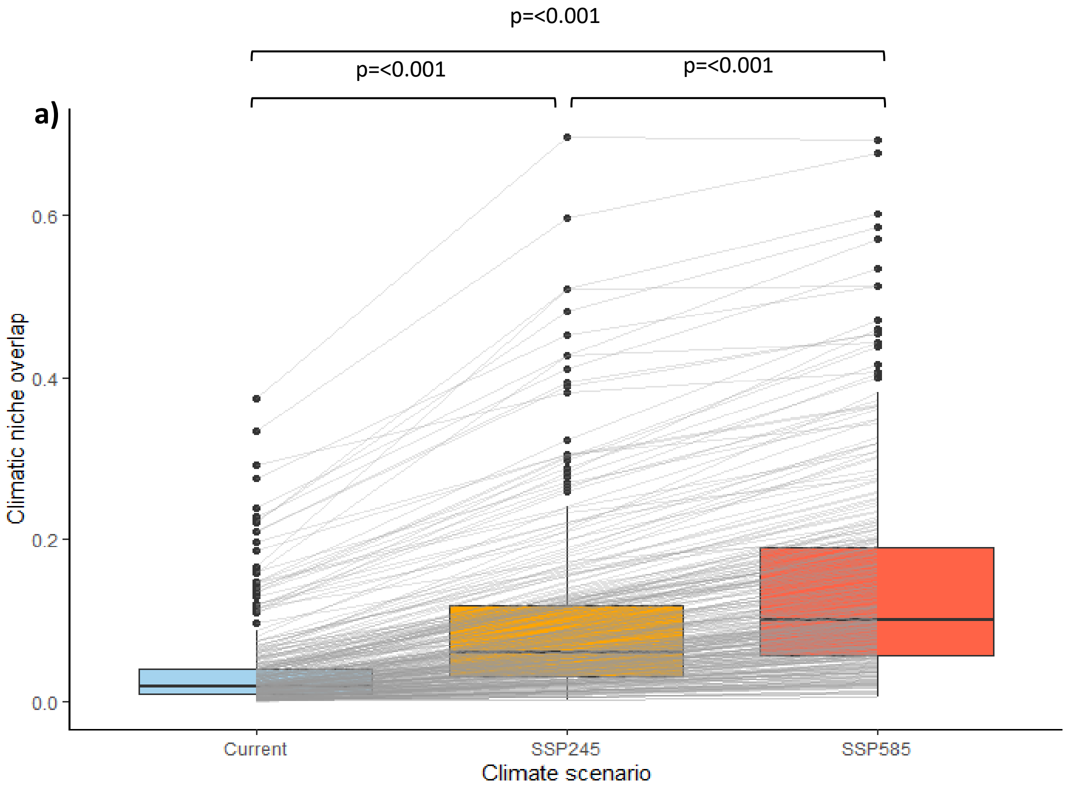


Figure 11: The most frequent Families observed in the list of 284 high-risk species. Families with <5 species were not plotted.



b)

Test	Estimate	T statistic	DF	Conf. interval	p-value
Current vs SSP2-45	-0.057	-17.881	283	-0.064 to -0.051	**<0.001**
Current vs SSP5-85	-0.106	-22.059	283	-0.115 to -0.096	**<0.001**
SSP2-45 vs SSP5-85	-0.048	-23.705	283	-0.053 to -0.044	**<0.001**

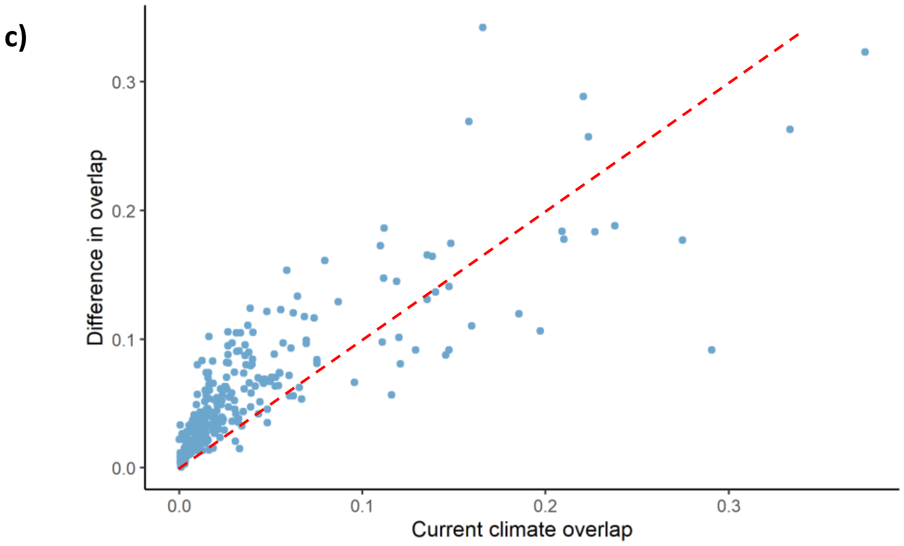


Figure 12: (a) climate overlap scores calculated between species' climatic niches and Norway's climate under current and future (SSP2-45, SSP5-85) climate change scenarios, (b) paired T-test results comparing hypervolume scores between each climate scenario (DF = degrees of freedom) and (c) a comparison of current climate overlap and the difference in overlap between current and SSP2-45 climates. Red line represents no change between current and SSP2-45 overlaps.

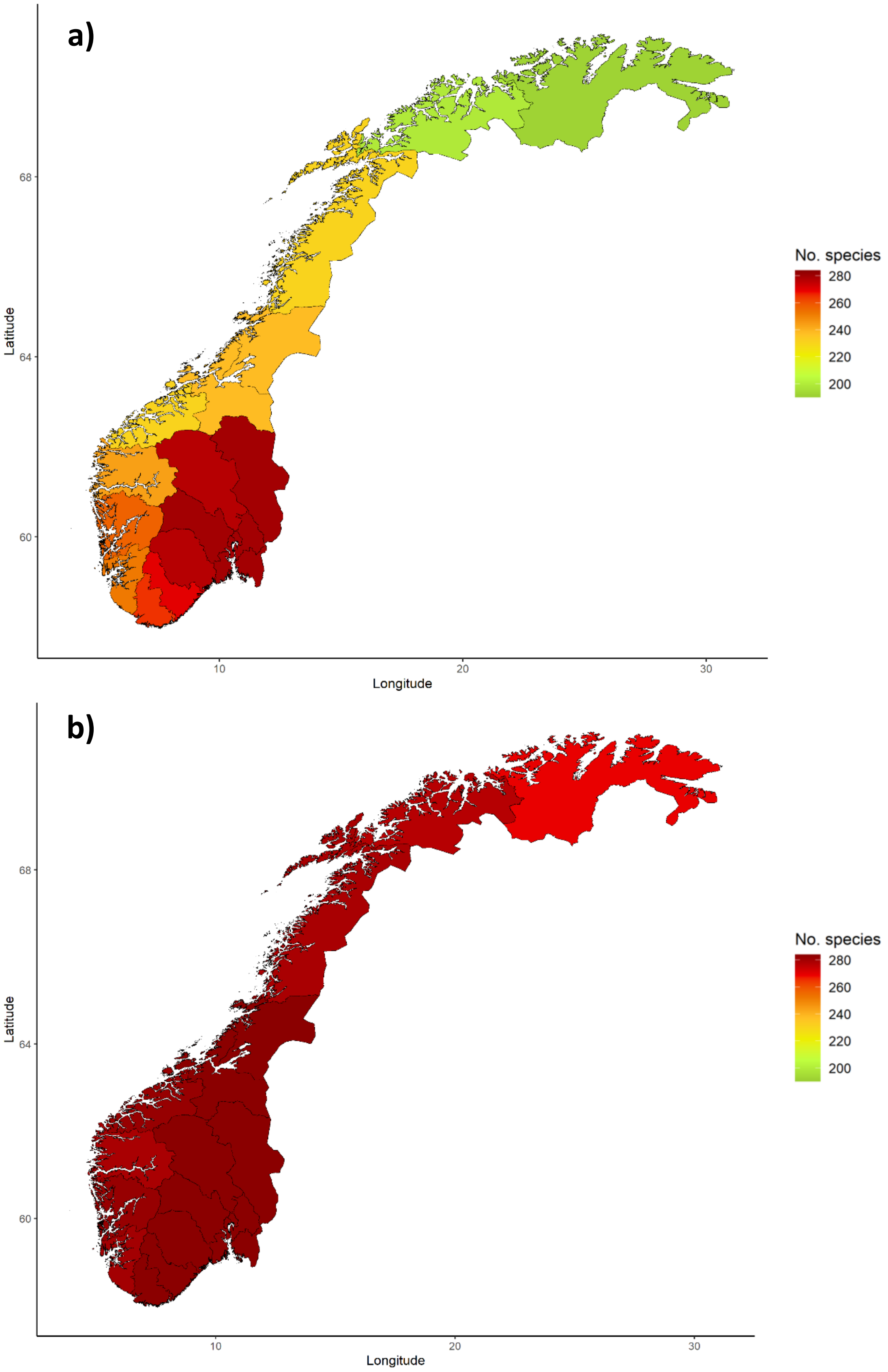


Figure 13: Number of species from the list of 284 high-risk species with climate overlap above 0 in each region of Norway under **a**) current and **b**) future climate (SSP2-45).

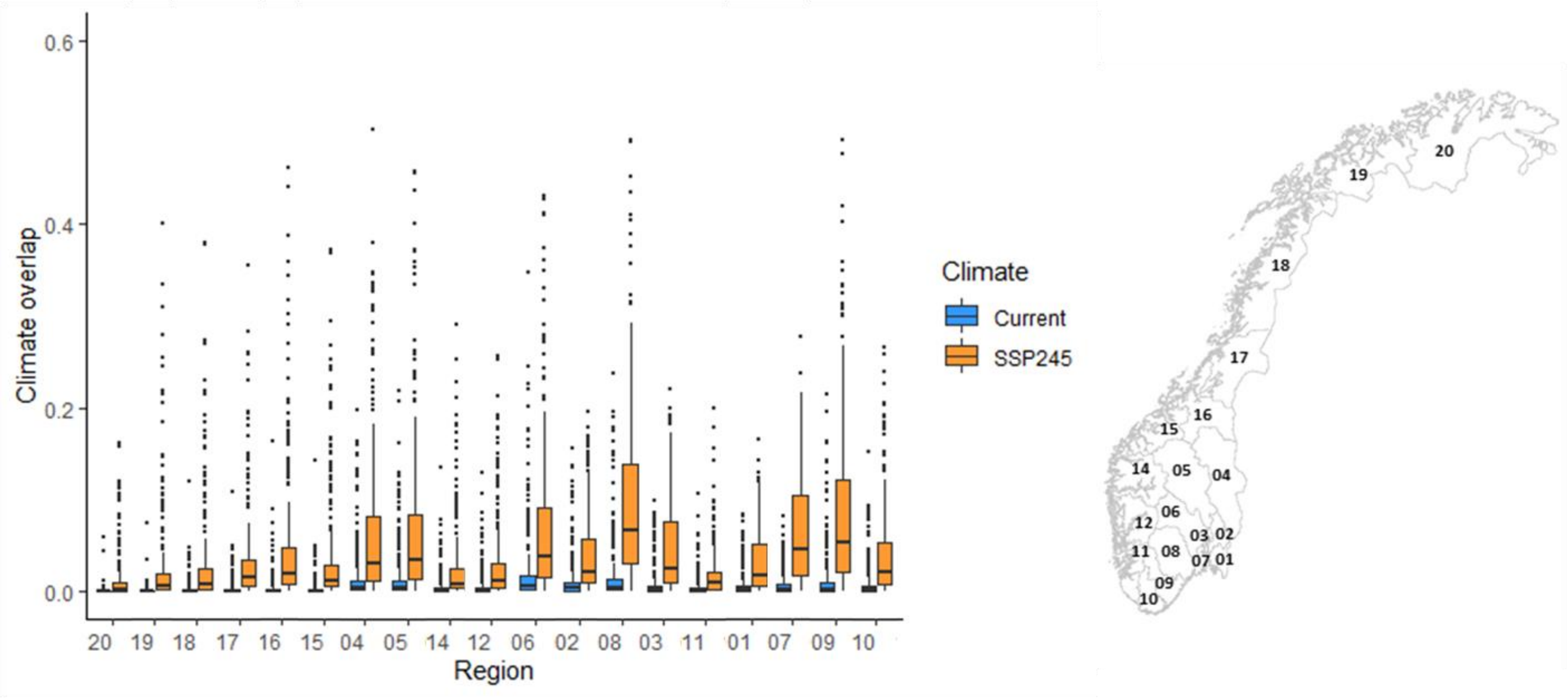


Figure 14**:** Range in climate overlap of high-risk 284 species in each region of Norway. Blue boxplots represent overlap with current climate, orange boxplots represent overlap with SSP2-45 future climate. Regions are represented by their ISO codes, ordered in descending order from highest to lowest latitude: 20 Finnmark; 19 Troms; 18 Nordland; 17 Nord-Trøndelag; 16 Sør Trøndelag; 15 Møre og Romsdal; 04 Hedmark; 05 Oppland; 14 Sogn og Fjordane; 12 Hordaland; 06 Buskerud; 02 Akershus; 08 Telemark; 03 Oslo; 11 Rogaland; 01 Østfold; 07 Vestfold; 09 Aust-Agder; 10 Vest-Agder.

2.4.2.2 Climate overlap sensitivity analysis

Removing outlying TWQ variables for the five high-risk species with highest climate overlap resulted in greater climate overlap for four of the five species (*A. decurrens, G. tinctoria, S. multiglandulosa* and *A. melanoxylon*) and did not affect the climate overlap of *P. pyrenaicus*. The species with the greatest change in climate overlap when outliers were removed was *A. decurrens*, where removing outliers resulted in an overlap increase from 0.38 to 0.55 under the current climate, from 0.70 to 0.96 under SSP2-45 and from 0.69 to 0.87 under SSP5-85 (Table S1 in File S2).

2.5 Discussion

2.5.1 High risk species

In this horizon scanning study I identified 284 high-risk species which cover a large range of families and most of which are used as ornamentals. The impacts of a number of these high-risk species have already been discussed widely in the literature. For example, *A. decurrens* is widely documented to occur in dense populations in Indonesia (Septiadi et al., 2018; Sulistijorini & Setyawati, 2017) and South Africa (de Wit et al., 2001; Mbedzi et al., 2021) and is reported to reduce biodiversity, increase erosion and fire risk and alter nitrogen levels in the soil, making the habitat unsuitable to a range of indigenous plants (de Wit et al., 2001). Multiple *Acacia* species (*A. longifolia, A. dealbata* and *A. melanoxylon*) are currently invasive in Portugal (Correia et al., 2014), with *A. longifolia* resulting in community composition changes (Marchante et al., 2003), increased fire risk (Marchante, 2001) and altered soil properties (Marchante et al., 2008). *Gunnera tinctoria* impacts have been discussed in Ireland, where its presence is reducing seed biodiversity of soil banks (Gioria & Osborne, 2009) and it has spread rapidly around disturbed areas of land (Skeffington & Hall, 2011). *Gunnera tinctoria* is also widespread across the Azores (Ares & Pena, 1996) and New Zealand, where it occurs in dense populations and displaces endangered native plants (Williams & New Zealand Department of Conservation., 2005). In addition, *G. tinctoria,* along with *Prunus lusitanica,* were chosen by Thomas (2010) as two of the most ‘critical’ or ‘urgent’ risk species to Great Britain, a landmass relatively close to Norway and where these species are already naturalising. The European Union’s Regulation 1143/2014 also included *G. tinctoria* as one of several species of ‘Union concern’ – that is, species whose movement and breeding is restricted. Multiple sources (Regulation 1143/2014, 2014; Thomas, 2010) within northern Europe having identified the same species as having a high invasion risk, having used different methods, reinforces the high-risk status of these species.

The Norwegian Biodiversity Information Centre (2020) produced a list of ‘door knocker’ species which may pose a risk to Norway, chosen via risk assessments by groups of experts (Sandvik, 2020; Sandvik et al., 2017). These door knockers fell into three categories: species already in Norway but unable to reproduce; species in neighbouring countries which may pass into Norway without human aid; species not in Norway but which may move into Norway through established transport pathways. This third category used by Sandvik (2020) is the most relevant to the aims of this study, and of their high-risk list of 1,392 species, 94 were shared with the 284 species identified here. The most significant difference between the methods employed in our study and the Norwegian Biodiversity Information Centre's project was climate matching of each species to Norway's climate. Whereas I carried out climate matching hypervolume calculations for every species, Sandvik (2020) discarded tropical or subtropical species and shortlisted the remainder based on their biogeography according to Plants of the World (POWO, 2022). This broader method of climate matching could explain the discrepancies between the two species lists. However, the number of shared species between lists is encouraging and gives more weight to both studies.

2.5.2 Climatic suitability of Norway

Invasion risk varies across Norway, as seen by the number of high-risk species with overlap in each region (Figure 13) and the range in overlap values in each region (Figure 14). Eastern regions of Norway seem the most hospitable for these species, and are therefore at most risk of invasion, the west and north of Norway less so. By comparing the regional maps (Figure 13 & Figure 14) with the bioclimatic variables TWQ, AP and PS of Norway (Figures A1-A3), it is possible to discern aspects of the Norwegian climate which may influence plant survivability. Mean temperature of the warmest quarter (TWQ) is highest in the southeast and southwest of Norway, but is lower in the central south and at higher latitudes. This might explain why the southeast has a higher number of species with overlap and a greater overall median overlap, and climate overlap analysis does suggest that temperature is the variable with the highest influence in determining climate overlap with Norway (Figure 9). However, Norway is situated at a relatively high latitude which suggests that winter temperatures might limit potential plant distribution more than the summer temperatures which were used in this analysis. Although no minimum temperature variable was used, mean temperature of the coldest quarter is strongly correlated with one of the chosen variables (annual precipitation; correlation = 0.70). It is therefore possible to infer that hypervolume analyses are quite robust to the effect of winter minimum temperature limitations of potential invasives. Further to this, I carried out a sensitivity analysis to determine whether temperature outliers influenced climate overlap. The highest risk species *A. decurrens* is native to Australia, as are many species in the high-risk species list, and its high overlap between its climatic niche and Norway's climate is somewhat surprising given that it is currently distributed across much lower latitudes than Norway (Figure

13). I therefore suspected that its high overlap may be due to lower temperature outliers, which may not be accurate if taken from regions with high climatic variation where this variation would not be picked up by the relatively low grid resolution (~9 km^2 at the equator). However, sensitivity analysis showed that for the five species ranked as highest risk to Norway, climate overlap increased for four species when outliers were removed and did not decrease for any species. This is probably because higher temperature outliers were also removed, which likely reduces climate overlap when included as such high temperatures are not found anywhere within Norway. These results suggest that the 'core' climatic niches of these five species do indeed show some overlap with Norway's climate, and that including even potentially inaccurate outliers do not considerably affect climate overlap.

Under climate change, climate overlap increased for all high-risk species suggesting that Norway will become more suitable for these species in the future. This increase was greatest in species which already had a relatively high overlap (Figure 12c). In addition, the number of high-risk species with climate overlap increased in every region. This increase was greatest in the northern half of the country. Temperature predictions for 2060-2080 show an increase throughout Norway by several degrees and the temperature of the northern regions begins to resemble that of the current southeast. It is therefore unsurprising that the number of species with climate overlap in the future at higher latitudes resembles current numbers in the southeast. The idea that species are likely to be able to survive at higher latitudes under climate change is widely supported in the literature (e.g. Grace, 2002; Pauchard et al., 2016; Walther et al., 2009), and it has been posited that plant populations may move further north of their own accord once established at lower latitudes. It is possible, based on the changes in climate overlap, that this may occur in Norway should the high-risk species become introduced in the more hospitable regions of the southeast.

2.5.3 Methodologies

This study used hypervolumes to calculate climate overlap, which has not been done in any previous horizon scanning studies. In contrast to the limited WRA options or more binary studies which answer either 'yes' or 'no' to the question of climate matching, hypervolumes show to what extent a species overlaps with a certain climate and therefore how likely it is to survive. To validate this method, various comparisons and analyses were carried out. These analyses showed that a large proportion of species which currently occur at higher latitudes have climate overlap with Norway, and that species currently occurring at lower latitudes show considerable increase in climate overlap under climate change. In addition, species which already occur at high latitudes (Figure 7) and in regions with lower temperatures (Figure 8) show decreased climate overlap in the future, suggesting that Norway will become less suitable for species which are already adapted to high-latitude regions with lower temperatures. The greatest increase in climate overlap occurred in species which currently live in areas averaging 15-17° TWQ, which falls within the upper range of Norway's predicted temperature in the future but falls outside of its current temperature range (mean ± SD). Based on the predictive ability of hypervolumes calculated in this study (Figure 4) and what is generally known about climate and niche conservatism (Liu et al., 2020; Peterson, 2011; Petitpierre et al., 2012), these results help validate the use of hypervolumes in determining the climatic suitability of Norway.

One of the limitations of this horizon scanning study is that it relies on a global list of known naturalised plants and established economic uses/invasive impacts. New species that have never been recorded as invasive before are emerging as new regions are exposed to new pools of potentially invasive plants through establishment of new and increasing trade and transport links (Seebens et al., 2018). New uses might also be found for other species, which then get introduced much more than in the past, meaning that potentially high-risk species may be missed. In addition, I shortlisted species based on their climate overlap with Norway's current climate rather than its predicted future climate, and then investigated the effects of climate change on these species. In fact, based on the results in Figure 7, a large number of species which had no overlap with Norway's current climate showed some overlap with Norway in the future. I decided to focus on species which currently pose a risk, rather than producing sets of high-risk species for each climate scenario, as these are the species which it is more important to highlight now. However, these points emphasise the importance of repeating such studies after a certain time span to ensure that newly emerging invasive species are considered and that we are continually risk-assessing species as Norway's climate changes. In addition, I focused on species which might be purposefully imported into Norway, whereas there are other factors which could be considered where plants are not introduced for economic reasons. Examples include taking into account the geographical proximity of invasive populations in countries close to Norway, which may spread their range across Norway's border in the future, or considering the trade routes into Norway and the potential of plants along these routes to be transported to Norway accidentally.

There is considerable variety in the methods employed to carry out horizon scanning studies. Roy et al. (2014), for example, interviewed experts in various taxonomic groups to get a consensus of questions to include in a risk assessment. Gallardo et al. (2016) did similar and additionally asked the experts to rank species based on their professional judgement. Many biosecurity agencies use the Australian Weed Risk Assessment (WRA) approach to determine species risk. This approach, although widely used (e.g. Bayón and Vilà, 2019; Thomas, 2010), would have been too time-consuming to use for the list of over 10,000 species taken from

GloNAF as it comprises of a questionnaire which should be applied to each individual species, whereas this horizon scanning study was designed to act as an initial rapid risk assessment. The type of horizon scanning method employed may well have a large impact on the identified high-risk species; for example, the Norwegian Biodiversity Information Centre (Sandvik et al., 2017), who had a similar aim to this study, identified many door-knocker species which this study did not.

Many species identified in this study had very low climate overlap values which may mean that in reality they would be unable to naturalised within Norway. However, due to the continuous nature of climate overlaps it would be unwise to use one value as a cut-off point, even if the models created to validate the use of hypervolumes (Figure 4) could be used to predict a threshold above which survival would be likely. Instead of identifying all 284 species as top priority it has allowed me to place them in a hierarchy of potential risk, but with the potential shortcoming of identifying species which are unlikely to be able to survive in Norway. Furthermore, the large size of some regions means that there is low accuracy in judging high risk areas. Analysing regions on a smaller scale would give a more accurate result of the specific areas of high risk.

2.5.4 Biosecurity

Horizon scanning studies are a valuable tool to identify high-risk species before they become an economic, environmental, ecological or human/animal health problem. Based on this study, I recommend that the identified high-risk species are fully screened as part of Norway's biosecurity policy to evaluate the potential costs of introduction of these species into Norway. More generally, it might be valuable to hold discussions with relevant institutions about the results of this study, such as agricultural agencies, environmental agencies or the National Biodiversity Information Centre, who may be able to give insight and recommendations for how to proceed with these identified species.

In addition to identifying particular high-risk species, it is possible to look at the areas from which these species might be imported based on their current distribution (Figure 10). Here, none of the high-risk species is currently found in Sweden, Canada or in most of Russia; it is possible to assume, therefore, that plant import from these countries will pose little risk. In contrast, however, a large proportion of high-risk species are currently found in France, Spain, eastern Australia and New Zealand. Stricter rules could therefore be placed around import from these countries. Predicting future invasion risk is increasingly important as climate change renders Norway's climate more habitable for introduced species and increases their suitable range into higher latitudes. In addition, the impacts of climate change on native biota (e.g. loss of species, range shifts) means that native communities will be in flux and therefore more susceptible to the impacts of invasive species (Thuiller et al., 2007). Early detection and prevention of invasion is always more cost effective than trying to eradicate or manage invasion post-introduction (CBD, 2010). By acting now to implement laws which will monitor the import of such species, Norway’s ecosystems and their biodiversity can be better protected for future generations.

2.5.5 Conclusions

Here I have presented a relatively simple protocol for rapidly screening large numbers of species based on their potential for introduction, naturalisation, and environmental impact which could precede and complement a full-scale invasive plant risk assessment and analysis. The method of climate matching used is arguably more accurate than other widely used methods and, in addition, takes into account both current and future scenarios, which has not been carried out before in horizon scanning studies. This approach can be easily adapted and implemented for different countries or regions and would provide quantitative support for established, consensus-based horizon scanning projects. However, due to the broad climate matching between species’ niches and Norway’s climate, the next step for these high-risk species is to carry out more detailed analysis on their potential distribution. This will enable me to observe the specific areas of Norway at risk from each of these species based on climate suitability and will further validate this horizon scanning study as a tool to help inform policy-makers.

Chapter 3

Predicting the distribution of potentially invasive plant species in Norway under a changing climate

3.1 Abstract

The most cost-effective way of managing invasive species is to prevent them from becoming introduced. In Chapter 2 I carried out a horizon scanning study and identified 284 high-risk species which are not yet present in Norway but could potentially naturalise and become invasive if introduced. Here, I implemented species distribution models (SDMs) to predict the potential distribution of these high-risk species in Norway under both current and projected future climate scenarios. This enabled me to observe in greater detail the areas of Norway most at-risk from invasions. Under the current climate, the distributions of high-risk species were mostly limited to the southeast and coastal regions of Norway. However, under future climate scenarios species' potential distribution increased significantly, with their ranges expanding northwards and further inland. Several invasion hotspots containing large numbers of species were identified close to urban areas such as Oslo, which is of particular concern as urban areas are amongst the most highly-invaded environments globally with particularly high propagule pressure in urban gardens. These results correspond with much of the literature which predicts range expansion of invasive plants to higher latitudes under climate change. I also investigated the correlation between climate overlap (overlap between a species' niche and the climate of Norway, calculated using hypervolumes), and the predicted distribution of species across Norway (proportion of Norway's grid cells which contained presence predictions, calculated using SDMs). Analysis showed positive correlation for both current and future scenarios ($r > 0.6$). Based on these findings I recommend that hypervolumes are used for assessing large numbers of species, and SDMs are then used on a limited set of high-risk species identified via horizon scanning to fully determine at-risk areas in the region of interest.

3.2 Introduction

Many high latitude regions have seen a rise in the number of invasive plants in recent years (Sandvik et al., 2020; Ware et al., 2012) which has coincided with increased human activity (Forbes et al., 2004). Invasive plants can have substantial negative impacts on native biotas, including outcompeting native plants (Bezemer et al., 2014), altering soil chemistry (Weidenhamer & Callaway, 2010) and affecting plant-pollinator interactions (Pyšek et al., 2012). Plant introductions can be intentional, e.g. for horticulture (Reichard & White, 2001) or forestry (Richardson, 1998), or unintentional, e.g. seed contamination of luggage, clothing or shipped goods (Rahman et al., 2003; Ware et al., 2012). Even if introduced at lower latitudes, however, non-native species could pose a risk to Arctic regions as climate change is resulting in invasive species' ranges shifting poleward (Merow et al., 2017; Pauchard et al., 2016). Norway is a country with more temperate regions in the south and more inhospitable Arctic tundra at its northern edge, which may mean that under climate change non-native species may not only become more prevalent in Norway's southern temperate regions but may move northwards and threaten its vulnerable Arctic ecosystems.

To avoid the ecological and economic costs of post-invasion management, preventing non-native species introductions is considered to be the best management strategy (CBD, 2010; Essl et al., 2011; Shine et al., 2010). Norway is already home to the second largest number of non-native plants in Europe (Sandvik et al., 2019), which makes further prevention of non-native species introduction vital. Preventative measures, such as horizon scanning studies, aim to predict which species are likely to become invasive within a country through factors such as environmental or socioeconomic impact (e.g. Bayón & Vilà, 2019; Gallardo et al., 2016). One of the main factors influencing potential plant distribution is climate (Woodward, 1987), which is therefore vital to include in predictions of plant invasion.

Species distribution models (SDMs) are a frequently used method to predict the potential distribution of a species both now and in the future, practised in fields of research such as invasion ecology, conservation planning and climate change studies (Barbet-Massin et al., 2018). The aim of SDMs is to relate environmental variables to species observations in the field, often in the form of presence or absence data (Guisan & Thuiller, 2005). Environmental variables are chosen to represent factors which limit a species' distribution, such as temperature, or resources to help a species survive, such as water availability (Guisan & Zimmermann, 2000). The efficacy of SDMs has been shown in several studies in which they were proved to successfully predict species' distribution change. Areias Guerreiro et al. (2016) carried out surveys on Eurasian otter distribution in Spain thirteen years apart, and found that otter occurrence in the second survey strongly resembled the distribution predicted by earlier models due to the otters' expanding ranges. Barbet-Massin et al. (2018) created models which accurately predicted the spread of the invasive Asian hornet throughout Europe. SDMs are particularly relevant in the context of managing invasive species, as they can be used to locate potential high-risk 'hotspots' where there is high climatic suitability for selected non-native species. By highlighting such areas, we can develop control strategies to prevent or limit movement of non-native species to these highly suitable locations (Barbet-Massin et al., 2018).

Based on the findings in Chapter 2, we know that certain regions of Norway are suitable for a greater number of potentially invasive plant species than others. Using hypervolumes to calculate climate overlap between a species' niche and Norway's climate was a valuable method for assessing large numbers of species and gave a general idea of which regions may be at higher risk from potentially invasive species. However, this method only calculates overlap between a species' climatic niche and a reasonably large area of land. It does not give a fine resolution prediction of suitable areas. In addition, I did not select a threshold overlap value below which species would be classed as 'unable to survive', and therefore might have included species not well suited to any area of Norway. To overcome these problems, I applied SDMs to each of the 284 high-risk species identified in Chapter 2. The main purpose of these SDMs was spatial projection of species' potential distributions, rather than to model their response to each environmental variable, which allowed me to determine (i) which areas of Norway were most at risk of invasion, (ii) how climate change affected invasion risk hotspots, and (iii) whether climate overlap values calculated in Chapter 2 were representative of SDM predictions.

3.3 Methods

3.3.1 Species of interest

The 284 high-risk species identified in Chapter 2 were used in this study (File S1). These species are known to be naturalised somewhere in the world, have some overlap between their climatic niche and the current climate of Norway, are used economically in a way which is common in Norway, and have known ecological impacts.

3.3.2 Data

3.3.2.1 Species occurrences

Species occurrences were downloaded from the Global Biodiversity Information Facility (GBIF) using the R package 'rgbif' (Chamberlain et al., 2020; see *2.3.1.1 Occurrence data*).

3.3.2.2 Environmental predictors

Climate data were downloaded at 5-minute resolution from WorldClim (Fick and Hijmans, 2017) for all of the 19 bioclimatic variables described on WorldClim using the R package 'raster'

(Hijmans and van Etten, 2012). The three bioclimatic variables used in Chapter 2 were chosen as the environmental predictor variables for SDMs (see *2.3.2.1 Climate data*): TWQ (mean temperature of the warmest quarter (° Celsius)), AP (annual precipitation (mm)) and PS (precipitation seasonality (coefficient of variation (CV)). Future data were also downloaded from WorldClim (see *2.3.2.1 Climate data*) for eight General Circulation Models (GCMs) in two CMIP6 scenarios, SSP (shared socioeconomic pathway) 2-45 and SSP5-85. In Chapter 2, the mean of all GCMs was calculated for analysis for simplicity due to the large number of species. In this study, however, GCMs were saved individually.

3.3.3 Species distribution models

3.3.3.1 Model building

The potential distributions of the 284 high-risk species were projected across Norway. All species distribution models (SDMs) were computed using the packages ‘biomod2’ (Thuiller et al., 2009) and ‘dismo’ (R. J. Hijmans et al., 2015). The framework used is summarised in Figure 1. Generalized linear models (GLM), generalized additive models (GAM), random forests (RF) and boosted regression trees (GBM) were selected, as in Dullinger et al. (2017), to represent two classical regression models (GLM and GAM) and two machine-learning models (RF and GBM). These algorithms all require both presence and absence data. There are different methods of sampling pseudo absences each with advantages and disadvantages. In target-group pseudo absence sampling, sampling is restricted to areas where presence points have been recorded. This means that the resultant models will not reflect the potential spatial bias of occurrence data, which is often limited to easily-accessible regions. However, this also means that the model is less reliable when predicting distribution across unsampled locations, e.g. polar regions, than if random sampling was used (Phillips et al., 2009). Random sampling was therefore chosen for this study since species distributions were projected across all of Norway which may contain regions where sampling is uncommon. Circles were created with a 200 km radius around each presence point and samples were taken randomly from outside the circles (Dullinger et al., 2017). For GLM and GAM 1,000 pseudo-absence points were sampled, and for RF and GBM the number of pseudo-absences selected equalled the number of presence points, following Barbet-Massin et al. (2012). Pseudo-absences were sampled ten times per species to control for any potential sampling bias. When fitting models, a five-fold cross validation approach was used, training models using 80% of model data and testing them with the remaining 20%. To minimise the impacts of spatial autocorrelation (SAC) (Dormann, 2007) cross validation samples were created using a blocking method (Bagchi et al., 2013). For this a world map of ecoregions according to WWF was downloaded (Olson et al., 2001) which was then grouped into five blocks, each with a similar mean and variance for the three bioclimatic variables selected for the SDMs.

For each training run, four of these five blocks were selected for model calibration and the final block was used for model evaluation. The resulting models were evaluated using the Relative Operating Characteristic (ROC) curve procedure which produce an AUC (Area Under Curve) metric. Models with an AUC of below 0.7 were rejected in accordance with Zhang et al. (2015) who state that evaluation scores of below 0.7 are considered poor, 0.7-0.9 moderate and above 0.9 good. Successful models were created for all four modelling techniques for all species except *Austrocylindropuntia subulata, Cereus jamacaru, Lathyrus subulata, Opuntia ficus-indica* and *Pelargonium capitatum.* These species had no GLMs with ROC values above 0.7, so only the three model types GAM, RF and GBM were used (see File S2 for information about species models). Four different models (GLM, GAM, RF, GBM) with ten pseudo-absence sampling runs, each with five training runs, resulted in up to 200 models (or up to 150 for species with no successful GLMs) in total per species.

3.3.3.2 Model projection & mapping

Each of the 200 models were projected across Norway for both current and predicted future climate data for SSP2-45 and SSP5-85. Unlike the hypervolume climate overlap calculations, each of eight future climate GCMs were projected individually instead of using the mean value for each scenario. Up to 3,400 projections were therefore computed for each species (200 current and 200 each of 16 future predictions, with some removed due to low AUC scores). We calculated the mean of each projection for each of the climate scenarios for all raster cells, resulting in three ensemble model projections for each species: current, SSP2-45 and SSP5-85. Averaging was unweighted as all models with an AUC below 0.7 were discarded. Mean model predictions were converted into binary presence/absence predictions by applying a threshold which optimised the True Skill Statistic (TSS) metric. Thresholds were averaged across all of the models for each species, so that each species' threshold was unique. This resulted in more accurate thresholds, as opposed to applying one threshold across all models regardless of species. The sum of all species' presence/absence scores was calculated to give the number of species with potential distribution in each 5-minute grid cell (equal to ~9km^2 at the equator) for all three climate scenarios, and mapped to identify 'hotspot' regions of invasion risk under current and future climates which contained high numbers of species.

3.3.3.3 Analysis of model results

For each climate scenario, potential % of Norway suitable for each species was determined by calculating the proportion of grid cells in Norway which contained presence predictions. Species' northern limits were also determined as the highest latitude which contained presence predictions. These values were then compared for all species between climate scenarios using paired T-tests to determine how range cover of Norway and latitudinal limits might be affected by climate change.

Finally, to determine whether climate overlaps were a good predictor of SDM results, Pearson correlation analysis was carried out between all 284 species' climate overlaps (File S1) and the proportion of grid cells in Norway which contained presence predictions for each climate scenario. Ten species with the highest climate overlap scores and ten species with the lowest overlap scores were isolated and their predicted distribution across Norway plotted separately to visualise the relationship between climate overlap and SDM predictions.

3.3.3.4 Model evaluation

After completing all SDMs, I carried out an evaluation using the guidelines suggested by Araújo et al. (2019) who suggest assessing the quality of SDMs based on four main categories: response variables, predictor variables, model building and model evaluation. Each category contains sub-categories which are each scored as gold, silver, bronze or deficient. Using these, I assessed my SDMs and assigned my model a score for each sub-category (File S3).

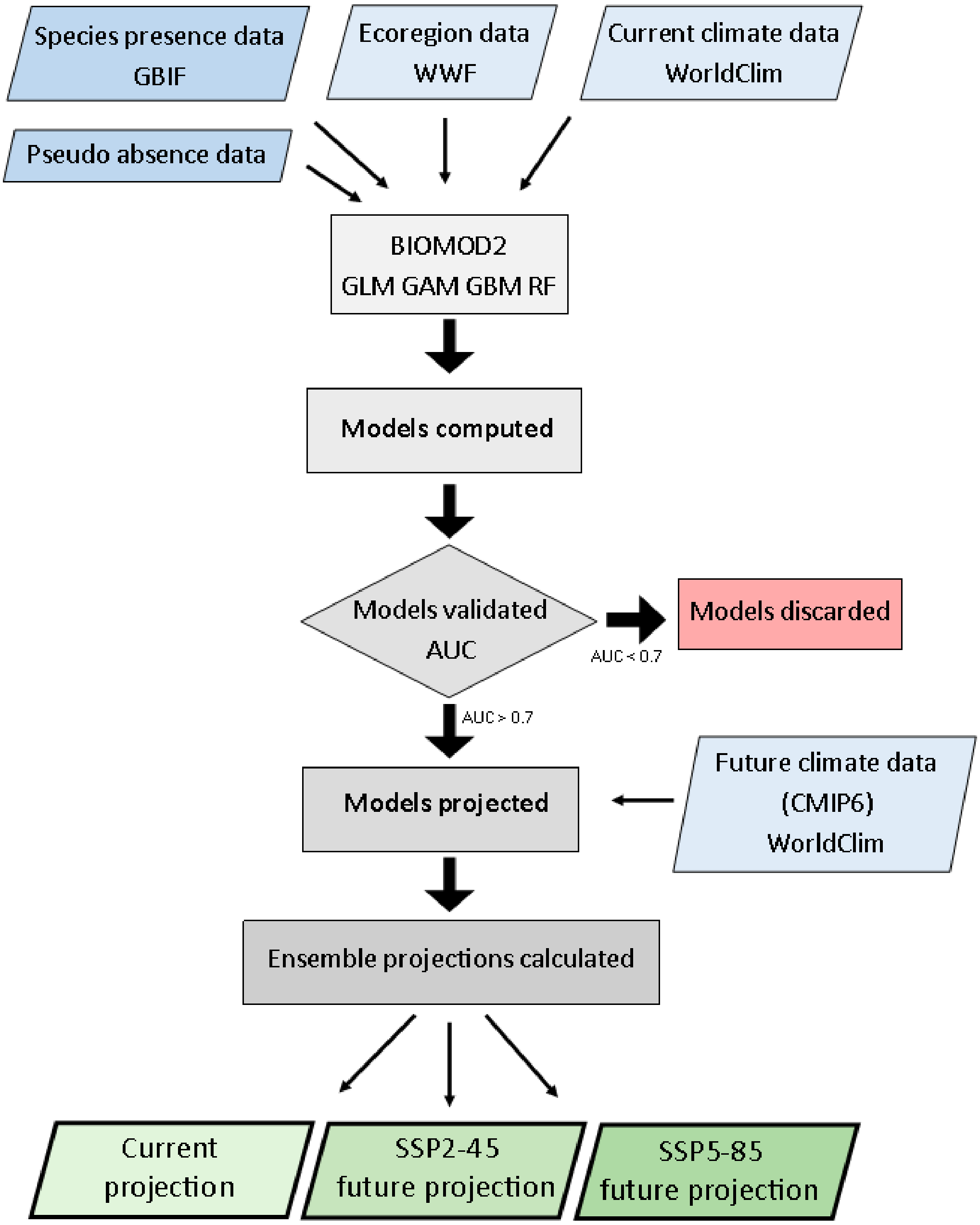


Figure 1: Framework used to carry out species distribution models (SDMs) on 284 high-risk species identified by horizon scanning study. Blue boxes represent data put into the model. Grey boxes represent stages within the model. Green boxes represent the final ensemble model projections.

3.4 Results

3.4.1 Species' distributions

Under the current climate, all grid cells within Norway contained at least one high-risk species, with a maximum of 83 species predicted to occur in any one location. The distributions of high-risk species were mainly clustered around the southern and western coast of Norway (Figure 3a). 150 high-risk species were not predicted to occur anywhere in Norway under the current climate, with corresponding climate overlap scores of <0.001 – 0.060. Under the future climate scenario SSP2-45, there was a maximum of 244 species in any one location. More species had predicted distributions further north along the coastline and further inland. The highest number of species was predicted to occur near Oslo, with a further cluster north of Trondheim in the boreal rainforest region (DellaSala et al., 2011) (Figure A5). A greater number of species were distributed along the northern coast and into the Arctic circle (Figure 3b) under SSP2-45 compared with the current climate. Under scenario SSP2-45, only 23 high-risk species were not predicted to occur anywhere in Norway, with corresponding climate overlap scores of 0.002 – 0.061. Under SSP5-85, there were a maximum of 260 species predicted to occur in any one location. The areas containing more than 200 species increased to cover the wider region in the south, around Oslo, and in the boreal rainforest north of Trondheim (Figure A5). The number of species distributed along the western coast increased. Few species were predicted to have potential distributions in the Arctic and alpine ecosystems of Norway under both current and future scenarios (Figure 3c). Only 15 high-risk species were not predicted to occur anywhere in Norway under SSP5-85, with corresponding climate overlap scores of 0.005 – 0.089. Invasion 'hotspots', here represented as areas containing at least 20 high-risk species, more than doubled in size from 19.0% of Norway suitable for at least 20 high-risk species under the current climate to 51.8% under SSP2-45 and 66.5% under SSP5-85.

The average potential range for all species, calculated as the mean of the percentage of Norway's grid cells each species is predicted to occur in, increased from covering 3.8% (2.3% lower quartile (LQ) to 5.3% upper quartile (UQ))) of Norway under the current climate to 15.8% (6.9% LQ to 24.8% UQ)) under SSP2-45, and to 24.1% (12.1% LQ to 36.1% UQ) under SSP5-85 (Figure 4a; see File S4 for all species' ranges). There were three species with potential ranges covering over 65% of Norway under current conditions, all of which had increased ranges under climate change to cover over 75% of Norway: *Acacia decurrens*, *Senna multiglandulosa* and *Cupressus lusitanica.* Species potential ranges shifted from an average latitude of 63.5°N under current climate conditions to 65.9 °N under SSP2-45 and 68.1°N under SSP5-85 (Figure 4b). The species with the most northerly potential range limit under current conditions was *A. decurrens*, predicted to occur at the most northern point in Norway (71.04°N; Figure A4) but under climate change scenarios the number of species predicted to occur at Norway's northern limit increased to 10 species under SSP2-45 and 27 species under SSP5-85. Both species' potential range sizes and their northernmost range limits increased significantly both from the current climate to SSP2-45, current climate to SSP5-85 and between SSP2-45 and SSP5-85, calculated using paired T-tests (Table 1). For full species' latitudinal limits see File S5.

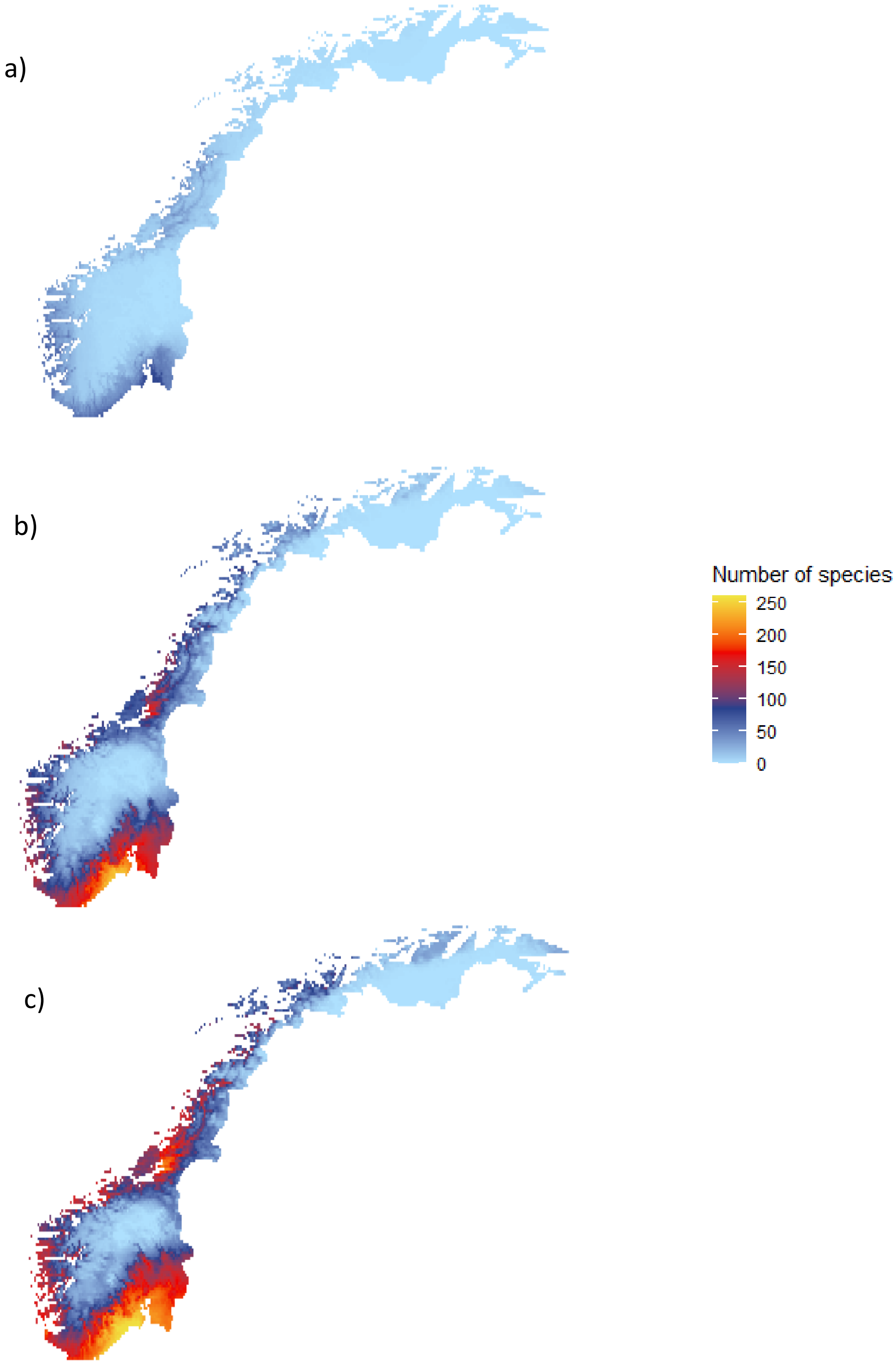


Figure 2: Potential distribution of 284 species identified as high-risk to Norway by a horizon scanning study under (a) current climate, (b) predicted climate for SSP2-45 and (c) predicted climate for SSP5-85.

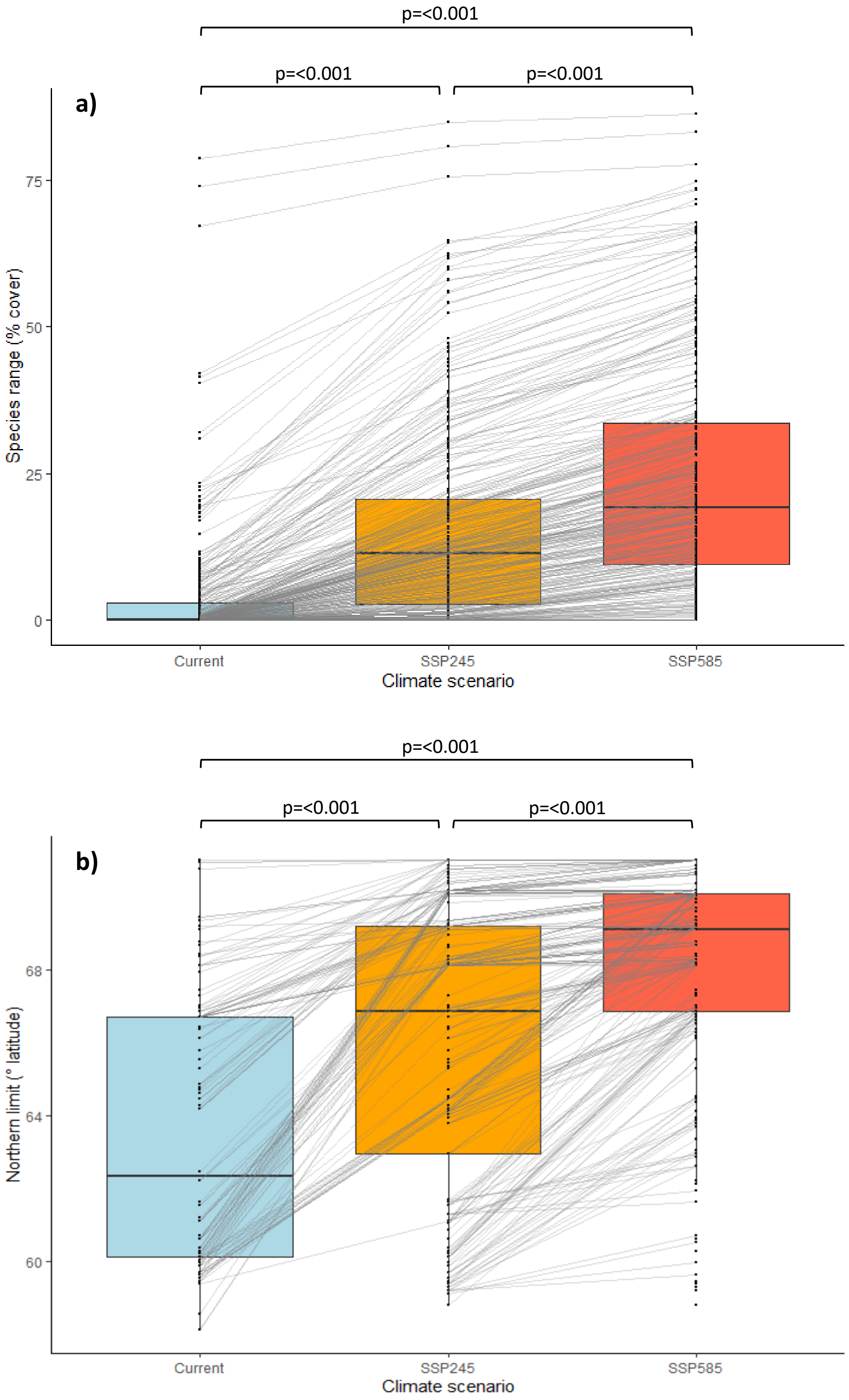


Figure 4: Predicted species ranges (% cover of Norway) **(a)** and northern limit of species' predicted ranges (° latitude) **(b)** under current climate conditions and predicted future climates SSP2-45 and SSP5-85. Grey lines join each species across different climate scenarios. Some species are not predicted to occur in Norway under current or SSP2-45 scenarios, so some lines are missing in plot (b).

Table 1: Paired T-test results comparing % range cover of Norway and northernmost range limit (highest latitude with predicted presence) for all species between each climate scenario. Bold p-values indicate significant result (p<0.01). DF = degrees of freedom.

Test	Estimate	T-statistic	DF	Conf. interval	p-value
% Range cover of Norway					
Current vs SSP2-45	-0.120	-19.002	283	-0.133 to -0.108	**<0.001**
Current vs SSP5-85	-0.204	-23.841	283	-0.221 to -0.187	**<0.001**
SSP2-45 vs SSP5-85	-0.084	-30.100	283	-0.089 to -0.078	**<0.001**
Northernmost range limit					
Current vs SSP2-45	-5.178	-20.201	133	-5.685 to -4.671	**<0.001**
Current vs SSP5-85	-6.546	-21.367	133	-7.152 to -5.94	**<0.001**
SSP2-45 vs SSP5-85	-2.513	-17.038	260	-2.803 to -2.222	**<0.001**

3.4.2 Top 10 and bottom 10 species

The potential range within Norway of the 10 species with the highest climate overlap (top 10) and 10 species with the lowest climate overlap (bottom 10) (Table 2; Figure 5) differed greatly from each other and in all climate scenarios. Under current climate conditions, the bottom 10 species only covered 5.2% of Norway. The maximum number of species in any one location under current climate conditions was 1 (Figure 6b). Distribution moved further north under SSP2-45 to cover 20.3% of Norway (Figure 6d) with their distribution limited to the south and central coasts. The maximum number of species in any one location increased to 4. This distribution spread further north under SSP5-85 to cover 35.1% of the projected area with a maximum of 5 species in any one location (Figure 6f).

In contrast, the top 10 species were already predicted to occur in 84.5% of the Norway under the current climate with all 10 predicted around the southeast and central coastal regions. Some species were predicted to occur within the Arctic circle (Figure 6a). The spread of these species increased under SSP2-45 to cover 86.0% of Norway, with all 10 species found in 35.9% of Norway, distributed across the southeast and central regions and some northern coastlines (Figure 6c). Under SSP5-85, these species increased further to cover more of the Arctic region (Figure 6e). All 10 species were present in 48.4% of Norway and only 12.7% of Norway contained no species at all. The increasing distribution of species between current and future climate scenarios corresponds with the increasing climate overlap values calculated using hypervolumes (Figure 5).

The correlation analysis carried out between climatic niche overlap scores and the proportion of Norway covered by each species showed strong positive correlation within each climatic scenario (r = 0.61, 0.72 and 0.69 respectively for current, SSP2-45 and SSP5-85 climate scenarios (Figure A6); Table 3).

Table 2: The top 10 and bottom 10 high-risk species ranked according to climate overlap with Norway's climate using n-dimensional hypervolumes.

Top 10 species **(highest-lowest)**	**Bottom 10 species** **(lowest-highest)**
Acacia decurrens	*Hiptage benghalensis*
Gunnera tinctoria	*Litsea glutinosa*
Senna multiglandulosa	*Hakea gibbosa*
Petasites pyrenaicus	*Opuntia stricta*
Acacia melanoxylon	*Cenchrus ciliaris*
Acacia dealbata	*Ceiba pentandra*
Erica lusitanica	*Schefflera actinophylla*
Pinus radiata	*Azadirachta indica*
Eucalyptus globulus	*Ruellia simplex*
Prunus lusitanica	*Parkinsonia aculeata*

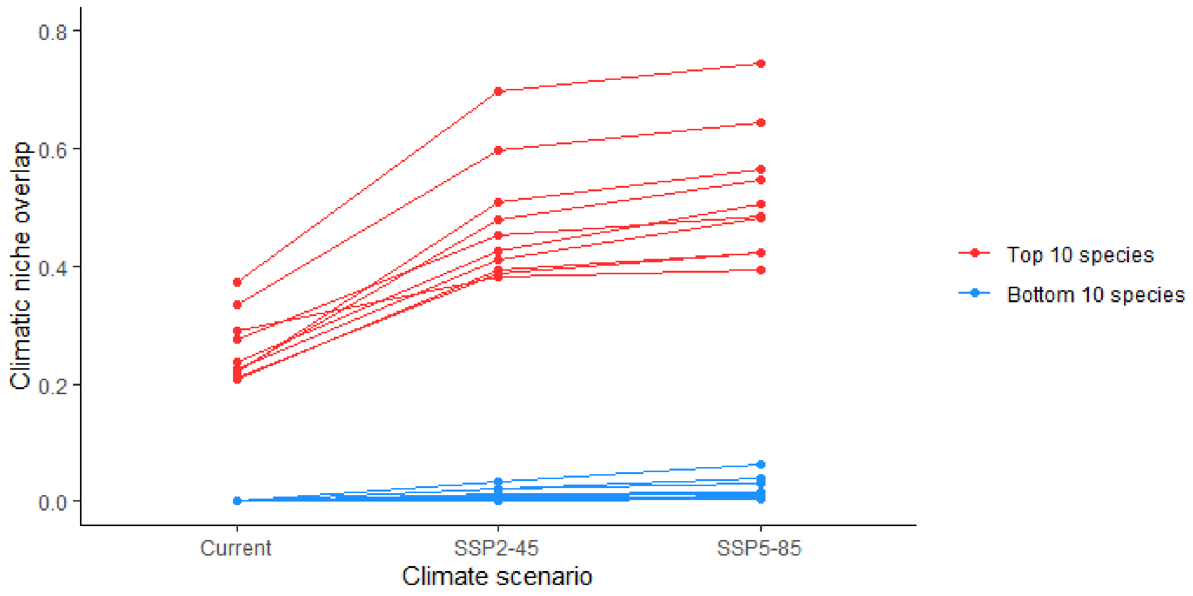


Figure 5: Climate overlap values calculated using 'dynRB' (Junker et al., 2016) between species' climatic niches and Norway's climate for the current climate and predicted future scenarios SSP2-45 and SSP5-85. Species are listed in Table 2.

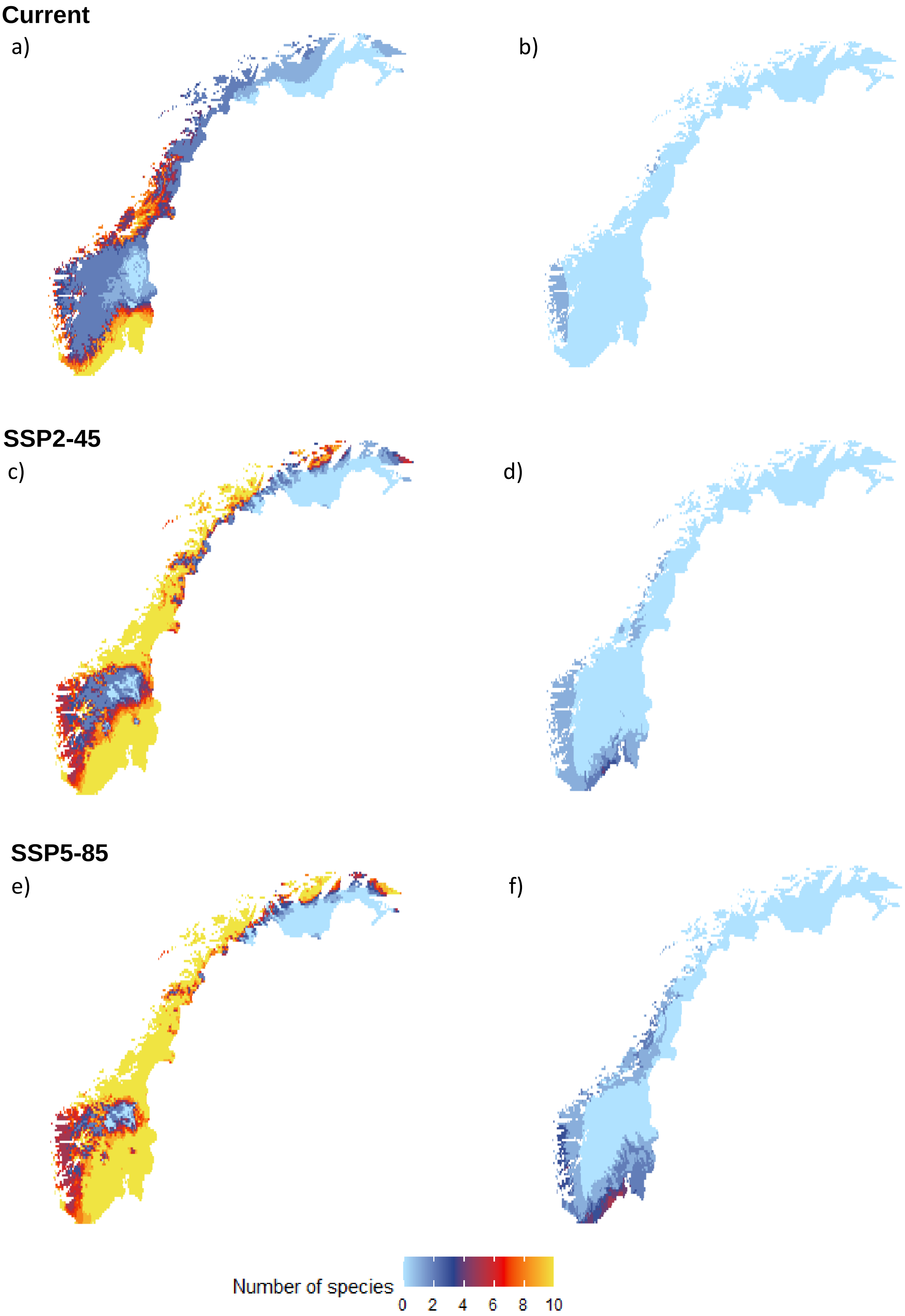


Figure 6: Potential distribution of top 10 (a, c, e) and bottom 10 (b, d, f) high-risk species ranked according to climate overlap with Norway's climate using n-dimensional hypervolumes. Predicted distributions are based on current climate (a, b), SSP2-45 (c, d) and SSP5-85 (e, f).

Table 3: Correlation between species' ranges (% cover of Norway; '% Cover') and climate overlap ('Overlap') scores for each climate scenario. Red numbers indicate correlations between values from the same climate scenario.

	% Cover current	**% Cover SSP2-45**	**% Cover SSP5-85**	**Overlap current**	**Overlap SSP2-45**	**Overlap SSP5-85**
% Cover current		0.81	0.70	0.78	0.73	0.65
% Cover SSP2-45	0.81		0.98	0.84	0.85	0.83
% Cover SSP5-85	0.70	0.98		0.80	0.82	0.83
Overlap current	0.78	0.84	0.80		0.96	0.91
Overlap SSP2-45	0.73	0.85	0.82	0.96		0.98
Overlap SSP5-85	0.65	0.83	0.83	0.91	0.98	

3.4.3 Model evaluations

I evaluated my models according to Araújo et al. (2019) and here describe my model scores in the same way (gold, silver, bronze or deficient). In terms of response variables, my models scored as deficient and bronze on taxon identification and the environmental/ geographical sampling of species' occurrences. The deficient aspects here were mainly because the response variables (presence of species) were downloaded from GBIF, and I was not able to assess the spatial accuracy of these occurrences or verify that the species were correctly identified by the recorders who entered this data originally. In terms of predictor variables, my models scored as deficient in determining the spatial and temporal resolution and uncertainty of my predictor variables. This was because my predictor variables were downloaded from WorldClim which only offers climate data from the years 1970-2000 to represent the near-current climate, and selecting a temporal scale appropriate to the taxa of interest (as suggested by Araújo et al. (2019)) was therefore not possible. In addition, I did not consider the uncertainty of these downloaded data. My models scored bronze in terms of predictor variable selection. In terms of model building, my models scored as deficient for the consideration of model complexity and the treatment of bias and noise in response variables, but scored as bronze in dealing with model uncertainty. My models scored as gold in terms of collinearity of predictor variables in the model. Finally, in terms of model evaluation my models scored as deficient for their evaluation of model assumptions, as I did not check whether my models violated statistical assumptions, bronze for their measures of model performance and silver for their evaluation of model outputs. For full evaluation and justification of results see File S3.

3.5 Discussion

This chapter built on a horizon scanning study which identified 284 potential high-risk species for future plant invasions in Norway (Chapter 2) by predicting the potential distributions of these species across Norway under current and future climate conditions. The key finding was that the distribution of the high-risk species in Norway was predicted to increase significantly from current to future climate projections, and this increase was more pronounced under the high-end future climate scenario SSP5-85 than under the intermediate scenario SSP2-45. In addition, the results suggest that species would be likely to expand their ranges further north under climate change and that the overall number of naturalised species will increase. In addition, the results show potential invasive species richness will increase across the southern regions of Norway, with potential implications for local biodiversity and ecosystem function. These findings are consistent with, but expand on, those of Sætersdal et al. (1998) who predicted an increase in native species richness in Scandinavia under climate change, particularly in the southern boreal regions, and with Petersen et al. (2022) who predict an increase in tall, woody species in Norway under climate change which applies to many species identified in Chapter 2; for example, six of the ten high-risk species with the highest climate overlap are trees or shrubs (File S1).

3.5.1 Distribution patterns

I observed a prevalence of high-risk species around the coasts of Norway but very few high-risk species inland. This pattern was present across both current and future climate scenarios (Figure 3a-c) and is probably due to the mountains which cover much of inland Norway (Figure A7). Of the three bioclimatic variables used in this study, the variable which showed the largest difference between the mountainous and coastal regions of Norway was the mean temperature of the warmest quarter (TWQ; Figures A1-A3), which suggests that temperature is the limiting factor preventing species from expanding their ranges. However, under SSP2-45 and SSP5-85 scenarios, species are predicted to occur inland at higher elevations, suggesting that these mountainous regions will become more hospitable in the future for high-risk species. This trend shows support for predictions that plants will move to higher elevations under climate change (Walther et al., 2009).

One of the most prominent high-risk 'hotspots' occurred near Oslo, with further high numbers of species predicted around the southeast and southwest coastlines where other larger cities are located (Bergen, Stavanger; Figure A5), a link which may be explained by these cities having been built in more temperate and hospitable climates. These hotspots are concerning as plants used for horticultural purposes are usually first imported and widely planted in urban areas

(Niinemets & Peñuelas, 2008; Smith et al., 2006). Urban sites were found to be among the most invaded types of land use (Chytrý et al., 2012; Lonsdale, 1999) and cities are often found to have increased plant species richness due to the high propagule pressure of introduced species (Kühn & Klotz, 2004; McKinney, 2008). Furthermore, spread of invasive plants often begins in urban areas from plantings (Dehnen-Schmutz et al., 2007) when ornamental plants 'escape' their garden environments and become naturalised (Niemiera & Holle, 2009). This means that these species are both more likely to be introduced to these cities than to less populated areas in Norway, and that if introduced these species are more likely to 'escape' gardens due to the suitable climate surrounding these cities. These results are concerning as introductions to these urban 'hotspot' areas would mean species avoid dispersal barriers such as geographical features which may otherwise prevent species from accessing climatically suitable regions of Norway. A further 'hotspot' was located in the boreal rainforest region of Central Norway. This ecosystem is categorised as 'vulnerable' by the Norwegian Biodiversity Information Centre (2020), and in fact a relatively high proportion of non-native species compared with native species already exists in this region (Olsen et al., 2017). This means that preventing further invasions is even more important to protect this vulnerable ecosystem.

The results of previous work suggest that plant species, both native and non-native, are likely to move polewards under climate change (Hellmann et al., 2008; Merow et al., 2017; Pauchard et al., 2016; Rew et al., 2020). This study supports these trends, showing a greater number of species predicted to occur at higher latitudes within Norway under climate change. Half of Norway's landmass lies within the Arctic circle and is classed as 'sub-Arctic' with much of the environment being forested. However, there are some areas of tundra at the northern edge of Norway which are characteristic of high-Arctic landscapes (Olson et al., 2001). The potential distribution of several high-risk species in these tundra ecosystems is particularly important as tundra has the lowest biodiversity of any terrestrial biome (Walker et al., 2001), making it less resistant to incoming species and therefore one of the most vulnerable ecosystems worldwide (Ims & Fuglei, 2005).

3.5.2 Are hypervolumes good predictors of climate suitability?

Predictions for the distribution of the top 10 and bottom 10 species, ranked according to their climate overlap value, were plotted separately to determine whether the climate overlap method using hypervolumes was representative of SDM predictions. In these SDMs, the top 10 species were already predicted to occur in a large proportion of Norway under current climate conditions and under future climate conditions, including regions within the Arctic circle. In addition, the notable trend observed in the model showing all 284 species, whereby only a few species were present around the mountainous regions of Norway, is not seen as strongly in the top 10 predictions. This suggests that these species are more adapted to a colder climate than the majority of the other 274 high-risk species. In contrast, only one species within the bottom 10 was predicted to occur in Norway under current conditions and was present only in one small region.

This discrepancy between the number of high-risk species with climate overlap calculated using the hypervolume method in Chapter 2 and the number of species with predicted distribution across Norway using SDMs may be explained by the different metrics of climate suitability represented by each method. The relationship between these methods will depend on the extent that Norway's climate is uniformly distributed, as hypervolumes consider the climate of Norway as a whole. However, Norway's climate is not uniformly distributed, with highly variable mean summer temperatures and varying levels of precipitation between coastal and inland regions. This means that although species' climatic niches may overlap with the full range of Norway's climatic variables, they may not share suitability with smaller-scale regions within Norway. In addition, species' risk was ranked according to their hypervolume climate overlap, and no threshold was applied at this stage below which a species was classed as 'low risk' and above as 'high risk'. Using SDMs, however, a threshold was applied to predict presence or absence of each species. This is likely to explain why so many species were not predicted to occur anywhere in Norway using SDMs, particularly under the current climate. In fact, species which were not predicted to occur anywhere in Norway under each climate scenario all had scores close to 0 for the corresponding climate scenario's climate overlap. This suggests that some of the high-risk species identified in this horizon scanning study may not pose such a risk to Norway if introduced, particularly those which are not predicted to occur in Norway even under SSP5-85. Conversely, some species currently distributed across lower latitude regions, such as *A. decurrens* (POWO, 2022), were predicted to occur throughout most of Norway even under current climate conditions. These projections are perhaps unexpected as species found at lower latitudes are unlikely to be adapted to the low temperatures found at Norway's high latitudes and altitudes. Sensitivity analysis into the effects of outlying temperature variables on climate overlap in Chapter 2 demonstrated that removal of species' temperature outliers did not reduce the climatic suitability of Norway. This suggests that the explanation for the large area of distribution across Norway for species such as *A. decurrens* may be because the SDM thresholds applied were not conservative enough to fully represent the species' true potential distribution and not because models included potentially inaccurate outlying climate variables. However, as mentioned above, applying SDM thresholds meant that some species which did have climate overlap with Norway were not projected to occur anywhere in Norway. Using a more conservative threshold may therefore increase the number of species with no projected distribution across Norway, which would mean we are unable to identify which areas are suitable for these species. It might be valuable instead to apply a threshold to the climate overlap values, based on whether there is a climate overlap value below which species are not predicted, using SDMs, to have any climatic suitability across Norway.

Despite these caveats, there was strong positive correlation between climate overlaps and the proportion of Norway with predicted presences for high-risk species (Table 3) which validates using hypervolumes as a method of calculating broad climatic suitability. This is particularly encouraging in the context of climatic niche predictions, as the hypervolume method is much less time-consuming and allows evaluation of a much greater number of species within a given timeframe than the SDM approach. For studies such as horizon scanning, where a large number of species are analysed, I therefore recommend initially using the hypervolume method to calculate the overlap between a species' climatic niche and the climate of a give country or region. For more in-depth analysis, however, hypervolumes do not give any information about where the overlap occurs within a region, so SDMs are valuable for determining which specific areas within a larger region are most at-risk after high-risk species have been identified.

3.5.3 Limitations of SDMs

The general limitation of SDMs is that they do not take into account biotic interactions and certain abiotic factors, e.g. plant herbivory, pollination, soil chemistry, which may mean that models have overestimated the true realized niche of the high-risk species within Norway. I show here the maximum potential range based on climatic suitability (i.e. the fundamental niche), but their distribution is likely to be much more limited due to dispersal limitations, soil suitability or natural enemies (delimiting the realized niche). In addition, although at least one species was predicted to occur within every grid cell in Norway in all climate scenarios, there are regions within Norway which are uninhabitable for plants such as glaciers and bare mountain tops. The cell size used here is also relatively large (5-minute resolution, equal to ~9 km^2 at the equator) so the models will not account for areas where conditions change on a small spatial scale, such as steep altitudinal gradients.

I assessed the performance of my SDMs in comparison to the 'gold standard' described by Araújo et al. (2019). My models scored well under certain criteria but for the majority of guidelines they scored as deficient or bronze. In most cases of 'deficient' classification, I had not evaluated the accuracy of the data I used such as occurrence records downloaded from GBIF and climatic data downloaded from WorldClim. In these cases my models were built on the assumption that occurrence records were geographically and environmentally unbiased and that taxon identification was correct. They also relied on WorldClim data being accurate. For some criteria, however, following the guidelines set out by Araújo et al. (2019) would have been possible; for example, GBIF includes measures of spatial uncertainty for each occurrence record which I could have used to select only records with high spatial accuracy. This evaluation highlights the complexity of SDMs and how many criteria must be considered to produce accurate models which can predict the true potential distribution of a species.

3.5.4 Conclusions

This study draws on the results from Chapter 2, which identified 284 high-risk species to Norway based on a set of characteristics such as climate overlap, economic uses and environmental impacts. Here, I have plotted the potential distributions of these species across Norway to identify which areas would be most at risk. The results, which predicted northwards expansion of species' ranges, correlated with much of the current literature. However, the predicted distribution of the 284 high-risk species depends on them first being introduced to Norway, and therefore their presence in the projected area is not guaranteed. If these species are monitored and their import into these regions is closely regulated, the risk they pose to Norway and particularly the vulnerable Arctic ecosystem will be greatly minimised.

Chapter 4

Testing enemy release of non-native plants across time and space using herbarium specimens in Norway

This chapter is now available at:

Ivison, K., Speed, J. D. M., Prestø, T., & Dawson, W. (2022). Testing enemy release of non-native plants across time and space using herbarium specimens in Norway. *Journal of Ecology*. https://doi.org/10.1111/1365-2745.13998

4.1 Abstract

The enemy release hypothesis predicts that invasive plant success is in part due to the absence of natural enemies in the invaded range. However, few studies have assessed how enemy release may vary over time or space. I used historical herbarium records to test whether ten non-native plant species in Norway have suffered less from natural enemies (foliar herbivores) at different latitudes and over the past 195 years, compared to closely related (congeneric) native species. I analysed over 2,200 specimens over 26 species. Chewing herbivory was lower at higher latitudes for both non-native and native species. However, there was no evidence of change over time in overall chewing herbivory for either native or non-native species on average. Chewing herbivory of native and non-native species differed within the genera *Centaurea, Epilobium* and *Salix* across latitudes, and in the genera *Acer, Barbarea, Campanula* and *Epilobium* across time. These results suggest that enemy release is unlikely to facilitate these non-native plants in Norway since herbivory levels are similar between both non-native and native plant species. Herbivory of these non-native plants did not change over time, suggesting that they were quickly recognised as food sources by native herbivores. Lower levels of herbivory at higher latitudes suggests that herbivory is currently unlikely to limit non-native plants further north, but that herbivory is likely to increase at higher latitudes as the climate warms.

4.2 Introduction

Invasive species are one of the key components of global change today (IPBES, 2019), affecting ecosystem function worldwide. Impacts to ecosystems include changes in insect diversity and hybridization or competition with native species (Litt et al., 2014; Pyšek et al., 2012) and there is an increasing amount of research aiming to understand the drivers of invasive species success. Enemy release, or the movement of a species outside the range of its natural enemies, is one of the leading hypotheses used to explain invasive plant success. However, the mixed results from tests of this hypothesis in the literature (Fenner & Lee, 2001; Siemann et al., 2006; Wolfe, 2002) suggest that enemy release is extremely system-specific and cannot be applied to all invasive plant scenarios.

When assessing the evidence for enemy release in non-native plants, the phrase 'natural enemies' often refers to insect herbivory. Herbivory can have a great impact on the success of non-native plants (Elton, 1958; W. Huang et al., 2012; van der Putten et al., 2005), but is influenced by a wide variety of factors which makes comparing herbivory damage between native and non-native plants difficult. However, it has been documented that biotic interactions are spatio-temporally dynamic and various studies exist which investigate links between herbivory and either latitude or time (e.g. Cronin et al., 2015; Harvey et al., 2013; Schemske et al., 2009; Siemann et al., 2006).

The Latitudinal Biotic Interaction Hypothesis predicts that there are fewer biotic interactions, and therefore less herbivory, at higher latitudes (Schemske et al., 2009). Some studies of native species have shown evidence for this (e.g. Schemske et al., 2009) whereas others show little or no difference in herbivory at different latitudes (Adams et al., 2010; Kelly et al., 2008; a meta-analysis of the literature by Moles et al., 2011). Studies between herbivory and latitude for non-native plant studies are equally mixed. Cronin et al. (2015) found no difference in herbivory of non-native species at different latitudes, and a meta-analysis by Xu et al. (2021) found that herbivory of non-native species was consistently lower than native species but that there was no difference between different latitudes. Nunes et al. (2016) found mixed support for the Latitudinal Biotic Interaction Hypothesis, and their results are highly dependent on the study species and tissue type being investigated. However, Kambo & Kotanen (2014) found that herbivory declined sharply at higher latitudes for a non-native plant, resulting in enemy release at the northern limit of its range.

Temperature is a key factor limiting growth and reproduction of plants (Walther et al., 2009) and is strongly linked to latitude; climate warming therefore means that non-native species globally are predicted to move to higher latitudes (Walther et al., 2002), particularly nearer the poles where warming is occurring at a faster rate (Serreze & Barry, 2011). How herbivory varies with latitude is therefore of particular importance in countries situated at relatively high latitudes such as Norway, which is one of several Arctic-bordering countries and is already home to thousands of non-native plants (*Norwegian Biodiversity Information Centre*, 2020). This large number of non-native plants in Norway is predicted to increase in abundance even further (Bjørnøy et al., 2007) in part because human activity is increasing (Crowl et al., 2008), which is likely to result in a greater extent and volume of plant introductions. Within Norway, an increase in non-native plant numbers and their range-shifting to higher latitudes means that there is likely to be an influx of new species to the vulnerable Arctic ecosystem (Alsos et al., 2015). Latitudinal studies are therefore valuable in determining how non-native plants and their enemies will respond at higher latitudes in the future, when higher latitudinal climate will resemble that of current lower latitudes. No studies investigating both latitude and herbivory have yet been carried out in Norway.

How herbivory of non-native plants changes over time is also key in determining the success of non-native plant spread in future. Herbivory of native plant species has increased over the last century (Meineke et al., 2019) but observed trends in non-native plants are so far mixed. It is proposed that low herbivory of non-native plants due to enemy release is followed by an increase in herbivory as herbivores adapt to their non-native hosts (Strong, 1974) or begin to recognise non-native species as a food source (Carpenter & Cappuccino, 2005). If this is the case, non-native herbivory may continue to increase until it is at a comparable level to that of native species. Some studies have observed this trend, and have found that herbivory gradually increases over several centuries until levels resemble herbivory of native species (Hawkes, 2007; Leather, 1986; Siemann et al., 2006; Strong, 1974). Other research, however, has found no relationship between time since introduction of a plant and herbivory levels (Carpenter & Cappuccino, 2005).

To determine how non-native plant herbivory changes over time, some studies substitute space for time and sample plants from their original introduction point (older samples) and at the edge of their introduced ranges (more recent samples) (e.g. Harvey et al., 2013; Siemann et al., 2006). However, it has been suggested that space-for-time substitutions lead to inaccurate patterns (Damgaard, 2019). This can be avoided by using natural history collections such as herbaria. Herbaria can be invaluable tools for tracking variation in plant-herbivore relationships over both time and space. Herbarium specimens and their associated records can span decades and are taken from a wide variety of locations, and can be used to provide information on herbivory at a point in time and space (Meineke et al., 2019). Sampling of multiple records can then be used to capture changes in the occurrence and level of herbivory suffered by plant species. By studying herbivory changes at higher latitudes and over time, it is possible to understand the role that herbivores might play in limiting the spread of non-native plants in these regions, and how temperature change in Norway under climate change, represented by latitude, may impact these interactions. Here, I used digitized herbarium records from the last 195 years in Norway to determine if herbivory differs between native and non-native plants (assessing enemy release), and whether differences between native and non-native plants have changed through time and with latitude.

Specifically, I sought to answer the following questions: 1) do herbivory levels differ between native and non-native species in Norway? 2) Do native and non-native plants both exhibit a decline in herbivory levels with increasing latitude (in line with the Latitudinal Biotic Interactions Hypothesis)? 3) How do herbivory levels of non-native plants change over time (using sample year as a measure of time)?

4.3 Methods

4.3.1 Area of study

The study focused on two regions in Norway from which to select native and non-native herbarium specimens, originally to compare two latitudinal groups. However, as is mentioned under *4.3.4 Data analysis*, latitude was later treated as a continuous variable. The first region was classed as 'southeast' Norway with a latitude below 62°N and a longitude above 9°E (Figure 1). This area contains the capital city of Oslo and the surrounding region, where a large number of non-native species were first introduced (Norwegian Biodiversity Information Centre, 2020), and therefore a large number of herbarium specimens (over 280,000 of vascular plants) have been sampled in this region (GBIF, 2022). The second region was classed as 'central' Norway, with a latitude of between 62 and 66 °N (Figure 1) and was included to increase the latitudinal range of the study in order to address Q2. This area contains the major city of Trondheim where again a large number of herbarium specimens have been collected (over 180,000 of vascular plants (GBIF, 2022 ; Speed et al., 2018)).

4.3.2 Species sampling and selection

A group of 30 non-native plant species were selected with populations in both central and southeast Norway, the majority of which were classed as having a severe impact in Norway according to the Norwegian Biodiversity Information Centre (2020) alien species impact classification. To compare these non-native species with native species, therefore addressing Q1 of the research aims, these species were then matched with at least one congeneric native species, the exception being *Myrrhis odorata* which was matched with a confamilial native species *Anthriscus sylvestris*. From now on, *A. sylvestris* and *M. odorata* will be referred to as congeners, for simplicity. Congeneric species were chosen to allow comparison of native and non-native status while minimising taxonomic bias, and to avoid the confounding of native status by phylogenetic differences between native and non-native species. Many species did not have sufficient samples for this study due to few older records and were discarded. This left a total of 26 species, 16 native and 10 non-native within 10 congeneric species 'sets' of trees and herbs from a range of Families (Table 1). All included species had sufficient records to allow herbivory rates to be analysed over a 100-year period, with some specimens dating back 200 years, and across a wide latitudinal range.

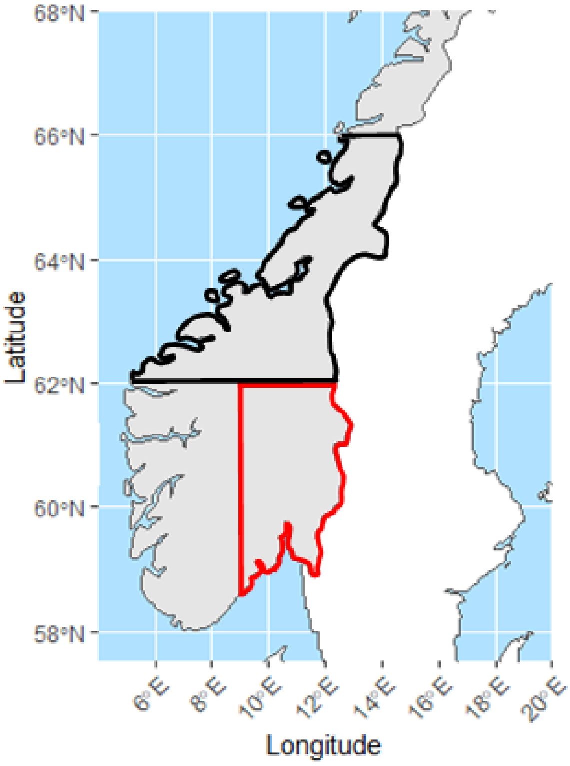


Figure 1: Two study regions in Norway. Red border = 'southeast' region. Black border = 'central' region.

Occurrence records with accompanying herbarium images were downloaded for each species using the R package 'rgbif' (Chamberlain et al., 2020). Two sampling methods were used to select (a) recent records (since the year 2000) across different latitudes within Norway to address Q2 and (b) records from the previous 100 years in the 'southeast' of Norway to address Q3. Sampling design was largely dictated by the availability of specimens for both native and non-native species. Specifically, while there were sufficient numbers of specimens available after the year 2000 in both regions (Figure 1) to assess the relationship between latitude and herbivory, the numbers of specimens available from earlier time periods in the central region were too low to assess sampling year and latitude simultaneously. Doing so would have led to a conflation of latitude and time, making it impossible to separate their effects. Sampling was therefore focused across the latitudinal gradient in both regions, constraining the time period to post-2000 (method a), and then across the 100-year period in SE Norway only (method b), where representation of species specimens through time was optimal. For sampling method (a), up to 15 records were taken for each species after the year 2000 from each of the 'central' and 'southeast' regions (Figure 1), unless there were fewer than 15 photos in which case all photos within that category were used for analysis (see Figure A8 for herbarium specimen distribution). This resulted in up to 30 photo specimens per species for the latitudinal study. For method (b), southeast records taken after the year 2000 (sampled in method (a)) were combined with samples from the following twenty-year categories, again in the 'southeast' region: 1980-2000; 1960-1980; 1940-1960; 1920-1940; before 1920. For each species, up to 15 photo records were randomly sampled within each 20-year category resulting in up to 90 photo specimens per species in the sample year study. The use of 20-year categories resulted in relatively even representation of species throughout the 100-year period. All shortlisted non-native species were first recorded in Norway during the 1800s (Norwegian Biodiversity Information Centre, 2020; Table 1). Identifying numbers for all sampled herbarium specimens can be found in File S1. Downloaded specimen images were from the following herbaria: Vascular Plant Herbarium, UiB (University of Bergen, 2022); Norwegian University of Science and Technology vascular plant herbarium TRH (Norwegian University of Science and Technology, 2022); University of Agder vascular plant herbarium KMN (University of Agder, 2022); Vascular Plant Herbarium, University of Oslo UiO (University of Oslo, 2022).

4.3.3 Image analysis

To analyse herbivory rate, the image software 'ImageJ' with the plug-in 'Fiji' was used (Schindelin et al., 2012; Schneider et al., 2012). Most herbarium photos in this study were photographed with a ruler measurement. Using this ruler as a guide, the image was overlaid with a grid, and each grid cell had an area of 625 mm^2 which gave a total of 240 grid cells across each specimen photo. This grid size was chosen as a compromise between a high grid cell resolution, for more accurately estimating proportion of each specimen with herbivory damage, and time constraints. If no ruler was present, the herbarium specimen labels were used to estimate scale. Each grid cell which contained part of a leaf was counted using the Fiji plug-in 'Cell counter', and all leaves in each herbarium photograph were counted regardless of size or position on the plant. Cells which contained each of the following types of leaf damage were then counted: 'Chewing', 'Galling', 'Leaf-mining' and 'Fungal' damage. Although galling, leaf-mining and fungal damage was not part of this analyses, the data are presented here for completeness.

4.3.4 Data analysis

All analyses were done in the R environment (R Core Team, 2019). Negative binomial GLMMs (generalised linear mixed models) were built using the R package 'glmmTMB' (Brooks et al., 2017) to assess the proportion of chewing herbivory damage between native and non-native species and in relation to (1) latitude and (2) year of specimen sample. Negative binomial GLMMs were chosen as model convergence was not possible when using other methods of binomial GLMM (e.g. the 'lme4' package (Bates et al., 2015)). Latitude and sample year were treated as continuous variables in all analyses due to relatively even spread of data across each delineated region/time period. Chewing was selected for analysis as this damage type was observed most frequently across samples (Figure 2). In each model, native status and either latitude or sample year were considered fixed effects and the interaction between native status and latitude/sample year was included. To account for non-independence between samples in a species and between species in a congeneric set, genus and species were included as nested random effects to investigate overall trends between native and non-native species across the whole dataset. Phylogeny was not included in the model structure, as the study was designed to account for phylogenetic relatedness by selecting closely-related congeneric species. Herbivory rates observed on records may also vary depending on the time of year which they were collected (Meineke et al., 2021). To account for this, day of year was added as a covariate in both models. Overdispersion was found in both models via investigation of model residuals using the package 'DHARMa' (Hartig, 2021) (Figures S1 & S2; these and all subsequent supplementary figures and tables are found in File S2). To address this, a further observation-level random effect (individual sample ID) was added (Maindonald & Braun, 2007). To determine whether certain genera had a high influence over the effects of latitude/sample year, the models were re-run, each time without one of the congener sets. The change in model effect sizes was then inspected and compared to the original models with all congener sets. Spatial autocorrelation between specimens was assessed using a correlogram from the R package 'pgirmess' (Giraudoux, 2013). Finally, negative binomial GLMMs were used to analyse proportion damage for each individual genus to assess single-species effects of latitude and sample year. For these models, latitude or sample year and their interaction with species were used as fixed effects, with a covariate of sample day of year. Individual sample ID was again used as an observation level random effect to account for overdispersion.

Table 1: List of congener sets of native and non-native species used in this study, with year each non-native species was first observed in Norway according to the Norwegian Biodiversity Information Centre (2020) and native range (POWO, 2022).

Native	**Non-native**			**Family**	**Growth form**
	Species	**First observed**	**Native range**		
Acer platanoides	*Acer pseudoplatanus*	1870s	Central & western Europe	Sapindaceae	Tree
Anthriscus sylvestris	*Myrrhis odorata*	1820s	Central & western Europe	Apiaceae	Herb
Barbarea stricta	*Barbarea vulgaris*	1820s	Europe, northern Africa, central Asia	Brassicaceae	Herb
Campanula cervicaria *Campanula latifolia*	*Campanula rapunculoides*	1820s	Europe, central Asia	Campanulaceae	Herb
Centaurea jacea *Centaurea scabiosa*	*Centaurea montana*	1870s	Central & western Europe	Asteraceae	Herb
Epilobium collinum *Epilobium montanum*	*Epilobium ciliatum*	1860s	Northern Europe, North America, southern South America, central Asia	Onagraceae	Herb
Lonicera periclymenum *Lonicera xylosteum*	*Lonicera tatarica*	1880s	Central Asia	Caprifoliaceae	Herb
Populus tremula	*Populus balsamifera*	1870s	North America, eastern Russia	Salicaceae	Tree
Primula veris	*Primula elatior*	1880s	Europe, central Asia	Primulaceae	Herb
Salix caprea *Salix pentandra* *Salix triandra*	*Salix fragilis*	1834	North Caucasus	Salicaceae	Tree

4.4 Results

A total of 2,224 herbarium record images were analysed, 1,534 native and 690 non-native species records. Of this total, 1,875 were sampled from southeast Norway and 349 from central Norway (Table A1). The earliest record was collected in the year 1821, and records ranged from a latitude of 58.59 ° to 66.18 ° N.

4.4.1 Damage types

Of the four damage types assessed (chewing, mining, galling, fungal infection) chewing damage was observed the most frequently, present in over 75% of all native and non-native samples in all six time periods. The proportion of samples with fungal damage was lowest before 1920 (23.8% of native and 22.0% of non-native species) and highest after 2000 (38.3% of native and 32.0% of non-native species) (Figure 2). Mining and galling were found in consistently low proportions of specimens. The proportion of samples with each damage type was similar across native and non-native species.

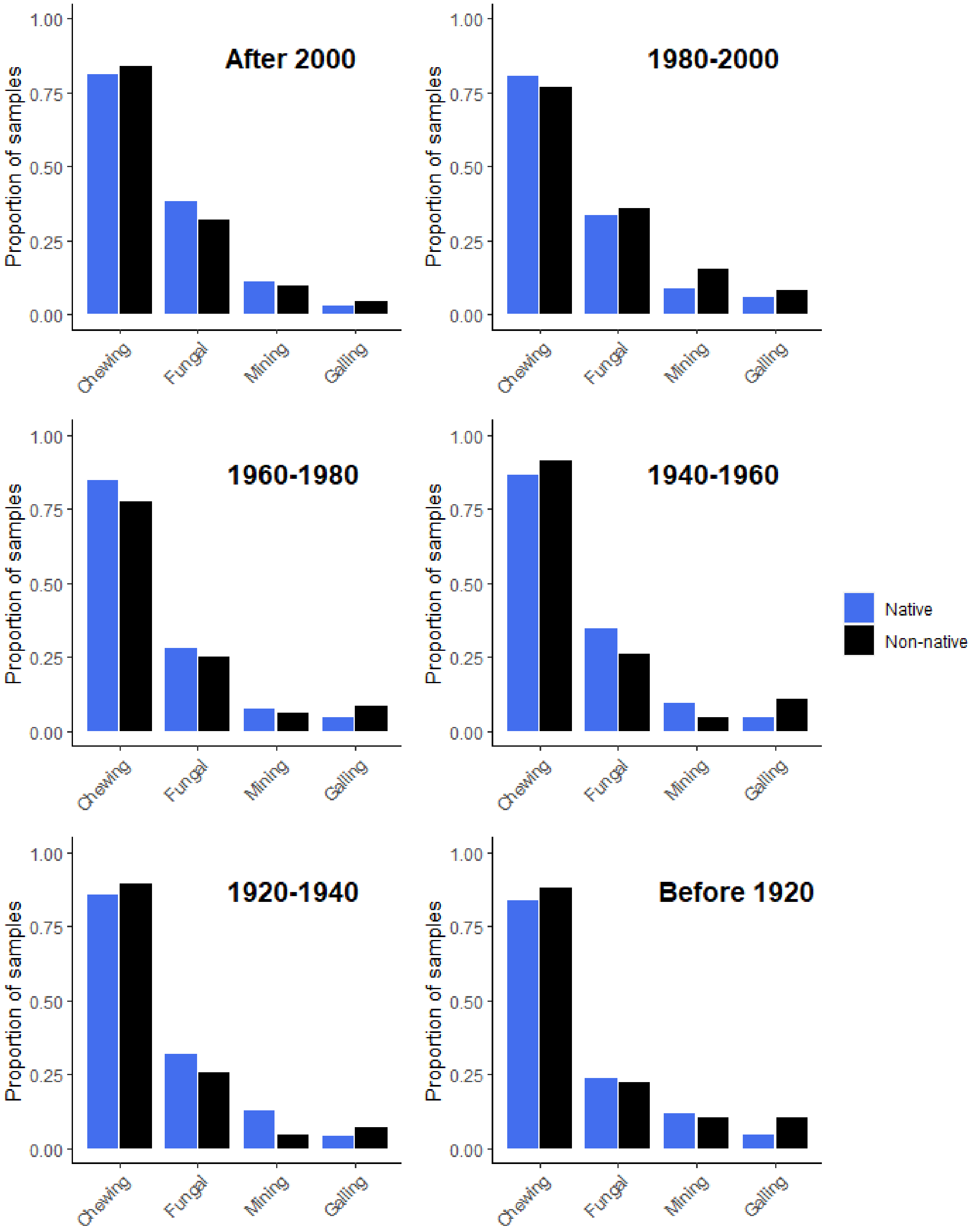


Figure 2: Proportion of herbarium samples with each damage type across all native and non-native plant species, split into year categories.

4.4.2 Overall trends of chewing herbivory

4.4.2.1 Latitude

There was strong evidence that the proportion of chewing herbivory damage on post-2000 herbarium records was lower at higher latitudes (P <0.01) (Table 2). However, this effect size was small compared to variation in damage proportions across genera (SD = 0.564); at the lowest latitude of 58.59 °N the model predicted 0.083 proportion chewing damage for native and 0.095 for non-native species, and at the highest latitude of 66.18 °N the model predicted 0.045 proportion chewing damage for native and 0.047 for non-native species (Figure 3). There was no evidence of any difference between chewing herbivory of native and non-native species on average and no evidence of any interaction between latitude and native status. There was strong evidence that removal of the genus *Campanula* resulted in a stronger negative relationship between chewing herbivory and latitude whereas the removal of *Anthriscus/Myrrhis* weakened evidence for this negative interaction further. The removal of *Centaurea* increased the difference between native and non-native chewing herbivory levels but evidence for this was weak. The removal of *Salix* had the biggest impact on results, creating a less strong positive relationship between chewing and day of year, and resulting in a stronger negative interaction between latitude and native status, so that latitude had a larger effect on non-native species (Figure A9; Table S1).

4.4.2.2 Sample year

There was no evidence of chewing herbivory change with sample year (p=0.604) and there was no evidence of a difference in chewing proportion between native and non-native species on average. There was no evidence of any interaction between sample year and native status (Figure 3; Table 2). The removal of *Barbarea* and *Salix* resulted in a stronger negative relationship between year and chewing herbivory levels and stronger evidence for this relationship, whereas the removal of *Campanula* resulted in this relationship becoming positive, although evidence for this was weak. The removal of *Centaurea* and *Salix* resulted in a greater difference between chewing on native and non-native species, but evidence or this did not differ greatly from the original model. Absence of *Salix* also resulted in a stronger positive relationship between chewing and day of year (Figure A10; Table S2).

Day of year

In both latitude and year models, there was strong evidence of an increase in herbivory with day of year (latitude: slope = 0.277, p < 0.001; year: slope = 0.181; p < 0.001; Fig. 4).

4.4.3 Spatial autocorrelation

There was no significant spatial autocorrelation within the residuals of the negative binomial GLMMs as all Moran's I coefficients were close to 0 (latitude vs chewing damage model coefficients range from 0.016 to -0.141; sample year vs chewing damage model coefficients range from 0.029 to -0.045) (Figure S3).

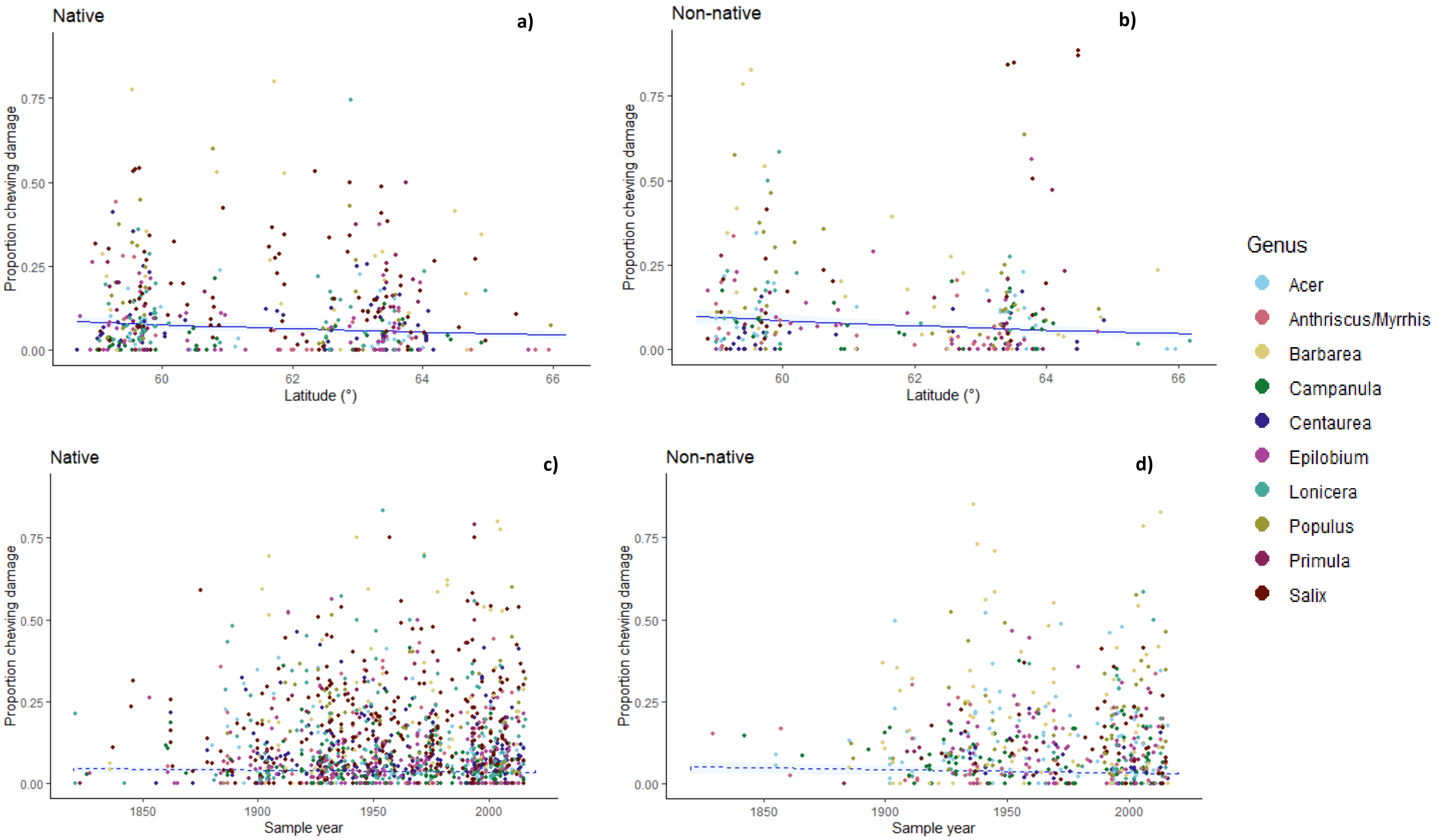


Figure 3: Effect of latitude (**a**, **b**) and sample year (**c**, **d**) on 16 native and 10 non-native plant species within 10 genera based on two negative binomial GLMMs (fitted values ±SE). Dashed lines represent non-significant and solid lines represent significant relationships ($p < 0.05$)

Table 2: Coefficients for negative binomial GLMMs determining the relationship between latitude/sample year and herbivory damage levels. Bold number indicate significant values (P = <0.05).

Latitude

	Est.	**SE**	***z***	***P***
Intercept (native)	-2.640	0.212	-12.466	**<0.001**
Latitude	-0.174	0.064	-2.704	**0.007**
Non-native	0.145	0.153	0.949	0.343
Day of year	0.277	0.052	5.294	**<0.001**
Latitude: non-native	-0.031	0.100	-0.305	0.760
Random effects:	**Std. deviation**		**Variance**	
Genus	0.564		0.318	
Species	0.292		0.085	

Sample year

	Est.	**SE**	***z***	***P***
Intercept (native)	-2.448	0.224	-10.936	**<0.001**
Sample year	-0.019	0.037	-0.518	0.604
Non-native	0.054	0.142	0.382	0.702
Day of year	0.181	0.032	5.743	**<0.001**
Sample year: non-native	-0.025	0.072	-0.341	0.733
Random effects:	**Std. deviation**		**Variance**	
Genus	0.555		0.308	
Species	0.302		0.091	

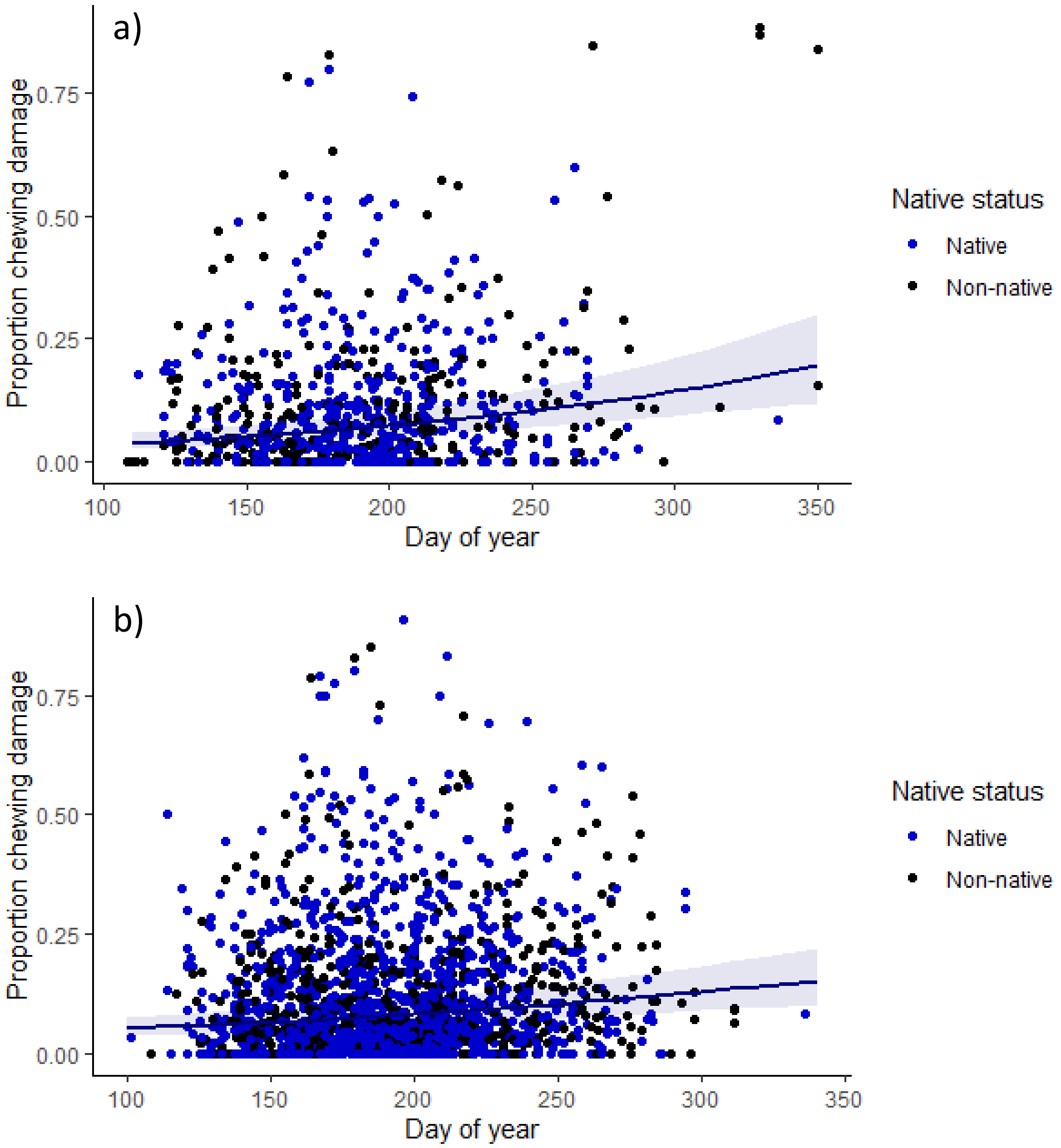


Figure 4: Day of year against proportion of chewing damage for specimens used in **(a)** latitude model (taken from both regions from year 2000) and **(b)** year model (taken from SE region over the last >100 years). Lines represent negative binomial GLMM fitted values (±SE).

4.4.4 Genus-specific trends of chewing herbivory

4.4.4.1 Latitude

Strong evidence of lower levels of chewing herbivory at higher latitudes were found in *Acer* and *Barbarea,* with weaker evidence of this trend observed in *Anthriscus/Myrrhis, Epilobium* and *Lonicera*. Higher levels of herbivory at higher latitudes were found in *Salix*. Differences in chewing proportion between native and non-native species varied greatly among genera, with greater chewing on non-natives in *Centaurea* but greater chewing herbivory on natives for *Epilobium* and *Salix*. Only *Salix* showed evidence of a negative interaction between latitude and native status, whereby latitude, which had a positive effect on chewing damage, had a stronger effect on non-native species (Figure 5; Table S3). Four of the ten genera showed an increase in herbivory with day of year (Table S3).

4.4.4.2 Sample year

There was evidence of herbivory decreasing over time in *Centaurea* only, and there was no evidence of any increase in herbivory over time. Greater herbivory was observed on native species than non-native species for the genus *Anthriscus/Myrrhis,* whereas greater herbivory was observed on non-native species for the genera *Acer*, *Campanula* and *Epilobium.* The only evidence of interactions between sample year and native status was found in *Centaurea*, where sample year had a stronger effect on non-native species (Figure 6; Table S4).

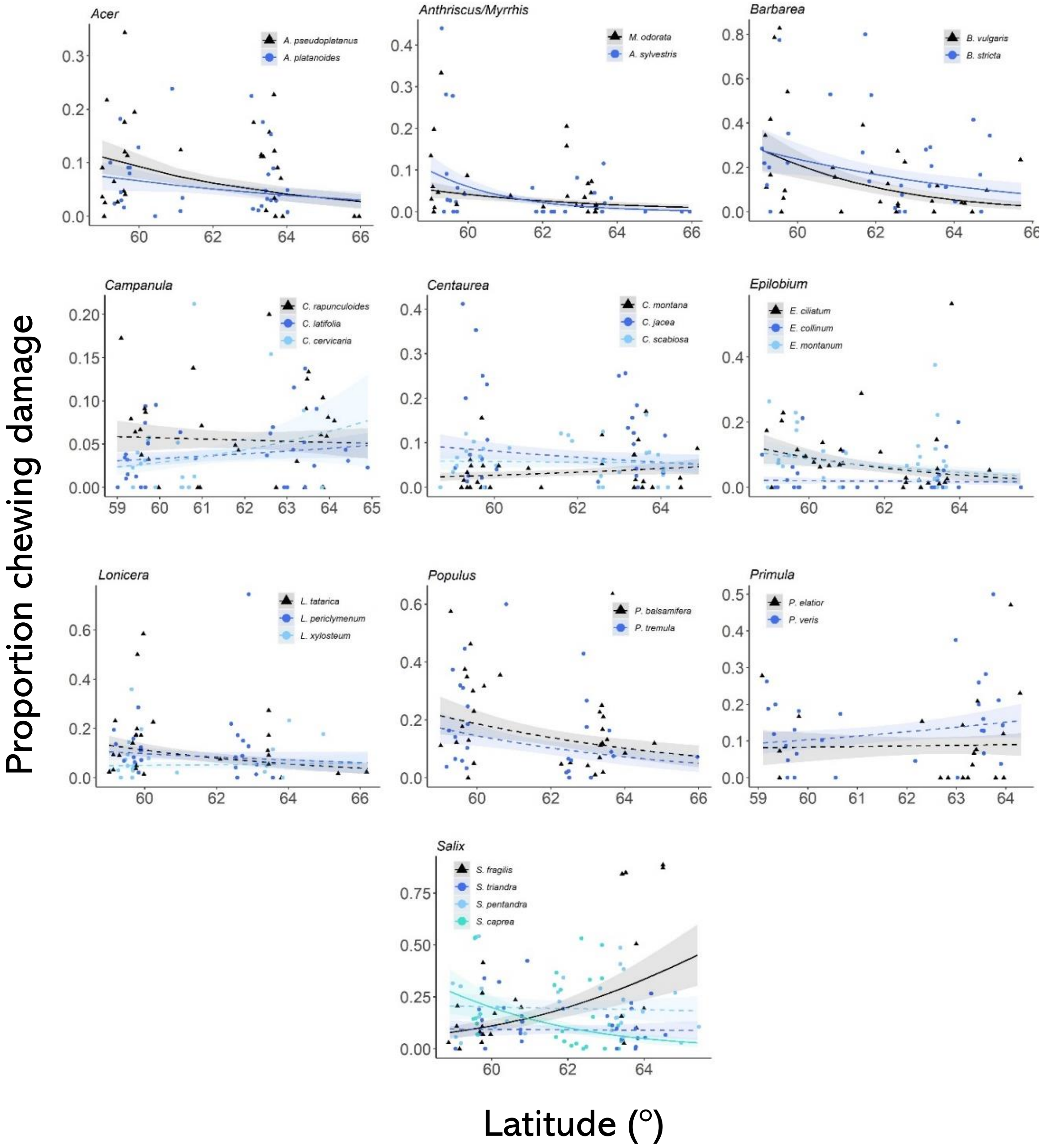


Figure 5: Proportion of chewing damage of herbarium samples in each genus across latitudes in Norway. Black triangles and black fitted lines (±SE) represent non-native species, and blue circles and blue fitted lines (±SE) represent native species. Dashed lines represent non-significant relationships and solid lines represent significant relationships ($p < 0.05$). Samples represented here are taken from the years 2000-2021.

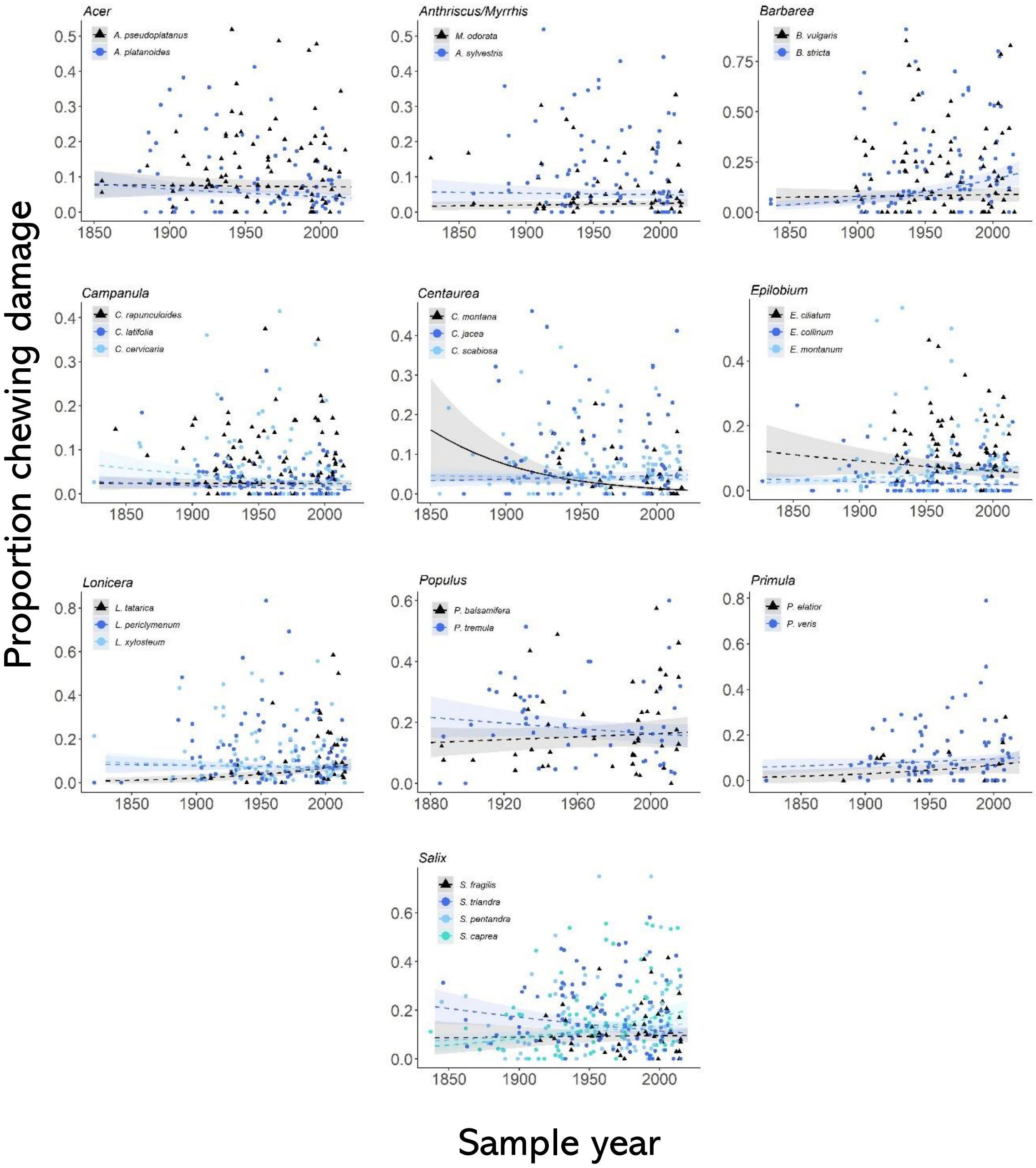


Figure 6: Proportion of chewing damage of herbarium samples in each genus. Black triangles and black lines (±SE) represent non-native species, and blue circles and blue lines (±SE) represent native species. Dashed lines represent non-significant trends and solid lines represent significant trends ($p < 0.05$). Samples represented here are taken from the southeast of Norway (latitude < 62°, longitude > 9°).

4.5 Discussion

4.5.1 Enemy release

In this study, I aimed to determine whether enemy release is occurring on non-native plants by assessing chewing herbivory and its variation through time and space on non-native and native plants in Norway. Firstly, I found little significant difference in chewing herbivory between native and non-native plants within each genus. All species groups were congeneric except for *Anthriscus sylvestris* and *Myrrhis odorata*, which are both in the same family, subfamily, tribe and subtribe (Apiaceae; Apioidea; Scandiceae; Scandicinae (Downie et al., 2000)). A link between phylogenetic relatedness and herbivory has been investigated by several past studies on herbivory levels of native and non-native species. These studies found that herbivory was lower in non-natives that were more distantly related to native species than those more closely related (Harvey et al., 2012; Hill & Kotanen, 2009; Pearse & Hipp, 2009). Pearse & Hipp (2009) concluded that biotic interactions are driven by leaf traits associated with phylogenetic relatedness. If true, this means that similar levels of herbivory between native and non-native congeners might be expected, particularly when concerning chewing herbivores, which may often be generalists (Vidal & Murphy, 2018) and might switch more readily from native to non-native food plants. However, closely-related species were chosen specifically to ensure that one of the main differences between each grouping was their native status.

4.5.2 Latitudinal and temporal patterns

Across species chewing herbivory rate was lower at higher latitudes, but I found no difference in the effect of latitude between natives and non-natives. These results contrast with much of the current literature which has frequently found that latitude has no effect on herbivory of non-native plants (Cronin et al., 2015; Moles et al., 2011; Xu et al., 2021). It also contrasts with the finding of the meta-analysis by Xu et al. (2021) that herbivory on non-native plant species is often significantly lower than herbivory on native species. It has been posited that non-native species have not existed in their invaded ranges for long enough to develop latitudinal patterns in herbivore damage (Lu et al., 2019). However, in this study, non-native plants appeared to follow the often-documented trend exhibited by native plants (Schemske et al., 2009) – that herbivory rates are lower at higher latitudes. This has implications for herbivory responses under climate change, suggesting that herbivory levels of these species at higher latitudes may increase to resemble the current lower latitude herbivory levels as temperatures rise in the future.

There was no evidence of a relationship between chewing herbivory and sample year across all genera in this system of study, or of any difference in sample year effects between native and non-native species. This corresponds with a study by Carpenter & Cappuccino (2005) who also found no significant change in non-native herbivory over time, although there are other studies which demonstrated an increase in herbivory of non-native plants over time (e.g. Hawkes, 2007; Siemann et al., 2006). One possible explanation for the similar levels of chewing herbivory between native and non-native species over time in this study is that any increase in herbivory levels occurred before the earliest sampling date. Herbivory of non-natives can increase to resemble herbivory levels of native species within several centuries of the species' introduction to its non-native range (Hawkes, 2007; Leather, 1986; Strong, 1974). All of the non-native species in this study were first observed in Norway well before the 1900s, with some as early as 1810-1820 (Norwegian Biodiversity Information Centre (2020); Table 1). There are too few herbarium records before the year 1900 to accurately observe their levels of herbivory when they were first observed in Norway. It is nonetheless possible that chewing herbivory was lower when each species first arrived in Norway and had increased to resemble that of their congeneric native species by the time herbarium specimens existed in sufficient number for this study, despite this time only spanning decades rather than centuries. This could also help to explain why the latitudinal gradients of non-native and native species showed similar trends to each other. Alternatively, due to the closely-related nature of the congeneric groups of native and non-native species, non-native plants may have been recognised as a food source soon after their introduction to Norway.

The absence of expected general differences between native and non-native species in the latitude and sample year relationships may have resulted from variation among congener sets. I determined how influential each genus was in affecting the estimated relationship between chewing herbivory rate and latitude or sample year, and differences between native statuses. Dropping of some genera (*Anthriscus/Myrrhis*, *Campanula*) markedly affected the latitude relationship, and in fact removing *Anthriscus/Myrrhis* led to a lack of any observed latitudinal trend. When considered alone, *Anthriscus*/*Myrrhis* showed some evidence of a negative relationship between latitude and chewing, whereas no such relationship was apparent for *Centaurea* or *Primula*. Despite these differences among genera, I still encountered an overall negative relationship between latitude and herbivory in most cases when a genus was removed. There was strong evidence of this negative trend for 3 out of 10 genera and weak evidence for a further 4 genera; I therefore argue that this latitude effect is general and robust. In contrast, removing certain genera (*Barbarea, Campanula, Salix*) affected the sample year relationship in a weak way, but when considered alone there was only evidence of herbivory change across sample year in one genus (*Centaurea*).

The smaller sample sizes per species may have prevented me from detecting evidence for sample year effects. I sampled up to 30 specimens per species for the latitude analysis, and up to 90 for the sample year analysis. This contrasts with Beaulieu et al. (2019) who analysed over 1,300 specimens of a single species of non-native plant *Lythrum salicaria* in Canada and observed in detail the gradual increase in chewing herbivory of this species over time. Instead of focusing on one species, I decided to look at a higher number of species but analysed fewer specimens for each, as my interest was primarily in comparing native and non-native species and assessing latitude and time relations across species more generally. To assess the generality of herbivory relationships and differences between native and non-native species, per-species sample sizes were therefore traded off against including more genera and species. This approach increases estimate accuracy more in a multispecies study than increasing the number of observations per species (van Kleunen et al., 2014). Moreover, I found strong evidence of latitude effects on herbivory with smaller sample sizes per species than for sample year (for which no evidence of effects was found). This may reflect that the effects of latitude are stronger and more directional than year and so are easier to detect with lower sample sizes, and/or that inter-year variability in herbivory rates is too high to detect biological meaningful trends. I am also confident that I was not biased in my selection of herbarium specimen images because the individual photo ID numbers were randomly selected without viewing the images *a priori* (Zvereva & Kozlov, 2019).

4.5.3 Herbaria as a tool

I carried out this study using herbarium records, which are an invaluable tool for observing trends over time and across regions. One of the key benefits of herbarium records is that specimens are increasingly digitised which allows specimens to be viewed online. This means that specimens can be analysed either in-situ using a microscope to assess damage (as in Meineke et al., 2019), or analysed digitally using image analysis software as was carried out in this study. Both methods have their benefits. In-situ analysis means that categorisation of damage types may be more accurate, and pre- and post-collection damage may be easier to differentiate; digital analysis, however, allows specimens from multiple herbaria to be incorporated into a study without the need to travel between locations.

However, there are certain downsides to using herbaria. The very nature of natural history collections means that there are only a limited number of historical specimens available for ecological studies. For many of these species, I used the maximum number of specimens that exist in the selected locations. This does mean that there may be limited statistical power available to detect subtle trends in herbivory over time due to lower numbers of historical than present-day samples. Despite this, I am confident that stronger, biologically meaningful effects would have been detected as significant, such as that found for the effect of latitude on herbivory. The variances in herbivory per species for the latitude data subset were similar to the variances of the sample year dataset (Table S5) and variance among genera in both latitude and year models was similar (Table 2). Given the similar variances and the larger sample sizes for the sample year dataset (Table S5), if there was an effect of year at least as strong as the effect of latitude, it should have been detected as significant. The fact that it was not indicates that evidence for a latitudinal trend in herbivory is stronger than the evidence for a temporal trend.

Sampling bias by collectors, such as selecting plants with little or no herbivory, is a problem which could significantly impact the results of any study based on herbarium collections. A recent study (Kozlov et al., 2020) found large differences between herbivory levels of ecological samples and herbarium records, with collectors favouring specimens with little or no chewing herbivory damage, but conversely choosing specimens with presence of other organisms such as leaf miners. These differences varied between species, which suggests that assuming lower levels of herbivory across all herbarium specimens is not valid when using herbarium data (Kozlov et al., 2020). However, a recent re-analysis of the data collected by Kozlov et al. (2020) showed that with sufficient samples (more than 10 data points), herbivory levels of field-observed samples and herbarium specimens are highly correlated, and that there is little difference in sampling bias across species (Meineke et al., preprint, 2020). For this study, I therefore assume that if a collection bias exists, it would be consistent for native and non-native species and would therefore not affect the interpretation of the results.

In addition to the above findings, it is possible that collection bias could be more apparent for the more abundant native species, particularly several decades ago when non-native species were less common and collectors sampled specimens regardless of their condition. In this data, all damage types were found in relatively similar proportions across all time periods and between native and non-native species, which indicates that in this case abundance of species does not seem to have influenced the proportion of damage on collected specimens. Moreover, the presence of the significant latitudinal trend corroborates findings from other studies carried out in the field rather than in natural history collections (Kambo and Kotanen, 2014; Nunes et al., 2016). This lends support to the view that, despite any potentially collection bias, herbarium data can reveal ecologically meaningful patterns in herbivory rates.

Another potential issue with using herbarium photos is that some damage can occur after sampling, such as by invertebrate herbivores living within the herbarium. Meineke et al. (2019) accounted for this problem by close observation of damage through microscopes to determine if the damage was done pre- or post-collection. In this study, I used only photographs of the samples. However, if significant post-collection herbivory occurred, I would expect to observe lower herbivory rate in newer than older samples. This was not the case, so I can assume that post-collection herbivory was not present in large quantities and a resulting source of error in the dataset. In addition, Norwegian herbaria are aware of the potential for post-collection damage, and measures have been in place to eradicate insects from collections.

Samples taken at the same time of year are more comparable than those taken at different times, as insect herbivory levels vary depending on ambient temperature (Lemoine et al., 2014) and therefore time of year. Day of year was included in the models to account for this, and found across the entire data set and for several genera individually (4 in latitudinal study and 4 in sample year study) that chewing herbivory was positively related to day of year. In the remaining genera the trend was still positive but evidence was weaker (Tables S2 and S3). This trend is consistent with Meineke et al. (2021) and was expected to be present in the data, as invertebrate herbivory is likely to accumulate throughout the year until senescence of leaves in the winter. The lack of consistent strong positive trends within each individual genus could have been due to the lower numbers of samples in each genus, giving lower statistical power to detect effects.

Finally, I must highlight that this study is system-specific, and the aims were not to test the general validity of the enemy release hypothesis. Instead, I have explored variation in herbivore damage (as a measure of enemy release) over space and time in phylogenetically related native and invasive plants, and found evidence in support of a latitudinal cline in herbivory which affects native and non-native plants in a similar way. Therefore, this study contributes to the general understanding of plant-herbivore interactions involving invasive plants in higher-latitude systems.

4.5.4 Conclusions

Plant introductions and invasions are a major contributor to global changes in ecosystem function and composition. A survey in 2019 revealed that there are almost 2,500 non-native species in Norway, over 1,000 of which are naturalised and the majority of which are plants. This means that Norway currently contains the highest number of non-native species in Europe outside the UK (Sandvik et al., 2019, 2020). To predict the long-term effects of these plant introductions on local ecosystems, it is important to determine how these non-native plants may survive in the future. To do this it is possible to investigate how they interact with, and may be controlled by, native enemies over time and across different areas. These results highlight three key points for the region of study. First, there is little evidence that non-native species will benefit from lower herbivory rates than related native species generally. Second, environmental conditions related to latitude, namely climate, constrain herbivory of non-native and native species in a similar way, with lower herbivory at higher latitudes. Third, herbivory levels have not changed through time in a directional manner for either native or non-native species in general. These findings have several implications for the future of these non-native plants in Norway. Lower chewing herbivory rates at higher latitudes fit with the Latitudinal Biotic Interactions Hypothesis, and similar herbivory levels of both native and non-native species mean that these plants might be impacted equally by these biotic interactions as they move further north, assuming that there is northward range expansion by herbivores occurring at lower latitudes under climate change. This would mean that enemy release is unlikely to play a major role in the success of non-native plants at higher latitudes in Norway under a warmer climate, at least for non-natives with close native relatives. Enemy release also seems to have been absent in over the period of time considered, indicated by the constant levels of chewing herbivory throughout the last 200 years in the southeast of Norway, suggesting that although herbivory on non-natives occurs, it is unlikely to increase relative to natives and so further limit non-native plants in the future. It remains to be seen if changes in herbivory will become more apparent at both lower and higher latitudes as temperatures increase. However, herbarium records provide a valuable baseline of herbivory levels for native and non-native plants alike, which will allow us to put current and future herbivory in context.

Chapter 5

Investigating enemy release of non-native plants in botanical gardens across a European latitudinal gradient

5.1 Abstract

Invasive plants threaten native biodiversity and can result in large economic costs, and it is therefore important to understand which factors might influence their invasive success. The enemy release hypothesis states that the success of invasive species is partly due to their escape from natural enemies, which gives them a competitive advantage over native plants. In addition, herbivory is predicted to decrease at higher latitudes (the latitudinal biotic interactions hypothesis) which would result in a reduction of enemy release at higher latitudes whereby non-native herbivory would remain at a constant low level but native herbivory would decrease across a latitudinal gradient. To test this hypothesis on a wide scale, collaborators and I carried out herbivory surveys in three botanical gardens and combined this data with surveys from a further twelve gardens, resulting in herbivory data ranging from Switzerland (46.95 °N) to Norway (63.45 °N). Botanical gardens are an ideal study system due to large quantities of plants living under common environmental conditions. The surveys took place from 2007-2021 and in each garden herbivory levels were measured (either % of plant damaged or proportion of leaves with herbivory damage) of as many native (n = 25-411) and non-native (n = 37-571) species as possible. Using MCMCglmms I carried out meta-analyses across all gardens to test 1. whether enemy release is occurring for (i) non-native species and (ii) non-naturalised or naturalised non-native species, 2. How enemy release changes across a latitudinal gradient, and 3. how absolute herbivory levels of native and non-native species change across a latitudinal gradient. Overall, I found that herbivory levels were lower on non-native species than native species. When non-native species were split into non-naturalised and naturalised categories, however, I found that non-naturalised plants suffered less herbivory than natives and that naturalised plants showed similar levels of herbivory to native plants. This suggests that naturalised species have become more established in their invaded communities and are therefore more susceptible to herbivory but that non-naturalised species are not yet recognised as food sources by native herbivores. I did not observe any latitudinal gradient in terms of absolute herbivory of species or in the extent of enemy release suffered by non-native species. My results show support for the enemy release hypothesis, but suggest that enemy release may be transient and may not apply to non-native species which have become integrated into the community.

5.2 Introduction

Biological invasions are considered one of the greatest threats to biodiversity, and can cause large economic and environmental costs (Chornesky & Randall, 2003; Dueñas et al., 2018; Essl et al., 2011; Welch & Leppanen, 2017). Plants make up a large proportion of invasive species and their impacts on native ecosystems include changing vegetation structure (Bezemer et al., 2014), altering soil properties (Weidenhamer & Callaway, 2010) and affecting local hydrological processes (Weidlich et al., 2020). It is therefore important to understand the factors that can limit invasion success of non-native plants. The role of natural enemies in invasion success has been widely studied, as the interactions plants have with other organisms, such as herbivores, can largely influence their success (Elton, 1958; W. Huang et al., 2012; van der Putten et al., 2005). One of the key hypotheses investigated is the enemy release hypothesis, which states that the success of invasive species is in part due to their movement away from their natural enemies (Darwin, 1859). This hypothesis has received mixed support (Fenner & Lee, 2001; Siemann et al., 2006; Wolfe, 2002), but tests of the enemy release hypothesis are often limited in terms of the number of species considered (e.g. Harvey et al., 2013; Lakeman-Fraser & Ewers, 2013).

In order to comprehensively test the enemy release hypothesis for numerous species, it is important to control for environmental conditions as these may affect insect herbivory (Stiling & Rossi, 1995). In addition, enemy release may not occur to the same extent across a range of locations, and latitude, in particular, has been predicted to influence herbivory. The latitudinal biotic interaction hypothesis predicts that there are fewer biotic interactions, and therefore lower levels of herbivory, at higher latitudes (Schemske et al., 2009). With both the enemy release hypothesis and the latitudinal biotic interactions hypothesis in mind, we would therefore expect to see a decrease in the difference in herbivory levels between native and non-native species (enemy release) with latitude. This is because herbivory levels on native species should decrease with latitude, whereas herbivory on non-native species would remain consistently low across all latitudes (Xu et al., 2021). Indeed, Cronin et al. (2015) found evidence for this when they investigated latitudinal trends in herbivory on *Phragmites australis* across its native and invaded ranges. However, evidence for the latitudinal biotic interactions hypothesis generally is varied (Adams et al., 2010; Coley & Aide, 1991; Cronin et al., 2015; Kambo & Kotanen, 2014; Kelly et al., 2008; Xu et al., 2021). Latitudinal studies also help us to understand the consequences of climate change on plant-herbivore interactions. Latitude is often used as a proxy for climate, specifically temperature, and we can often use trends observed at lower latitudes to predict how higher latitude ecosystems will respond to warming. With the additional prediction that non-native plants will move to higher latitudes under climate change (Walther et al., 2002), latitudinal studies are an invaluable way to investigate the future of non-native plant/herbivore interactions.

Botanical gardens are an ideal study system for investigating general trends between native and non-native plants (e.g. Razanajatovo et al., 2015) and how widely mechanisms such as enemy release can be observed. Indeed, botanical gardens currently house around 30% of all plant species (Mounce et al., 2017) and have long been used for scientific research (Donaldson, 2009). In addition, the distribution of botanical gardens around the world means that hypotheses can be tested in multiple locations, which is vital in determining if trends exist on a broader scale or are dependent on local factors. Botanical gardens are also relevant in the field of invasion ecology as they are often considered a pathway for invasions and have contributed to the introduction of invasive plant species around the world, including half of the world's worst invasive species according to the IUCN (Boudjelas et al., 2000; Hulme, 2011). In addition, at least 93% of global naturalised alien flora is currently grown in botanical gardens globally (van Kleunen et al., 2018).

Most of the relevant literature investigating latitude and herbivory (with the exception of Xu et al. (2021) and Coley & Aide (1991)) focus on one or only a few species which may not demonstrate general trends (e.g. Kelly et al., 2008; Lu et al., 2019). In this study, I combined data from herbivory surveys conducted in 2007-2009 with surveys carried out by myself and collaborators in 2021, resulting in data from fifteen botanical gardens across Europe ranging from 46.95 °N (Switzerland) to 63.45 °N (Norway). With this I aimed to answer the following questions: 1) Is enemy release occurring across botanical gardens? 2) Does enemy release differ across a latitudinal gradient? 3) How do absolute herbivory levels differ across a latitudinal gradient?

5.3 Methods

5.3.1 Garden surveys

Surveys were carried out between the years 2007-2021 in fifteen botanical gardens across Europe. The botanical gardens spanned a latitudinal range of 46.95 °N (Bern, Switzerland) to 63.45 °N (Trondheim, Norway; Figure 1). Herein, individual surveys will be referred to by the botanical garden's location (see Table 1). In each garden, as many species as possible (n = 94 to 982) were surveyed in the timeframe available, with an effort to include a good proportion of native plants. Only plants growing outside were selected, as herbivores might not have had access to plants growing in greenhouses. The following information was documented for each surveyed species: species name and family, native status (native, non-native to the respective country), plant growth form (grass, herb, shrub, tree, succulent), plant phenological stage (vegetative, flowering, fruiting), plant height (cm), ground area covered by plant (cm^2), level of herbivory (see below). The following databases were used to determine the native status of each species: the Online Atlas of British and Irish Flora (2022) for species in the UK; the Norwegian Biodiversity Information Centre (2022) for species in Norway; Euro+Med (2006) for species surveyed in mainland Europe. Tree or shrub growth form was confirmed by checking Plants of the World (POWO, 2022). There were three methods employed to record level of herbivory. In Durham and Aberdeen (surveyed in 2021), herbivory was measured as the proportion of a subset of leaves with herbivory damage, categorised into chewing, leaf mining or galling. The subset of leaves was chosen by randomly selecting 2 stems/branches (or one quarter of leaves for rosette plants) and counting the total number of leaves, then counting the number of leaves with each damage type. If 2 stems/branches contained fewer than 10 leaves, more stems/branches were selected until the total number of leaves exceeded 10. In Trondheim (surveyed in 2021), a similar method was applied but instead of subsetting 2 stems/branches, a total of 10 leaves were randomly chosen and the proportion with damage recorded. For the other twelve gardens (surveyed in 2007-2009), herbivory was measured as the estimated % chewing leaf damage on the entire plant (Table 1). In thirteen gardens only one observation was made per species, but in Aberdeen and Durham an average of 3 observations were made per species.

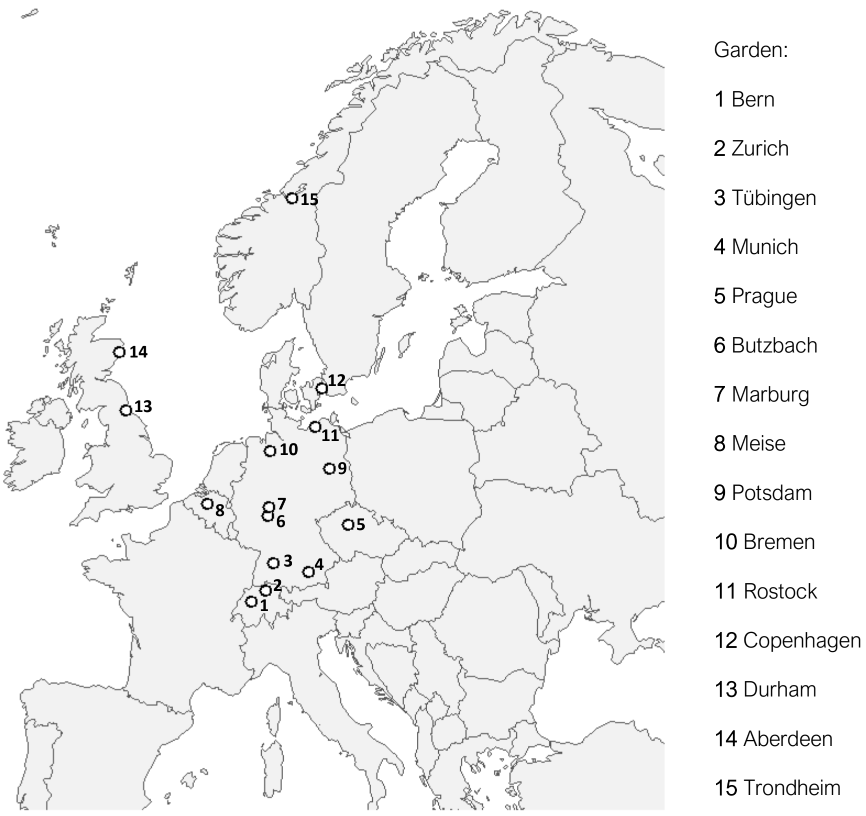


Figure 1: Locations of all botanical gardens.

A total of 5,986 observations were made of 2,752 different species across all surveys. The vast majority of species (1,796) were found in only one garden each. The most frequently found species was the common ivy *Hedera helix,* surveyed in ten gardens (Figure A11). The most common growth form was herbs, making up 64.4% of all observations, followed by shrubs, which made up 20.6% of observations, and trees, which made up 14.9% of observations. In each group except grasses, there were a greater number of non-native than native species (Figure A12). There were only 7 observations of succulents in total, all of which were non-native. The species surveyed belonged to a total of 191 different families, the most frequently surveyed being Rosaceae with 568 observations, followed by Asteraceae and Lamiaceae with 499 and 262 observations, respectively (Figure A13; for full list of families see File S1).Generally, there were a higher number of non-native species observed than native species in each botanical garden, with the exception of Butzbach, Prague and Rostock. There were a much greater number of non-naturalised species compared to naturalised species in all gardens (Table 1; Figure 2).

Table 1: Location of botanical garden surveys, number of observations made in each and method of measuring herbivory. Numbers in brackets indicate how many species were surveyed; if there are no numbers in brackets, the number of species surveyed was equal to the number of observations. Division of non-native species into non-naturalised and naturalised subgroups is based on the Global Naturalised Alien Flora database (van Kleunen et al., 2019).

Botanical garden	**Location**	**Latitude (°N)**	**Country**	**Year**	**No. survey observations**			**Herbivory measurement**
					Native	**Non-native**		
						Non-naturalised	**Naturalised**	
Bremen Botanical Gardens	Bremen	53.1	Germany	2009	96	87	25 (24)	Estimated % damage of entire plant
Butzbach private garden	Butzbach	50.4		2008	88	36 (35)	29 (28)	
Botanical Garden Marburg	Marburg	50.8		2008	31	60 (59)	11	
Botanical Garden Munich-Nymphenburg	Munich	48.1		2009	111	230 (221)	46 (45)	
University of Potsdam Botanic Garden	Potsdam	52.4		2009	51	120 (119)	15 (14)	
Rostock Botanical Garden	Rostock	54.1		2009	137	88	21	
University of Tübingen Botanic Garden	Tübingen	48.5		2009	95	169 (167)	27 (26)	
Meise Botanic Garden, Bouchout Castle	Meise	50.9	Belgium	2009	138 (132)	293 (279)	47 (45)	
The Botanical Garden of the University of Bern	Bern	46.9	Switzerland	2007-2009	595 (411)	687 (529)	61 (42)	
University of Zurich Botanical Gardens	Zurich	47.4		2009	25	87	14 (13)	
Botanical Garden of the Natural Sciences Faculty, Charles University	Prague	50.1	Czech Republic	2008	140 (136)	37	0	
University of Copenhagen Botanical Garden	Copenhagen	55.7	Denmark	2009	29	52	14 (13)	
Durham University Botanic Garden	Durham	54.8	UK	2021	121 (41)	434 (145)	111 (36)	Proportion of subset leaves (2 branches/stems) with damage
Cruickshank Botanic Garden	Aberdeen	57.1		2021	263 (84)	485 (161)	153 (49)	
NTNU Ringve Botanical Garden	Trondheim	63.4	Norway	2021	107	403 (400)	117 (113)	Proportion of subset leaves with damage

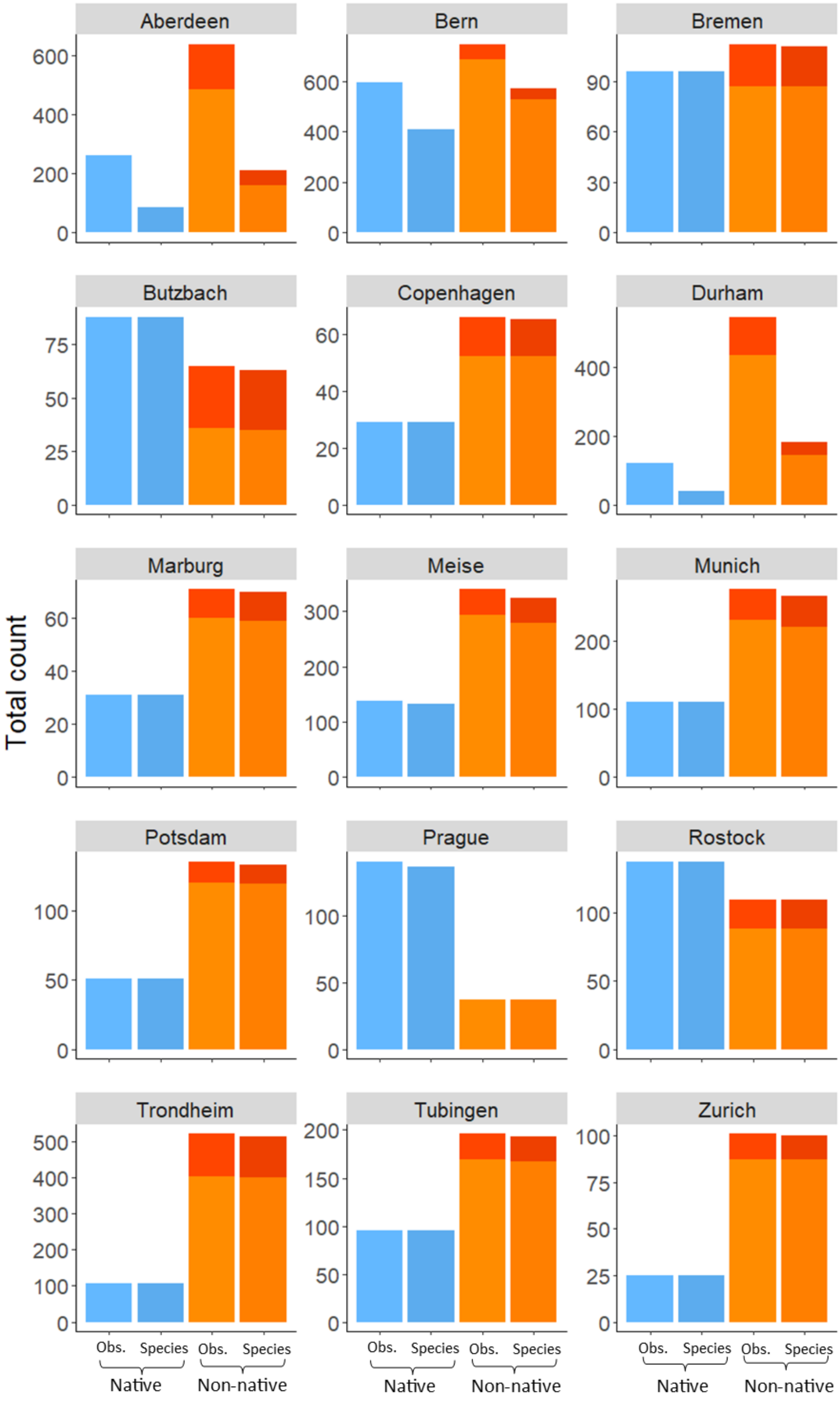


Figure 2: The number of observations (Obs.) made in each garden compared to the number of species observed split into native and non-native species. Note different y-axis scales for each garden.

5.3.2 Phylogenetic data

All species names were harmonized according to The Plant List using the R package ‘Taxonstand’ (Cayuela et al., 2012). Species, genus and family names from The Plant List were then used to create phylogenetic trees for each individual garden with the package ‘V.PhyloMaker’ (Jin & Qian, 2019). These phylogenetic trees were incorporated into the models outlined below.

5.3.3 Investigating enemy release

Markov chain Monte Carlo generalised linear mixed models (MCMCglmms) were built using the R package ‘MCMCglmm’ (Hadfield, 2010) to test for differences in herbivory damage between native and non-native species, taking into account phylogenetic relatedness (henceforth referred to as ‘herbivory models’). MCMCglmms were carried out for each botanical garden individually due to the different sampling methods used. Only leaf-chewing as a form of herbivory was analysed, since this was recorded across all gardens. Native status was treated as a fixed effect. For each garden, one model was created with native status categorised as ‘native’ or ‘non-native’ (2 levels), and a second model was created with ‘native’ species and non-native species split into ‘non-naturalised’ and ‘naturalised’ (3 levels). Here, ‘non-naturalised’ refers to a non-native species which has not become established in its non-native range. These more specific categorisations were achieved using the Global Naturalised Alien Flora (GloNAF; van Kleunen et al., 2019) and the National Biodiversity Network (*NBN Atlas*, 2022) databases to determine the naturalisation status of non-native species. If a non-native species was not documented by these databases as being naturalised in the botanical garden’s country, they were listed as ‘non-naturalised’. To account for the potentially confounding effect of plant height on herbivory levels, plant height (cm) was included as a covariate. Plant height was chosen here as this was measured to a higher degree of accuracy compared to plant area, which was categorised into bins (e.g. 0.5 m^2, 1 m^2). Species names and phylogenetic trees specific to the garden in question (created using ‘V.Phylomaker’ (Jin & Qian, 2019) – see above) were treated as random effects. Species names were chosen as random effects because, although most species only had one observation per garden, there were a few instances where multiple observations were made. Models where non-native status was split into non-naturalised and naturalised were repeated using non-naturalised species as a baseline to allow direct comparison between these and naturalised species. The priors and number of iterations used varied for each garden model and were altered to optimise model mixing; an uninformative prior was used where possible but an expanded prior was necessary for 12 of the 15 gardens. The number of iterations used ranged from 400,000 to 800,000, with a burn-in of 20,000 and a thinning interval of 100 for all gardens. (Table S1; this and all subsequent supplementary tables can be found in File S2). The priors and iterations were consistent for each of the two models created per garden. For full model summaries see Tables S2-S4. From these analyses I obtained per-garden mean effect sizes that estimated the difference between native and non-native (or non-naturalised and naturalised) plant herbivory levels which I used in the meta-analyses described below.

5.3.4 Meta-analysis across botanical gardens

To investigate herbivory on native and non-native plants across all gardens, garden model effect sizes and associated errors were extracted and analysed in a meta-analytical framework. ‘MCMCglmm’ (Hadfield, 2010) was used to conduct meta-analyses. Models were built to investigate both overall trends in herbivory damage and to investigate how latitude of the garden might affect herbivory levels. 500,000 iterations were used with an expanded prior to estimate the overall mean difference in herbivory between native plants and (i) non-native, (ii) non-naturalised and (iii) naturalised plants as intercept models. The effect of garden latitude on differences in herbivory between native and non-native (or naturalised/non-naturalised) plants was then investigated. The posterior means for each garden’s effect sizes were treated as response variables and the precision of effect sizes was accounted for using the standard deviation of the effect sizes. Meta-analyses were repeated with latitude included as a fixed effect to determine whether enemy release changed across latitudes (Table S5). The posterior means showing the difference between non-naturalised and naturalised herbivory were extracted from each garden’s MCMCglmm. A meta-analysis was then carried out separately to determine the difference between non-naturalised and naturalised species’ herbivory across all gardens (Table S5), as the general meta-analysis only showed the trend between native and non-naturalised herbivory or native and naturalised herbivory. Meta-analyses were repeated using only data from data obtained in 2007-2009 to determine whether the survey year or herbivory measurement method affected the observed results (Table S6).

5.3.5 Latitudinal trends in absolute herbivory

To better understand how latitude affects absolute levels in herbivory, herbivory of species according to their native/naturalised status was analysed separately, per garden. Intercept models were used for this, resulting in 4 models per garden: i) mean herbivory on natives; ii) mean herbivory on non-natives; iii) mean herbivory on non-naturalised non-natives; iv) mean herbivory on naturalised non-natives (Tables S7-S10). Plant height (cm) was again included as a covariate. Individual phylogenetic trees were created per group of species in each garden and MCMCglmms carried out to determine the intercept of herbivory, with species and phylogenetic trees as random effects. The number of iterations and the priors used were the same for each garden as those used in herbivory models, with the exception of Rostock’s naturalised species model, which required a more informative prior for successful model mixing (see Table S1).

Meta-analyses were carried out for each of the 4 groups of species (native, non-native, non-naturalised and naturalised) with MCMCglmms using the intercepts calculated in these models, with latitude as a fixed effect (Table S11). The precision of effect sizes was accounted for using the standard deviation of the effect sizes. All latitude meta-analyses had 500,000 iterations. Meta-analyses on native and non-naturalised species used the same expanded priors as were used in the majority of herbivory models, whereas models for non-native and naturalised species required marginally more informative expanded priors to create successful model mixing (Table S1). The more informative priors used here and for Rostock's model on naturalised species did not significantly change the outcomes of the models. Meta-analyses were then repeated using only data obtained in 2007-2009 to determine whether the survey year or herbivory measurement method affected the observed results (Table S12). The data manipulation and analyses were carried out in R version 3.6.1 (R Core Team, 2019).

5.4 Results

5.4.1 Damage types

In surveys where different damage types were recorded (Durham, Aberdeen and Trondheim), the most common damage type was chewing, which was found in 75.7% of observations, followed by leaf mining which was found in 7.6% of observations and galling which was only found in 2.1% of observations (Figure 3). Due to low occurrences of leaf mining and galling, analysis of these types of herbivory was not possible.

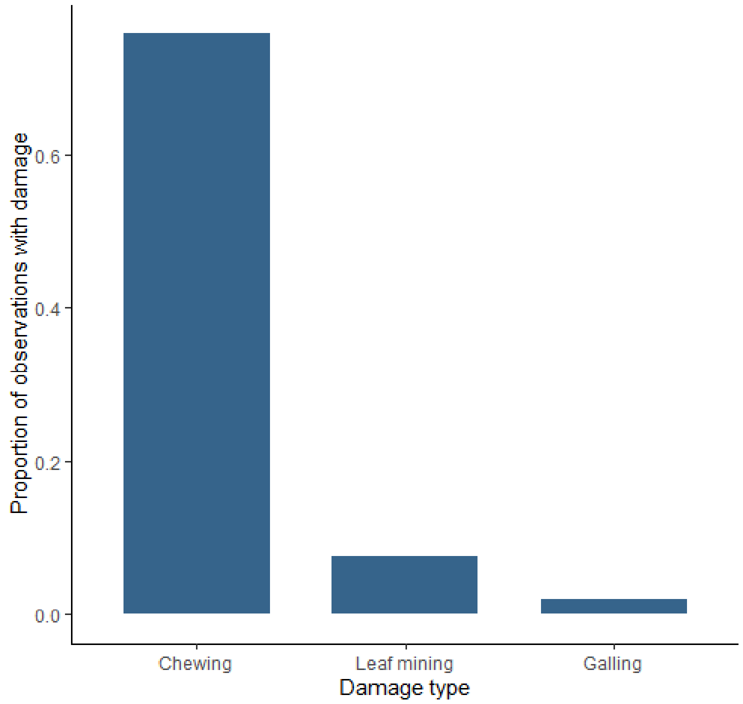


Figure 3: Proportion of observations from gardens surveyed in 2021 with each type of herbivory damage.

5.4.2 Is enemy release occurring across botanical gardens?

Two analyses were carried out to investigate differences in herbivory levels between native and non-native species. Firstly, non-native species were classed as a single group and secondly, non-native species were split into the two groups (non-naturalised and naturalised). The first meta-analysis showed strong evidence of lower herbivory levels on non-native plants across all gardens compared to natives (pMCMC = 0.004; Table 2a; Figure 4). When investigating herbivory levels of natives compared with non-naturalised and naturalised species, the second meta-analysis showed non-naturalised species had lower herbivory than native species (pMCMC = 0.002), but there was only very weak evidence of lower herbivory on naturalised species (pMCMC = 0.099; Table 2c & e; Figure 4). There was weak evidence for a difference in herbivory between non-naturalised and naturalised species (pMCMC = 0.062; Table 2g). For full meta-analysis summaries see Table S5.

5.4.2.1 Individual garden models

The models comparing native vs non-native species revealed strong evidence for lower herbivory levels in non-native species in 4 of the 15 gardens (Butzbach, Durham, Munich and Potsdam; pMCMC = <0.05). Weaker evidence of the same trend was observed in a further 4 gardens (Bern, Bremen, Prague, Trondheim; pMCMC = <0.1). There was no evidence for greater herbivory levels on non-native species in any garden (Figures 4 & 5; Table S2). The models comparing native vs non-naturalised and naturalised species revealed strong evidence of lower herbivory on non-naturalised species in 3 gardens (Butzbach, Durham, Trondheim) and on naturalised species in 2 gardens (Butzbach and Durham; pMCMC = <0.05) than on native species. Weaker evidence of lower herbivory on non-naturalised species was observed in 5 gardens (Bern, Bremen, Munich, Potsdam, Prague) and lower herbivory on naturalised species in 3 gardens (Meise, Munich and Tübingen; pMCMC = <0.1). There was no evidence of higher herbivory levels on non-naturalised or naturalised species compared to natives in any gardens. Differences in herbivory between non-naturalised and naturalised species were only observed in Trondheim, where naturalised species had higher levels of herbivory than non-naturalised species, but evidence for this was weak (pMCMC = 0.08; Figures 4 & 5; Table S4).

Height was included as a covariate to account for the potentially confounding effects of plant size on herbivory levels. Height was found to affect herbivory levels in 6 gardens, five of which (Bremen, Copenhagen, Durham, Marburg, Trondheim) showed that taller plants had greater levels of herbivory and one of which (Aberdeen) showed that taller plants had lower levels of herbivory.

5.4.3 Does enemy release differ across a latitudinal gradient?

There was no evidence that the difference in herbivory between natives and non-natives, or between native and non-naturalised/naturalised non-natives, changed across a latitudinal gradient (Table 2b, d & f). This was also the case when the meta-analysis was repeated using only data from 2007-2009 (Table S6), which was done to investigate whether the absence of a latitudinal gradient was caused by differences in sample year or sampling method. However, there was weak evidence for a difference in herbivory between non-naturalised and naturalised species increasing across latitude (Table 2h; pMCMC = 0.054).

5.4.4 How do absolute herbivory levels differ across a latitudinal gradient?

There was no evidence of any latitudinal trend in herbivory levels for native, non-native, non-naturalised or naturalised species (Figure 6; Table 3; Table S11). There was also no evidence of any latitudinal trend for any species groups when the meta-analyses were repeated using only data from 2007-2009 (Table S12).

Table 2: Results of a meta-analysis using 'MCMCglmm' to investigate the differences in herbivory between (a) native and non-native species, (c) native and non-naturalised non-native species, (e) native and naturalised non-native species, (g) non-naturalised and naturalised species, and (b, d, f, h) the relationship of herbivory with latitude between the status groups across 15 botanical gardens. Bold pMCMC indicate significant results (<0.05) where the 95% CI (credible interval) does not cross 0. For a full summary, see Tables S5.

	Posterior mean	95% CI	pMCMC
(a) Native vs non-native herbivory			
Intercept	-0.17	-0.27 to -0.06	**0.004**
(b) Native vs non-native herbivory across latitude			
Intercept	0.28	-0.86 to 1.35	0.586
Latitude	-0.01	-0.03 to 0.01	0.379
(c) Native vs non-naturalised herbivory			
Intercept	-0.18	-0.28 to -0.08	**0.002**
(d) Native vs non-naturalised herbivory across latitude			
Intercept	0.51	-0.54 to 1.55	0.320
Latitude	-0.01	-0.03 to 0.01	0.181
(e) Native vs naturalised herbivory			
Intercept	-0.11	-0.25 to 0.03	0.099
(f) Native vs naturalised herbivory across latitude			
Intercept	-0.36	-1.97 to 1.17	0.613
Latitude	<0.01	-0.02 to 0.03	0.736
(g) Non-naturalised vs naturalised herbivory			
Intercept	0.04	-0.06 to 0.12	0.399
(h) Non-naturalised vs naturalised herbivory across latitude			
Intercept	-0.94	-1.91 to 0.08	0.062
Latitude	0.02	0 to 0.04	0.054

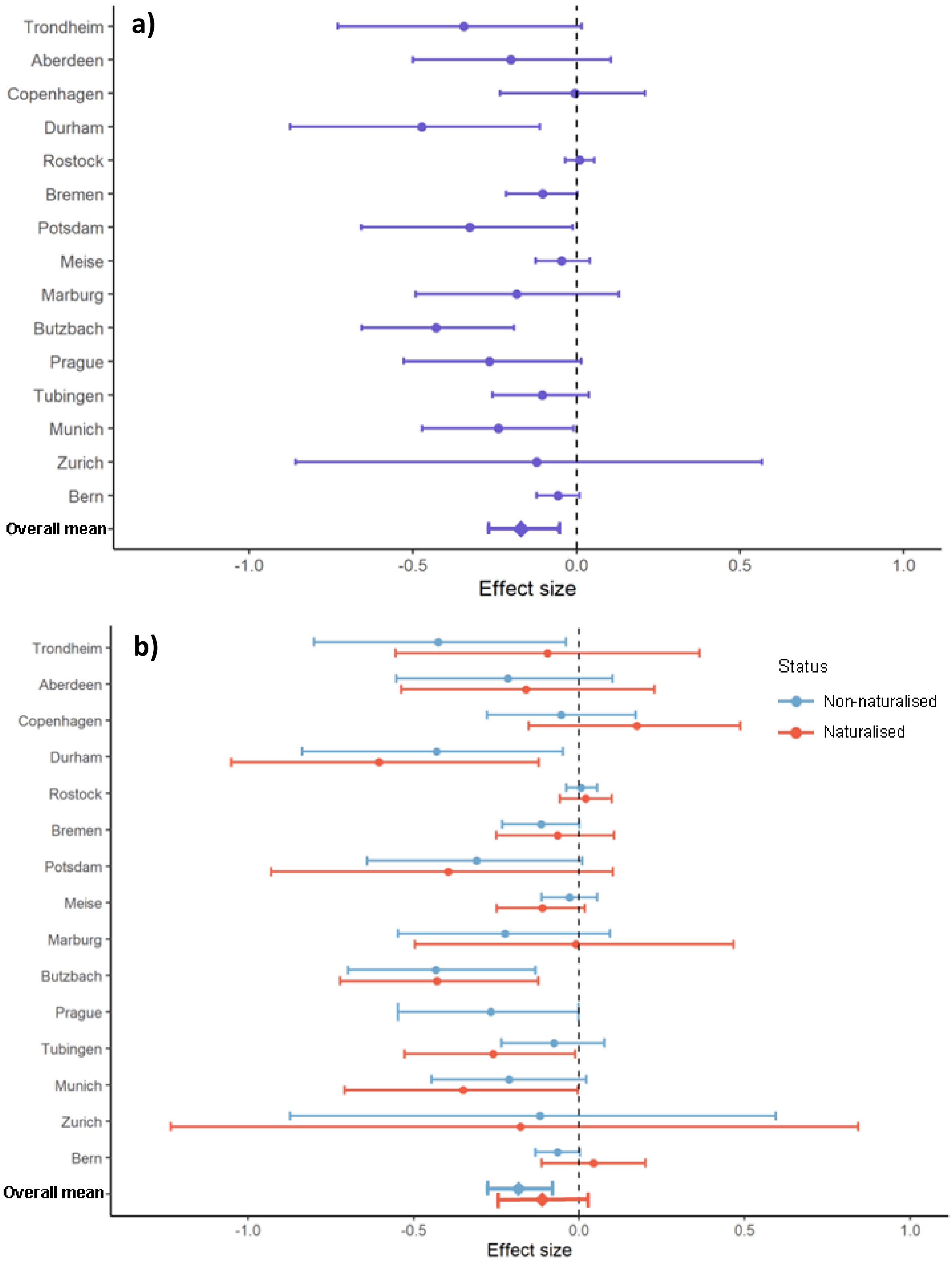
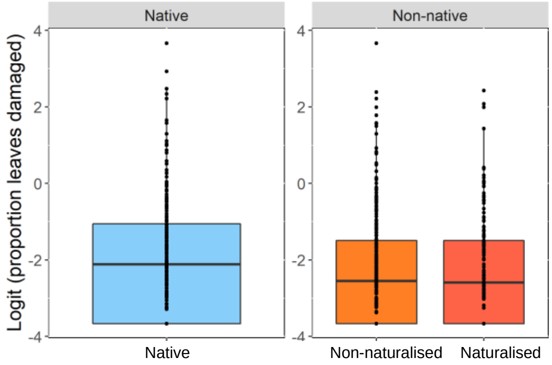
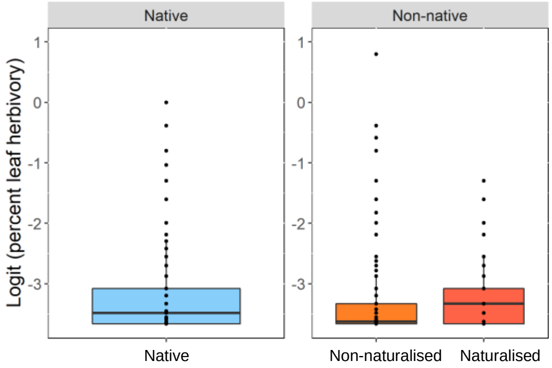


Figure 4: Effect sizes of MCMCglmms for 15 botanical garden surveys comparing herbivory levels of **(a)** native and non-native plant species and **(b)** native and non-native plant species split into non-naturalised (blue) and naturalised (red), ± 95% credible interval (CI). Prague did not contain any naturalised species. Overall means in bold show mean effect sizes across all gardens ± 95% CI: **(a)** non-native species herbivory (pMCMC=0.005, CI did not cross 0); **(b)** non-naturalised species herbivory (pMCMC = 0.001; CI did not cross 0) and naturalised species herbivory (pMCMC = 0.08; CI crossed 0)). Mean effect sizes were calculated using a meta-analysis with MCMCglmm. Negative effect indicates lower herbivory levels on non-native species, positive effect indicates higher herbivory levels on non-native species. Gardens are listed by latitude from most northern (Trondheim) to most southern (Bern).

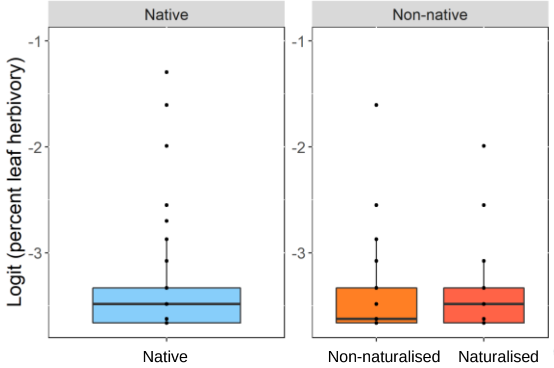
Aberdeen (n = 901)



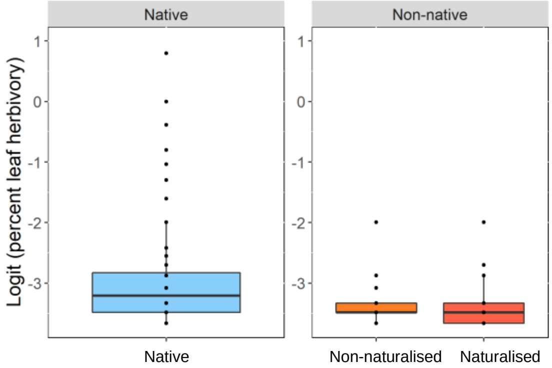
Bern (n = 1,343)



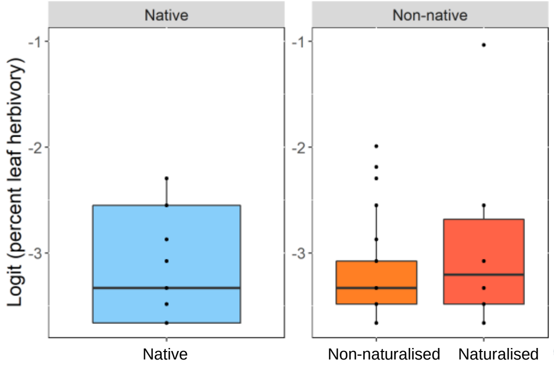
Bremen (n = 208)



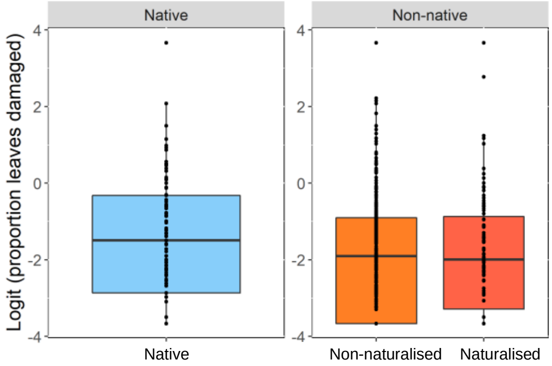
Butzbach (n = 153)



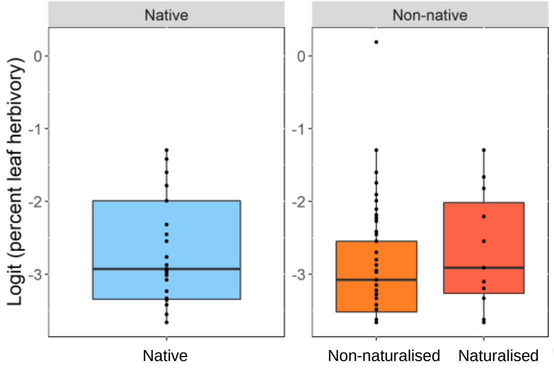
Copenhagen (n = 95)



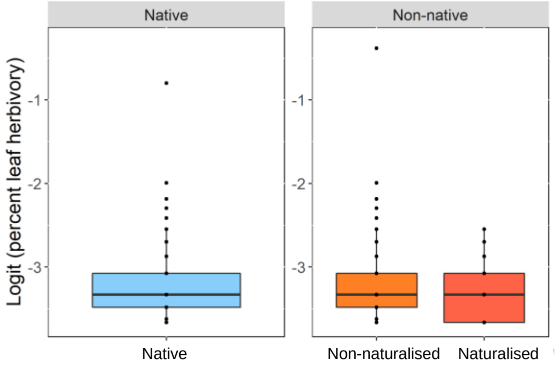
Durham (n = 666)



Marburg (n = 102)



Meise (n = 478)



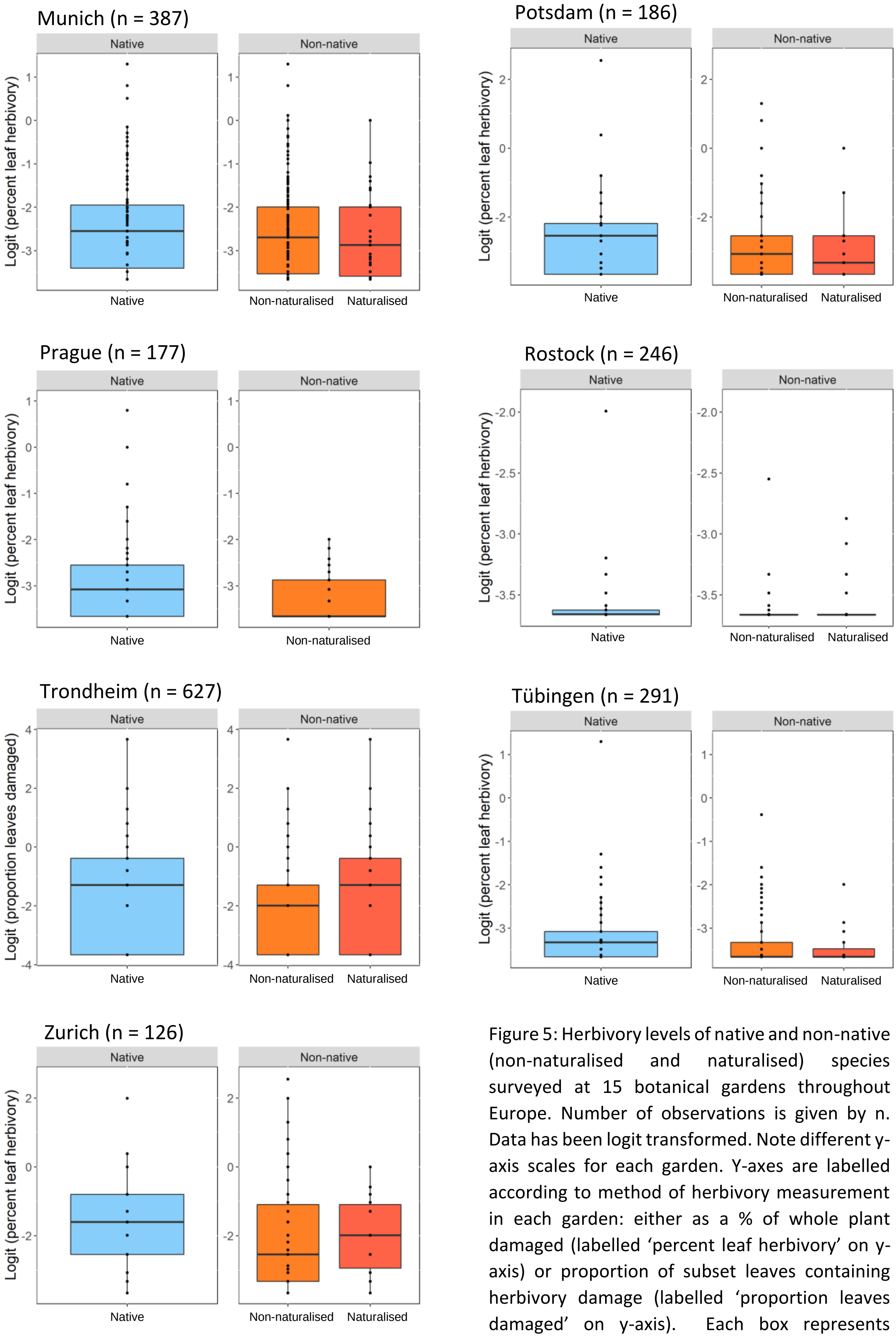


Figure 5: Herbivory levels of native and non-native (non-naturalised and naturalised) species surveyed at 15 botanical gardens throughout Europe. Number of observations is given by n. Data has been logit transformed. Note different y-axis scales for each garden. Y-axes are labelled according to method of herbivory measurement in each garden: either as a % of whole plant damaged (labelled 'percent leaf herbivory' on y-axis) or proportion of subset leaves containing herbivory damage (labelled 'proportion leaves damaged' on y-axis). Each box represents interquartile range of data, lines represent minimum and maximum values and points show raw data (including outliers).

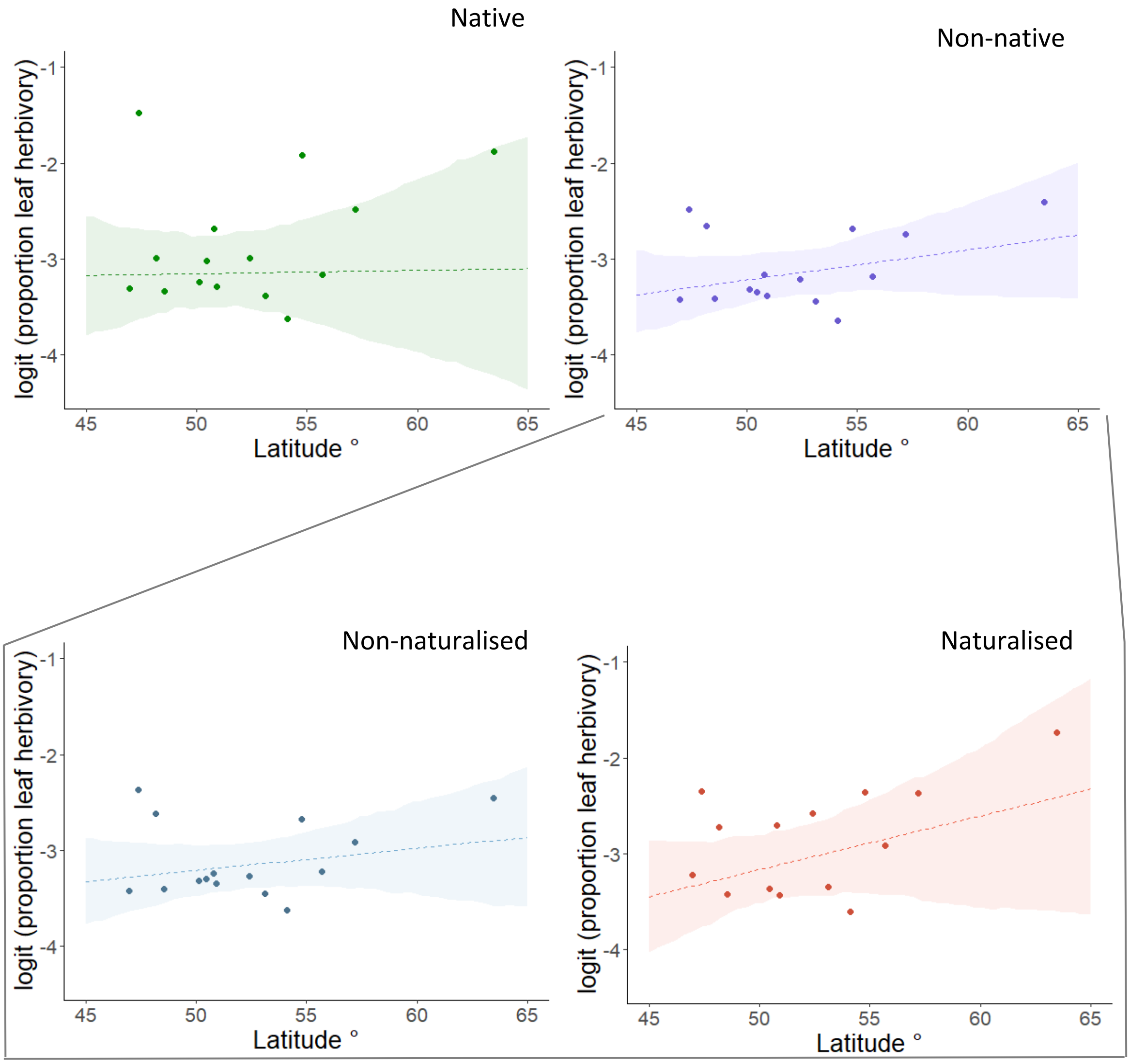


Figure 6: Herbivory of native and non-native species (treated as a single group and split into non-naturalised and naturalised) compared with latitude for 15 botanical gardens. Dashed lines represent non-significant relationships between latitude and herbivory calculated using MCMCglmm meta-analyses where 95% CI (credible interval) crossed 0 (Table 3).

Table 3: Summaries of meta-analyses of herbivory levels on native and non-native species (treated as a single group and split into non-naturalised and naturalised subgroups) in relation to latitude of the botanical gardens. Bold pMCMC indicate significant results (95% CI (credible interval) does not cross 0). For full summary see Table S11.

	Posterior mean	95% CI	pMCMC
Native herbivory across latitude			
Intercept	-3.33	-8.04 to 0.86	0.128
Latitude	0.00	-0.08 to 0.09	0.961
Non-native herbivory across latitude			
Intercept	-4.79	-7.43 to -2.14	**0.002**
Latitude	0.03	-0.02 to 0.08	0.208
Non-naturalised herbivory across latitude			
Intercept	-4.36	-7.18 to -1.59	**0.007**
Latitude	0.02	-0.03 to 0.08	0.360
Naturalised herbivory across latitude			
Intercept	-5.98	-10.17 to -1.86	**0.014**
Latitude	0.06	-0.03 to 0.14	0.172

5.5 Discussion

Surveys were carried out in fifteen botanical gardens across Europe to investigate the enemy release hypothesis and how enemy release varies across a latitudinal gradient. I found evidence of a wide-scale enemy release across all gardens where herbivory levels were lower on non-native than native species. In addition, while this trend was observed for non-naturalised species, naturalised species showed similar levels of herbivory to native species. There was no effect of latitude on enemy release or on absolute herbivory levels within each native status group.

5.5.1 Enemy release

The overall trend of herbivory across all gardens showed lower levels on non-native species than on natives. This result supports the idea of a wide-scale enemy release occurring at multiple locations across Europe, despite some gardens showing no significant difference in herbivory levels between native and non-native species. This wide-scale enemy release has also been found in meta-analyses carried out by Liu & Stiling (2006) and Xu et al. (2021) who combined data from multiple datasets and found overall lower levels of herbivory on non-native species than native. However, to my knowledge this is the first study to collect directly-comparable data on such a large spatial scale to investigate enemy release. In terms of non-native subgroups, non-naturalised species showed overall lower levels of herbivory compared to natives whereas this was not observed for naturalised species. These results might be explained by some naturalised species having become more established into the local community, and therefore accumulating more herbivores, whereas the less established non-naturalised species may not yet have been identified as a food source by native herbivores. A similar trend, whereby naturalised flowers received comparable visitation rates to native flowers but non-naturalised flowers received fewer visitations, was found in another botanical garden study (Razanajatovo et al., 2014). Several other studies, however, found the opposite trend of lower herbivory levels on naturalised than non-naturalised species (Cappuccino & Carpenter, 2005; Huang et al., 2020; Jogesh et al., 2008), with the suggestion that lower herbivory levels have contributed to such species becoming naturalised (Huang et al., 2020). These two opposing patterns call for further research into herbivory on non-naturalised and naturalised non-native plant species to shed light on the interactions of non-native plant species with other biota in their invaded communities.

5.5.2 Latitudinal patterns

There was no latitudinal change in herbivory differences between native and non-native species, or enemy release, regardless of whether the non-native species are naturalised or not. This lack of latitudinal gradient was also observed when comparing absolute herbivory levels of each species group (native, non-native, non-naturalised or naturalised). These results do not support the latitudinal biotic interactions hypothesis, which predicts a decrease in herbivory at higher latitudes, which if occurring would show a decrease in the extent to which non-native plants undergo enemy release. This would be because the herbivory levels of native plants would decrease but herbivory of non-native plants would remain at a low, constant level. This lack of latitudinal gradient is echoed by Xu et al. (2021), who collected herbivory data from almost 200 studies globally and compared enemy release with latitude. As mentioned above, Xu et al. (2021) did find evidence of enemy release, but found no evidence of interaction effects between enemy release and latitude. With the exception of Xu et al. (2021), however, most studies investigating the interaction between enemy release and latitude only concern one or few study species and herbivores (e.g. Kelly et al., 2008; Lu et al., 2019). Evidence for the latitudinal biotic interactions hypothesis has been found in some studies (e.g. Ivison et al., 2022; Kambo & Kotanen, 2014; Moreira et al., 2018) with mixed results in others (e.g. Anstett et al., 2014; Moreira et al., 2015), and some find no evidence for the latitudinal biotic interactions hypothesis at all (Andrew et al., 2005). There are several potential explanations for why herbivory levels might not vary with latitude and therefore contradict the latitudinal biotic interactions hypothesis. Firstly, the specialism of herbivores may affect latitudinal trends in herbivory, with specialist herbivores such as stem borers or seed herbivores showing latitudinal trends but generalist herbivory levels remaining constant (Anstett et al., 2014). My study focused solely on chewing herbivores which are often generalists (Vidal & Murphy, 2018), and unfortunately there were too few occurrences of leaf mining or galling damage types in the 2021 dataset to analyse these. In addition, the species surveyed varied greatly between gardens, with most species occurring in only one garden. Although phylogenetic analyses were carried out for each individual garden MCMCglmm, meta-analyses only took effect size of each garden MCMCglmm into account and not the phylogenetic relationships within the gardens. Many latitudinal trends in the literature are found to be species-specific (Nunes et al., 2016) and therefore herbivory levels between different species at different latitudes may not be comparable. Furthermore, the latitude range in this study was relatively small compared to studies such as Kozlov et al. (2015) and Lim et al. (2015) who used data spanning both northern and southern hemispheres. Finally, elevation differences between study sites might have an effect on climate and therefore may mean that the latitudinal gradient did not exhibit the expected corresponding gradient in climate; however, Figure A14 shows that for most gardens there was a broad latitudinal gradient in summer temperatures.

The data for this study originated from different time periods; one dataset was collected in 2007-2009, and the second dataset in 2021. One caveat of using data collected at different times is that herbivory levels may differ from year to year, or even exhibit overall trends through time; Meineke et al. (2019) found in herbarium specimens that herbivory levels have been increasing in the northeastern US over the past several decades. This trend, if occurring within these European study sites, might significantly alter the results, particularly since the more recent study sites are all at higher latitudes which may therefore affect the latitudinal trends observed. In addition, the different methods employed for each study might affect the observed latitudinal trends. To control for this, I repeated the latitudinal meta-analysis using only the 12 gardens of the 2007-2009 surveys to determine whether latitudinal trends might be observed if excluding the second studies. There were no trends observed in the repeated meta-analyses, suggesting that these caveats are not affecting the observed result (Table S12).

Latitudinal gradients can give an indication of how higher latitude ecosystems may respond to climate change, as in the future the climate will warm at higher latitudes to resemble that of lower latitudes currently (IPCC, 2014). If there had been a latitudinal decrease in herbivory, I could therefore have predicted that herbivory at higher latitudes might increase as the climate warms to resemble herbivory at lower latitudes. In this study, there was no evidence of any latitudinal trend in herbivory. This suggests that temperature is not affecting herbivory in these study systems, and therefore that climate change might not cause herbivory levels to increase over time. This means that non-native plants may not become more limited by herbivory in the future and that their herbivory levels and enemy release may remain at a constant level under climate change. This would have negative connotations for native species, as the current competitive advantage of non-native species over native species whereby they suffer lower herbivory levels would not change.

5.5.3 Botanical gardens & Methodologies

Botanical gardens can act as both valuable tools in the conservation of endangered species (O'Donnell & Sharrock, 2017) and, sometimes, sources of potentially naturalising or invasive species (Hulme, 2011). The high diversity in such gardens make them ideal field sites for surveying large numbers of species to address key questions in invasion ecology. To my knowledge, this is the first study to investigate wide-scale enemy release using botanical gardens as study sites. Furthermore, only one other study has used a botanical garden to investigate enemy release and this only took place in one location (Kirichenko & Kenis, 2016). Botanical gardens are a valuable source of non-native species and enable many hundreds of species to be surveyed at a single location, which makes them valuable tools for comparing widespread trends across native and non-native plants in a variety of locations. However, it is important to consider that within many botanical gardens, at least in Europe, there are a greater number of non-native than native species, whereas in wild environments native species are more abundant. This calls into question how much herbivory is a result of forage selectivity and how much is simply due to which plants are available. Despite these considerations, however, I was still able to observe lower levels of herbivory on non-native species, which suggests that herbivores are able to exhibit forage selecting behaviours within these gardens to a quantifiable extent.

This survey aimed to make observations of as many species as possible, resulting in most species only having one observation per garden (with the exception of Durham and Aberdeen, where multiple observations were made). This method of prioritising the number of species over the number of observations per species is recommended by van Kleunen et al. (2014), who state that using more species gives a higher statistical power when comparing groups of species, and found that during simulations estimate accuracy was increased by increasing number of species rather than increasing number of species observations.

5.5.4 Conclusions

In this study I found evidence for the enemy release hypothesis on a wide spatial scale. Perhaps more interesting, however, is the finding that when a species becomes naturalised in its non-native range, the differences in herbivory between native and such non-native species become less detectable. This suggests that herbivory release is transitory, and that it may not play a long-term role in invasion success. Moreover, as naturalised species become more abundant and integrated into communities, they may therefore over time become an established part of local food webs. Future research investigating the specific interactions between non-naturalised and naturalised species and their non-native ecosystems, such as visitation by pollinators and herbivores, might be valuable in determining the extent to which naturalised species have become integrated and how native biota are responding.

Chapter 6

Investigating the effects of warming and biotic interactions on invasive plant success in Norway

6.1 Abstract

There are a variety of factors which can influence the success of non-native plants. These can take the form of biotic interactions, such as competition with native plants or herbivory by invertebrates which may limit non-native plants, or climate change which has been predicted to increase non-native plant performance. To investigate the effect of these factors on five non-native plant species I set up a common-garden experiment in Trondheim, Norway, using herbivore exclusion and artificial warming treatments and planting non-native plants either alone or in competition with a native plant community. I found that three non-native species had greater biomass under artificial warming and all five were taller under warming. Competition with native species reduced the biomass of three non-native species and herbivore exclusion resulted in taller plants for three non-native species. The only non-native species to affect the native plant community was *Centaurea montana*, where native plants grown in competition with this species had reduced biomass. However, with the exception of non-native species *Alchemilla mollis*, where competition with a native community reduced the positive effects of warming on biomass, there were no generally-observed interactions between the three factors of warming, herbivore exclusion and competition. These results suggest that climate change is likely to increase the performance of these non-native species but that they may be limited by other biota in their invaded range. They also suggest that *C. montana* is likely to be the most detrimental non-native species to native communities.

6.2 Introduction

Invasive species are currently considered one of the greatest threats to biodiversity, causing significant economic costs and harming native biota in their invaded ecosystems. In particular, invasive plants have been found to alter soil chemistry (Weidenhamer & Callaway, 2010), affect insect populations (Litt et al., 2014), hybridize with native plant species (Pyšek et al., 2012) and decrease species richness (Hejda et al., 2009).

Native biota play a large role in the success of non-native plants, interacting with non-native plants such as through pollination by insects, competition with native plants or predation by herbivores. One of the leading hypotheses in invasion ecology is that that the success of non-native plants is in part due to the relative lack of effects of natural enemies such as herbivores in areas where the non-native plants are introduced (enemy release). The effects of herbivory on plant success include reducing plant survival and reproduction (Huang et al., 2012) and limiting the range that a plant can expand into (van der Putten et al., 2010). However, there are mixed results from tests of the enemy release hypothesis in the literature (Fenner & Lee, 2001; Siemann et al., 2006; Wolfe, 2002) which suggests that enemy release is extremely system-specific and cannot be applied to all non-native plant scenarios. It is therefore important to understand, for each non-native plant species, whether herbivore release is occurring and to understand the effect of herbivory on non-native plant performance.

Another form of biotic interaction influencing the success of non-native species is competition with native species. The outcompeting of native plants is a frequently described ecological impact of non-native plants within their invaded community (Mack et al., 2000), and it has been found that non-native species often possess greater competitive ability than native species (Gioria & Osborne, 2014). For example, Lee et al. (2021) found that non-native dandelions outcompeted their native competitors in a pairwise experiment, and Corbin & D'Antonio (2010) found that native plant productivity in a Californian grassland was reduced when native plants were in competition with non-native grasses. However, there are also documented effects of native species affecting non-native species performance. A review of pairwise experiments showed that although non-native plants affect native plants strongly, there was still some effect of native competition on non-native plant performance (Vilà & Weiner, 2004). Revegetation of land using native species was found to suppress non-native plant establishment (Schuster et al., 2018) and non-native species biomass was reduced when in competition with either native or naturalised non-native species (Haeuser et al., 2019). In one study, native plants were even found to outcompete their non-native competitors in a pairwise experiment using native and invasive populations of garlic mustard *Alliaria petiolata* (Bossdorf et al., 2004). These studies demonstrate how the competitive balance between native and non-native plants can vary between systems and species.

Climate change has been predicted to influence non-native plant success and increase their competitive advantage over natives in their invaded ranges. The traits which enable plants to naturalise and reproduce in non-native environments (e.g. broad climatic niche, high phenotypic plasticity) are traits which are likely to help plants adapt to a changing climate (Davidson et al., 2011; Liu & Stiling, 2006; Liu et al., 2017). Indeed, a meta-analysis revealed that non-native plants performed better than native plants under both increased temperature and atmospheric CO_2 concentration (Liu et al., 2017). In addition to the potential for giving established non-native plants a competitive edge, global warming is likely to lengthen the suitable seasons during which an introduction could happen and extend the range in which an invasive plant could survive. Longer warm periods also mean invasive plants may be able to produce fruit and reproduce within the growing season in areas with climates which, in the past, would not have supported such quick growth (Liu et al., 2017). High-latitude countries such as Norway are warming at a faster rate than elsewhere in the world (IPCC, 2014), which makes research into the response of non-native species to warming in these locations even more important. Based on a survey carried out in 2018, Norway is currently home to over 2,000 non-native species, around half of which are naturalised and stably reproducing and over 70% of which are plants (Sandvik et al., 2019). In fact, Norway was found to have the most naturalised plant species of all European countries except the UK (Sandvik et al., 2019). This makes understanding the response of non-native species to warming in highly-invaded locations such as Norway even more important to predict how the threat of these plants may develop.

There are very few studies which consider the interactive effects of climate change warming, herbivory and competition on non-native plants. Such studies include field experiments by Lu et al. (2016) who found that native species gain the competitive advantage over non-native species under artificial warming but only in the presence of a biocontrol beetle herbivore, and Zhang et al. (2021) who found that warming increased plant performance of two aquatic non-native plants in China but that the competitive balance between them was dependent on the ecosystem zone (tropical/temperate) and the presence of biocontrol herbivores. However, these studies both focused on biocontrol herbivores rather than native herbivores, and therefore do not indicate how general herbivory might mediate competition or warming.

In this study, I aim to investigate how climate warming, herbivory and competition with native species influence the performance of non-native plants species in Norway. To achieve this I created a common-garden experiment containing warming and herbivore exclusion treatments within which I planted non-native species both individually and in close proximity to native species. Herbivore exclusion allowed me to determine whether enemy release is benefitting non-native species, and how creating an artificial enemy release for both native and non-native plants affected their response to warming. In addition, my design allowed me to investigate both the effects of a native plant community on non-native plants and the effect of non-native plants on a native community. This is the first experiment to investigate the three factors of warming, herbivore exclusion and native plant competition in Norway and will help determine which factors are likely to influence non-native species both now and in the future.

6.3 Methods

6.3.1 Study species

The starting pool of non-native plant species was taken from the Norwegian Biodiversity Information Centre's (2020) list of high or very high risk alien species in Norway. These species are rated according to invasion potential (plant lifespan, rate of expansion, ability to colonise habitats) and ecological impacts (effect on native species, genetic transfer, transmission of pathogens; Norwegian Biodiversity Information Centre, 2020). Species considered for this experiment had to meet the following criteria: short germination time (4 weeks or less) as seeds were planted in spring and re-potted outside in early summer, and ground cover area of less than roughly 30 cm^2 due to limited space within the experiment. Germination times of each species were checked on plant information websites (Plants For A Future; Thompson & Morgan (Accessed January 2021)). Ground cover area was discussed with an expert (Vange, personal communication, January 2020). The following five herbaceous species were selected which fulfilled these criteria: *Arabis caucasica, Alchemilla mollis, Centaurea montana, Cerastium tomentosum* and *Hesperis matronalis* (Table 1). All species have considerable ecological impacts or high invasion potential and are therefore classed as invasive to Norway. *A. caucasica* became naturalised around 1912 and has approximately doubled its rate of occurrence every 20 years since, found to displace native species particularly in shallow soils. *A. mollis* was first found in Norway in 1938 and is now widespread across Norway and throughout Troms og Finnmark, the northernmost Norwegian county. *C. montana* and *C. tomentosum* both became naturalised within Norway in the late 1800s and began to expand their range in the 1940s, and *C. tomentosum* can form large mats which displace native species. *H. matronalis* began to expand its range in Norway around 1830 and since 1900, rate of occurrences have increased by 20-50% every decade. Norwegian native species were then chosen to act as competitors against the non-native species, again prioritised by germination time and size (Vange, personal communication, January 2020). Three were selected to represent a Norwegian native grassland community in the wild: a grass, red fescue *Festuca rubra,* and two herbs; red campion *Silene dioica* and red clover *Trifolium pratense.*

Table 1: Non-native species chosen for common-garden experiment including species family and native range (POWO, 2022). Risk ratings are according to the Norwegian Biodiversity Information Centre (2020). For full native and non-native distributions see Figure A15.

Species	**Family**	**Native range**	**Risk rating**
Arabis caucasica	Brassicaceae	NW Africa, SE Europe & Arabian Peninsula	High
Alchemilla mollis	Rosaceae	Romania to Caucasus	Very high
Centaurea montana	Asteraceae	Western & Central Europe	High
Cerastium tomentosum	Caryophyllaceae	Italy	Very high
Hesperis matronalis	Brassicaceae	Southern Europe and Caucasus	High

6.3.2 Study site and experimental layout

A common-garden experiment was set up in the Norwegian University of Science and Technology (NTNU) Ringve Botanical Gardens in Trondheim, Norway (approximately 63.4° N, 10.5° E). The experiment was positioned on a grass lawn with little or no shading from trees. Within the experiment there were ten replicate blocks of four treatment plots: control, herbivore exclusion, warming, and warming + herbivore exclusion (Figure 1). Each of the ten replicate blocks was positioned within a 2.5 x 2.5 m raised bed filled with soil. Warming was achieved by using open top chambers (OTCs), hexagonal structures made of clear plastic which warm inside air temperature by 1-3° Celsius (C) (Molau & Mølgaard, 1996). Herbivore exclusion was achieved by creating six-sided insect-proof mesh covers roughly one metre tall, fitted over six bamboo canes tied together at the top to form a point. For treatments which did not include herbivore exclusion, insect-proof mesh covers with gaps at the bottom and top were attached to bamboo structures as a procedural control for light levels, wind and precipitation which may be affected by the mesh. Control plots therefore had a half cover of mesh, herbivore exclusion plots had a full cover of mesh, warming treatments had an OTC and half-cover of mesh, and warming + herbivore exclusion treatments had an OTC and a full cover of mesh (Figure 1). To prevent aboveground insects accessing plots from the ground, full mesh covers were tucked under either the base of OTCs in plots which included warming, or tucked under six lengths of bamboo, one for each edge of the mesh cover, which were fixed to the ground using metal staples in exclusion-only plots. Around 2 cm of soil was built up around the base of the full mesh covers to ensure that there were no gaps at ground level where aboveground insects could access the plants.

Seeds were planted at the end of April 2022 in the greenhouses in the botanical garden. Non-native species were each sown into a single tray and native species were each sown across three trays due to higher numbers of native species required for the experiment. Trays contained two layers of soil; a bottom layer of 90% potting soil (phosphorus 40 mg l^{-1}, calcium 220 mg l^{-1} and nitrogen 950 mg l^{-1}) and 10% perlite, and a top layer around 5cm deep of potting soil only (phosphorus 30 mg l^{-1}, calcium 150 mg $l^{-1}$and nitrogen 750 mg l^{-1}). Seedlings were thinned out and re-potted at least once before being placed within the experiment, with the exception of the grass *F. rubra*. The non-native *A. mollis* seeds did not germinate so to replace these, *A. mollis* seedlings growing wild in the garden were transplanted into trays. There were also insufficient *C. montana* seedlings, as only 53 seeds germinated, so again wild-growing seedlings were transplanted from the garden to ensure there was a sufficient number of plants.

At the beginning of June 2022, seedlings were separated into pots containing (by volume) 90% potting soil (phosphorus 40 mg l^{-1} calcium 220 mg l^{-1} and nitrogen 950 mg l^{-1}) and 10% perlite for planting out. Each of the four treatment plots across ten replicate blocks (Figure 1) contained eleven 2 litre pots: five containing one of each non-native species only (no competition for non-natives), five containing one of each non-native species potted with one each of all three native species (competition), and one pot containing one each of all three native species (no competition from the non-natives). Each treatment plot therefore contained 2 individual plants for each non-native species and 6 individual plants for each native species (Figure 2). For most species there was a surplus of seedlings, so it was possible to select seedlings of a similar size to transplant into pots. The grass *F. rubra* was very dense within the seedling trays so clumps of grass 1 x 1 cm were treated as one individual 'plant'. Each pot was labelled according to the replicate block (1-10), the treatment and the composition of the pot's species. Before pots were moved outside into the experiment, measurements were made of each non-native plant: number of leaves, number of leaves where over 10% of leaf was damaged by herbivory, the proportion of each damaged leaf missing due to herbivory, plant height (cm; measured from the soil to the highest point of the plant as it lay naturally), length of the largest leaf (mm), and width of the largest leaf (mm). Plant pots were then sunk into the soil within the raised bed replicate blocks so the top of the pot was level with the soil surface, which i) reduced the risk of pots drying out, ii) increased the realism of belowground temperatures experienced by the plants, and iii) increased the volume of space for plant growth within experimental plots. Finally, temperature loggers were placed within each plot to determine whether the OTCs were successful in warming the air and soil. TMS-4® dataloggers measure soil moisture and temperature at 6 cm below the soil surface, and air temperature +2 cm and +15 cm above the surface (Wild et al., 2019). One TMS-4® was placed within each of the four treatment plots for five randomly chosen replicate blocks and set to measure temperatures every 15 minutes. HOBO 64K Pendant® dataloggers, which measure soil temperature only, were placed within each of the four treatment plots of the remaining five replicate blocks and set to measure soil temperature every hour. A further eight HOBO® loggers were distributed so that two replicate blocks contained both TMS-4® and HOBO® loggers.

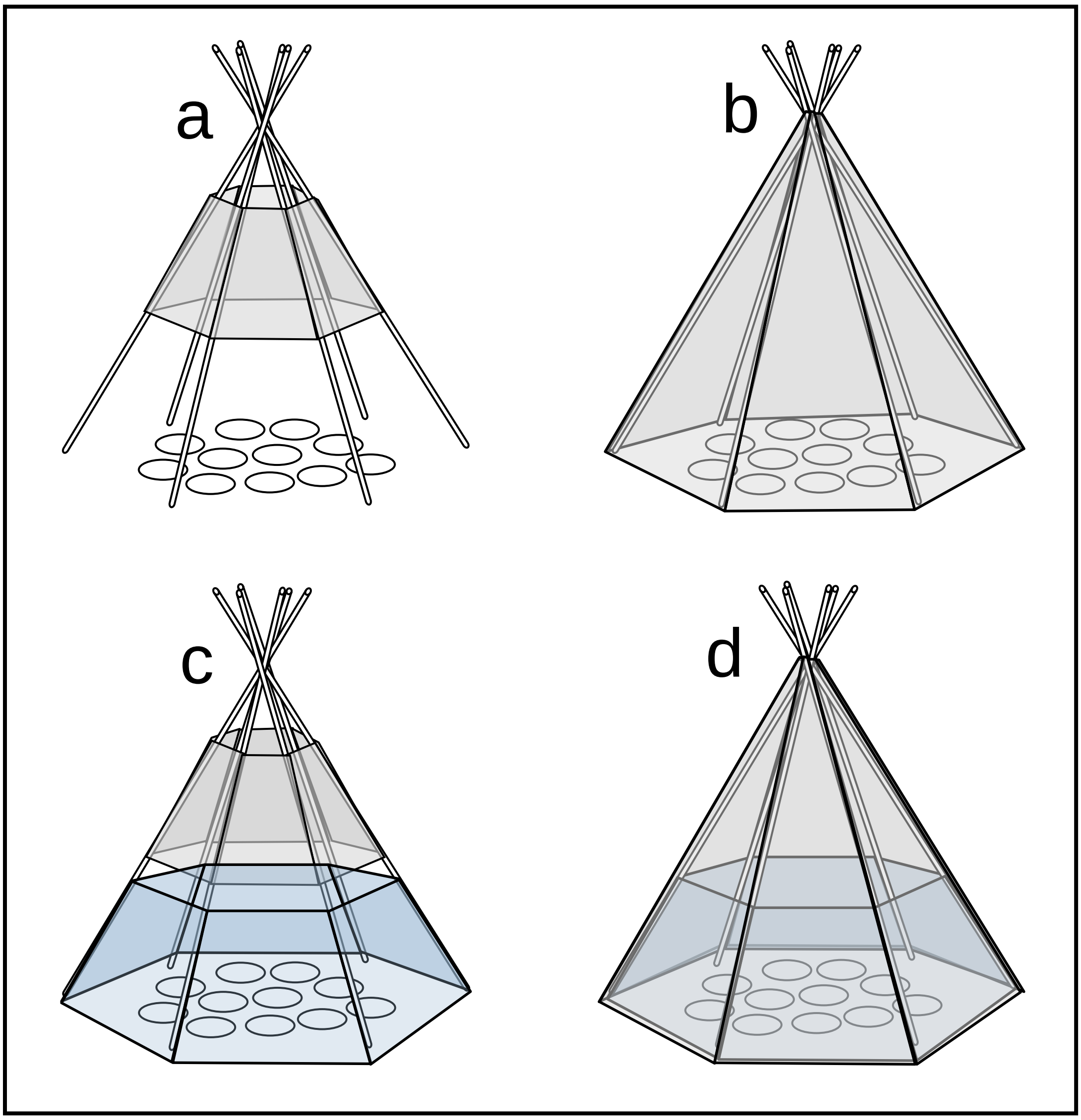


Figure 1: Experimental layout of common-garden experiment investigating how climate warming, invertebrate herbivory and competition affect non-native plant success, comprising ten replicate blocks of four treatment plots. Figure shows one block, represented by outer box. Control (a) is ambient and contains only a half mesh cover. Herbivore exclusion (b) is ambient and has a full mesh cover. Warming (c) has an OTC to increase air temperature and a half mesh cover. Warming and exclusion (d) has an OTC and full mesh cover. Half covers were used to account for potential effects of mesh on light, wind and precipitation levels.

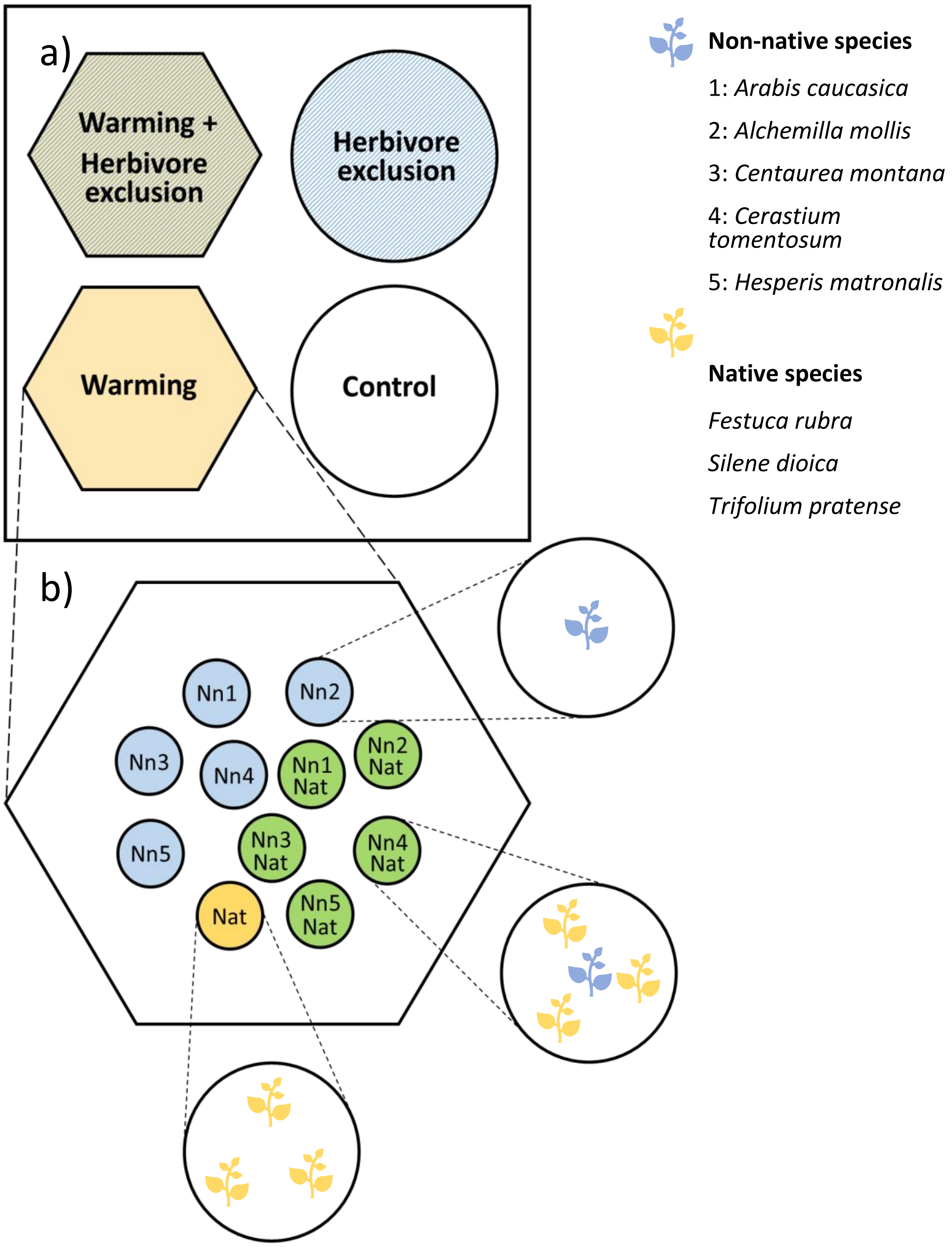


Figure 2: Experimental layout showing one of ten repeated experimental blocks. In part (a), hexagonal warming sections represent treatments with OTCs and herbivore exclusion sections represent treatments covered in insect-proof mesh (for more detail about treatment plot design see Figure 1). Within each of the four treatments (b) were 11 pots, represented by coloured circles, each containing either one of five non-native species, one of five non-native species with three native species, or three native species alone. NB pot types (non-native, non-native with native competition and native only) were randomly distributed within treatment plots.

6.3.3 Data gathering

The experiment ran from 17th June to 17th August 2022. Watering was carried out once two weeks after the experimental start date. When pots were removed from the experiment the following measurements were made of all non-native plants: height (cm, measured as length from soil to highest point of plant to more accurately represent the growth of the plant in contrast to height measurements made before the experiment), number of leaves with herbivory (proportion of all leaves if plant contained less than fifty leaves; proportion of a random subset of fifty leaves if plant contained more than fifty leaves), length of the largest leaf (mm), width of the largest leaf (mm), presence/absence of chewing or leaf mining damage across whole plant, number of flowers, surface area of largest leaf, and dry biomass of largest leaf. To measure surface area of largest leaf, the largest leaf was removed from the plant and placed on a large sheet of white paper. A grid of 1 mm^2 graph paper was placed beside the leaf for scale. A clear sheet of glass was then placed over the leaf to keep it flat and a photograph taken from above. Photographs were later analysed using the image software 'ImageJ' with the plug-in 'Fiji' (Schindelin et al., 2012; Schneider et al., 2012). The graph paper was used to set the scale and a contrast applied to the image to select only the leaf. Missing leaf parts due to herbivory were excluded from area measurements; if damage occurred on the edge of a leaf there was no way to accurately predict the full area of the leaf without damage, so all damage was therefore excluded regardless of location. Biomass of the largest leaf was measured by placing each leaf in an envelope and drying them within a drying oven at 60° C for 48 hours. Weight was then measured in grams to four decimal places. Specific leaf area (SLA) was calculated by dividing leaf area (mm^2) by leaf weight (g). For the native plants *S. dioica* and *T. pratense*, proportion of leaves with herbivory was measured as a random subset of up to twelve leaves for the entire plant. Twelve leaves were chosen because for *T. pratense* this equalled four separate leaves each with three leaflets. It was not feasible to randomly select up to fifty leaves for native plants due to time constraints. No herbivory measurements were made of the grass *F. rubra*. Finally, dry biomass of all native and non-native plants was measured by cutting all plants at the base and placing them in individual envelopes. These were placed in drying ovens at 60° C for 72 hours and weighed in grams to 2 decimal places.

6.3.4 Data analysis

Firstly it was important to determine whether the OTCs had successfully increased temperatures within warming treatments. Data from the dataloggers were downloaded resulting in four separate temperature measures (three measurements at -6, +2 and +15 cm relative to soil surface for TMS4 dataloggers; one measurement (roughly -3 cm) for HOBO dataloggers). Dataloggers within the control plots for two replicates recorded temperatures at least 6° C warmer than all other recorded temperatures which was likely due to an error within the dataloggers, so these data were not considered. Mean temperatures for all four measures were calculated for the entire experimental timeframe (17th June – 17th August). A linear mixed effects model was then used in the R package 'glmmTMB' (Brooks et al., 2017) to analyse temperature measures across treatments, to confirm whether or not the OTCs had increased temperatures in warmed plots. Mean temperature across the entire experimental timeframe (for a given soil surface depth/data logger) was used as a response variable and treatment type (control, exclusion, warming, warming + exclusion) as a fixed effect with replicate block number (1-10) as a random effect to account for spatial patterns in temperature across the experiment.

Soil moisture data were also downloaded from TMS4 dataloggers and the mean moisture calculated across the entire experimental timeframe. Linear mixed models were used to determine whether soil moisture was affected by treatment, using mean soil moisture as a response variable, treatment as a fixed effect and replicate block number (1-10) as a random effect.

To determine whether the exclusion mesh covers were successful in excluding herbivores, a binomial generalised linear mixed model was used in the R package 'lme4' (Bates et al., 2015). Herbivory was represented as proportion of leaves with damage. Competition (non-native plants grown either alone or with native plants) and treatment (control, exclusion, warming, warming + exclusion) were used as interaction terms and whether plants were grown from seed or picked from the wild as seedlings was included as a covariate. Species was treated as a random effect in order to estimate overall herbivory differences among treatments across all non-native plants. Replicate block number (1-10) was an additional random effect. The resulting model was validated using the R package 'DHARMa' (Hartig, 2021), which showed normal distribution of residuals, and the interactions between competition and treatments were investigated further using the R package 'emmeans' (Russell, 2021).

To investigate the effects of competition, warming and herbivore exclusion on non-native plant performance, linear mixed models were created using the R package 'lme4'. Separate models were created for each non-native species to determine how each was affected individually by warming, exclusion and competition, and in each model plant performance was represented by one of three measurements as response variables: total plant biomass, SLA or plant height. Biomass was square root-transformed due to a skewed distribution of data. SLA was natural log- or square root-transformed depending on each species' data distribution. Height data did not indicate a skewed distribution so no transformation was necessary. Warming and exclusion were included in the model as two factors (warming or no warming, exclusion or no exclusion) to assess whether the effects of warming on plant performance were dependent on exclusion of herbivores. Competition with native species was treated as a third term and the interactions between warming, exclusion and competition were included. To account for the initial size of plants at the beginning of the experiment, length of the largest leaf at the time of planting was added as a covariate. For *C. montana*, an additional covariate of plant origin (seed grown or wild-growing seedling) was included as too few seeds germinated in the greenhouse and plants were supplemented with wild-growing seedlings. Finally, replicate number (1-10) was added as a random effect.

Finally, models were created to investigate treatment effect on native plant biomass, again in ‘lme4’. Native plants were firstly treated as a community, and total biomass of the native community was therefore treated as a response variable. Warming and exclusion were included in the model as two factors (warming or no warming, exclusion or no exclusion). A further term of community status comprising six factors was added (native community alone or competition with one of five non-native species) to investigate the effects of competition, and specifically which non-native species had the largest competitive ability. The interactions between warming, exclusion and competition were included. Replicate number (1-10) was added as a random effect. Further species-specific models were then created, where biomass of either *S. dioica, T. pratense* or *F. rubra* were response variables and species composition, exclusion and warming were interaction terms. The summed biomass of the remaining two species within each pot was added as a covariate, with replicate number as a random effect. Residual diagnostics for all regression models were carried out using the R package ‘DHARMa’ (Hartig, 2021) and all models showed normal dispersion of residuals. All significant interactions in both native and non-native models were investigated using the R package ‘emmeans’. All data handling was completed in R version 3.6.1 (R Core Team, 2019).

Due to an insufficient number of flowers observed on non-native plants, analysis of the effect of treatments on reproductive success was not possible; for information about number of flowers across species see Figure A16.

6.4 Results

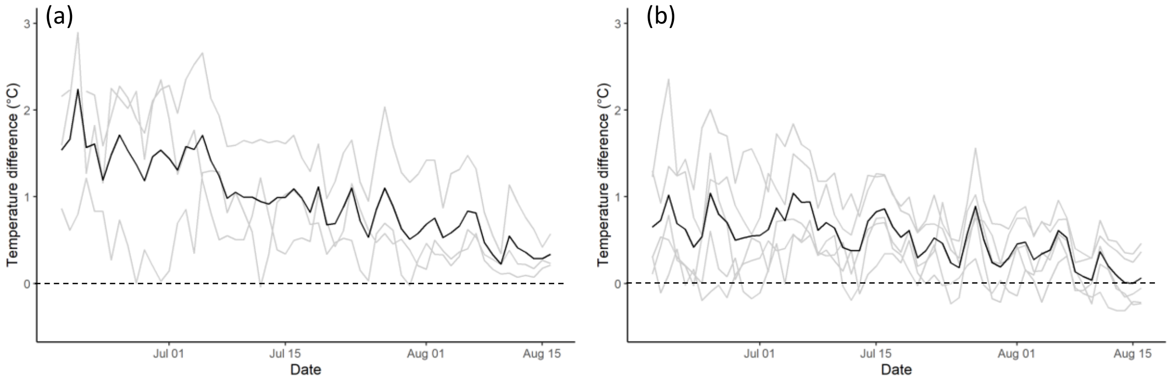
6.4.1 Warming

The warming treatments were found to increase temperatures for all below-ground and above-ground measurements, and the increase was greater for warming than for warming + exclusion treatments. The biggest effect of warming was found 6 cm below ground level where temperatures increased by an average of 0.91°C for warming and 0.74°C for warming + exclusion treatments (Table 2a). HOBO dataloggers showed an additional slight increase in temperatures for exclusion plots. The mean daily difference between warming and control plots, and between warming + exclusion and exclusion plots, was mostly positive but did decrease throughout the summer for all datalogger measurements (Figure 3). There was no difference in soil moisture levels across any treatment plots (Table 2b).

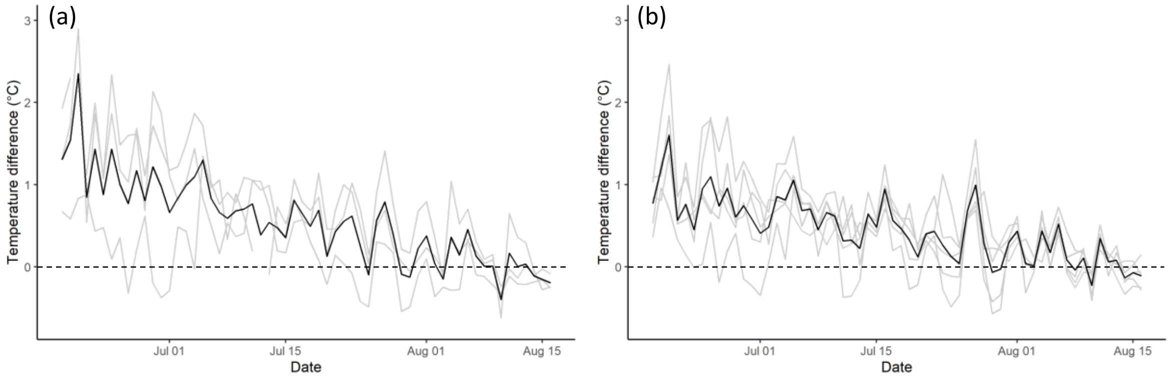
Table 2: Model summaries investigating (a) the warming effects of OTCs placed around warming and warming + exclusion treatments (highlighted in grey) compared to control and exclusion treatments, and (b) the difference in soil moisture across all treatments. Temperature/soil moisture measurements were taken as mean values per datalogger across entire experimental timeframe (17th June – 17th August). C = control, E = exclusion, W = warming & W + E = warming + exclusion treatments. Bold numbers indicate significant results ($p < 0.05$). SE = standard error. Soil moisture is measured using time-domain transmission (TDT) method with raw TDT data as units (Wild et al., 2019).

Logger		*Estimate*	*SE*	*z-value*	*p-value*
(a)					
TMS4 -6 cm Temperature (°C)	Intercept (C)	14.84	0.14	104.6	**<0.01**
	E	0.25	0.18	1.38	0.17
	W	0.91	0.18	5.07	**<0.01**
	W + E	0.74	0.18	4.15	**<0.01**
TMS4 +2 cm Temperature (°C)	Intercept (C)	14.76	0.09	155.8	**<0.01**
	E	-0.07	0.10	-0.70	0.49
	W	0.50	0.10	4.81	**<0.01**
	W + E	0.36	0.10	3.50	**<0.01**
TMS4 +15 cm Temperature (°C)	Intercept (C)	14.50	0.09	160.0	**<0.01**
	E	0.09	0.11	0.79	0.43
	W	0.67	0.11	5.81	**<0.01**
	W + E	0.59	0.11	5.17	**<0.01**
HOBO -3 cm Temperature (°C)	Intercept (C)	15.11	0.07	206.2	**<0.01**
	E	0.29	0.11	2.65	**0.01**
	W	0.81	0.11	7.73	**<0.01**
	W + E	0.71	0.11	6.72	**<0.01**
(b)					
TMS4 Soil moisture	Intercept (C)	1479.1	360.6	4.10	**<0.01**
	E	493.0	401.6	1.23	0.22
	W	664.5	435.4	1.52	0.13
	W + E	617.9	426.1	1.45	0.15

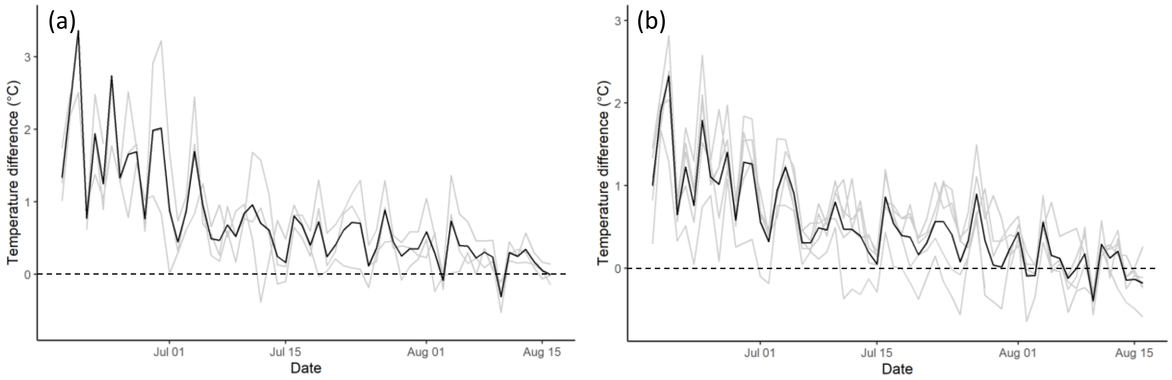
TMS4 -6 cm



TMS4 +2 cm



TMS4 +15 cm



HOBO -3 cm

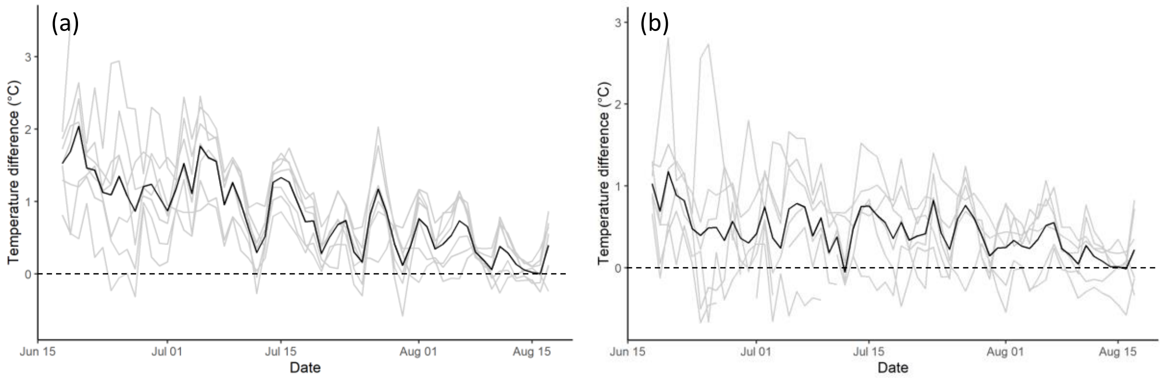


Figure 3: Mean daily difference in temperature between (a) warming and control and (b) warming + exclusion and exclusion plots across experimental timeframe. Grey lines represent temperature differences between dataloggers within the same replicate block (1-10) and black lines represent overall means across all dataloggers in all replicate blocks. Black dashed lines show 0° C. There were fewer TMS-4 dataloggers than HOBO dataloggers and therefore fewer comparisons between dataloggers (grey lines) in TMS4 panels. In addition, two discarded TMS-4 dataloggers in control plots resulted in fewer comparisons between warming and control plots in (a) panels for TMS-4.

6.4.2 Herbivory

Herbivory levels were lower in exclusion and warming + exclusion plots compared to controls (p < 0.01 for both), and higher in warming plots. There was weak evidence of lower herbivory levels on non-native plants with native competition (p = 0.06) which was more pronounced in warming + exclusion plots (Table 3; Figure 4). There was no effect of plant origin (seed grown or wild-collected seedlings) on herbivory levels.

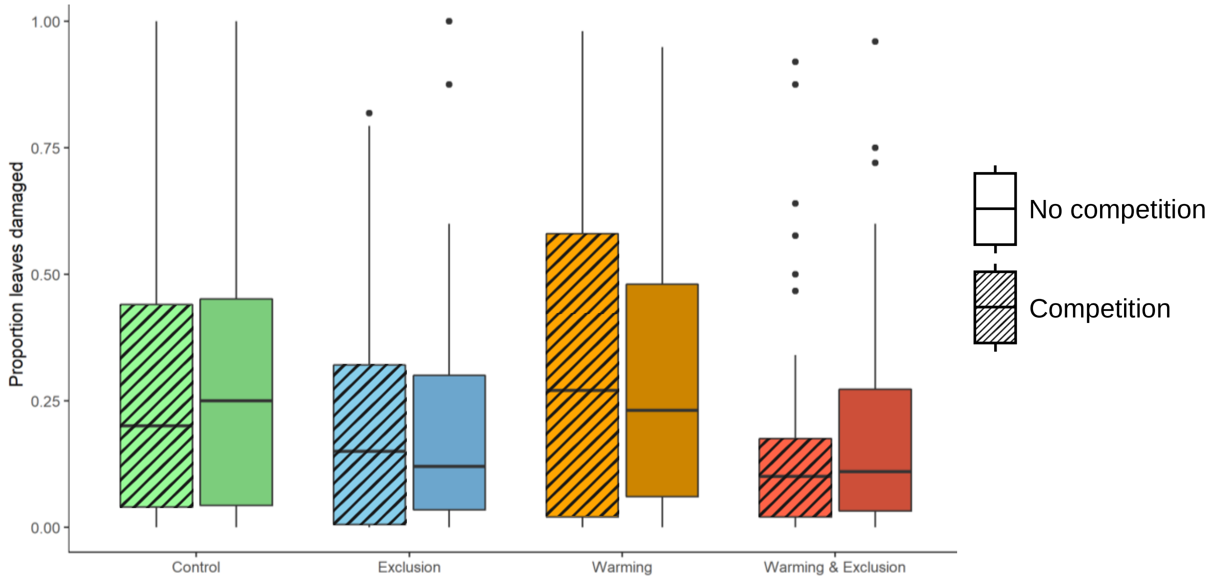


Figure 4: Herbivory levels (proportion of leaves damaged) of non-native plants in each treatment type and with/without native competition.

Table 3: Summary of model investigating herbivory levels between treatment plots and between plants with or without native competition, to determine whether exclusion treatments (highlighted in grey) were successful. Bold numbers indicate significant results (p < 0.05). SE = standard error, SD = standard deviation.

	Estimate	*SE*	*z-value*	*p-value*
Intercept (control; no competition)	-1.24	0.68	-1.81	0.07
Competition	-0.14	0.08	-1.88	0.06
Exclusion	-0.77	0.08	-9.85	**<0.01**
Warming	-0.02	0.07	-0.33	0.74
Warming + exclusion	-0.84	0.08	-10.9	**<0.01**
Competition: exclusion	0.27	0.12	2.29	0.89
Competition: warming	0.48	0.11	4.56	**0.02**
Competition: warming + exclusion	-0.10	0.12	-0.88	**<0.01**
Seed grown/wild	-0.02	0.11	-0.15	0.38
Random effects	*Variance*		*SD*	
Species	2.29		1.51	

6.4.3 Non-native species-specific performance

6.4.3.1 Biomass

Biomass was reduced for three species when in competition with native species: *A. caucasica, A. mollis* and *C. tomentosum*. There was strong evidence that warming resulted in increased biomass for *A. mollis* and *H. matronalis,* with weaker evidence for *A. caucasica*. There was no effect of herbivore exclusion on any species' biomass (Figure 5). For all species except *H. matronalis*, the initial size of the plant before being planted into the experiment (length of largest leaf) was positively linked to higher biomass. The only interactions between competition, warming and exclusion were observed in *A. mollis* where there was strong evidence that plants' increase in biomass in warmed plots was greater without competition than with competition (Figure 6), and weaker evidence that plants' increase in biomass in warmed plots was greater where herbivores were not excluded than where herbivores were excluded. Weak evidence for a further three-way interaction was also observed. If herbivores were excluded, plants with no competition showed no change in biomass and plants with competition showed increased biomass under warming. If herbivores were not excluded, however, biomass increased for plants without competition and decreased for plants with competition under warming (Table S1 (this and all subsequent supplementary tables can be found in File S1); Figure A17).

6.4.3.2 SLA

SLA was lower for *A. caucasica* plants in competition. For *A. caucasica, A. mollis* and *C. montana*, longer leaves at the beginning of the experiment were linked to higher SLA. For *C. montana*, plants picked as seedlings from the wild had a lower SLA than seed-sown plants. *C. montana* also showed evidence of interactions between competition, exclusion and warming. If herbivores were excluded, plants with no competition had a greater SLA in warmed than ambient plots. If herbivores were not excluded, plants with no competition had a lower SLA under warmed than ambient plots (Table S2; Figure A18).

6.4.3.3 Height

Plant height increased under warming for all five non-native species and increased under herbivore exclusion for three (*A. caucasica, A. mollis* and *H. matronalis*). Competition with native plants resulted in reduced height for *A. mollis* (Figure 7). For three species (*A. caucasica, C. montana* and *C. tomentosum*), longer leaves at the beginning of the experiment were linked to increased height. For *C. montana*, wild seedlings were shorter than seed-grown plants. There was evidence of an interaction between competition, exclusion and warming for *A. mollis*. Height increased under warming but the extent of this increase was different across treatments. If herbivores were excluded, height increase under warming was more pronounced for plants with competition. If herbivores were not excluded, the increase in height under warming was more pronounced for plants without competition. (Table S3; Figure A19).

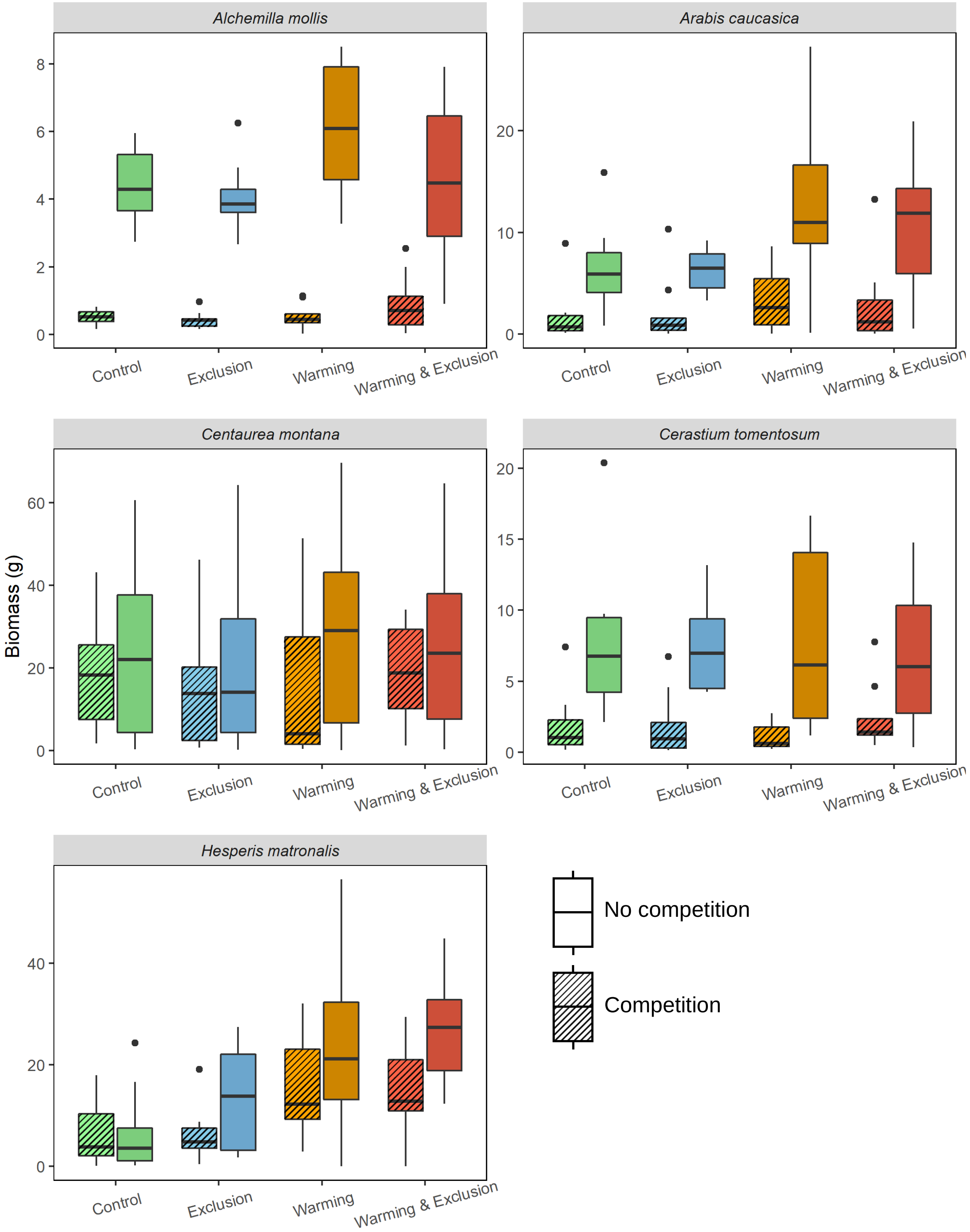


Figure 5: Biomass of each non-native species across each treatment type and with/without native competition.

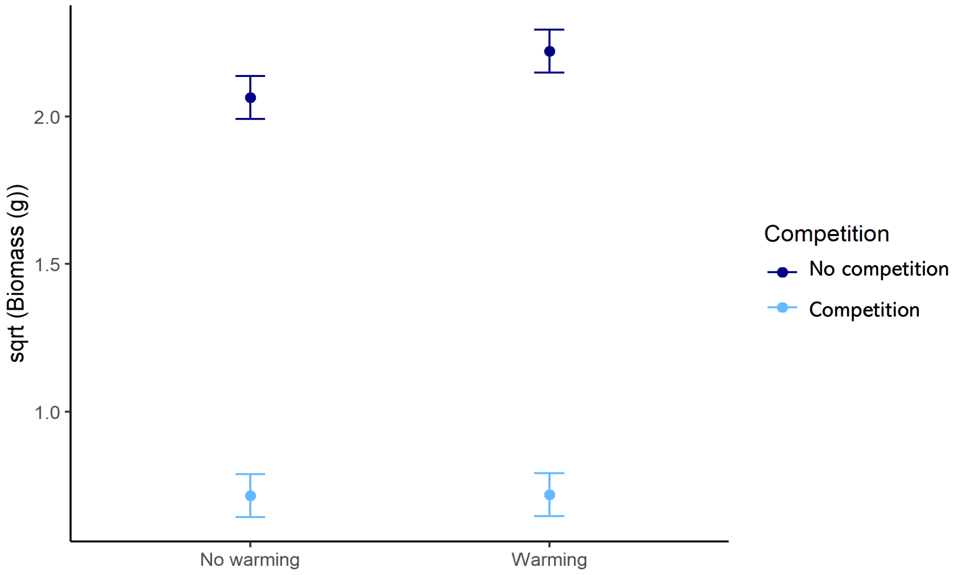


Figure 6: The interactive effects of warming and competition with native species on the biomass (±SE) of *Alchemilla mollis* based on a linear regression model.

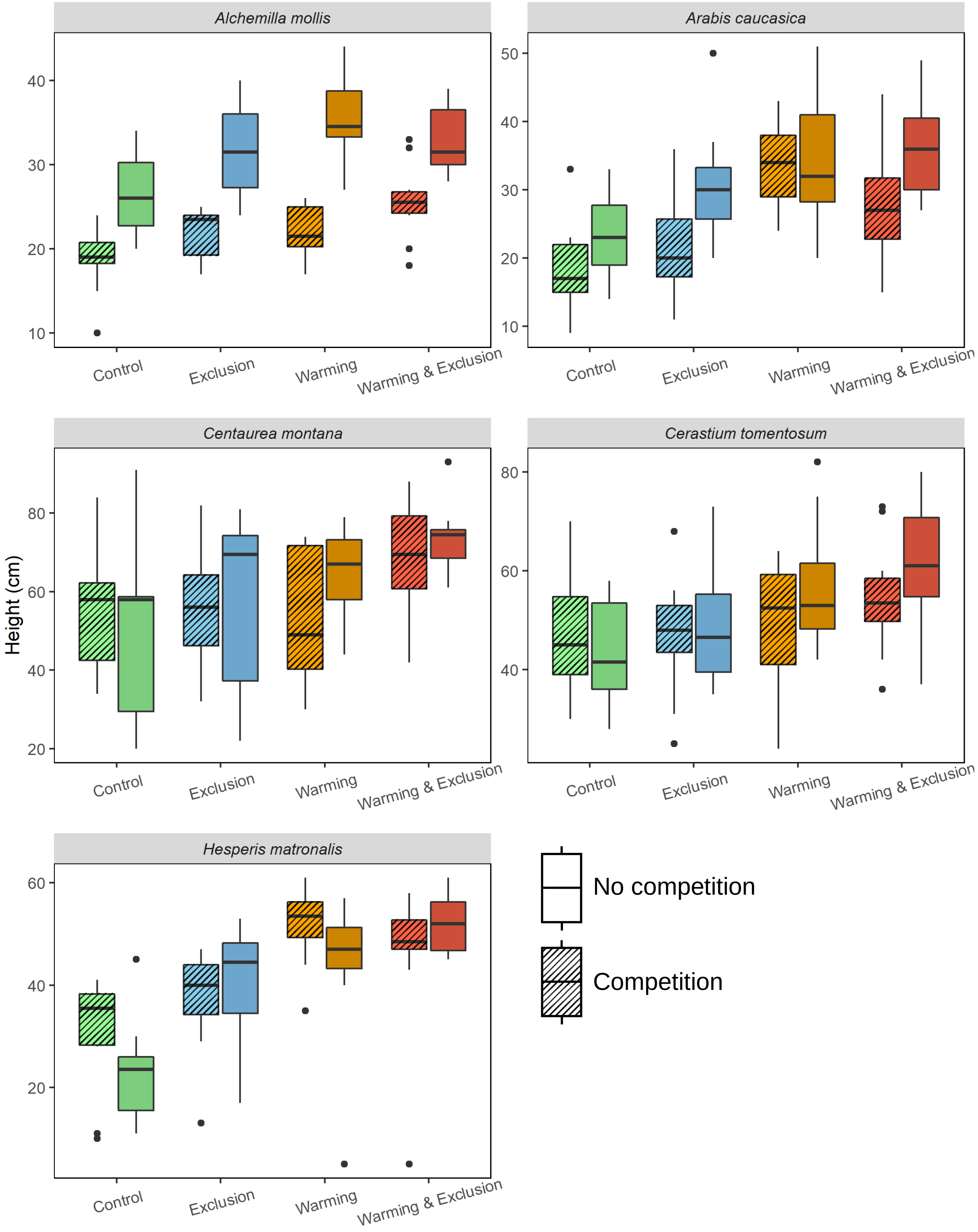


Figure 7: Height of each non-native species across each treatment type and with/without native competition.

6.4.4 Native species performance

There was no evidence of warming or herbivore exclusion affecting the total biomass of native species. The only effect of competition on native species was competition with *C. montana*, which resulted in reduced community biomass. Competition with other species did not affect biomass of native species compared to native species grown without competition (Figure 8; Table S4). When each native species was considered separately, there was no effect of warming, competition or herbivore exclusion for *S. dioica* (Table S5). *C. montana* resulted in lower biomass for *F. rubra* and there was weak evidence of this effect for *T. pratense* (p = 0.01 & 0.09 respectively; Tables S6 & S7). *F. rubra*’s biomass increased as the summed biomass of *S. dioica* and *T. pratense* increased (Table S7). *T. pratense* biomass showed strong evidence of an interaction between exclusion, warming and competition with *C. tomentosum*, where plants with no competition had increased biomass under warming and plants with competition had decreased biomass under warming if there was no herbivore exclusion. If there was herbivore exclusion, the opposite trend was observed where plants with no competition had decreased biomass under warming but plants with competition had increased biomass under warming (Table S6; Figure 9).

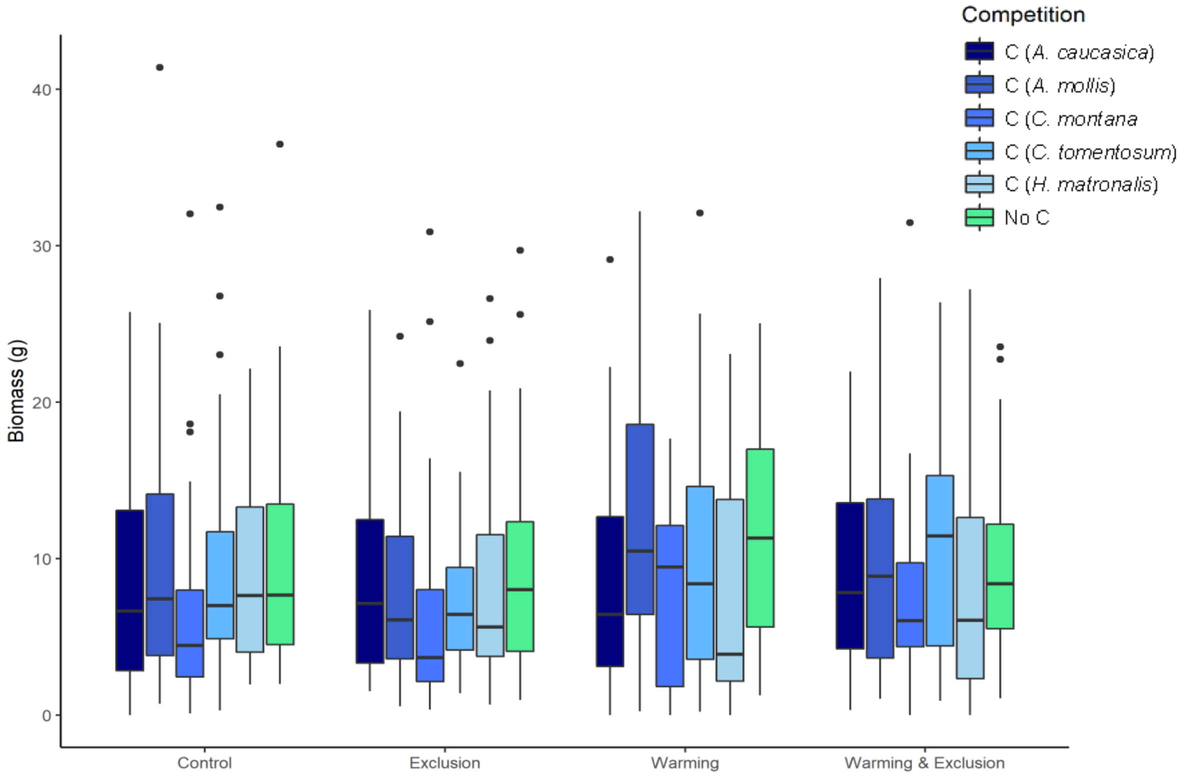


Figure 8: Biomass of native species communities in each treatment type and either in competition with each non-native species or alone. In legend C = competition.

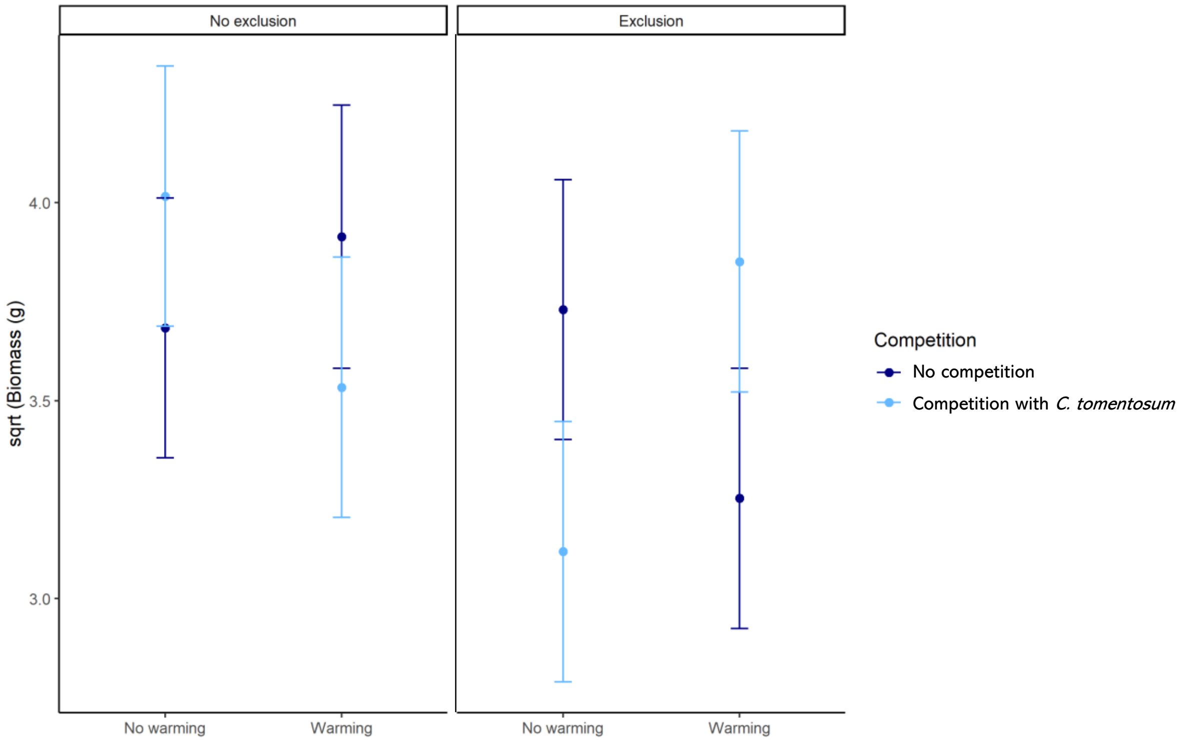


Figure 9: The interactive effects of warming, herbivore exclusion and competition with *C. tomentosum* on biomass (±SE) of *Trifolium pratense* based on a linear regression model.

6.5 Discussion

In this common-garden experiment, I aimed to investigate the effects of warming, invertebrate herbivore exclusion and native plant competition on non-native plant performance. I found strong evidence that warming increases plant performance (biomass and height) for non-native species, that herbivore exclusion results in increased non-native plant height and that competition with native species reduces non-native plant biomass. The native species community, however, showed no response to warming or herbivore exclusion and were only affected by competition with *C. montana*.

6.5.1 Effects of climate change

All non-native plants showed an increase in height, whereas only two species (and to a weaker extent a third species) showed strong evidence of increased biomass and no species showed an increase in SLA under warming. This corresponds with predictions by Petersen et al. (2022) that plants will become taller in Norway under climate change. In terms of experimental warming, this trend was also observed by Bjorkman et al. (2018) who found that over multiple locations in the Arctic tundra, plant height responded strongly to warming but SLA was not affected, and Walker et al. (2006) who found that height responded rapidly to warming, again in tundra ecosystems. The ecosystem of my experiment was not tundra but I still observed an effect on height, indicating that the warming effects of plant structure may be extensive across higher latitude ecosystems. Elsewhere, warming increased height and biomass both in the Qinghai-Tibetan Platea (Zhang et al., 2015) and in a common-garden experiment in Belgium (de Frenne et al., 2011). However, these studies placed warming chambers upon areas of natural landscape and therefore observed these trends within native communities, whereas biomass of the native species community as a whole in my experiment did not respond to warming and increased biomass trends were only observed for two non-native species. This suggests that these two non-native plants are more phenotypically plastic than the native species, fitting with the idea that plasticity promotes establishment of non-native plants in a wide range of climates (Richards et al., 2006). A study by He et al. (2012b) supports this idea, because they found that experimental warming of congeneric non-native and native plants grown together had a greater positive effect on non-native biomass than native biomass. The positive response of both height and biomass to warming highlight the species *A. mollis* and *H. matronalis*, and to a weaker extent *A. caucasica* which showed weak evidence of increased biomass under warming, as those which are likely to benefit from warming in the future. This has implications for Norwegian ecosystems as all three species are documented to displace native plants (Norwegian Biodiversity Information Centre, 2020), an impact which is likely to be exacerbated as climate warming enables them to grow larger in a short timeframe.

6.5.2 Effects of herbivory

Herbivory of non-native plants was reduced in herbivore exclusion plots which probably resulted in increased performance of three non-native species (increased height). If enemy release was occurring I would expect to see similar levels of herbivory and a similar level of plant performance in plots with and without herbivore exclusion. My results therefore suggest that these non-native plants are not currently benefitting from enemy release. However, I have shown that if these non-native plants were to escape their natural enemies this may lead to their greater success. This shows partial support for the enemy release hypothesis which states that reduced herbivory may help to explain non-native plant success. It is difficult to make assumptions about the corresponding response of native plants to enemy release to determine whether this response is specific to non-native species, as the only measurement for native species in this experiment was biomass which showed no difference between plots with and without exclusion for either non-native or native species. This contrasts with experiments by Geppert et al. (2021) who carried out a large experiment in Italy using herbivore exclusion cages, and by Dawson et al. (2014) who excluded herbivores experimentally by applying insecticides, which both found that excluding herbivores increased the biomass of both native and non-native species. However, the general observation that herbivore exclusion increases plant performance is consistent in this study and those by Geppert et al. (2021) and Dawson et al. (2014), despite being represented by different metrics. A further interesting observation was made for *T. pratense*, where presence of herbivores resulted in contrasting interactions between the response of *T. pratense* to warming and competition with one non-native species; plants in competition with *C. tomentosum* had increased biomass under warming where herbivores were not excluded, but had decreased biomass under warming where herbivores were excluded. This suggests that herbivores might be mediating the competitive balance between native and non-native plants and that herbivory may affect different native species differently, as *T. pratense* was the only native species for which I observed interaction effects within the experiment. However, there was no significant response of *C. tomentosum* to either herbivory or competition with native species which means it is difficult to fully understand the context of the *T. pratense* competitive interactions with this species.

6.5.3 Native and non-native competition

My experimental design allowed me to observe both the impact of a native community on non-native plant performance, and the impact of a non-native plant on a native community and the native species within it. Competition with native species negatively impacted the biomass of three non-native species. This result is supported by a meta-analysis by Schuster et al. (2018) which suggests that revegetation of grasslands by native species can suppress non-native plants, and by Haeuser et al. (2019) who found that biomass of non-naturalised non-native species was lower when grown in competition with either native or naturalised non-native plants.

One particularly interesting observation was the interaction between competition and warming on plant performance of *A. mollis*, where presence of native competition reduced the positive effects of warming on biomass and height. This, in addition to the trend discussed above where non-native plant performance was sometimes lower when herbivores were not excluded, suggests that some species may well be limited by native biota comprising both plants and insect herbivores in their invaded Norwegian ecosystems, and that the benefits of climate warming to non-native plants may be limited by presence of native plants.

C. montana and *H. matronalis* were the only non-native species to be unaffected by competition with native species, showing no difference in biomass, SLA or height between pots with and without competition. In addition, *C. montana* was the only non-native species which negatively impacted native plant performance. This strong competitive ability suggests that populations of *C. montana* could suppress native plant diversity in its invaded range. However, with the exception of *C. montana*, there was no overall competitive effect of non-native species on native community biomass. This contrasts with much of the literature which has frequently found evidence that non-native plants outcompete and suppress native species (Lee et al., 2021; Mack et al., 2000; Stinson et al., 2006). For example, a meta-analysis by Vilà & Weiner (2004) found both that non-native plants have a greater impact on native plants than vice versa, and that native species are more productive when grown alone than with non-native competitors. In my experiment, I designed the competition pots specifically to investigate the effects of native plant competition on non-native plants, with less emphasis on the effect of non-native plants on natives; it is therefore likely that the design, where three native plants were potted alongside one non-native plant, favoured native species and this was the reason for the lack of suppression by the non-native plants. In addition, there was no interaction between warming and the competitive effect of non-native species on native species, despite warming increasing non-native plant performance but not native plant performance. This was also found by Verlinden et al. (2013), where warming had no effect on the competitive balance of native and non-native plant pairs but did result in increased biomass for some study species. However, most of the literature has found some effect of warming on non-native competitive ability, for example warming increased the competitive ability of a non-native plant *Centaurea maculosa* but not its growth (He et al., 2012a).

The differences in competitive ability of the non-native species in this experiment might be due to the growth conditions. For example, *A. caucasica* and *C. tomentosum* frequently grow in shallow, calcareous soils (Norwegian Biodiversity Information Centre, 2020) and therefore may not have been well adapted to the conditions within this experiment where they were grown in deep, nutrient-rich soils. In contrast, *C. montana* mostly grows in deep meadow soils (Norwegian Biodiversity Information Centre, 2020) and would therefore have found growth conditions much more suitable during this experiment, which may explain why *C. montana* had such a large competitive effect compared with plants suited to shallow soils.

6.5.4 Experimental design

One of the key benefits of common-garden experiments such as this is that in-depth studies can be made of the few species of interest, and that general patterns within species can be picked up on. The relatively low number of species also meant that I could create a more complex experimental design, with three interacting factors, which would be more difficult with a greater number of species due to time and space constraints. In addition, in common-garden experiments it is possible to control for the environment as all plants are grown within the same plot and under the same conditions, which means that results can be attributed more to differences across treatments rather than differences within the environment.

The OTCs used in this experiment increased the average summer temperature by 0.6-0.9°C (Table 2) which, although less than the documented temperature increase by OTCs of 1-3° C (Molau & Mølgaard, 1996), resulted in increased performance by the five non-native plant species. However, the effects of OTCs on plant growth has been found to vary depending on context: Welshofer (2017) found that non-native plants only benefitted from growing within OTCs at the further north of two study sites, where their abundance increased and native plant abundance decreased, whereas this trend was not observed at the southern field site; Cowles et al. (2018) found that the effect of OTCs on plant communities differed across landscape types and precipitation levels, causing a decrease in plant diversity which was much greater at warmer and drier locations. Although the results of my experiment show similar trends to other studies which employed OTCs (Bjorkman et al., 2018; de Frenne et al., 2011; Walker et al., 2006; Zhang et al., 2015), it is important to acknowledge that the location and climate of this experiment may influence the warming effects. However, OTCs remain a simple and effective method for artificially warming experimental plots and continue to be widely used to simulate climate change.

In this common-garden experiment, herbivore exclusion was carried out by placing fine mesh covers around the exclusion treatments which were buried at the base and tied at the top (Figure 1). This was done as an alternative to using insecticide spray. Despite levels of herbivory being lower in exclusion plots, however, herbivore damage was still observed in reasonably high amounts at the end of the experimental timeframe despite the exclusion mesh covers, and slugs were frequently observed in pots. It is therefore possible that the mesh covers were not buried sufficiently to exclude slugs, which may have burrowed beneath the soil surface. It is also possible that the topsoil was contaminated with slug eggs. In addition to this, a potential disadvantage of this method was that, once herbivores had accessed the plants within the treatment, the mesh covers prevented the natural enemies of these herbivores (such as birds) from predating on them and reduced the ability of herbivores inside to escape again.

6.5.5 Conclusions

In this chapter I aimed to investigate how warming, herbivore exclusion and competition with native plants affects non-native plant performance in Norway. This is the first experiment to investigate these three factors together on non-native plants in Norway, and has helped to shed light on how these factors may interact to influence non-native plant success in the future. I have identified species that will benefit overall from warming but for some, biotic interactions can either exaggerate or limit this response. Interaction experiments are therefore vital to determine how multiple factors contribute non-native plant success, to increase our understanding of how non-native species may be managed in future.

Chapter 7
General Discussion

7.1 Synthesis

In this thesis I aimed to answer questions relating to how climate change might impact non-native plants in Norway, the extent of biotic interactions experienced by non-native plants within Norway, and how both biotic interactions and climate change might interact to influence non-native plant success. Research investigating these questions, although prevalent for some parts of the world (e.g. North America (Carroll et al., 1997; Cronin et al., 2015; Parker & Hay, 2005) and Asia (Fan et al., 2016; Lu et al., 2013)), is lacking in Norway. However, due to Norway's high number of non-native plant species and the faster rate of warming predicted for high-latitude countries (IPCC, 2014), investigating the interactions and responses of non-native species is vital in understanding the future of Norway's ecosystems. To carry out this research, I first identified a set of potential high-risk species to Norway then investigated which areas of Norway are most at risk from these species and how this might be affected by climate change. I then investigated how herbivory levels differ between non-native and native species and how this changes across a latitudinal gradient, using herbarium specimens within Norway and botanical garden surveys across Europe. Finally, I investigated how biotic interactions and climate change impact non-native plant success through a common-garden experiment containing artificial warming, competition and herbivore exclusion treatments. Here I will summarise my findings in terms of (i) the impact of climate change on non-native plants in Norway, (ii) the interactions of non-native plants with other biota in Norway, and (iii) the interplay between biotic interactions and climate change.

7.1.1 The impact of climate change on non-native plants in Norway

In this thesis I investigated the effect of climate change on non-native species using both modelling and experimental methods. I showed that Norway is already climatically suitable to a large number of species and that its suitability increases under climate change (Chapter 2), and found for a subset of species that larger areas of Norway become suitable under climate change, including regions at higher latitudes and around urban settlements (Chapter 3). In terms of plant performance, I found that non-native species responded positively to artificial warming by growing taller, having increased biomass or both. These results demonstrate first how climate change will benefit potentially invasive species by increasing the size of their climatically-suitable ranges, and second how climate change is likely to increase the performance of individual plants in Norway. This supports much of the literature which predicts northward range expansion of plants (Hellmann et al., 2008; Merow et al., 2017; Rew et al., 2020) and an increase in plant size (Bjorkman et al., 2018; Petersen et al., 2022; Walker et al., 2006; Zhang et al., 2015) under climate change.

7.1.2 The interactions of non-native plants with other biota in Norway

7.1.2.1 Enemy release

To explore the enemy release hypothesis, which states that the success of plants is in part due to release from natural enemies (Mitchell et al., 2006), I quantified and compared the levels of herbivory damage on native and non-native plants by employing two different methods: first, using herbarium records from Norway (Chapter 4) and second, using combined survey data from 15 botanical gardens across Europe (Chapter 5). In my first study (Chapter 4), I found that although herbivory levels of non-native species were lower in some genera of study, there was no trend when considering all study species together. This suggested that non-native species as a whole are undergoing similar levels of herbivore interaction to native species and that non-native species are not benefitting from enemy release. In addition, herbivory levels remained constant throughout the time period studied which suggests that herbivores recognised these non-native species as a food source soon after their introduction. In my second study (Chapter 5), I found contrasting results to Chapter 4 whereby in some individual gardens (including Trondheim, Norway) there were significantly lower herbivory levels on non-native species. A meta-analysis of all gardens showed an overall trend of lower herbivory levels on non-native species, therefore finding evidence of a wide-scale enemy release across Europe. Furthermore, when comparing overall herbivory of native species with that of non-native non-naturalised species and non-native naturalised species, enemy release was only observed in non-naturalised species. Trondheim was again one of the individual gardens where this trend was strongest. Interestingly, the non-native species in Chapter 4 were chosen from an initial pool of naturalised (not non-naturalised) species and it is therefore possible to observe further correlation between naturalised status and a lack of enemy release. However, I am hesitant to firmly link naturalisation status and herbivory in Chapter 4 based solely on the findings of Chapter 5, as the methods employed in both studies were so different.

7.1.2.2 Impact of biotic interactions on non-native plants

Chapters 4 & 5 investigated whether non-native plants in Norway are undergoing biotic interactions, but did not determine how these interactions affect the performance of non-native plants. In my common-garden experiment (Chapter 6), I found that the presence of other biota, either herbivores or native plants, negatively impacted three species by reducing either height or biomass. Although Chapter 5 demonstrates that non-native species suffer lower levels of herbivory and therefore undergo enemy release, this is only one facet of the enemy release hypothesis and does not address the hypothesis that this reduced herbivory contributes to non-native plant success. In Chapter 6, however, I found evidence that herbivore exclusion does in fact lead to increased plant performance, even if the non-native species in this experiment are not currently benefitting from enemy release.

7.1.3 The interactions between biotic interactions and climate change

Latitudinal gradients have frequently been used to study climate change (Cronin et al., 2015; Lu et al., 2013), as current lower latitude ecosystems climatically represent future higher latitude ecosystems under global warming (Frenne et al., 2013). Observations made at lower latitudes can therefore act as predictors for the consequences of climate change at higher latitudes. In terms of biotic interactions, the latitudinal biotic interactions hypothesis posits that there are more frequent and stronger biotic interactions at lower latitudes due to more tolerable climates and higher species diversity (Schemske et al., 2009). If the latitudinal biotic interactions hypothesis is accurate, I would therefore expect to observe lower levels of herbivory at higher latitudes, and could then infer that under climate change herbivory levels at higher latitudes may increase due to rising temperatures and range-shifts of lower-latitude species further north. In this thesis, I used data from across a latitudinal gradient in Chapters 4 & 5 to investigate how biotic interactions may be influenced by climate and therefore to predict how they might respond to climate change. In Chapter 4, there was evidence of a decrease in herbivory levels at higher latitudes for both native and non-native species. This supports the latitudinal biotic interactions hypothesis and suggests that as higher latitudes warm, herbivory is likely to increase for these species based on the assumption that native herbivores will shift their ranges north (e.g. Vanhanen et al., 2007). In contrast to these results, I found no change in herbivory levels across a latitudinal gradient in Chapter 5. The latitudinal gradient in Chapter 5 is much larger than the gradient in Chapter 4, spanning from Switzerland to Norway, and I would therefore have expected a correspondingly more significant latitudinal gradient of both absolute levels of herbivory and enemy release. However, many other studies have found no latitudinal trend across large gradients (e.g. Andrew et al., 2005; Xu et al., 2021). This result suggests that for these species, herbivory intensity may not be affected by latitude-specific factors such as temperature, and therefore that climate change may not affect herbivory levels in the future. The benefit of carrying out a Europe-wide survey is that we can determine how herbivory of non-native plants in Norway sits within the wider context of non-native plant interactions. Here, I have shown that Norwegian non-native species have comparable levels of herbivory damage to non-native species across a broader scale in Europe and therefore that, even if a non-native species is tolerant to Norway’s climate, there is no advantage to establishing in Norway in terms of escape from herbivory over establishing at lower latitude countries with more tolerable climates.

The results in Chapters 4 & 5 oppose each other; in one study I found a latitudinal gradient in herbivory and in the other I found no effect of latitude on herbivory. This could be due to the different methods employed in each study. For example, in Chapter 4 I used the same species across the latitudinal gradient where in Chapter 5 different species were sampled in each garden. This might mean that herbivory levels across the latitudinal gradient in Chapter 5 were less comparable, as different species will suffer different levels of herbivory even at the same location. Furthermore, the method of quantifying herbivory damage was different in each study. In Chapter 4, herbivory was measured as a proportion of grid cells which contained damage, and for most species each leaf was large enough to cover multiple grid cells. In Chapter 5, however, herbivory was measured as proportion of leaves damaged so herbivory levels were at a much coarser scale. This finer scale in Chapter 4 might have resulted in greater power to detect latitudinal changes in herbivory. In addition, the botanical gardens used for surveying in Chapter 5 were all located in urban areas where the climate is often milder due to the urban heat island effect (Yang et al., 2016). These more tolerable climates are not necessarily representative of typical climates found at similar latitudes in non-urban areas, which may mean that the climatic gradient across latitudes, which is a key assumption the latitudinal biotic interactions hypothesis, is not as strong when considering urban areas alone. Conversely, herbarium specimens were sampled from both urban and rural areas within Norway. Although many herbarium specimens were located close to urban settlements, the presence of specimens taken from more climatically harsh rural locations may have influenced the overall herbivory levels so that a latitudinal gradient could be observed. However, this theory relies on the assumption that herbivore abundance is correlated only with climate, whereas multiple studies have found that urban areas have reduced invertebrate abundance (e.g. Denys & Schmidt, 1998; Steibl et al., 2021) which means it is difficult to make assumptions about herbivory levels between urban and rural herbarium specimens. However, in terms of Chapter 5 it has been suggested that botanical gardens may act as refuges to various invertebrate species (Pinilla-Rosa et al., 2022) which might mean that the negative impact of urbanisation on herbivore abundance is mitigated in gardens and therefore that invertebrates may be able to exhibit responses to climate.

7.2 Management of invasive species

As discussed in previous chapters, Norway is already home to over 2,000 non-native species, the majority of which are plants (Sandvik et al., 2019). This number is much greater than expected, as it is generally observed that the number of non-native species decreases as latitude increases. It has been suggested that the high number of non-native species in Norway could be due to its long history of agriculture, which is often associated with species introductions, or that the Gulf Stream around Norway means its climate is milder and more tolerable to plants than other regions at similar latitudes (Sandvik et al., 2019). This second hypothesis is supported by the large number of species (almost 7,000) identified in Chapter 2 which had some climatic niche overlap with Norway's current climate. Although the majority of these species did not fulfil the other criteria in the horizon scanning study, they demonstrate that parts of Norway are suitable for a wide range of species with sometimes unexpected native ranges; for example, the species ranked as highest risk to Norway in Chapter 2 was *Acacia decurrens*, native to Australia. In terms of invasive species management, this perhaps surprising result highlights how important it is to include both native and non-native ranges in climatic suitability calculations. The climatic niche of *A. decurrens* shared very similar levels of precipitation with Norway, but based on its Australian native ranges alone may not have shared temperature variables with Norway's climate. However, its invaded ranges include regions such as New Zealand and the Andes (POWO, 2022) which highlight that this species is capable of living in more temperate and cooler environments and therefore that regions of Norway may well be suitable for it.

My horizon scanning study in Chapter 2 is a novel approach to assessing large numbers of species as it is the first of its kind to consider climate suitability in such detail under both current and future conditions and is applicable to any region. Using this method, I have shown that climatic suitability of Norway increases under climate change, making invasions in the future more likely as climatic tolerance is one of the largest limitations of plant distribution (Woodward, 1987). This work may help to advise Norwegian policy-makers about which species should be monitored for trade and import. Examples of such policies include the European Union's Regulation 1143/2014 (2014), New Zealand's National Plant Protection Accord (NPPA, 2020) and the USA's Plant Protection Act (1999), which all place restrictions on certain plant species which are known to have harmful effects the environment or economy. Currently, Norway's import policy contains the Regulations on Foreign Organisms (Forskrift Om Fremmede Organismer, 2015), most recently amended in 2020, which lists 24 plant species whose import and trade is banned. However, the policies mentioned above only include plants which are currently causing ecological damage within each country and do not include species which may cause damage if introduced. Due to the high number of non-native species currently present in Norway and the importance of preventing further introductions, I strongly recommend that the import of the high-risk species identified in Chapter 2 should be restricted. I also recommend that horizon scanning studies such as this are repeated in the future to ensure that any arising high-risk species are identified quickly, particularly as Norway's climate changes and becomes suitable for a greater number of species.

More generally, by identifying high-risk species I have also identified the regions where they are currently distributed which in itself can advise in a broader way about which regions might be more likely to source invasive species. For example, I found that Norway's neighbouring countries (Sweden and Finland) and Canada do not contain any of the high-risk species identified, meaning that introduction of invasive species from these countries are less likely and therefore that regulations around plant import may not be as necessary. Many other countries however, such as France, Spain, New Zealand and parts of Australia contain high numbers of high-risk species. Stricter regulations should perhaps be prioritised on plant imports from these countries. However, it is important to remember that these potentially risky origin countries are specific to this study, and that other countries might currently host species not identified here.

I have shown that climate change is likely to increase the performance of some plants already invasive in Norway which may exacerbate their ecological and economic impacts. This means that in the future, invasive species management may become more necessary to prevent these plants causing further damage to their invaded ecosystems. Eradication is one such management technique, but this is more commonly applied to invasive mammals than plants and there have been few successful invasive plant eradications (Pyšek & Richardson, 2010). The other widely-applied method for managing invasive species is use of biological controls (biocontrols). Biocontrols, whereby host-specific enemies are introduced from an invasive species' native range, may be a viable method for managing species which are not currently limited by enemies in their invaded range (Thomas & Reid, 2007). Meta-analyses of studies quantifying the effectiveness of biocontrols have shown that they reduce plant density, biomass, seed production and flower production (Clewley et al., 2012; Thomas & Reid, 2007). However, even enemies which have not co-evolved with plants can impact their success; in Chapter 6 I found evidence that for some non-native species, presence of native herbivores resulted in lower plant performance compared to when herbivores were excluded. This suggests that if growth of these species can be affected by a non-specialised herbivore, a more specialised herbivore which has co-evolved with a non-native plant may be much more detrimental.

In terms of making decisions about invasive species management, the surveys carried out in Chapter 5 showed that non-native species, particularly non-naturalised species, are indeed benefitting from enemy release and therefore are likely to be less limited by natural enemies. This means that implementing management techniques such as biocontrols for these species might be valuable to reduce their likelihood of becoming naturalised, as naturalised species are more likely to become invasive than non-naturalised species as they have already formed self-sustaining populations in their non-native range (Richardson et al., 2000). I also found that in general the naturalised species in this study were already suffering similar levels of herbivory to native species. This observation, if seen more widely, may have implications for the use of biocontrols for naturalised plants, because if such plants are already suffering high amounts of herbivory then introducing enemies may not limit them any further. However, if naturalised species are currently suffering herbivory from generalists only, introducing specialist biocontrol herbivores may have a much more limiting effect. By carrying out surveys like those in Chapter 5, we can determine which species are not likely to be controlled by native herbivores in their non-native ranges which can inform policy-makers about where to focus management efforts. However, there are some major concerns of utilising biocontrols such as their functional replacement of native biota within the ecosystem or their introduction into the native foodweb (Pearson & Callaway, 2003). They can also target other hosts apart from the non-native species they were introduced to control or become invasive themselves (Thomas & Reid, 2007). Specifically to biocontrol herbivores, non-native plants may produce secondary compounds or increase their growth in response to high herbivory levels which can increase, not decrease, the performance of non-native plants (Pearson & Callaway, 2003). Alternative methods to reduce the spread of non-native plants may therefore be preferable. Such species are already established in Norway, so creating policy to ban their import as discussed above is not a viable method. However, policy restricting their breeding and trade within Norway would be valuable to ensure that human activity is not directly increasing their populations sizes. In a broader context, if native herbivores are the only limiting factor for these species, efforts could be made to preserve herbivore populations such as through restrictions on potentially harmful pesticides or conservation of particularly important insect habitats.

7.3 Methodologies & Limitations

In this thesis I have used a wide variety of techniques to investigate climate change and biotic interactions. I used online databases as resources to obtain information about species and carried out predictive modelling techniques based on this information (Chapters 2 & 3). I looked at preserved plant specimens obtained through herbaria (Chapter 4) and used garden surveys to observe plants *in situ* (Chapter 5). Finally, I carried out my own common-garden experiment (Chapter 6). Each technique has its own benefits. Using online databases enabled me to look at a huge range of species and allowed me to access information about these species on a global scale, for example their distributions and what is currently known about their uses and impacts around the world. Using herbarium data meant I gained a deeper appreciation of how plants have historically been preserved and enabled me to investigate how biotic interactions have changed over centuries, a method which is only possible when using historical collections. Carrying out surveys in botanical gardens meant I could observe real-life interactions which are happening in the present day, as opposed to relying solely on preserved specimens, and the wide range of locations in the combined dataset meant I could investigate these interactions across a large latitudinal gradient. It is one of very few studies to utilise botanical gardens for non-native plant research (Kirichenko & Kenis, 2016; Razanajatovo et al., 2015). Finally, my common-garden experiment allowed me to investigate several factors at once and observe the direct impacts of each on plant performance. Each method has therefore given me insight into different facets of invasion ecology: predicting species' distributions, observing historical trends and wide-scale patterns of plant biotic interactions, and investigating plant responses to artificial conditions. A consistency across all of my studies, however, is that each concerns multiple species rather than focusing in detail on the biotic interactions or effects of warming on one species. As mentioned in previous chapters, experiments investigating multiple species have been shown yield more accurate estimates in statistical models compared with increasing the number of samples for fewer species (van Kleunen et al., 2013). Investigating multiple species also allowed me to observe how widely patterns could be seen across non-native species, which is important when investigating ecological questions such as the enemy release hypothesis which makes general assumptions about a group of species. However, it has also demonstrated how the answers to these ecological questions can differ depending on the study species and highlights how important it is to avoid making generalisations about these key hypotheses.

However, there have been limitations within my thesis. At the beginning of this PhD, I aimed for the majority of my data collection to be based on fieldwork so that I could investigate non-native plants *in situ* and gain a fuller understanding of their responses to climate change and biotic interactions. However, due to the Covid-19 pandemic which began during my first year a lot of my work has been based on resources accessible online. Although these resources are extremely valuable, databases such as those used in Chapter 2 may not be fully up-to-date and species may therefore be missed, and in terms of the data used in Chapter 4 it has been suggested that herbarium records are biased and do not represent trends observed in the wild (Kozlov et al., 2020). Furthermore, due to travel restrictions I was only able to carry out the common-garden experiment in Norway during one summer in my final year whereas I originally wanted to keep the experiment for at least two summers to determine the survival rate of non-native plants over winter under different treatments. This means that less work about the impact of biotic interactions on non-native species has been carried out, and more focus has been on whether non-native plants in Norway are undergoing biotic interactions via data collection about herbivory.

7.4 Further work

There are so many facets to invasion ecology, and specifically the questions of biotic interactions and climate change, that even when studying invasive plants within a single country there are countless study systems and species to investigate. In addition, the response of each ecological system will vary to such a degree that it is unviable to provide complete answers to ecological hypotheses such as the enemy release hypothesis and latitudinal biotic interactions hypothesis; evidence for this is seen in Chapters 4 & 5, whereby Chapter 4 found support for the latitudinal biotic interactions hypothesis but no evidence of enemy release, and Chapter 5 found no support for the latitudinal biotic interactions hypothesis but did find evidence of enemy release. With this in mind, there is a large amount of work which could be carried out to further address the questions asked at the beginning of this thesis. In terms of biotic interactions, I only investigated the resulting herbivore damage and not the invertebrates which created the damage. This means that we do not know whether herbivory is being carried out by generalists, specialists, or even non-native herbivores, which may influence observed trends; Keane & Crawley (2002) suggest that non-native plants are more likely to escape specialist herbivores, whereas they may not be released from generalists. Invertebrate surveys or trapping would therefore be valuable to identify which herbivore species are consuming non-native plants.

In terms of climate change, although latitudinal studies are important they do not directly show the response of plants and biotic interactions to warming. Due to the Covid-19 pandemic travel restrictions I was only able to carry out the artificial warming experiment for a single season at just one site, whereas response to warming may depend on location; for example, Prevéy et al. (2017) found that plant phenological responses to warmer summers were stronger in regions with colder climates. This is particularly important in high latitude ecosystems, which are warming at a faster rate than the rest of the world (IPCC, 2014). In addition, as discussed in Kozlov et al. (2015), the change in latitudinal biotic interactions has been found to be more pronounced in polar regions. Additional warming and herbivore exclusion experiments within Norway’s Arctic tundra would therefore provide important answers about how plants in polar regions are affected by herbivores and how they might respond to climate change. These experiments could run for a longer timeframe, giving more information about the long-term response of plants to warming and how this might influence their winter survival rates. In particular, investigating reproductive output under different climate conditions would be valuable to determine how populations of non-native plants might grow in the future.

Alternative methods of investigating the effect of climate change on plant growth include temperature-controlled growth chambers. These have the benefit of consistent growing conditions, which are difficult to achieve when carrying out common-garden experiments using OTCs. In addition, herbivores can be placed inside growth chambers to observe their interactions with plants. There was some evidence that native competition or herbivory affected non-native plant response to warming in the common-garden experiment (Chapter 6), so using growth chambers may therefore be a valuable method to investigate how climate change might mediate the biotic resistance of a native ecosystem to invasions.

Finally, in my horizon scanning study I identified a set of potentially high-risk species but this method was relatively rapid. A more in-depth risk analysis could now be carried out on these species to explore specific invasion pathways, such as trade routes into Norway, to investigate fully the potential impacts of these species and how this might affect Norwegian biota in particular, and to discuss likelihood of introduction with Norwegian industries, such as the horticultural and timber trades. This will give a fuller understanding of how risky these species might be and will provide further evidence for policy-makers.

7.5 Conclusions

In this thesis I have used a variety of methods to ask the following questions: 1) How climatically suitable is Norway to non-native plants and how might this change under climate warming? 2) How do non-native plants in Norway interact with native herbivores and will this change under climate change? 3) How do biotic interactions (insect herbivory and native plant competition) and climate change interact to affect non-native plant success in Norway? To answer question 1, I show that Norway is already suitable for a great number of non-native plants and that climate change is likely to increase Norway's suitability to these plants. To answer question 2, I show that some non-native plants in Norway do interact significantly with native herbivores but that some undergo enemy release, and that the potential effects of climate change on these plant-herbivore interactions is context-dependent. Finally, to answer question 3 I show that climate change is likely to benefit non-native plant growth in Norway, but that interacting with native biota may limit non-native plant performance or even reduce their ability to respond positively to climate change. This has contributed to the ever-increasing field of invasion ecology research, and the mixed results, particularly in terms of enemy release, highlight the diversity of non-native plant behaviours and the importance of carrying out system-specific research. The management implications of such research are varied, as I have shown that Norway is likely to become even more susceptible to further invasions in the future but that some species already established in Norway may face limitations in the form of native plant communities or invertebrate herbivores. I hope that invasion ecology within such fascinating high-latitude ecosystems continues to be investigated, and that the results of this thesis may contribute to our understanding of non-native plant behaviours both in Norway and globally.

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Appendices

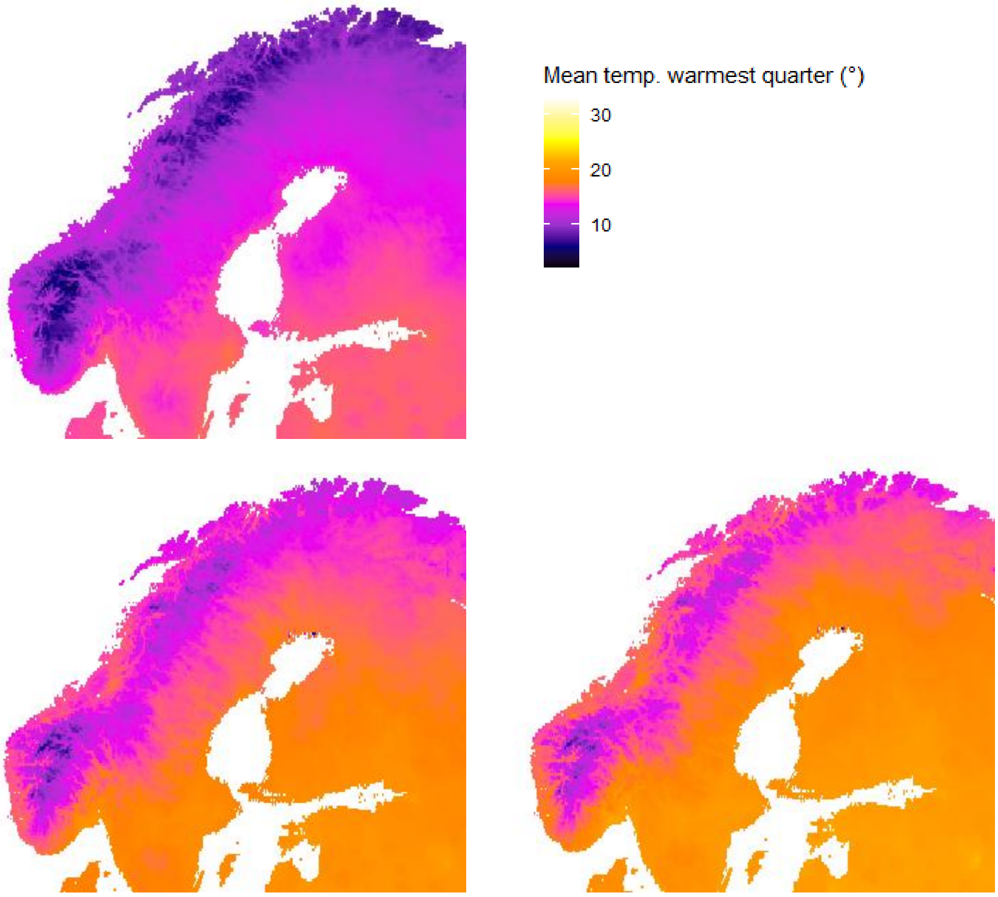

Figure A1: Climate map of western Fennoscandia showing mean temperature of the warmest quarter (TWQ; ° C) for (a) current, (b) prediction for climate change scenario SSP2-45 and (c) prediction for climate change scenario SSP5-85. Future climates were calculated as the mean between eight Global Climate Models (GCMs): BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6 and MRI-ESM2-0. All climate data were downloaded from WorldClim version 1.0 (Fick & Hijmans, 2017.

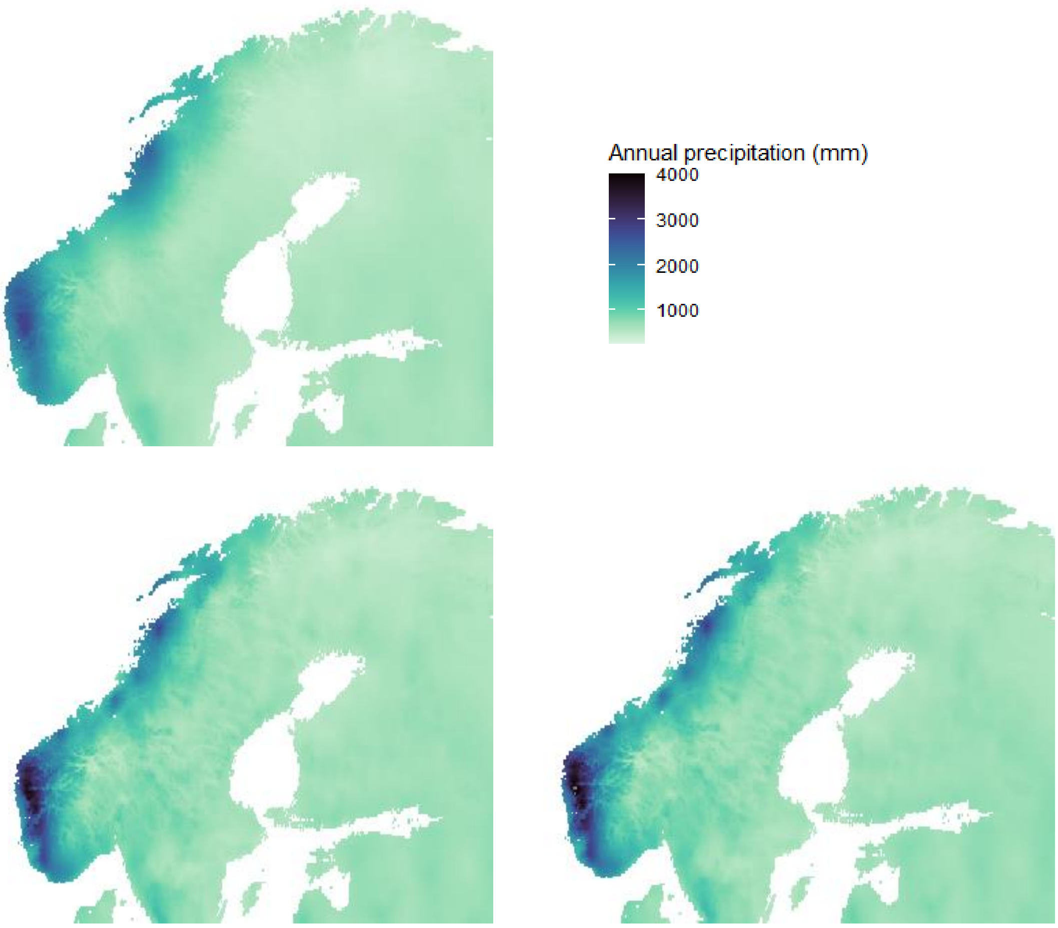

Figure A2: Climate map of western Fennoscandia showing annual precipitation (AP; mm) for (a) current, (b) predicted climate for climate change scenario SSP2-45 and (c) predicted climate for climate change scenario SSP5-85. Future climates were calculated as the mean between eight Global Climate Models (GCMs): BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6 and MRI-ESM2-0. All climate data were downloaded from WorldClim version 1.0 (Fick & Hijmans, 2017).

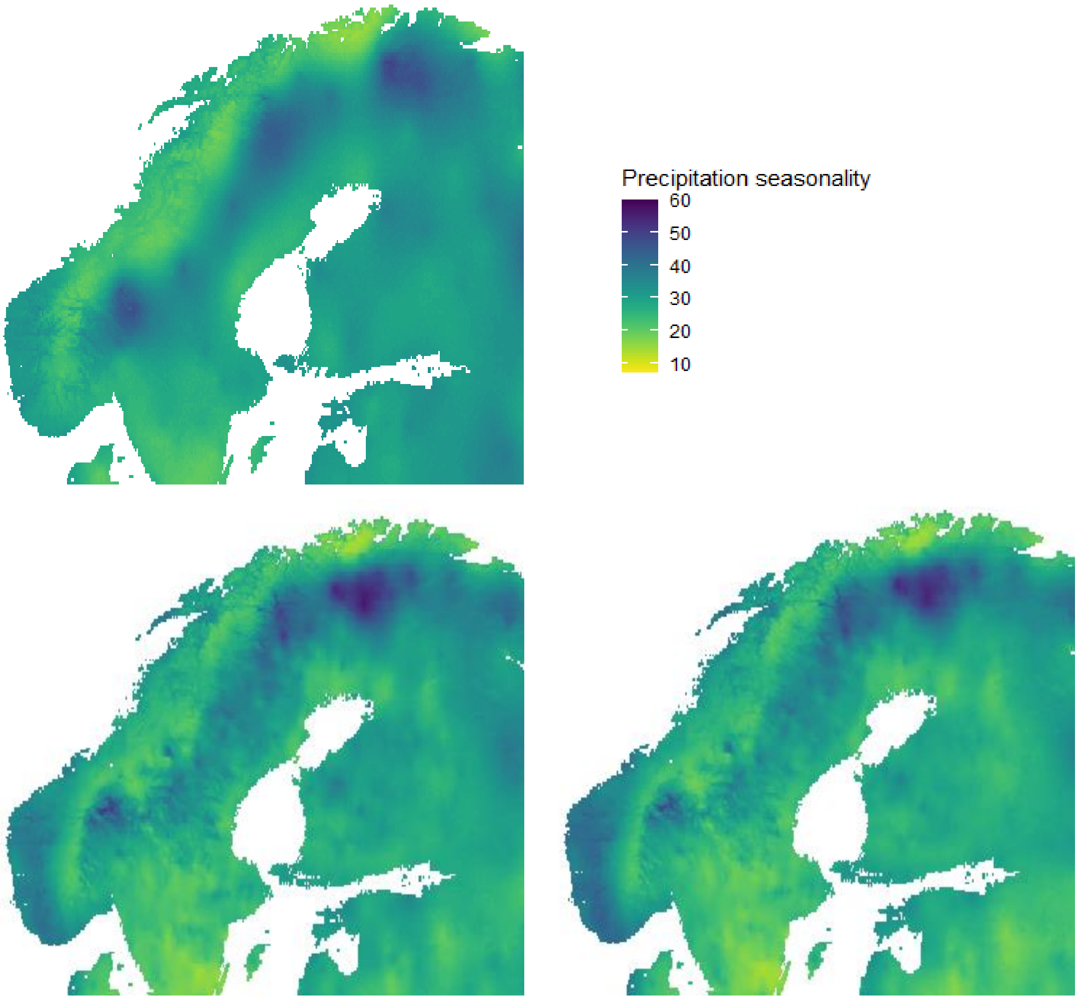

Figure A3: Climate map of western Fennoscandia showing precipitation seasonality (PS; coefficient of variation) for (a) current, (b) predicted climate for climate change scenario SSP2-45 and (c) predicted climate for climate change scenario SSP5-85. Future climates were calculated as the mean between eight Global Climate Models (GCMs) downloaded from WorldClim: BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6 and MRI-ESM2-0. All climate data were downloaded from WorldClim version 1.0 (Fick & Hijmans, 2017).

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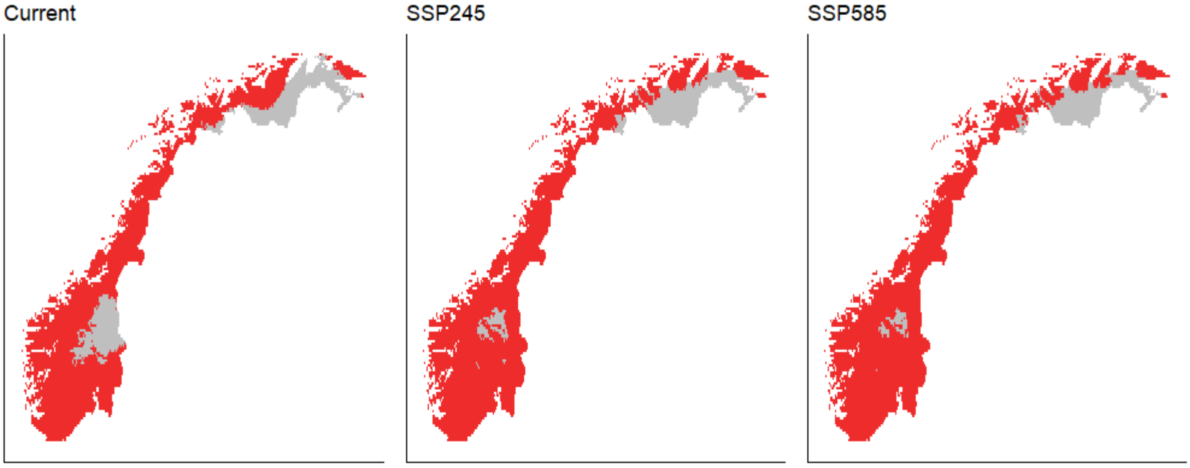

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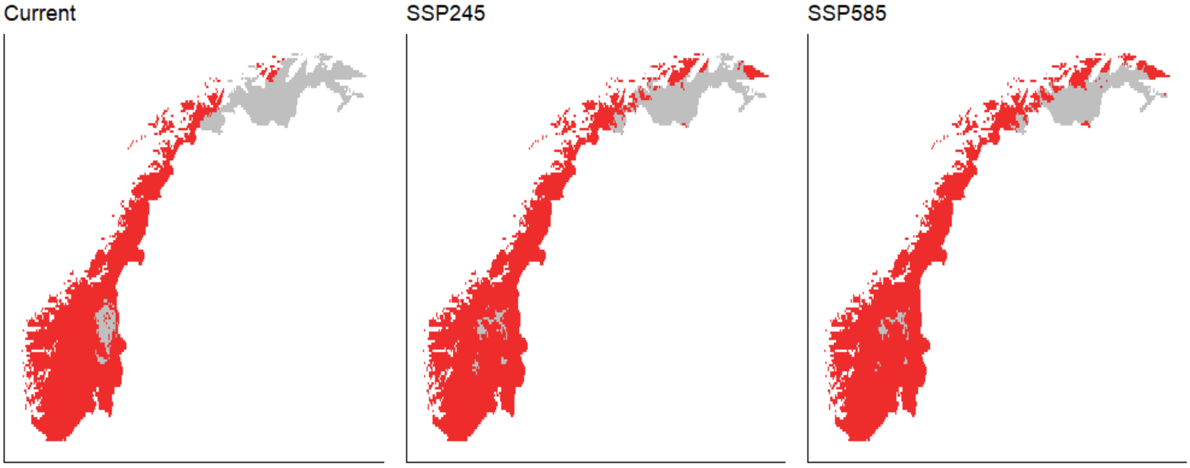

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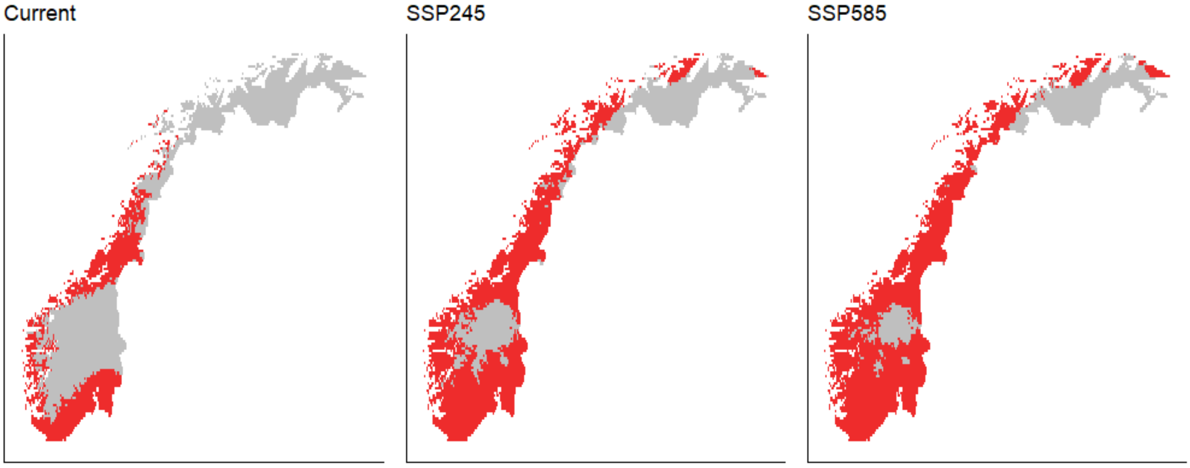

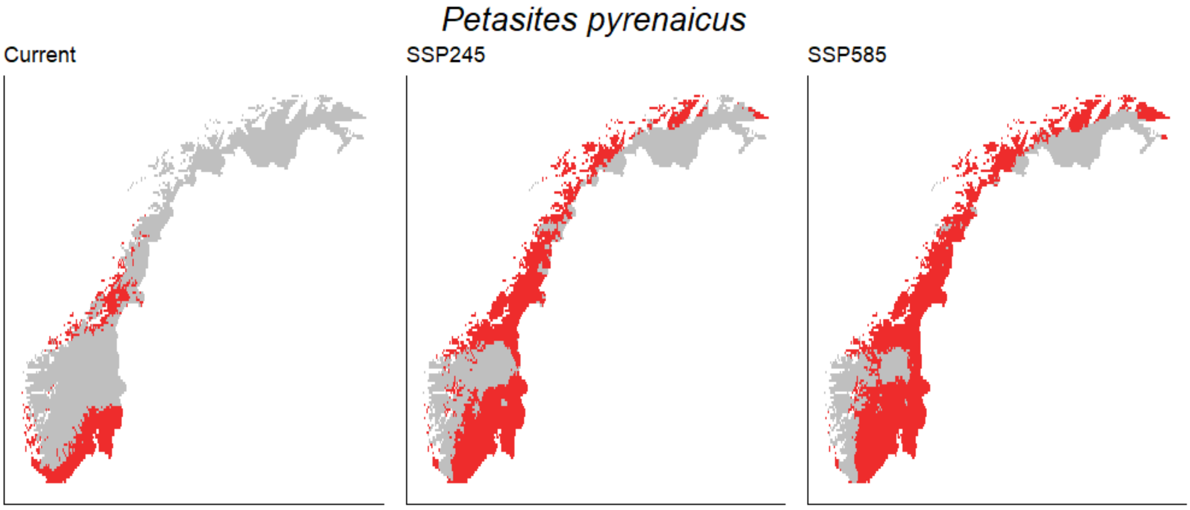
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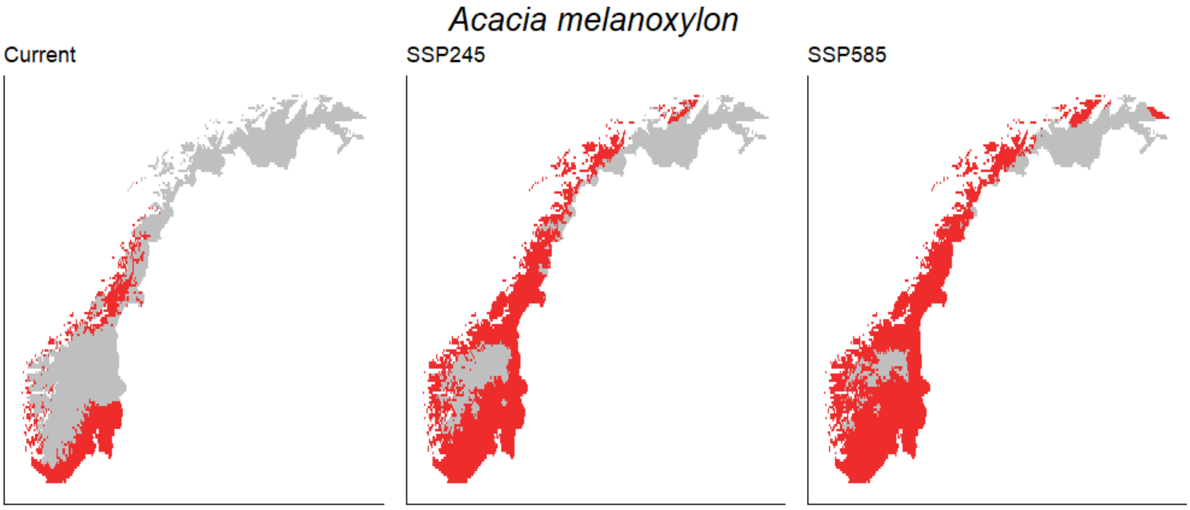
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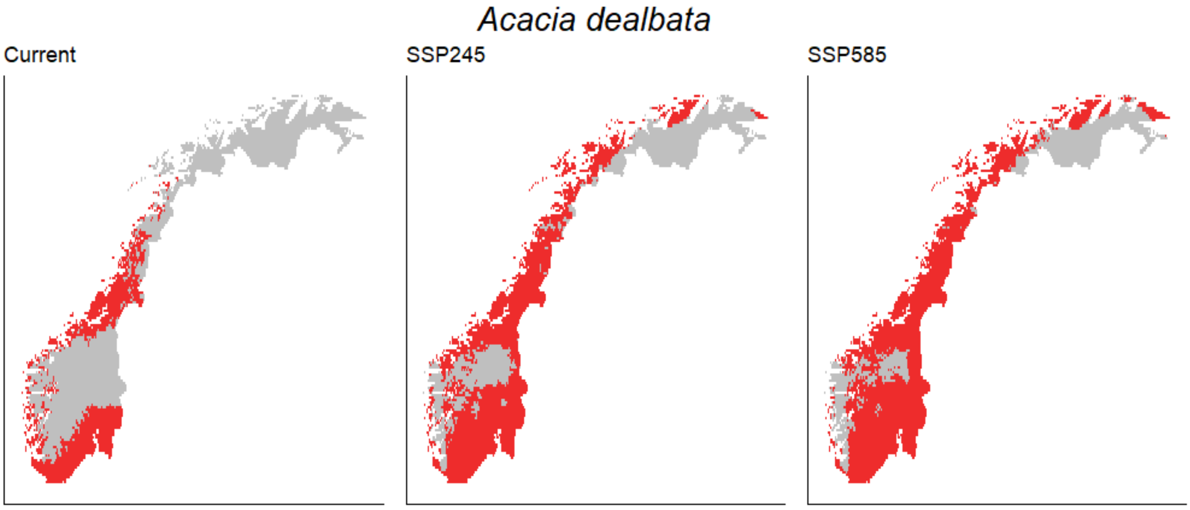
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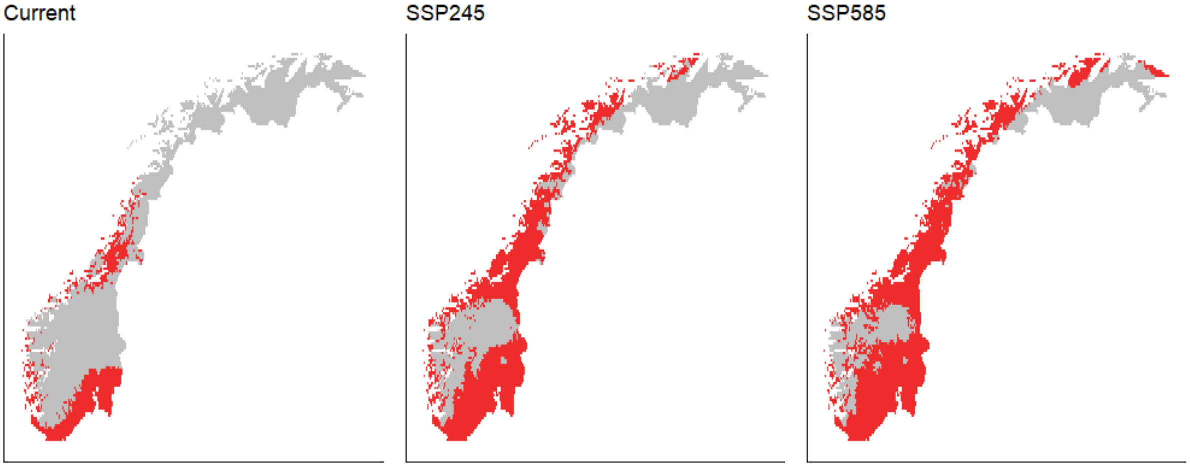

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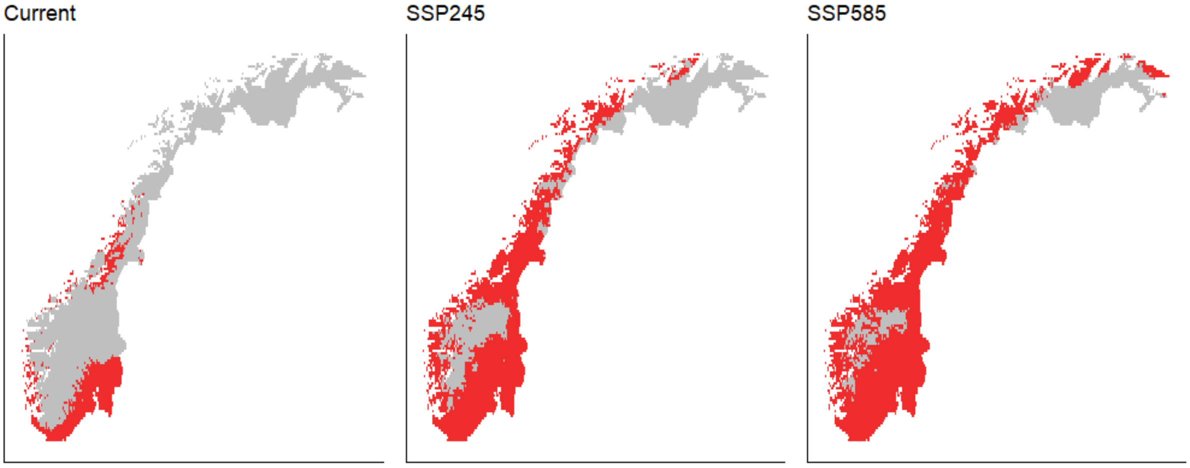
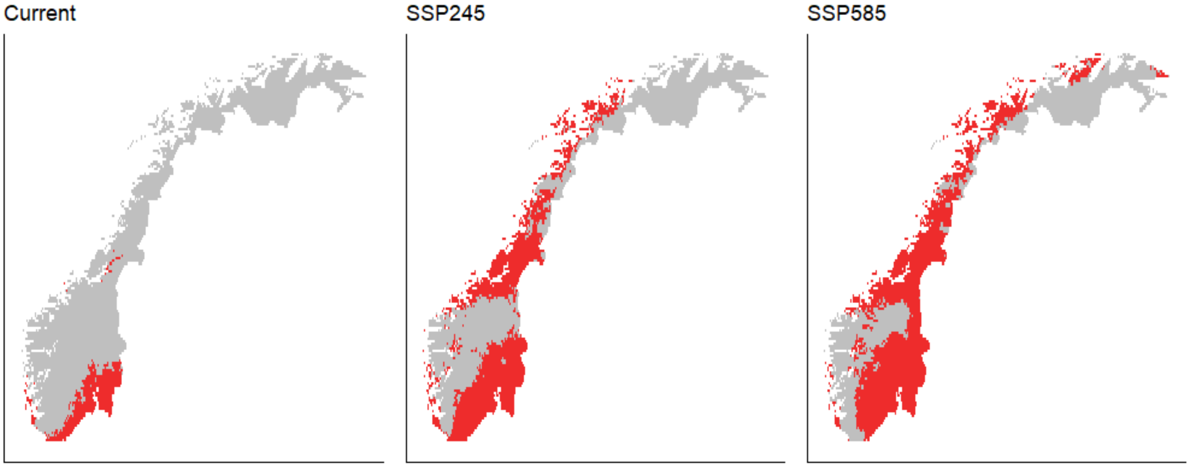


Eucalyptus globulus



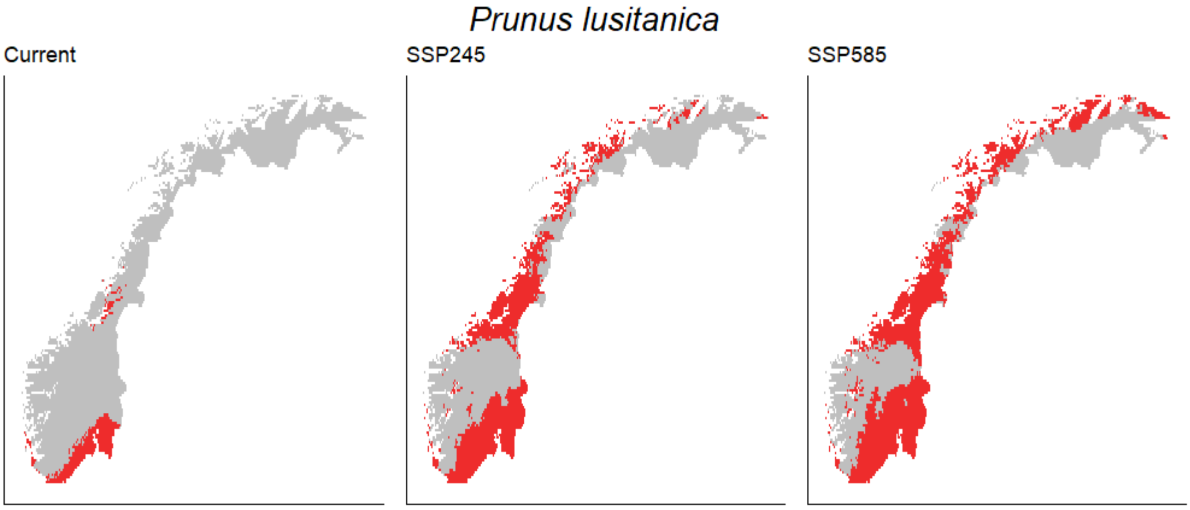


Figure A4: Potential distribution of top 10 high-risk species identified in horizon scanning study, ranked based on climatic niche overlap with Norway. Distribution calculated using species distribution models and predictions converted into binary presence/absence using a prediction threshold which maximised TSS. Red indicates predicted presence; grey indicates predicted absence.

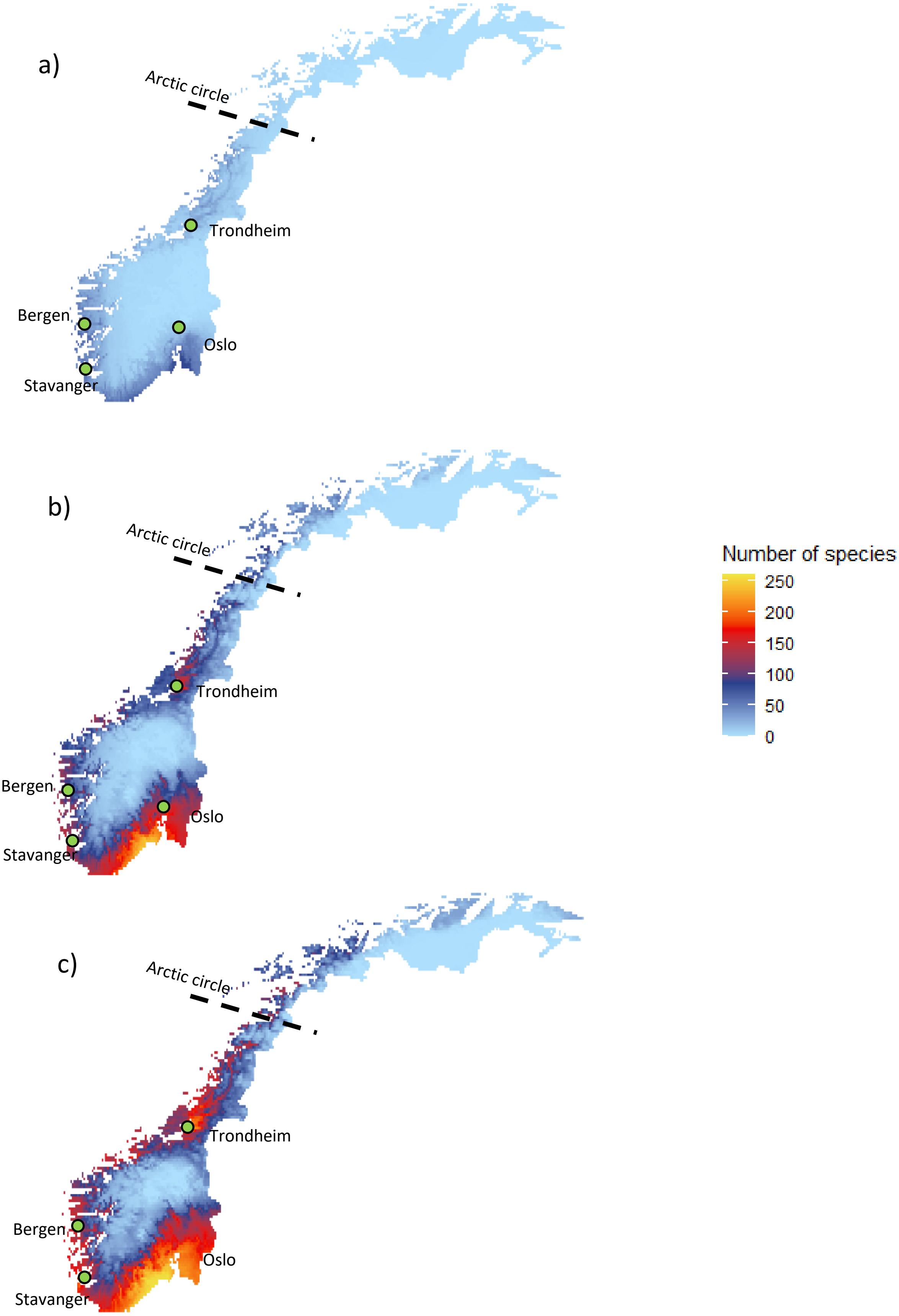


Figure A5: Predicted distribution of high-risk species across Norway and the locations of key sites (cities and Arctic circle) under (a) current, (b) SSP245 and (c) SSP585 scenarios.

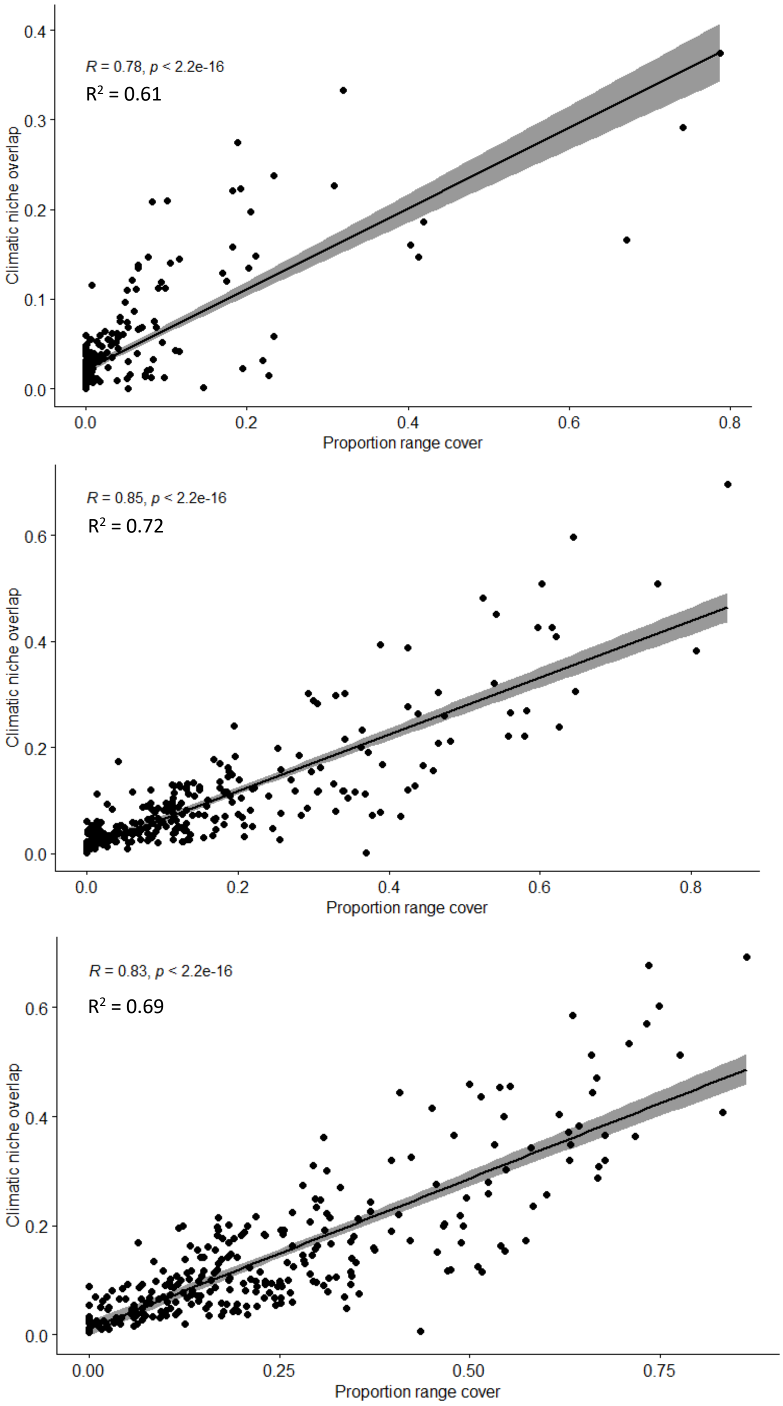


Figure A6: Climatic niche overlaps of 284 high-risk species compared to proportion of Norway with predicted range cover. *R* and *p* values were calculated using Pearson correlation.

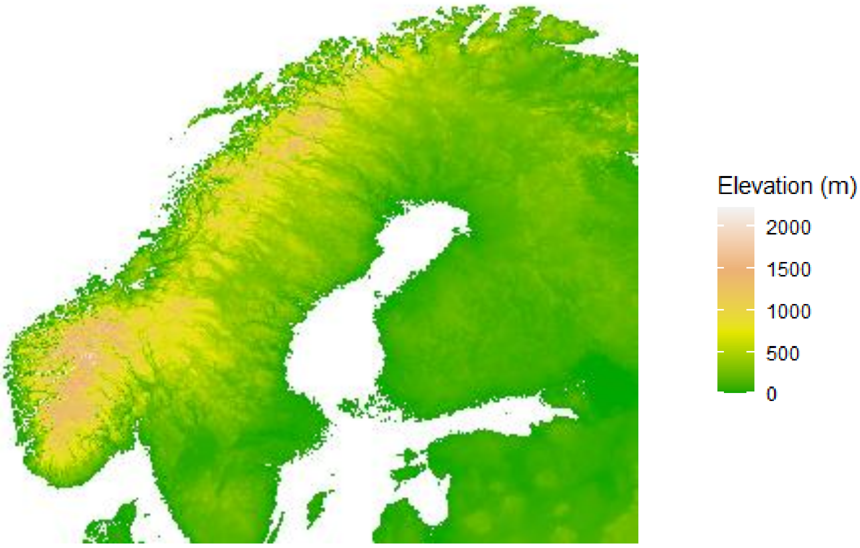


Figure A7: Elevation (m) of western Fennoscandia.

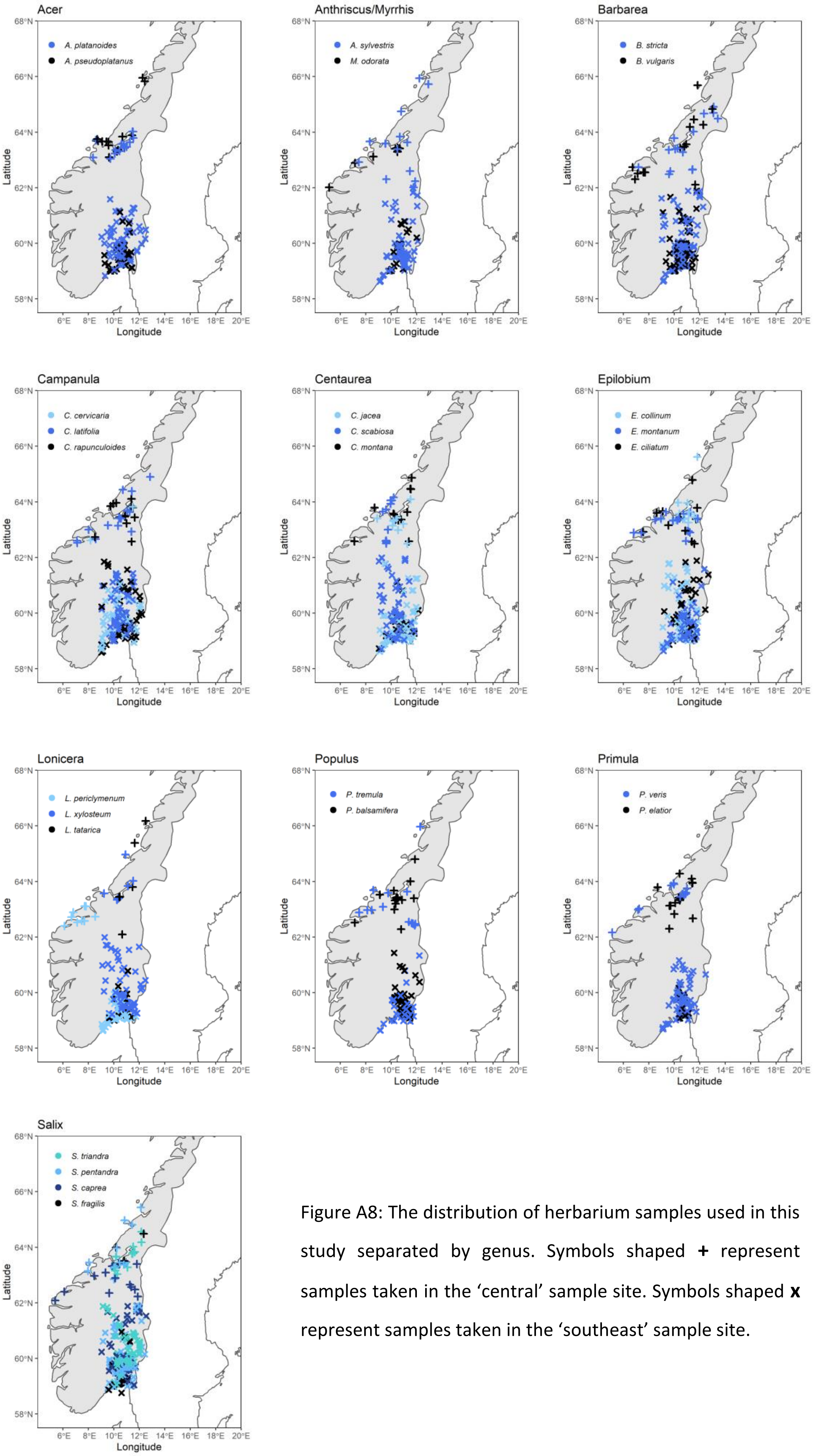
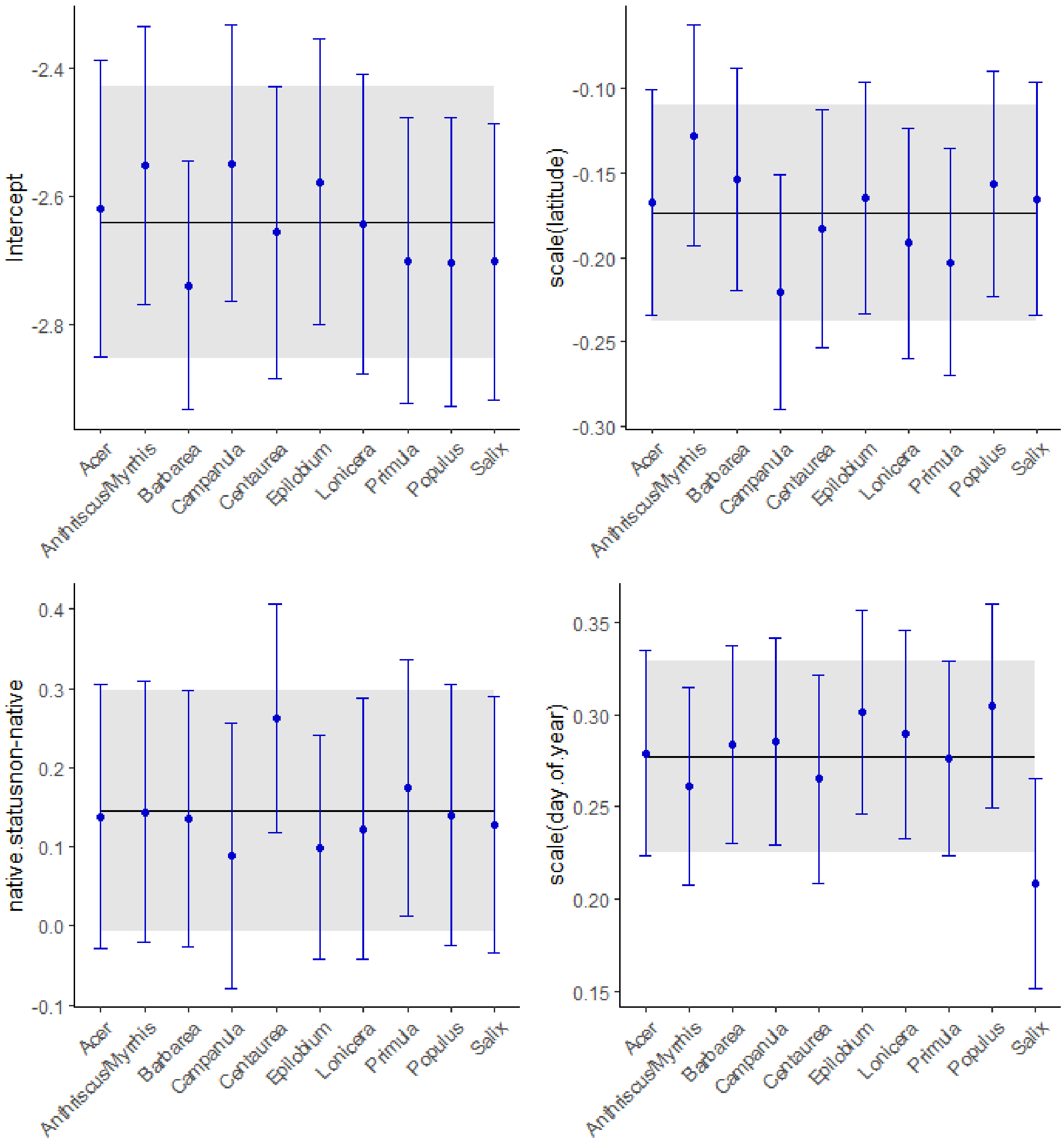


Figure A8: The distribution of herbarium samples used in this study separated by genus. Symbols shaped **+** represent samples taken in the 'central' sample site. Symbols shaped **x** represent samples taken in the 'southeast' sample site.

Table A1**:** Number of specimens sampled for each species, in each dataset (southeast region and central region) and in each time period.

Native		Non-native	
Species	**No. specimens**	**Species**	**No. specimens**
Acer platanoides	90	*Acer pseudoplatanus*	99
Anthriscus sylvestris	94	*Myrrhis odorata*	64
Barbarea stricta	98	*Barbarea vulgaris*	97
Campanula cervicaria *Campanula latifolia*	81 103	*Campanula rapunculoides*	102
Centaurea jacea *Centaurea scabiosa*	98 103	*Centaurea montana*	53
Epilobium collinum *Epilobium montanum*	104 104	*Epilobium ciliatum*	86
Lonicera periclymenum *Lonicera xylosteum*	100 94	*Lonicera tatarica*	43
Populus tremula	64	*Populus balsamifera*	63
Primula veris	99	*Primula elatior*	27
Salix caprea *Salix pentandra* *Salix triandra*	95 106 101	*Salix fragilis*	56
No. specimens in southeast dataset			
1323		552	
No. specimens in central dataset			
211		138	
No. specimens in each time period			
After 2000	444	After 2000	272
1980 – 2000	217	1980 – 2000	112
1960 – 1980	219	1960 – 1980	80
1940 – 1960	217	1940 – 1960	81
1920 – 1940	222	1920 – 1940	86
Before 1920	214	Before 1920	59



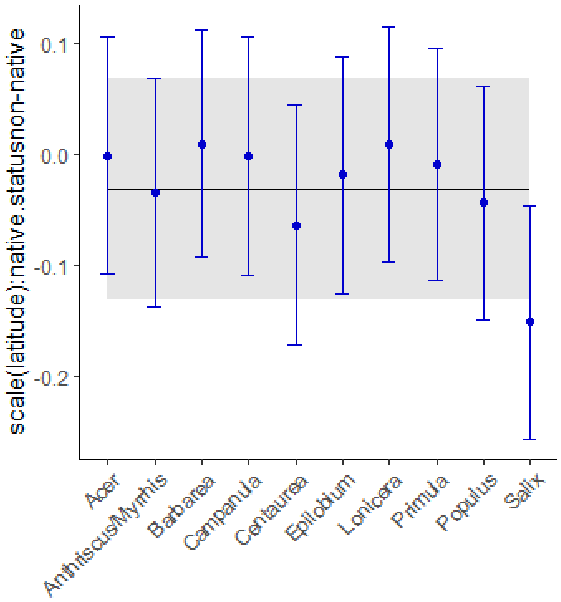


Figure A9: Estimates of negative binomial generalised linear mixed effects models exploring the relationship between proportion of chewing damage and latitude for a range of native and non-native plant species, where each of 10 genera were dropped. Y axis shows which genus was dropped to give the resulting estimate value ± 1 standard error (SE). Black line represents estimate in original GLMM containing all 10 genera and grey ribbon represents the original GLMM estimate's SE.

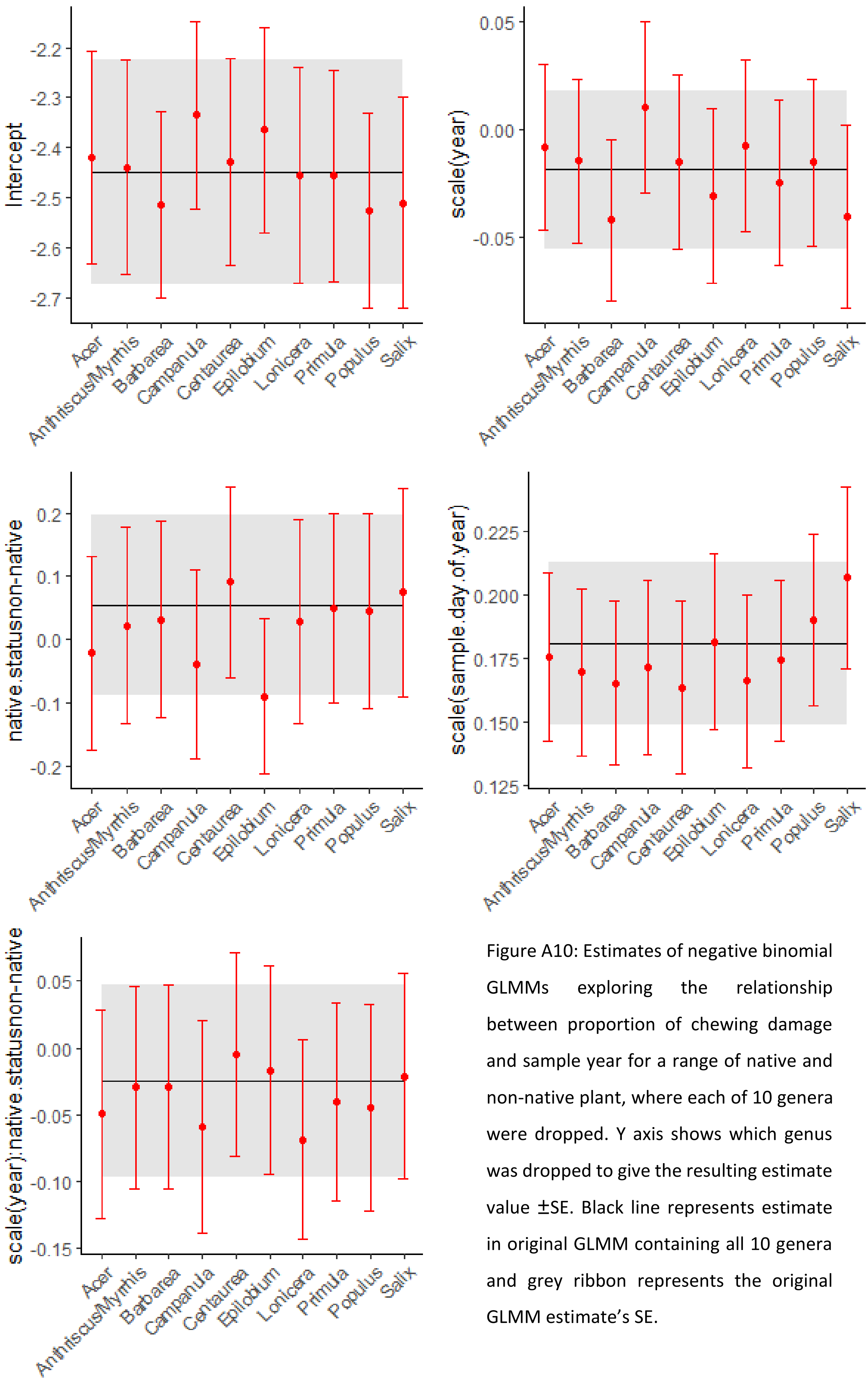


Figure A10: Estimates of negative binomial GLMMs exploring the relationship between proportion of chewing damage and sample year for a range of native and non-native plant, where each of 10 genera were dropped. Y axis shows which genus was dropped to give the resulting estimate value ±SE. Black line represents estimate in original GLMM containing all 10 genera and grey ribbon represents the original GLMM estimate's SE.

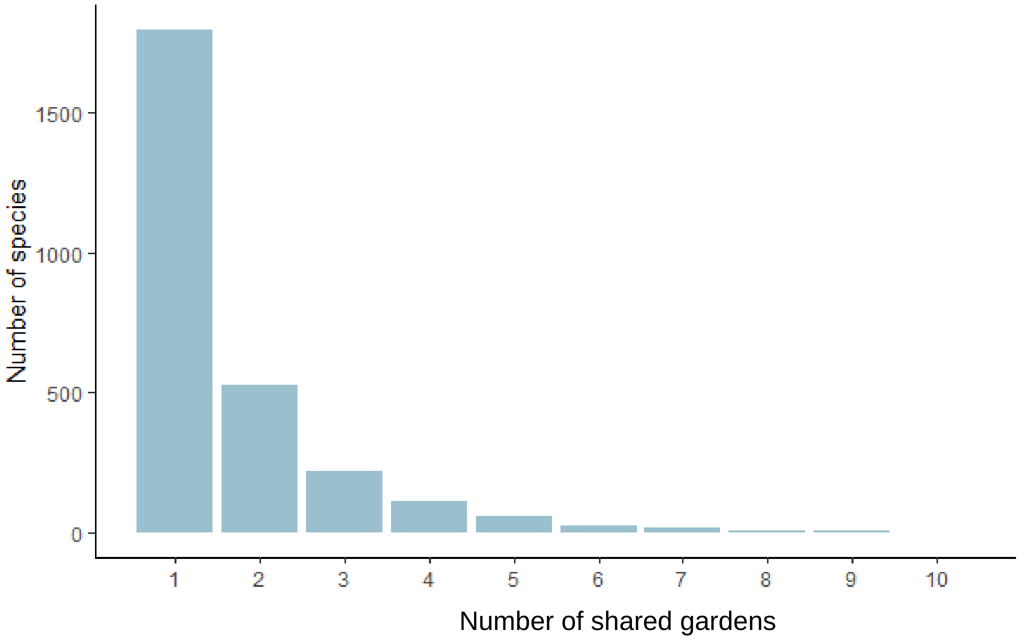


Figure A11: The distribution of species throughout 15 botanic gardens, showing number of species compared with how many gardens each occurred in.

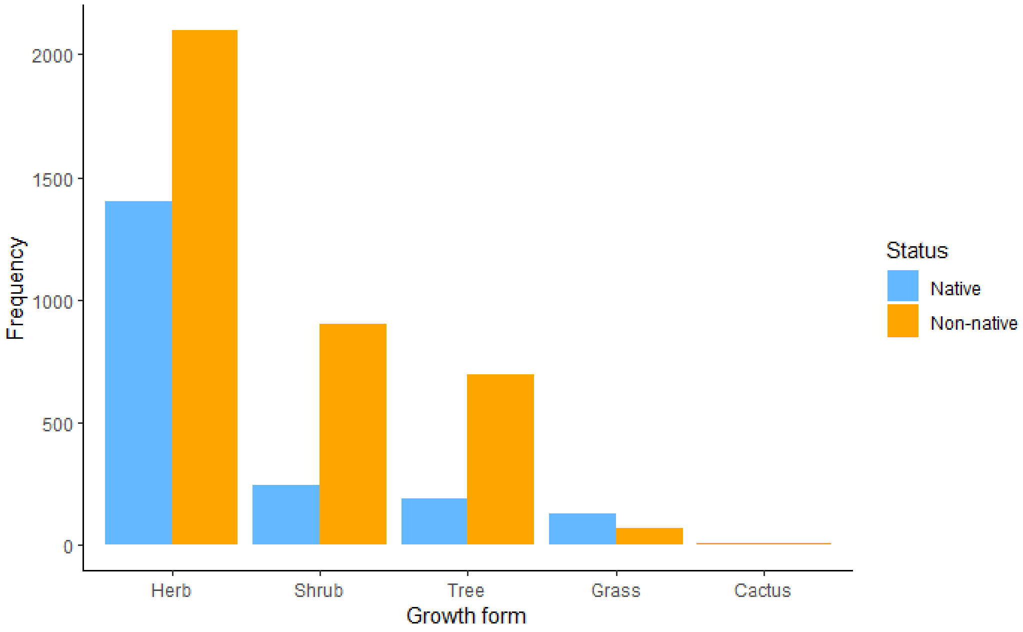


Figure A12: Frequency of growth forms observed across all 15 botanic gardens.

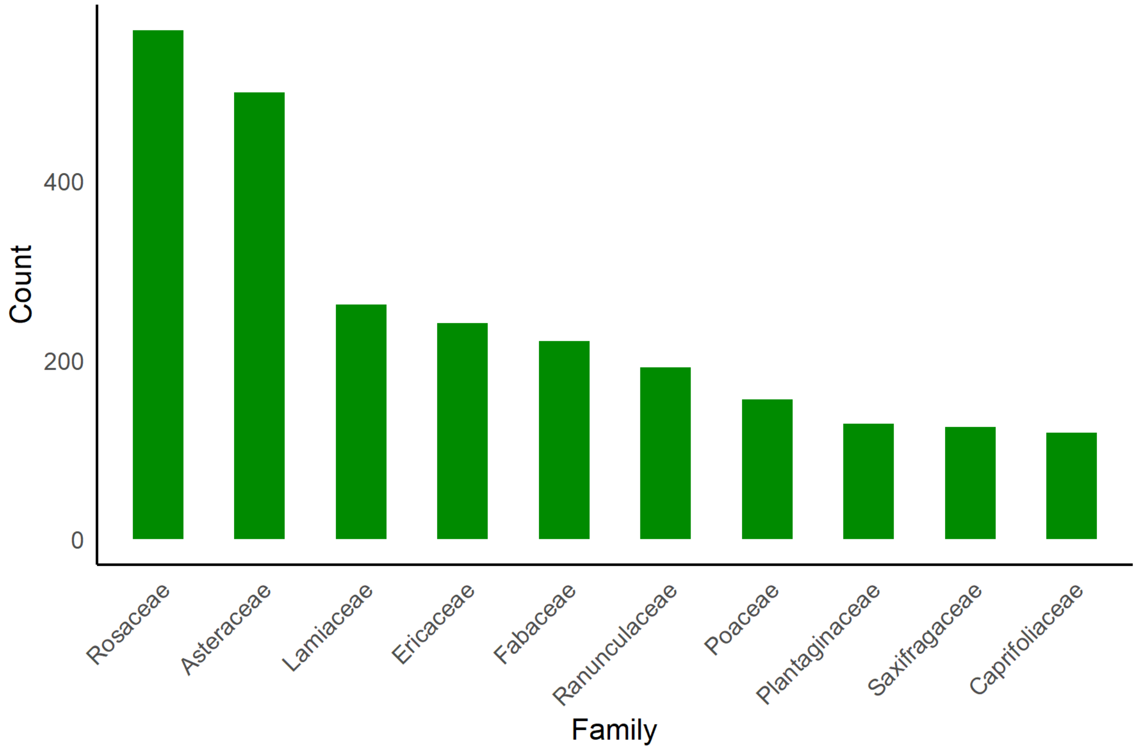


Figure A13: The ten most frequently observed families across all 15 botanic gardens.

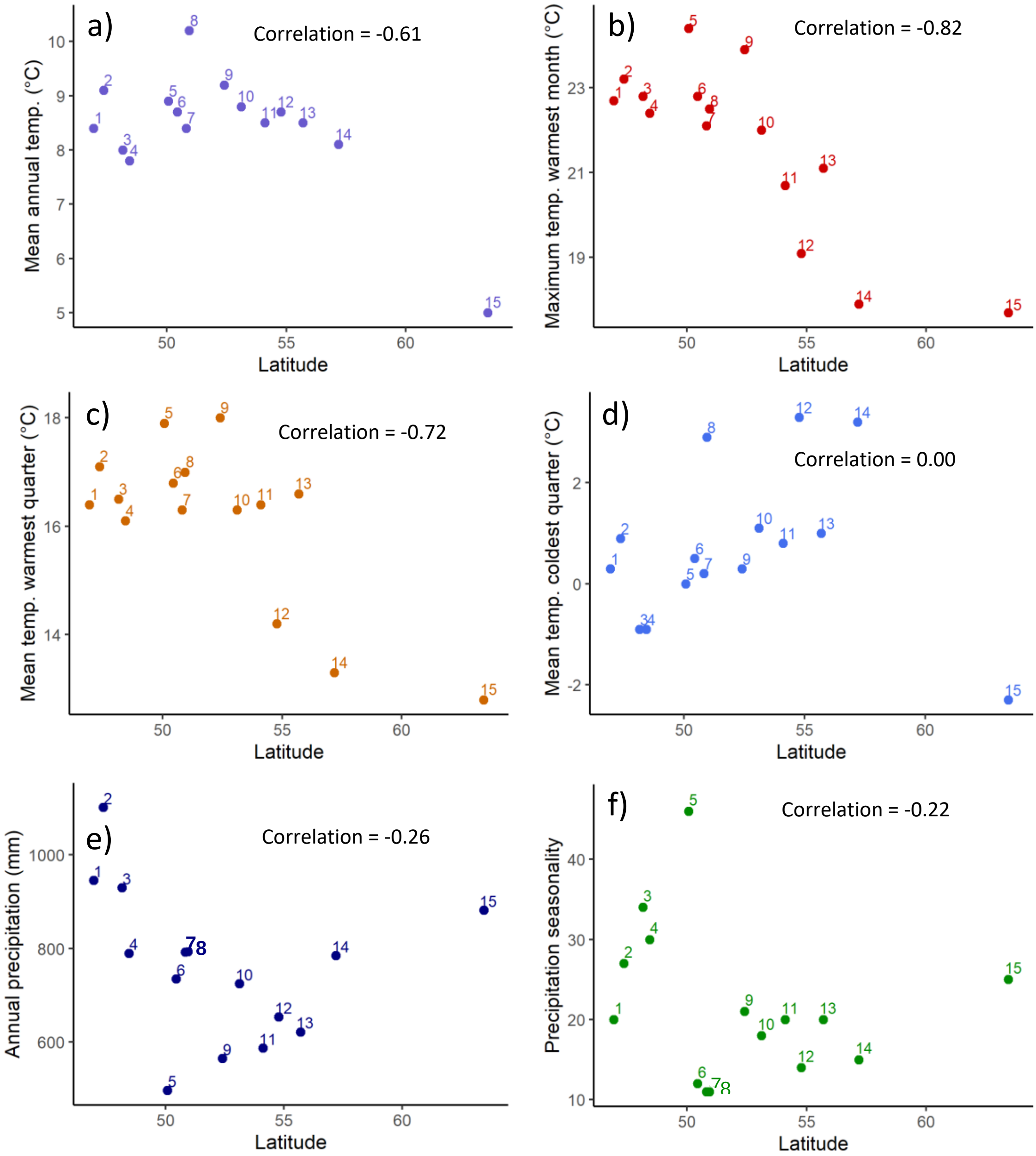
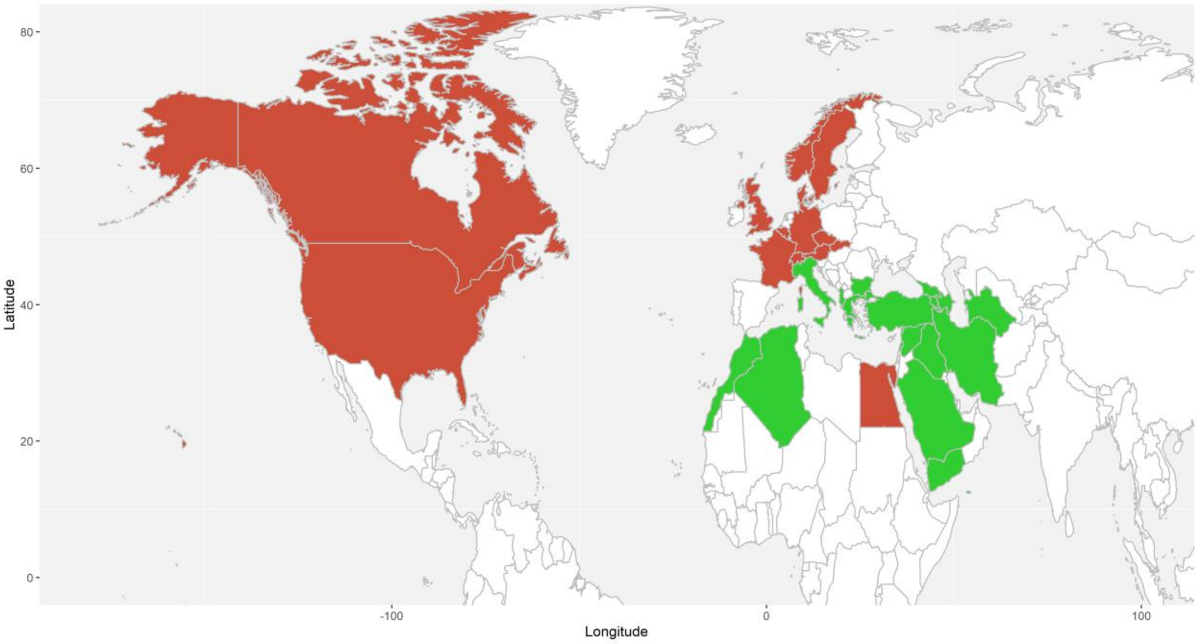
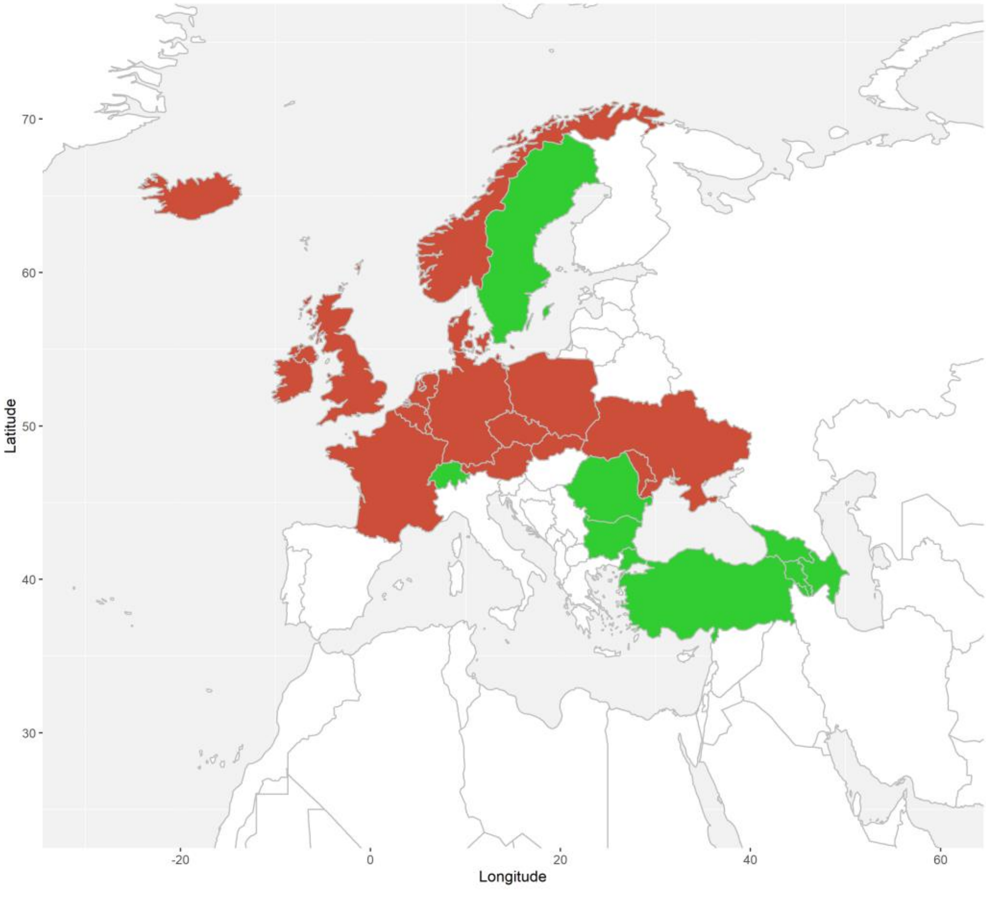


Figure A14: Bioclimatic variables associated with each botanical garden compared with the latitude of each garden for (a) mean annual temperature (° Celsius), (b) maximum temperature of the warmest month (°C), (c) mean temperature of the warmest quarter (°C), (d) mean temperature of the coldest quarter (°C), (e) annual precipitation (mm) and (f) precipitation seasonality (coefficient of variation). Correlation indicates correlation between latitude and climatic variable. Bioclimatic variables were extracted from the closest coordinate to each garden on a 2.5 minute resolution raster (grid cell size ~4.5 km at the equator) downloaded from WorldClim version 1.0 (Fick & Hijmans, 2020) using the 'raster' package (Hijmans & van Etten, 2012) on R version 3.6.1 (R Core Team, 2019). Gardens are numbered in order of latitude: (1) Bern, (2) Zurich, (3) Munich, (4) Tübingen, (5) Prague, (6) Butzbach, (7) Marburg, (8) Meise, (9) Potsdam, (10) Bremen, (11) Rostock, (12) Durham, (13) Copenhagen, (14) Aberdeen and (15) Trondheim.

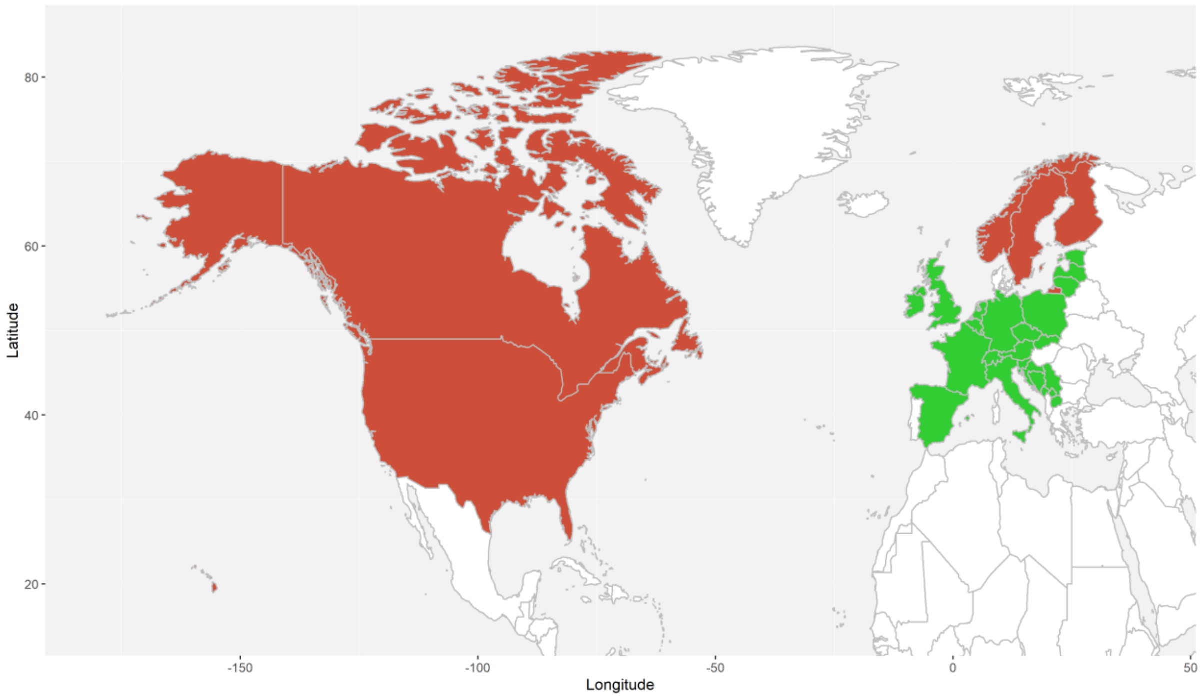
Arabis caucasica



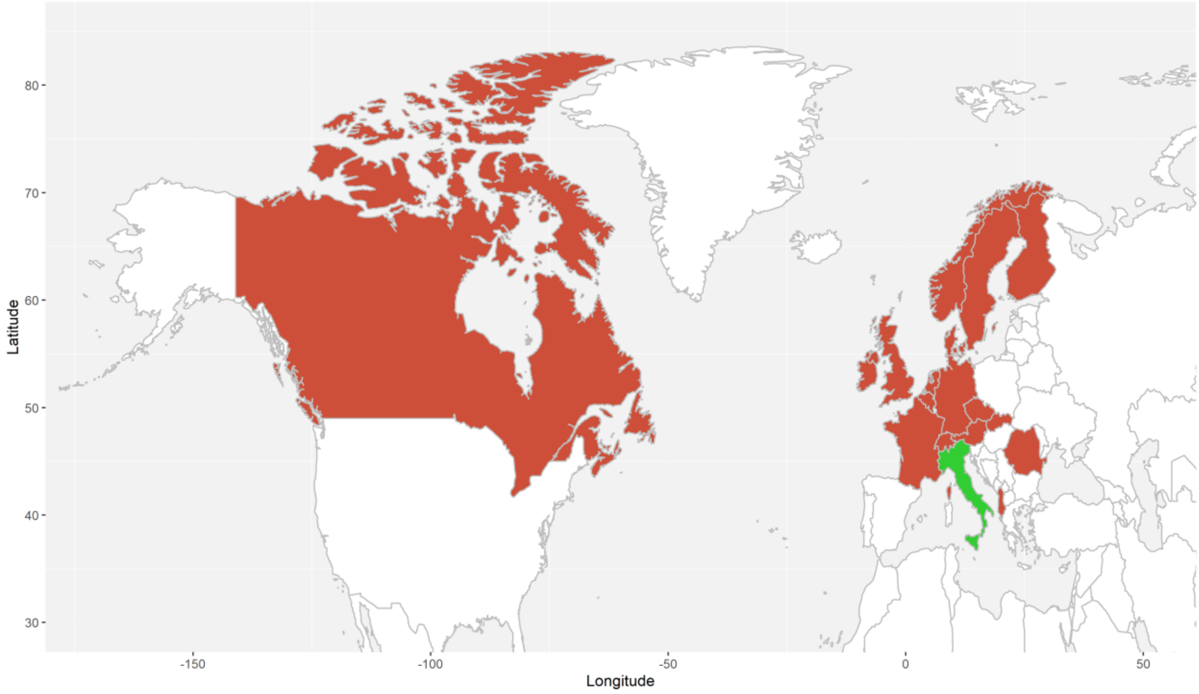
Alchemilla mollis

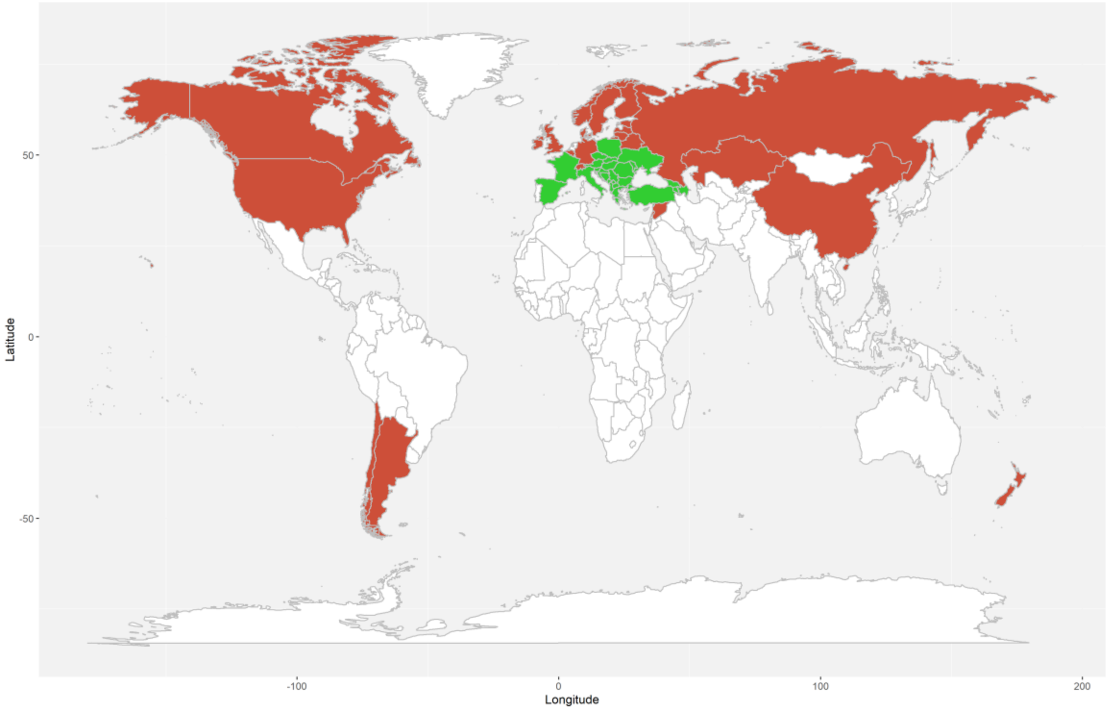


Centaurea montana



Cerastium tomentosum





Hesperis matronalis

Figure A15: Native and non-native distribution of the five non-native species used in common-garden experiment in Norway (POWO, 2022). Green regions represent species' native ranges and red regions represent species' non-native ranges.

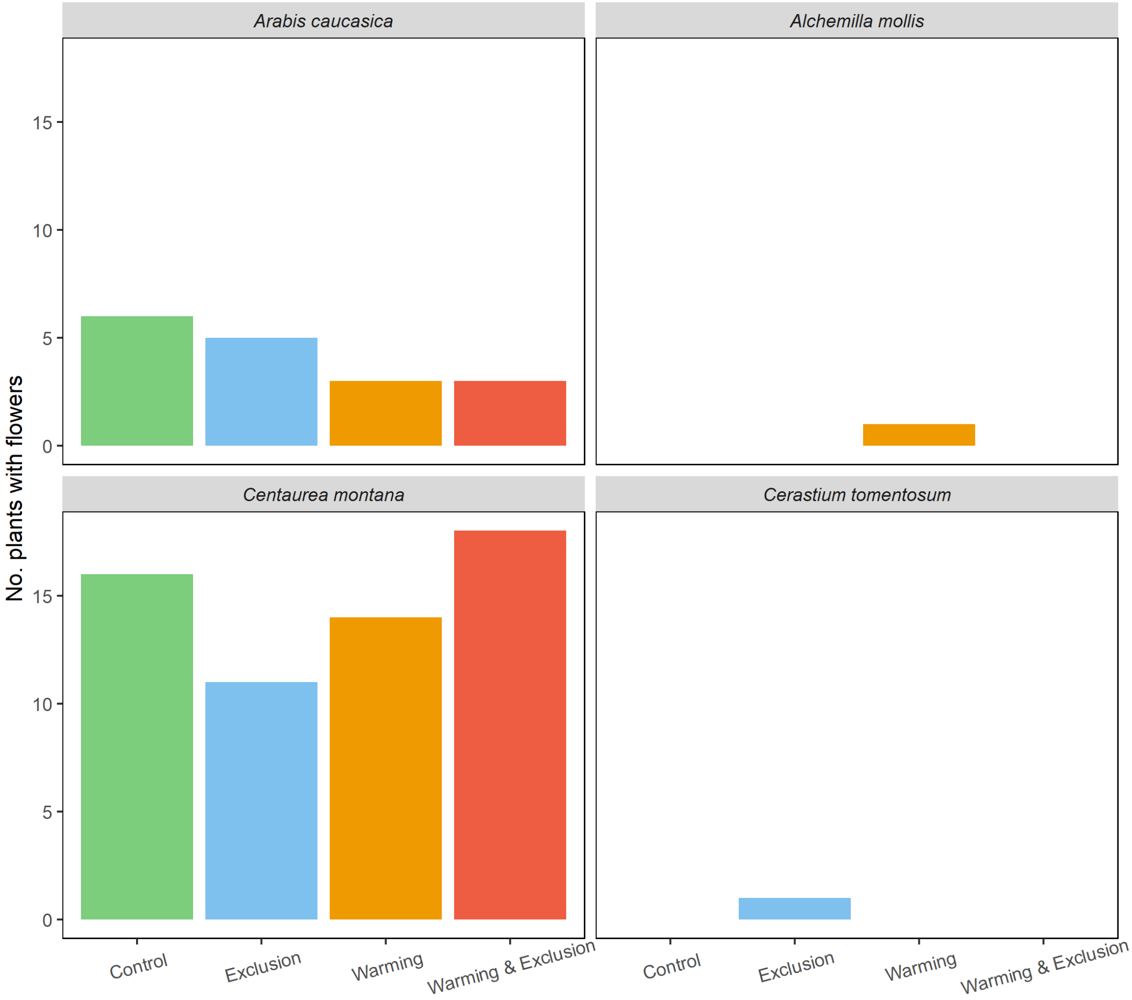


Figure A16: Number of plants with flowers in each treatment for four species. No flowers were recorded for *Hesperis matronalis*.

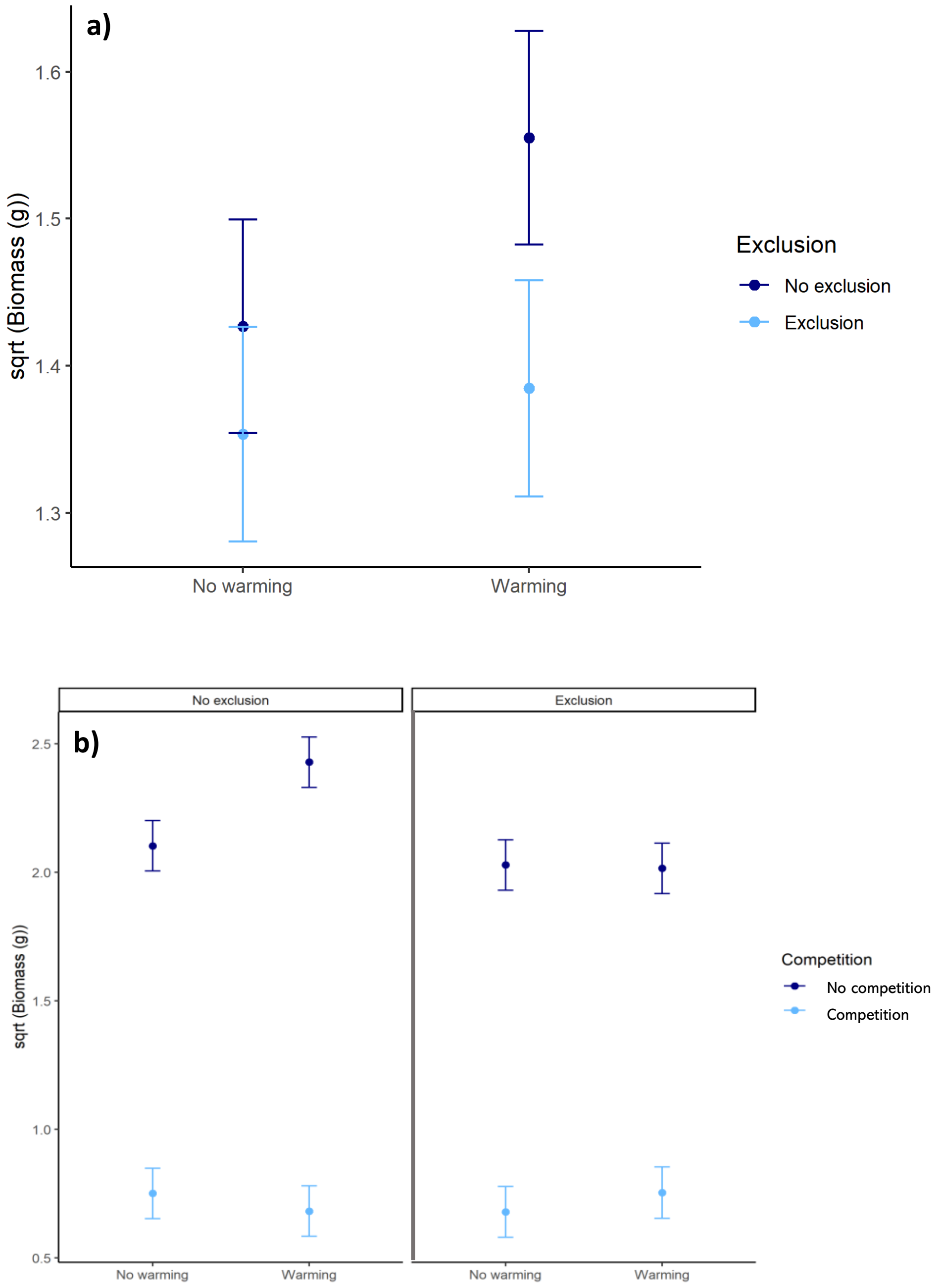


Figure A17: The predicted biomass (±SE) of *Alchemilla mollis* based on a linear regression model and the interactive effects of (a) warming and exclusion and (b) warming, exclusion and competition on plant biomass.

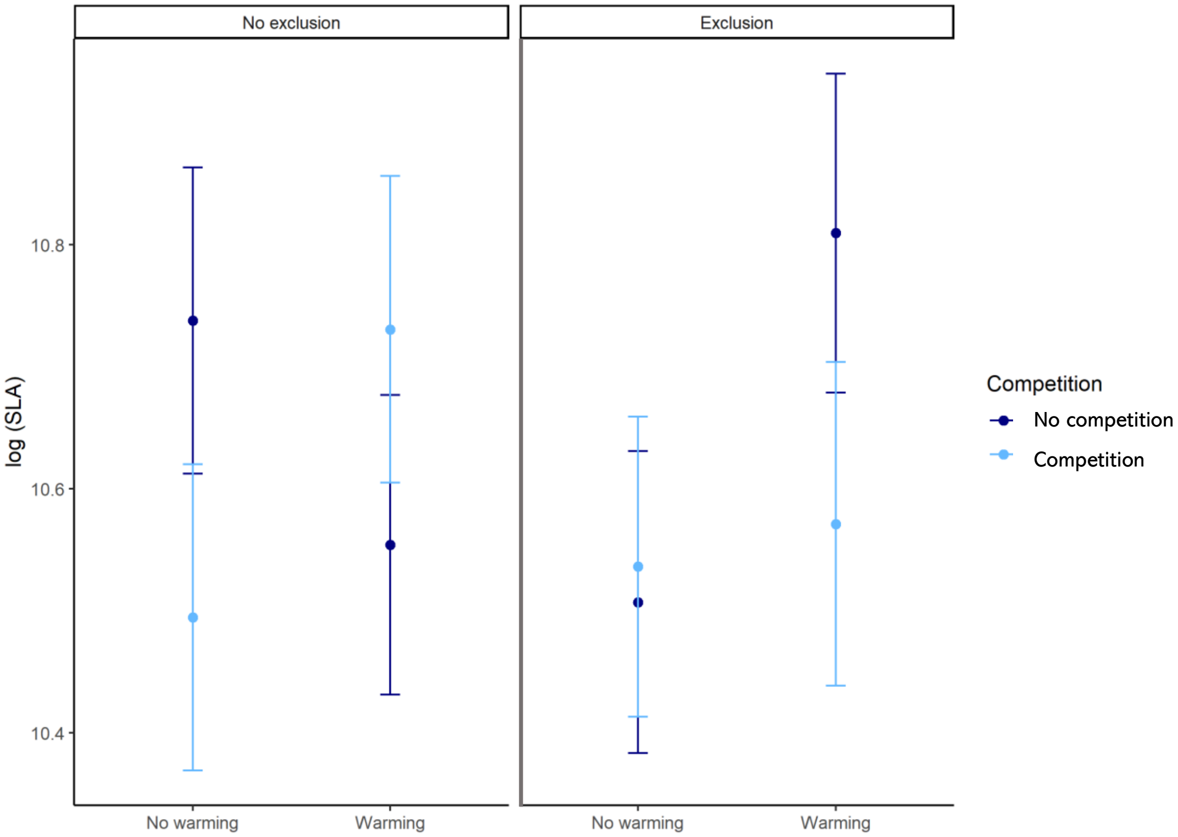


Figure A18: The predicted specific leaf area (SLA) (±SE) of *Centaurea montana* based on a linear regression model and the interactive effects of warming, competition with native species and herbivore exclusion on SLA.

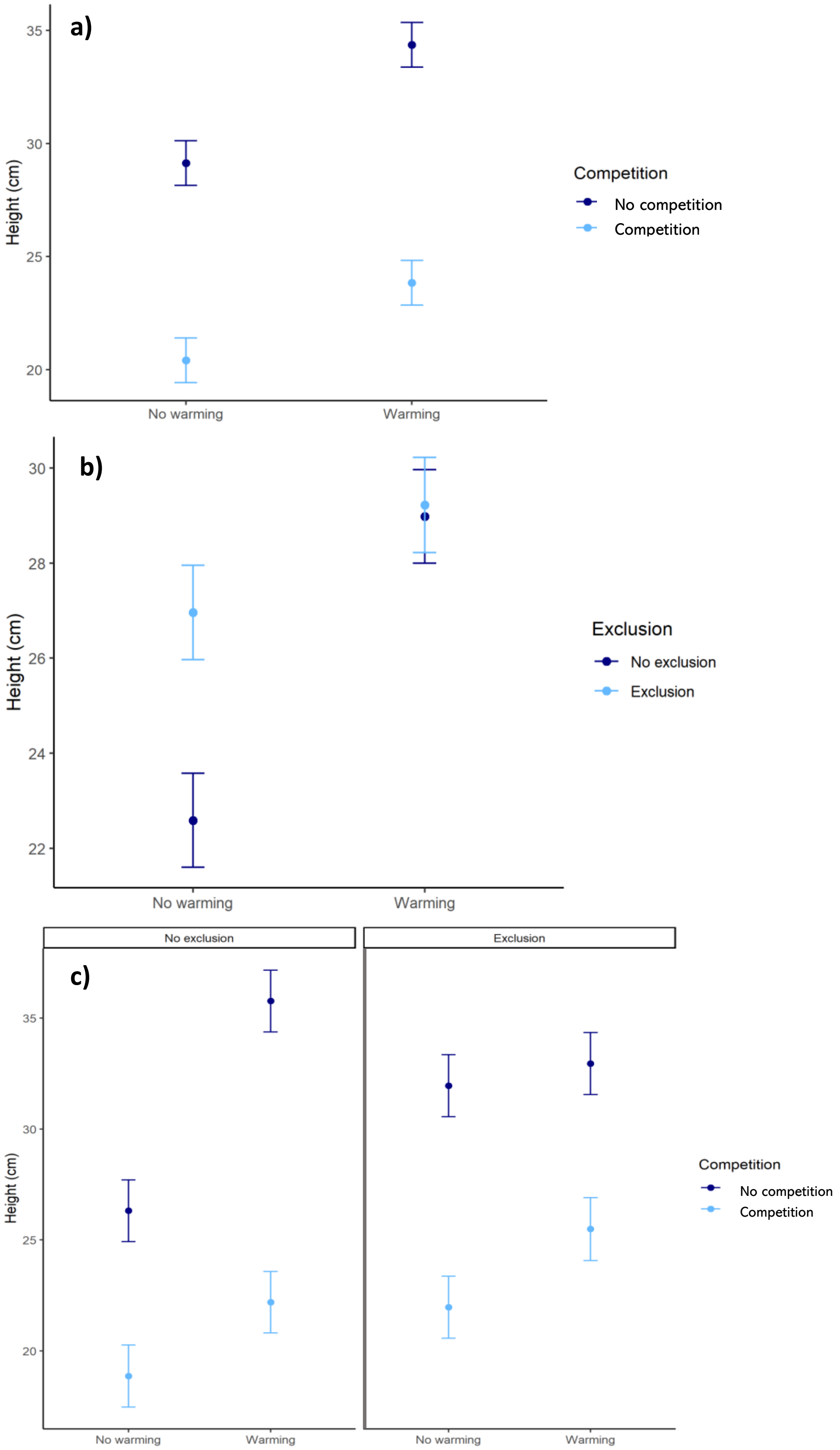


Figure A19: The predicted height (±SE) of *Alchemilla mollis* based on a linear regression model and the interactive effects of (a) warming and competition, (b) warming and exclusion and (c) warming, exclusion and competition on plant height.