Assessing range limits and niche shifts in invasive weeds

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Thomas Frank Carlin

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Invasive species pose global threats to the environment, human health, and endemic species. Being able to predict which species will become invasive, and which countries are vulnerable, helps prevent species invasions before they occur. Current methods consider which environments a species occupies in the native range and extrapolates this onto new regions. However, when species undergo niche shifts they occupy different environments in the introduced range than those they occupied in the native range. In this thesis I will combine statistical and empirical approaches to uncover what processes lead to niche shifts, and provide a better understanding of how to predict species' distributions in the presence of niche shifts. To accomplish this I consider three globally invasive ruderal weed species: *Rumex obtusifolius* Linnaeus, *R. crispus* L., and *R. conglomeratus* Murray.

I begin by assessing where *Rumex* species undergo niche shifts globally. I found that *Rumex* species undergo different niche dynamics in each of the three non-native regions considered. In New Zealand, the climatic niche expanded towards warmer, wetter climates; in Australia, the niche was largely conserved; and in North America the niche predominantly expanded into drier, less stable climates. From here, I wanted to understand which variables were best at predicting species' distributions both in the native and introduced range where the species were shown to have undergone a niche shift. Here I considered land use, human-related, and hydrological non-climatic variables. Whilst climatic variables are the most commonly used variables in predicting species' distributions, I found that climate models often underperformed when compared to non-climatic models. In particular, when projecting models from the native range onto the introduced ranges the inclusion of climatic variables was detrimental to model performance. Utilising non-climatic variables, such as human impact, resulted in more accurate model projections. Finally, I conducted a large-scale common garden experiment in the introduced range to ascertain whether individuals from the introduced range had evolved to occupy new niche space beyond what individuals from the native range tolerate. Contrary to my expectations, I found that climatic niche shifts in *Rumex* species are the result of preadaptation rather than rapid evolution.

This study is the first of its kind to consider niche shifts across multiple introduced regions and provide experimental evidence of how species are capable of shifting their niches into non-analogue climates. In this thesis I will provide new insights into how we assess niche shifts, and open new avenues for future research. I suggest that we should first focus on better understanding the species' fundamental niche, before assessing whether species have undergone rapid adaptation in new regions.

Keywords: niche shift, introduced plant, niche dynamics, range limits, species' distribution model, macroecology, niche expansion, invasive species, *Rumex*, weed, common garden, preadaptation, rapid adaptation, fundamental niche, realised niche, evolution, climate change

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Chapter 1

General Introduction

Plants transported beyond their native range by humans can have profound impacts on their new environments (Hulme, 2020; Weidlich et al., 2020). Introduced plants can outcompete native species for resources (Buerdsell et al., 2021; Funk, 2013; Matzek, 2011), introduce novel diseases (Goss et al., 2020; Pimentel et al., 2001), and disturb the community making it easier for more introduced plants to establish (Green et al., 2011; Prior et al., 2014). Introduced plants can cause direct negative consequences for human health (Mazza et al., 2014) and communities (Booy et al., 2017; McLean, 2010; Seawright et al., 2009). Agriculturally, introduced plants compete with crops for water, light, and nutrients (Spitters & Van Den Bergh, 1982), reduce pasture yield by replacing productive pasture species (Tozer et al., 2011), and are difficult to remove (Broadfield & McHenry, 2019). As a result, estimates have suggested that the cost to the New Zealand (NZ) agricultural industry from introduced weeds and weed control is at least NZD 1.7 billion annually (Saunders et al., 2017). Whilst humans have been both directly and indirectly transporting plant species beyond their native ranges for millennia, the modernisation of trade and transport routes has dramatically accelerated this process (Hulme, 2009). The increased pace of plant invasions, and negative effects that occur post-invasion, motivate us to predict where successful introductions will occur.

Current methods of predicting the distributions of introduced species generally rely on characterising the species' niche (Bradley et al., 2008, 2012; Bradley, Blumenthal, et al., 2010; Bradley, Wilcove, et al., 2010; Broennimann et al., 2007; Chapman et al., 2019; Early & Sax, 2014; Petitpierre et al., 2012, 2017; Srivastava et al., 2019). The niche is the set of environments in which it can, on average, experience a population growth rate greater than or equal to 0 (Godsoe, 2010; Holt, 2009; Hutchinson, 1957). In other words, the species' niche is the set of environments under which species can establish and thrive. One way to characterise a species' niche involves looking at where it occurs and describing the environmental attributes of those locations. Many methods focus on the range of climates species occupy, otherwise known as the climatic niche (Atwater et al., 2018; Bradie & Leung, 2017; Bradley et al., 2008; Broennimann et al., 2007; Chapman et al., 2019; Early & Sax, 2014; Gallagher et al., 2010; Petitpierre et al., 2012, 2017; Srivastava et al., 2019). The climatic niche is particularly useful when predicting distributions at continental scales, where the climates a species can tolerate dictate their large-scale distributions (Ashcroft et al., 2011; Petitpierre et al., 2017). Often forecasts of the distribution of introduced species rely on the assumption that the climatic niche a species occupies in the introduced range will be the same as the climates it occupies in the native range, known as climatic niche conservatism (Atwater et al., 2018; Bradley et al., 2012; Bradley, Blumenthal, et al., 2010; Bradley, Wilcove, et al., 2010; Chunlong Liu et al., 2020b; Petitpierre et al., 2012).

Unfortunately introduced species frequently occupy climates dissimilar to those found in the native range, a phenomena known as a climatic niche shift (Atwater et al., 2018; Atwater & Barney, 2021; Christina et al., 2019; Comte et al., 2017; Gallagher et al., 2010; X. Liu et al., 2017; Silva et al., 2016; Tingley et al., 2014). Niche shifts are unfortunately difficult to define, with many studies using vague descriptions (Atwater et al., 2018; Atwater & Barney, 2021), whilst others attempt to impose stricter yet ultimately controversial definitions (Chunlong Liu et al., 2020b; Petitpierre et al., 2012). In this thesis niche shifts are generally defined as the niche in the introduced range being significantly dissimilar to that in the native range, described using metrics of overlap or expansion. Liu et al. (2020b) suggest that niche shifts are rare across taxa, however other studies have suggested they may but common in introduced plants (Atwater & Barney, 2021; Atwater et al., 2018; but see - Petitpierre et al., 2012). Nevertheless, little is currently known about which species are likely to shift their niche or why niche shifts occur (Lantschner et al., 2019). For example gorse, *Ulex europaeus,* occupies warmer areas in Australia and South America than in its native range (Christina et al., 2019), but the cause of this climatic niche shift is unknown. Furthermore, studies investigating niche shifts tend to compare only two regions, the native range and an introduced range (Atwater et al., 2018; Early & Sax, 2014; Petitpierre et al., 2012). This approach unfortunately provides little information on the consistency of niche shifts, particularly whether species that have undergone niche shifts tend to do so in all the ranges in which they are introduced. If a species consistently undergoes niche shifts when introduced in different climates across the world we can use this information to predict how its range limits will shift in a new region. Furthermore, this analysis could provide insight into whether regions with certain climates are more vulnerable to species invasions than others.

The presence of climatic niche shifts may indicate that climate is not the limiting factor of species' distributions at their niche limits (Benning & Moeller, 2019). Human mediated dispersal along trade routes is a prominent driver of plant species introductions (Essl et al., 2020; Hulme, 2020; Seebens et al., 2018), and thus where human influence is high the likelihood of species introductions will also increase (Kołodziejek & Patykowski, 2015; Pysek et al., 2010; Redpath & Rapson, 2015; Venter et al., 2018). Furthermore, environments disturbed by human activity are more vulnerable to the establishment of introduced plants compared to undisturbed environments (Kołodziejek &

Patykowski, 2015; Pysek et al., 2010; Redpath & Rapson, 2015). Both biotic (Jones & Gilbert, 2016) and non-climatic environmental factors can influence species' distributions, such as soil type (Mahgoub, 2019), topography (Bello et al., 2013), and hydrology (Bradie & Leung, 2017). Therefore non-climatic variables rather than climate may be more reflective of introduced plant distributions in the introduced range and may better predict their potential future distributions (Bradie & Leung, 2017; Gardner et al., 2019). Non-climatic variables have been shown to be useful in a number of studies utilising species distribution models (SDMs; Bello et al., 2013; Bradie & Leung, 2017; Gallien et al., 2015; Gardner et al., 2019; Iturrate-Garcia et al., 2016). Unfortunately they are rarely considered when assessing niche shifts (Atwater et al., 2018; Early & Sax, 2014; Lantschner et al., 2019; Petitpierre et al., 2012). It is possible that utilising non-climatic variables in SDMs may help us make stronger predictions of species' distributions and interpret observed climatic niche shifts more diligently (Roura-Pascual et al., 2011).

When species move to a new region they can shift their niches into both climates that are equivalent to those in the native range (analogue climates) or climates not found in the native range (non-analogue climates) (Guisan et al., 2014). When species establish in non-analogue climates, known as niche pioneering (Atwater et al., 2018), the traditional methods of predicting their distribution based on the climatic niche in the native range provide incomplete information on how species will react to the new climates (Guisan et al., 2014; Petitpierre et al., 2012). At present it is unclear if niche shifts in non-analogue climates are the result of evolution in the introduced range or simply preadaptation to climates previously unreachable (Anderson & Song, 2020; Atwater et al., 2018; Petitpierre et al., 2012; Webber et al., 2012). As such, the implications of niche shifts into non-analogue climates are often ignored (Chunlong Liu et al., 2020b; Petitpierre et al., 2012; Webber et al., 2012). Understanding whether niche shifts into non-analogue climates represent rapid evolution in the introduced range or simply preadaptation will help clarify this issue and dictate the course of niche shift research in the future.

If species are evolving to meet the requirements of the introduced range this may constitute a shift in the fundamental niche, i.e. the set of all abiotic environments a species could tolerate once dispersal limitations and biotic interactions are removed (Soberón, 2007). However if species are shifting their niche into climates they're preadapted to it would only constitute a shift in the realised niche. The realised niche is the subset of the fundamental niche in which the species is actually present. Most current methodologies are correlative, only considering the realised niche, which makes it difficult to quantify the fundamental niche (Banerjee et al., 2017; Dreyer et al., 2019; Guisan et al., 2014; Webber et al., 2012). However if we can better quantify the fundamental niche of a species we can determine whether a climatic niche shift is the result of preadaptation or rapid evolution to non-analogue climates. Unfortunately characterising the fundamental niche is difficult, requiring experiments of environmental tolerances. Such experiments are logistically challenging and difficult to complete for all species that may potentially be introduced.

Some have argued that rapid evolution is the most likely explanation for expansion into new climates in the introduced range (Boheemen et al., 2019; Dlugosch & Parker, 2008a, 2008b; Grant & Kalisz, 2020; Hulme & Barrett, 2013; Luo et al., 2019; Maron et al., 2004; Wan et al., 2020). Introduced plants, such as *Spartina alterniflora* Loisel, have been shown to have evolved greater fitness in the introduced range compared to the native range (Liu et al., 2020). This greater fitness in the introduced range may allow the introduced populations to tolerate different climates than those of the native range, leading to a climatic niche shift (Matesanz et al., 2014; Sultan & Matesanz, 2015). Similarly, rapid evolution has been observed in species such as *Polygonum cespitosum* Blume which evolved greater physiological plasticity and increased reproductive output in response to the higher sunshine hours of its North American introduced range (Sultan et al., 2013). If climatic niche shifts are primarily caused by rapid evolution in the introduced range it would suggest that species capable of rapid adaptation, such as those with short generation times, are more likely to experience climatic niche shifts (Barraclough, 2015; Bradley, Blumenthal, et al., 2010; Friedman, 2020; Grant & Kalisz, 2020; van Kleunen, Bossdorf, et al., 2018). Furthermore, if climatic niche shifts are primarily caused by rapid evolution in the introduced range, our current methods of projecting the species range may have limited applications in predicting the distribution of introduced species.

However, others have argued that species are more likely preadapted to the climates they are shifting into and that climatic niche shifts are restricted to changes in the realised niche, meaning other factors limit their distribution in the native range (Cadotte et al., 2018; Dlugosch & Parker, 2007; Early & Sax, 2014; González-Moreno et al., 2015; Parker et al., 2003). Species native to areas with strict dispersal limitations through geographic barriers, such as mountains or islands (Alexander & Edwards, 2010), or non-climatic environmental requirements, such as land use or hydrology restrictions (Bradie & Leung, 2017), would likely show preadaptation to climates beyond their native range limits. Similarly, species may be preadapted to climates beyond their native range if their range is restricted by biotic factors such as the distributions of pollinators (Chen et al., 2018; Gigante et al., 2020; Warren et al., 2010), herbivores (Lau et al., 2008), or mutualists (Lopez et al., 2020). The absence of non-climatic variable interactions from the native range or presence of new non-climatic variable interactions in the introduced range may allow species to expand their realised niche in the introduced range, leading to a climatic niche shift. If preadaptation to new climates is the primary driver of climatic niche shifts it would mean we need to focus on better quantifying the species' fundamental niche. Nonetheless, projections of the species' niche in the introduced range may still help us predict climatic niche shifts. Whether this can be accomplished by utilising non-climatic variables in models is yet to be determined.

1.1 Study species

This thesis utilises three perennial herbaceous weed species: *Rumex obtusifolius* L., *Rumex crispus* L., and *Rumex conglomeratus* Murray. These *Rumex* spp. are ruderals typically colonising open, disturbed environments associated with human activity, including pastures (Cavers & Harper, 1964, 1966; Grime et al., 2007; Holm et al., 1997; Lousley & Kent, 1981). They are native to Eurasia but have been spread across the world at least as early as the 16th century (Vibrans, 1998) and have colonised every continent except Antarctica (Cavers & Harper, 1964; Holm et al., 1977; Lousley & Kent, 1981). All three species were introduced to New Zealand (NZ) as agricultural seed contaminants and have subsequently established and spread (Grossrieder & Keary, 2004; Halsted, 1889; Zaller, 2004).

Where these species have been introduced they infest pasture and reduce pasture yield (Cavers & Harper, 1964; Grime et al., 2007; Harrington et al., 2014). They are unpalatable (Cavers & Harper, 1964; Grime et al., 2007), hence many grazing animals avoid consuming them, allowing populations to spread through pastureland unless management practises are implemented. Broad-scale management of *Rumex* spp. is difficult, with seed able to survive in the seedbank for years (Cavers & Harper, 1966; Foster, 1989; Totterdell & Roberts, 1979). Individual plants can survive grazing or mowing, and plants readily regenerate through taproot fragments (Alshallash, 2020; Weaver & Cavers, 1980). *Rumex* spp. are a particular nuisance in NZ as it’s agricultural sector is proportionally larger than that of other countries, with >6% of NZ GDP coming from agriculture in 2015 (*New Zealand Economic and Financial Overview 2016*, 2016) compared to only ~0.5% UK GDP for the same year (*Contributions of UK Agriculture FINAL REPORT*, 2017). A large proportion of NZ is pasture (Walker & Lee, 2000; Chapter 3) which provides an ideal environment for *Rumex* spp. to establish and spread through seed stock contamination or by agricultural machinery (Stefano Benvenuti, 2007; Grossrieder & Keary, 2004; Halsted, 1889; Zaller, 2004). Furthermore, *Rumex* spp. in NZ have been shown to develop greater seed production than in the native range without compromising seed size due to an increase in available resources (Bufford & Hulme, 2021).

Rumex spp. are ideal candidates to test whether they have evolved adaptations to climates in the introduced range. They are short lived, capable of demonstrating annual, biennial, or perennial life strategies, however tend to reproduce annually if conditions are favourable (Cavers & Harper, 1964; Grime et al., 2007). They have not been the subject of horticultural selection which could affect their invasiveness or climatic tolerances (Kitajima et al., 2006). These species have a long history of introductions, and as such have likely reached climatic equilibrium in their introduced ranges.

Despite the broad range of climates available in their native range, the ranges they have been introduced to possess novel climates which may require adaptations to establish in. Their short lifespan combined with their long invasion history and lack of artificial selection make them likely candidates for detecting possible evolutionary adaptations to new climates.

By studying three closely related species I can determine whether climatic niche shifts are common among congeners, and see if climatic niche shifts cause divergences in species' distributions among closely related species. Some studies have considered niche shifts among multiple congeners only descriptively (Finch et al., 2019; Klonner et al., 2017; Wan et al., 2019; You et al., 2018), with others either combining data from similar species (Atwater et al., 2018) or assessing congeners only as part of a much wider species pool (Dullinger et al., 2017; Early & Sax, 2014). Therefore, this thesis aims to more thoroughly examine the extent of climatic niche shifts among congeners than previously done. Although these *Rumex* species are closely related, they still possess different microhabitat requirements, with varying preferences for soil pH, moisture, and nitrogen content (Grime et al., 2007; Hill et al., 1999; Lousley & Kent, 1981). These differences may well encourage diverging adaptations between species in the introduced region, or may suggest factors other than climate largely constrict their niche. *Rumex* spp. are well studied in the native and introduced ranges, and as such I have access to more high quality distribution data than is typically available.

Furthermore, *Rumex* spp. are amenable to experimentation because they are short-lived, already widespread across their introduced ranges, and are not subject to controls or removal campaigns. They can also be controlled with herbicide and routine maintenance. These traits allow them to be responsibly planted beyond their native range. For these reasons *Rumex* spp. can provide us with information which could be extrapolated to other introduced plant species. By employing *Rumex* spp. I can utilise their abundant high quality presence data to combine correlative SDM approaches with empirical experiments to deeply examine the climatic niche shifts of an introduced nuisance plant.

1.2 Thesis objectives

My thesis seeks to understand where and why niche shifts occur. To do this I will first examine whether three related *Rumex* species show consistent niche shifts across multiple introduced ranges (Chapter 2). In this analysis I aim to determine whether we can use information from a niche shift in one region to help predict whether a species will shift its niche in other introduced ranges. We currently have many examples of a niche shift between the native range and a single introduced range (Atwater et al., 2018; Early & Sax, 2014; Petitpierre et al., 2012; Tingley et al., 2014). If niche shifts in individual plant species move consistently towards certain climates then information from one range could be utilised to improve predictions into other ranges.

In Chapter 3 I will examine whether the variables that most accurately predict *Rumex* species' distributions are consistent between the native and introduced ranges, and evaluate whether data from the native range can accurately predict the species' distribution in the introduced range. To do this I will contrast the accuracy of predictions generated using climatic variables with those using non-climatic variables. The findings from this analysis will provide us with a better understanding of which variables best predict the distributions of introduced plant species. If these are different between the native and introduced ranges it may suggest species are limited by different factors in the introduced range. Models of data from the native range will then be projected onto the introduced range and compared with models from the introduced range. This analysis will assess the accuracy of models projected from the native range of species that undergo niche shifts, and which variables provide the most accurate predictions.

Finally, in Chapter 4 I will test for preadaptation of *Rumex* species to the introduced range using a large scale common garden experiment. This can help determine the underlying cause of niche shifts for introduced species, particularly into climates not available in the native range. The findings of this field experiment will suggest whether niche shifts into non-analogue environments are fundamental niche shifts, where species adapt to new environments, or realised niche shifts, where species are preadapted to these environments prior to introduction.

In summary, I aim to determine whether:

1. Niche shifts within *Rumex* species are consistent across multiple introduced ranges in magnitude and direction.

2. Non-climatic factors can better predict the distributions of *Rumex* species which have undergone niche shifts and in non-analogue climates.

3. Niche shifts into non-analogue climates are the result of preadaptation or rapid evolution in the introduced range.

Together, the findings of this thesis will not only contribute to the environmental niche modelling literature, but also better inform stakeholders of how to predict the establishment and spread of introduced species.

Chapter 2

Global assessment of climatic niche shifts in three *Rumex* species

2.1 Introduction

Attempts to predict the establishment of introduced plants in new regions have commonly assumed species inhabit similar environments across the globe, usually termed climatic niche conservatism (Bradley et al., 2012; Bradley, Blumenthal, et al., 2010; Bradley, Wilcove, et al., 2010). A species' realised climatic niche is the set of climates a species currently occupies and in which it experiences stable or positive population growth (Atwater et al., 2018; Holt, 2009; Hutchinson, 1957), and niche conservatism occurs when a species inhabits that same niche in both the native and introduced range (Petitpierre et al., 2012). However, studies have revealed shifts in the climatic niche between introduced and native ranges across many taxa and environments (Atwater et al., 2018; Christina et al., 2019; Comte et al., 2017; Liu et al., 2017; Silva et al., 2016; Tingley et al., 2014). Niche shifts can occur when species occupy new climates in the introduced range that are either available but unoccupied in the native range (expansion) or unavailable in the native range (pioneering), or by failing to occupy climates in the introduced range that are occupied in the native range (unfilling) (Atwater et al., 2018; Guisan et al., 2014). Where climatic niche shifts occur between the native and introduced range, the question remains whether, for any one species, such shifts are predictable and consistent in both direction and magnitude across different regions of the world. A better understanding of when niche shifts are consistent will make it easier to predict the establishment and future range dynamics of introduced species. To date, most studies have focused on shifts between only two regions (Atwater et al., 2018; Early & Sax, 2014; Gallagher et al., 2010; Petitpierre et al., 2012), or consider the transferability of species distributions between ranges in the absence of climatic niche shifts (Fernández & Hamilton, 2015; Chunlong Liu et al., 2020a; Randin et al., 2006; Soberón & Peterson, 2011). Currently the transferability of introduced plant species distributions which undergo climatic niche shifts has been little explored (Datta et al., 2019; C.-J. Wang et al., 2017), however has been assessed for some animal species (Hill et al., 2017; Pili et al., 2020; Silva et al., 2016).

When comparing niche shifts across multiple ranges there are a number of potential outcomes (Figure 2.1). Firstly, a species may consistently shift into certain climates across all observed ranges (Figure 2.1A). Consistent niche shifts across ranges may be expected in species with strong tolerances to particular climates or when its native range does not fully encapsulate its fundamental tolerances. This would suggest that the species is either pre-adapted to, or able to rapidly adapt to, specific climates. Silva et al. (2016) showed that independent invasions of a dung beetle, *Onthophagus taurus,* all expressed niche shifts towards more humid climates than those occupied in the native range. Alternatively we may see idiosyncratic patterns in the direction of niche shifts, with the species shifting in different directions across regions (Figure 2.1B), or experiencing niche shifts in some regions but niche conservatism in others (Figure 2.1C). In this instance it may suggest species are able to rapidly adapt to some climates, but struggle to adapt to others. This could also indicate that non-climatic factors in the introduced range are facilitating a niche shift, or that a niche shift represents an escape from non-climatic factors which restrict the species' niche in some ranges (Bulleri et al., 2016). For example gorse, *Ulex europaeus,* occupies warmer areas in Australia and South America than in its native range, yet cooler areas in North America, but the mechanisms behind these niche shifts are unknown (Christina et al., 2019). Alternatively, niche shifts may be inconsistent in magnitude, where niche shifts in two independent regions could both be towards similar climates, but may be more extreme in one introduced region than the other. Variations in magnitude of a niche shift would amplify the difficulty in predicting the climatic thresholds a species may be able to tolerate, and subsequently which areas are susceptible to establishment. Inconsistent niche shifts across ranges may be expected in species which have a propensity for rapid adaptation, or have broad climatic tolerances but are limited by available climates.

It is currently not well understood whether closely related species show consistency across niche shifts. Previous niche shift studies have usually looked at a single species (Christina et al., 2019; Silva et al., 2016; Tingley et al., 2014), or considered multiple species without accounting for taxonomy (Atwater et al., 2018; Olivier Broennimann et al., 2012; Early & Sax, 2014), but comparisons of closely related species would provide new insights into whether they experience consistency in niche shifts across regions. Studies of multiple species within a similar functional group are required to compare whether species show similar responses across regions, or whether species responses are idiosyncratic. If closely related species share a similar climatic niche, and experience niche shifts consistently, we may conclude that common factors, such as climate availability, in the introduced region may be a larger driver of niche shifts than individual species' attributes. If this is the case then data from related species could be used to supplement our knowledge of the species niche, and potentially aid in predicting shifts (Smith et al., 2019). We could then use the presence of a known species to make strong inferences about where a related species could potentially spread.

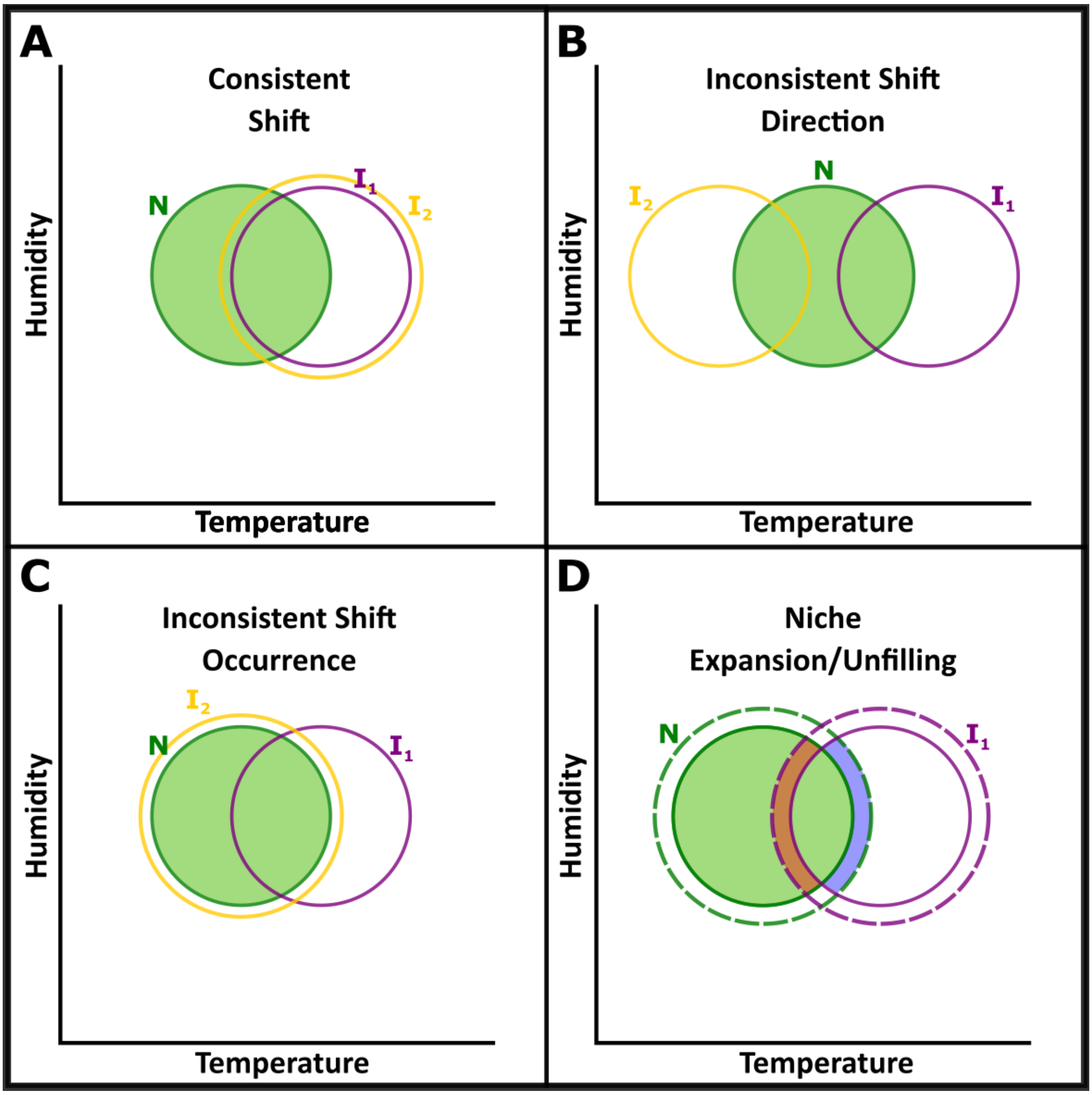

Figure 2.1 Possible niche shift scenarios between regions. Axes represent two different environmental gradients across which a niche shift could be observed. Areas occupied in a species' native range (N) are shown by the green shaded circle; areas occupied in two different introduced ranges (I_1, and I_2) are shown by the purple and orange circles respectively. A) Niche shifts are consistent across independent ranges. B) Niche shifts are inconsistent across independent ranges. C) Niche shifts occur in some ranges, whilst the niche is conserved in others. D) Two niche dynamics that lead to niche shifts are shown. Niche expansion (blue) refers to areas of analogue, or overlapping, climate space between the native and introduced ranges that are only occupied in the introduced range. Niche unfilling (red) refers to areas of analogue climate space that are only occupied in the native range. Dashed circles denote available climate space for the native range (green) and introduced range (purple).

In this chapter I will test whether climatic niche shifts are consistent across regions for three closely related, globally invasive, herbaceous species. Specifically I will ask: Do species shift their niches in multiple introduced ranges? Do species shift their niches in the same direction across regions? Are climatic niche shifts consistent across closely related species? I expect that species with broad environmental tolerances or widespread distributions will be able to undergo climatic niche shifts in independent ranges, constrained mainly by the available climates. Widespread species may be likely to undergo niche shifts into non-analogue climate space, as their native range is unlikely to possess all climates that would be suitable for these species (Atwater et al., 2018). Less widespread species with more restrictive climatic tolerances will be more likely to exhibit niche conservatism (Petitpierre et al., 2012), however if niche shifts are observed they would likely be consistent across ranges. Alternatively, less widespread species may experience unexpected niche shifts if their distribution in the native range is otherwise constrained by dispersal limitations, biotic, or non-climatic abiotic factors (Early & Sax, 2014). Finally, I expect that closely related species that occupy similar climates would likely experience similar niche shifts, allowing information from the distribution of one species to help inform others. With this analysis I hope to shed light on when and where niche shifts occur, and whether the direction of niche shifts can be predicted.

2.2 Methods

2.2.1 Study Area and Species

Three common dock species were studied: *Rumex obtusifolius* L., *R. crispus* L., and *R. conglomeratus* Murray. These species are all ruderals, typically colonising open, disturbed environments associated with human activity, including pasture (Cavers & Harper, 1964, 1966; Grime et al., 2007; Holm et al., 1997; Lousley & Kent, 1981). All three species are of Eurasian origin yet have been introduced and established across the globe as agricultural seed contaminants (Figure 2.2; Holm et al., 1997; Holm et al., 1979). *Rumex* spp. have been unintentionally spread for over five hundred years (Table 2.1; Vibrans, 1998). Furthermore, data for these species are numerous in both the native and introduced ranges, making them ideal candidates for large scale climate matching analyses. Despite the wide variety of ecoregions *Rumex* spp. inhabit (Olson et al., 2001) they generally occupy similar habitats across the globe, indicating that any possible niche shifts would likely be driven by climate rather than habitat limitations (Figure 2.2; Cavers & Harper, 1964; Grime et al., 2007; Holm et al., 1997; Lousley & Kent, 1981).

Rumex spp. are short lived and capable of demonstrating annual, biennial, or perennial life strategies, however tend to reproduce annually if conditions are favourable (Cavers & Harper, 1964; Grime et al., 2007). Their long invasion history suggests they are likely to have reached climatic equilibrium in their introduced ranges, and that sufficient generations have passed for adaptations to new climates to develop (Table 2.1; Vibrans, 1998). As such, it stands to reason that *Rumex* spp. have had ample opportunities for niche shifts to occur. *Rumex* spp. were not deliberately introduced for agricultural or horticultural purposes, and as such have not been subjected to artificial selection which may affect their invasiveness or climatic tolerances (Kitajima et al., 2006). Therefore any niche shifts observed are likely due to natural processes.

These congeners all prefer open environments with minimal shading, nitrogen rich soils, and can tolerate either weakly acidic or basic soils. They are capable of hybridising with one another (Cavers & Harper, 1964; Holm et al., 1979; Lousley & Kent, 1981) and share broad environmental tolerances (Grime et al., 2007; Hill et al., 1999; Lousley & Kent, 1981). Despite this, small differences in environmental tolerances are observed between species, with *R. obtusifolius* in particular able to tolerate extremely nutrient rich or polluted soils and waterways (Grime et al., 2007). *Rumex conglomeratus* has a smaller range size and is restricted to more mild temperatures and wetter habitats such as along waterways (Hill et al., 1999; Lousley & Kent, 1981). In comparison, *R.*

obtusifolius and *R. crispus* can tolerate cooler, drier climates, with their native distributions extending to the Arctic Circle (Hultén E, 1950).

We modelled these species' niches across the native range, predominantly in Europe, and 3 regions where the species are recorded as naturalised introduced species by national organisations and the Global Invasive Species Database (Invasive Species Specialist Group, 2019): western North America (USDA & NRCS, 2019), south-eastern Australia (*Atlas of Living Australia*, 2019), and New Zealand (New Zealand Plant Conservation Network, 2019a). These regions have an abundance of occurrence records for all three species, a wide variety of climates, and a long history since the species were first introduced (Table 2.1).

Table 2.1 **Number of usable records obtained for each region of interest and earliest known date of record. Usable records were of sufficient identifying information, coordinate precision, and were counted after spatial thinning.**

Region	Species	No. Records	Earliest Record	Reference
Native Range	*R. conglomeratus*	21855	-	-
	R. crispus	47122	-	-
	R. obtusifolius	42417	-	-
Eastern Australia	*R. conglomeratus*	3717	1770	(Victorian Biodiversity Atlas, 2019a)
	R. crispus	12242	1770	(Victorian Biodiversity Atlas, 2019b)
	R. obtusifolius	627	1887	(Australia's Virtual Herbarium, 2019)
New Zealand	*R. conglomeratus*	202	1867	(New Zealand Plant Conservation Network, 2019b)
	R. crispus	437	1832	(New Zealand Plant Conservation Network, 2019c)
	R. obtusifolius	651	1835	(Darwin & Keynes, 1835)
Western North America	*R. conglomeratus*	103	1872	(Grant & Niezgoda, 2019)
	R. crispus	2014	1822	(Gall, 2019)
	R. obtusifolius	435	1550	(Vibrans, 1998)

Defining the Native range

I define the native range for each of these species as spanning Europe, the Middle East, and Northern Africa (Figure 2.2). Multiple databases, including the Global Biodiversity Information Facility (GBIF; GBIF.org, 2019) the Atlas Florae Europoaea (AFE, 1979), the Flora of Japan (FOJ; Flora of Japan, 2019), Calflora (Calflora, 2019), Centre for Agriculture and Bioscience International (CABI, 2019), U.S. Germplasm Resources Information Network (USDA, 2019), and the Global Weed Compendium (Randall, 2017), were consulted to determine where these species were classified as native (Table A.1). Areas of continuous species occurrence contiguous with these regions were likewise considered native, unless otherwise stated as a known introduction, as these occurrences were considered likely to be naturally distributed from the same range. A literature search was conducted to determine whether historical records indicated known introductions (Table A.2).

There is no consensus on whether Japan is part of the native or introduced range for *R. obtusifolius* and *R. crispus*. Some sources include eastern Asia and Japan as part of the native range for *R. obtusifolius* and *R. crispus* (Flora of Japan, 2019; USDA, 2019), while other sources consider the species introduced there (Grossrieder & Keary, 2004; Makuchi & Sakai, 1984; Miyagi et al., 2010; Nishida, 2002). Additionally, the available data for these species in Asia show a large geographic distance between the European and Asian populations suggesting that they are likely to be genetically isolated, or that there are large gaps in sampling. As a result, I do not consider Japan to be part of *R. obtusifolius* and *R. crispus*' native range. However, the analyses were repeated with the inclusion of Japan as part of the native range of *R. obtusifolius* and *R. crispus* in order to see whether this affected our results (Table A.5). Table A.1 displays a full list of the countries considered in this study and whether I classified these *Rumex* species as native or introduced in that country. *Rumex conglomeratus* is not considered native to eastern Asia by any of the assessed sources.

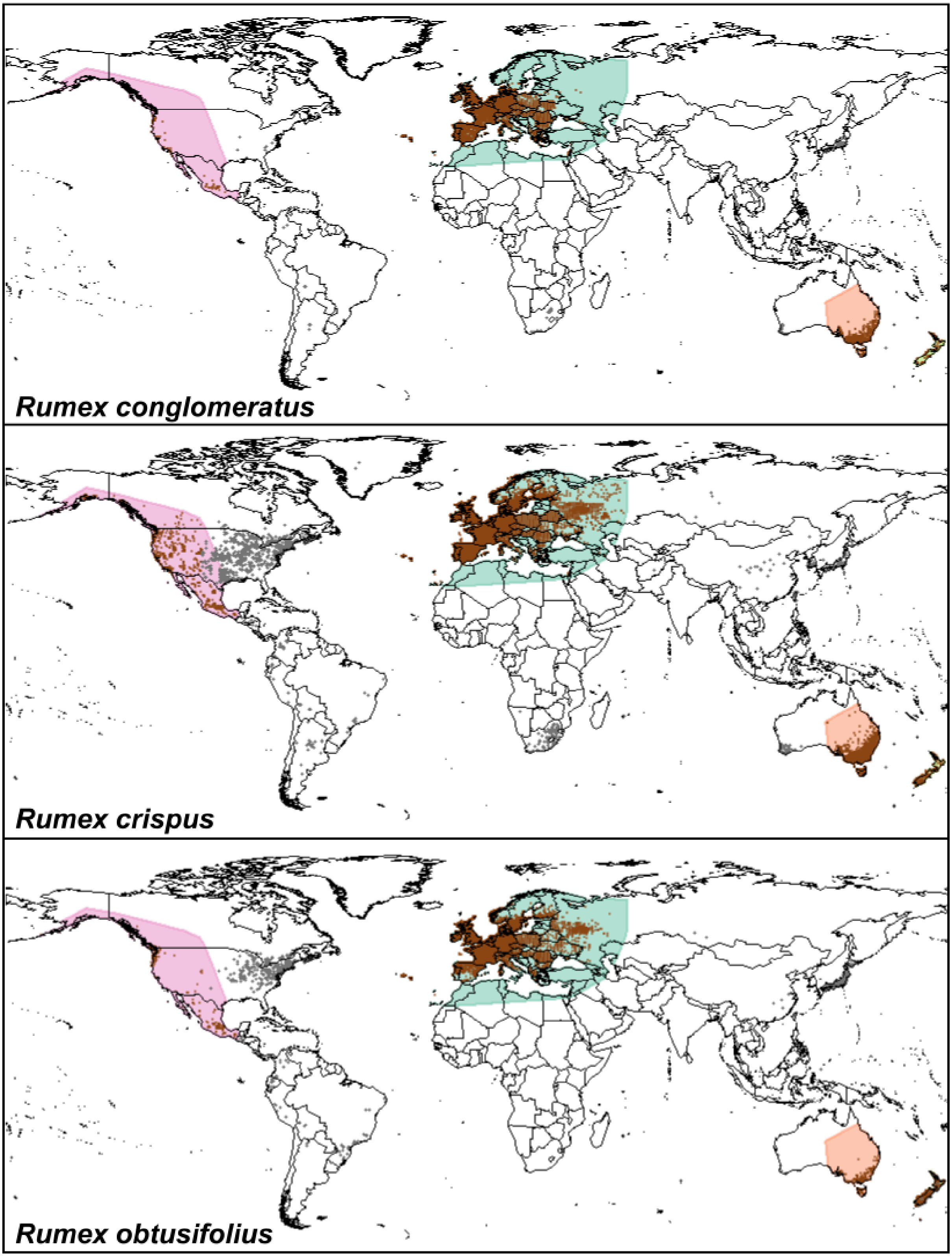

Figure 2.2 Worldwide distribution of *Rumex conglomeratus* (top), *Rumex crispus* (middle) and *Rumex obtusifolius* (bottom) records. Records span temperate and tropical zones. Records in brown were used in our analyses, and records in grey are considered introduced but fall outside of the assessed regions. Note that sources disagree on whether Japan is part of the native range for *Rumex* species, hence I classified Japan as an introduced range. Background climates considered are displayed by shaded minimum convex polygons: Native range – Teal; Western North America – Magenta; Eastern Australia – Orange; New Zealand – Green.

2.2.2 Data Collection

Species’ occurrence data

Occurrence records were collected for the three *Rumex* spp. from: GBIF, AFE, the Atlas of Living Australia (ALA), the Early Detection and Distribution Mapping System (EDDMapS; University of Georgia, 2019), Calflora, records georeferenced from targeted journals (Table A.2), and personal collections in the UK and NZ. Due to the underreporting of *Rumex* spp. distribution records in New Zealand, I examined New Zealand journals that commonly publish floristic inventories, using the search term “*Rumex*” and checked all results for occurrence records. Records were georeferenced at the highest possible resolution using Google Maps (google.com/maps). Table A.3 shows a breakdown of the number of records obtained for each species, and associated databases.

Occurrence records were cleaned by removing records with missing or inaccurate coordinates and records with coordinate uncertainties over 10,000m. Records were separated into the native range and three introduced ranges and thinned by applying a 2.5 arc minute grid over the occurrence points, and selecting one random point per grid cell using the R package GSIF (Hengl, Kempen, Heuvelink, & Malone, 2014). Thinning the occurrence records was necessary to reduce geographic sampling bias and remove duplicate results.

Climate data

To encompass variation in temperature and precipitation six of the 19 WorldClim (Booth, Nix, Busby, & Hutchinson, 2014; worldclim.org) variables known to affect plant distributions were selected at a 2.5 arc minute resolution (Dullinger et al., 2017; Root et al., 2003). The six selected variables were: temperature seasonality (BIO4), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), precipitation seasonality (BIO15), precipitation of the wettest quarter (BIO16), and precipitation of the driest quarter (BIO17). Both temperature (Benvenuti et al., 2001; Cavers & Harper, 1964, 1966) and precipitation, through soil moisture (Cavers & Harper, 1964), are of importance in determining plant species’ distributions at local scales and using fewer, more biologically relevant variables, helps to make results more interpretable (Fourcade et al., 2018).

2.2.3 Niche Analysis

In order to assess whether the climatic niche of these species changed in their introduced range I utilised the environmental principal component analysis (PCA-env) approach proposed by Olivier Broennimann et al. (2012). This method corrects for sampling biases by applying a kernel density smoother to estimate the density of occurrences. I adapted the standard approach by extracting climatic data from minimum convex polygons (MCPs) fitted around all three species' occurrence points combined, for each region, as opposed to each species individually. This allowed us to compare all three species within the same climatic boundaries and provided clearer comparisons between species. Following methods developed by Silva et al. (2016), a buffer zone of 1 decimal degree (~111km at the equator) was added around species' presences and MCPs were fitted around this area for each assessed region (Figure A.1). In order to reduce the number of variables to two, which the PCA-env approach requires, I performed a principal component analysis (PCA) on the climate data and used values of the PCA axes at the species' known occurrence points to calculate the conditions that are occupied by the species in each range. Following guidelines from Guisan et al. (2014) and amended by Silva et al. (2016), I performed pairwise comparisons between all three introduced ranges.

In order to determine whether climatic niche shifts occurred between the native and introduced ranges, comparisons were made between the available environmental conditions of each of the three introduced ranges and the native range, following metrics suggested by Guisan et al. (2014). The observed niche overlap in each comparison was calculated using Schoener's *D* (Olivier Broennimann et al., 2012; Schoener, 1970; Warren et al., 2008), a metric which varies from 0, indicating the greatest possible distance between the predicted occurrences of each range (no niche overlap), and 1, indicating no differences (complete niche overlap). I calculated niche similarity to determine whether the niches in the native and introduced ranges are more or less similar than expected by chance given their available climates (Aguirre-Gutiérrez et al., 2015; Warren et al., 2008, 2010). Significant values of niche similarity between the native and introduced ranges indicate the niches are more similar than expected by chance, and hence are good predictors of one another.

Proportions of niche expansion and niche unfilling were calculated to determine in what dimensions the niches of the native and introduced ranges are dissimilar to one another (Guisan et al., 2014). For consistency with other studies, I considered observations in analogue and non-analogue climates separately (Atwater et al., 2018; Guisan et al., 2014; Petitpierre et al., 2012). I define niche expansion as the proportion of environmental space present in both the native and introduced range, but only occupied in the introduced range, and niche unfilling as the proportion of environmental space present in both the native and introduced range, but only occupied in the native range. Niche pioneering was defined as the proportion of occupied environmental space in the introduced range which is only present in the introduced range. Using the values of these niche metrics I determined whether a species' niche shifted between the native and introduced ranges. I further used the PCA output to determine the direction, and hence consistency, of the shifts in climate space across regions for each species. The same methods were then applied across species within each region individually to detect differences between the occupied climate spaces of each species. All metrics were calculated using the *ecospat* package (Di Cola et al., 2017) in the statistical software R version 3.5.1 (R Core Team, 2013).

2.3 Results

2.3.1 Principal Component Analysis

The first two principal components explained 76.6% of the variation in the original six climate variables (44.0% and 32.6% for PC1 and PC2 respectively) and I take these to represent the available environmental space adequately. Increasing values of PC1 correspond to colder, wetter areas with more seasonal variation in their temperatures, and less seasonal variation in precipitation. Increasing values of PC2 indicate areas with greater wet-season precipitation and less seasonality in their temperatures (Figure 2.3).

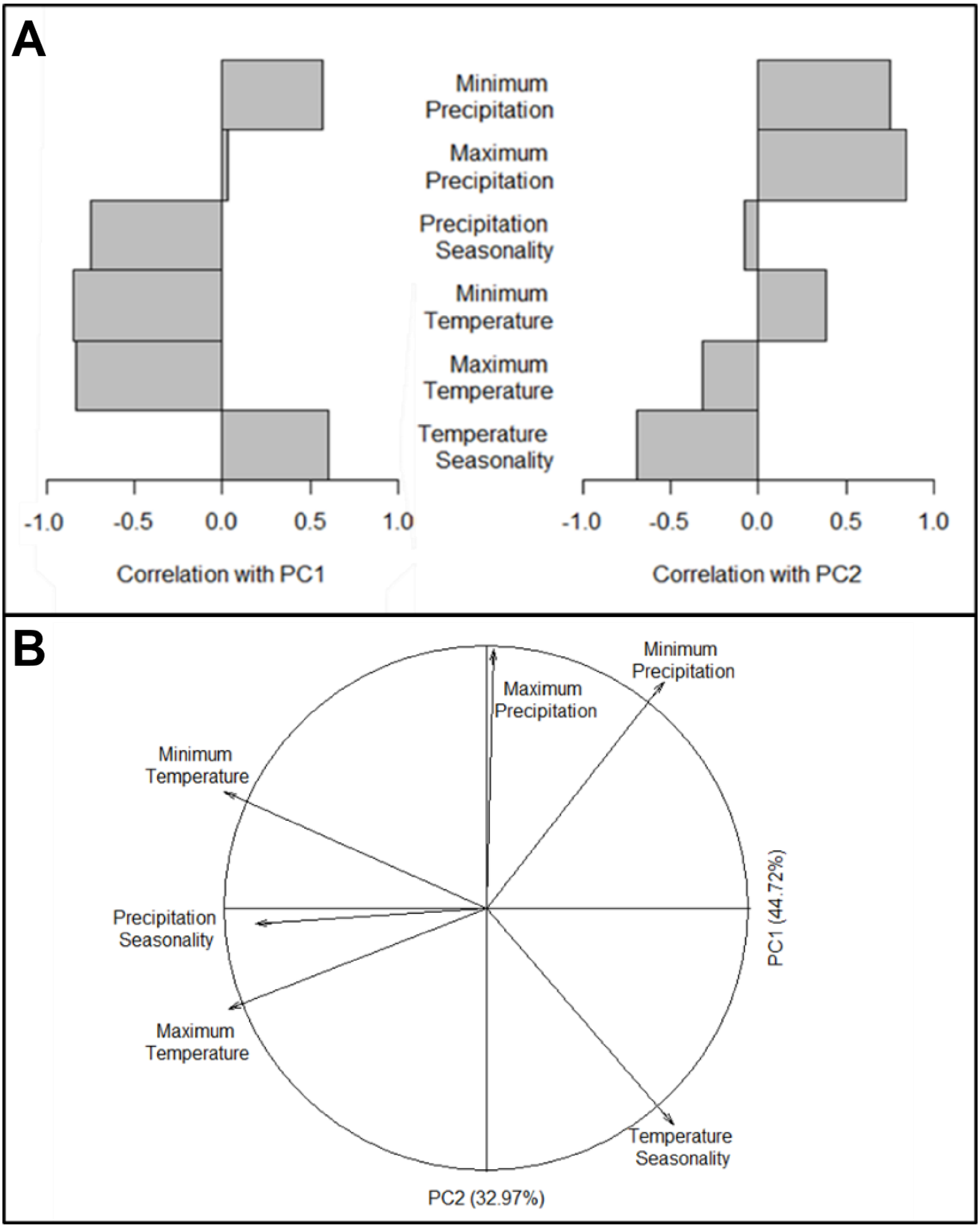

Figure 2.3 A) Contributions of variables to the first two axes of the principal component analysis. B) Direction of variables with respect to the first two principal components. Direction of arrows indicates increasing values of corresponding variable. The first two principal components represent the environmental space used for further niche analysis. Some variable names are shortened for simplicity: Minimum Precipitation = Precipitation of the driest quarter (BIO17), Maximum Precipitation = Precipitation of the wettest quarter (BIO16), Minimum Temperature = Minimum temperature of the coldest month (BIO6), Maximum Temperature = Maximum temperature of the warmest month (BIO5).

2.3.2 Niche shifts are inconsistent across regions

Climatic niche shifts were idiosyncratic across regions for all species, with one region characterised by niche conservatism (Figure 2.4; Australia) and two regions characterised by large niche shifts (Figure 2.4; New Zealand and North America). *Rumex* spp. exhibited climatic niche shifts into both analogue and non-analogue climate space (Table 2.2). Both the direction, and presence, of climatic niche shifts was broadly consistent across *Rumex* species (Figure 2.4), however, niche overlap between species was low in all introduced ranges compared to the native range (Table 2.3). Similarly, niche overlap when comparing species' distributions between the introduced regions was low despite significant values of niche similarity (Table A.6).

In New Zealand all three species expanded into warmer, wetter areas with more variable precipitation (lower values of PC1 and higher values of PC2; Figure 2.4). Levels of niche overlap and unfilling between the occupied climates in NZ and the native range were low (Table 2.2). The climatic niche shifts in NZ were primarily into non-analogue climate space, however niche expansion into analogue climate was also present (Table 2.2; Figure 2.4). New Zealand was the only introduced range that was not significantly similar to the occupied analogue climates in the native range for any species (Table 2.2).

In North America the climatic niche expanded into predominantly into warmer, drier climates (lower values of PC1 and PC2), but also into wetter cooler climates with less stable temperatures (higher values of PC1; Figure 2.4). North America had significant values of niche similarity with the native range for both *R. crispus* and *R. conglomeratus,* despite low levels of niche overlap, suggesting there is high niche overlap under analogue climates (Table 2.2). Two species, *R. obtusifolius* and *R. conglomeratus*, showed high levels of niche unfilling in North America where wetter, cooler areas remained unoccupied despite being available (high values of both PC1 and PC2; Figure 2.4). Climatic niche shifts in North America were observed across analogue and non-analogue climate space (Table 2.2; Figure 2.4).

Australia is the only region in which *Rumex* spp. largely conserved their climatic niche (Figure 2.4), and was the region with the highest level of niche overlap with the native range (Table 2.2). Furthermore, Australia is the only region that had significant niche similarity values compared to the native range for all three species (Table 2.2). *Rumex* spp. in Australia experienced low levels of niche expansion, in both analogue and non-analogue climates, and high levels of niche unfilling. Niche unfilling in Australia occurred in wet areas with highly seasonal temperatures and drier areas with less seasonal temperatures (both higher and lower values of PC2; Figure 2.4).

Comparisons of niche overlap between *Rumex* spp. within each region show little consistency across introduced regions (Table 2.3). *Rumex* spp. show high degrees of niche overlap and similarity in the native range, however levels of niche overlap are significantly lower in each introduced range. New Zealand is the introduced range that consistently has the highest level of niche overlap between species, and the only range in which all species' distributions are significantly similar to one another. The highest niche overlap was between different species pairs in each region (Table 2.3).

The inclusion of Japan within the native range of *R. obtusifolius* and *R. crispus* had minimal effects on the results (Table A.5). Because the occupied climate in the native range was slightly larger, niche expansion values in the introduced ranges were slightly reduced and niche unfilling was slightly increased. Additionally, niche expansion in North America was predominantly into non-analogue climates, rather than into both analogue and non-analogue climates. Most other measurements of niche overlap, expansion, and unfilling remain broadly similar (Table A.5).

Table 2.2 Results from pairwise comparisons between the native and introduced ranges of three *Rumex* species. "N" shows the number of occurrence records for each species and region. All comparisons are projected from the native range to the introduced range and consider analogue climate space only, except for niche pioneering. All metrics vary from 0-1, where 1 indicates complete similarity, complete expansion, complete unfilling, or complete pioneering; niche similarity is displayed as a p-value which, if significant, indicates regions are more similar than chance alone. Note that niche metrics are weighted according to the density of occurrences in climate space.

Species	Region	N	Niche Overlap (*D*)	Niche Similarity (p-value)	Niche Expansion	Niche Unfilling	Niche Pioneering
Rumex obtusifolius	Eastern Australia	275	0.319	0.01	0.071	0.399	0.059
	Western North America	242	0.077	0.07	0.686	0.516	0.569
	New Zealand	345	0.111	0.06	0.289	0.016	0.369
Rumex crispus	Eastern Australia	4035	0.341	0.01	0.029	0.389	0.015
	Western North America	823	0.150	0.01	0.467	0.283	0.317
	New Zealand	271	0.158	0.07	0.236	0.050	0.298
Rumex conglomeratus	Eastern Australia	1537	0.198	0.01	0.011	0.602	0.012
	Western North America	89	0.167	0.04	0.397	0.907	0.416
	New Zealand	125	0.152	0.06	0.334	0.066	0.364

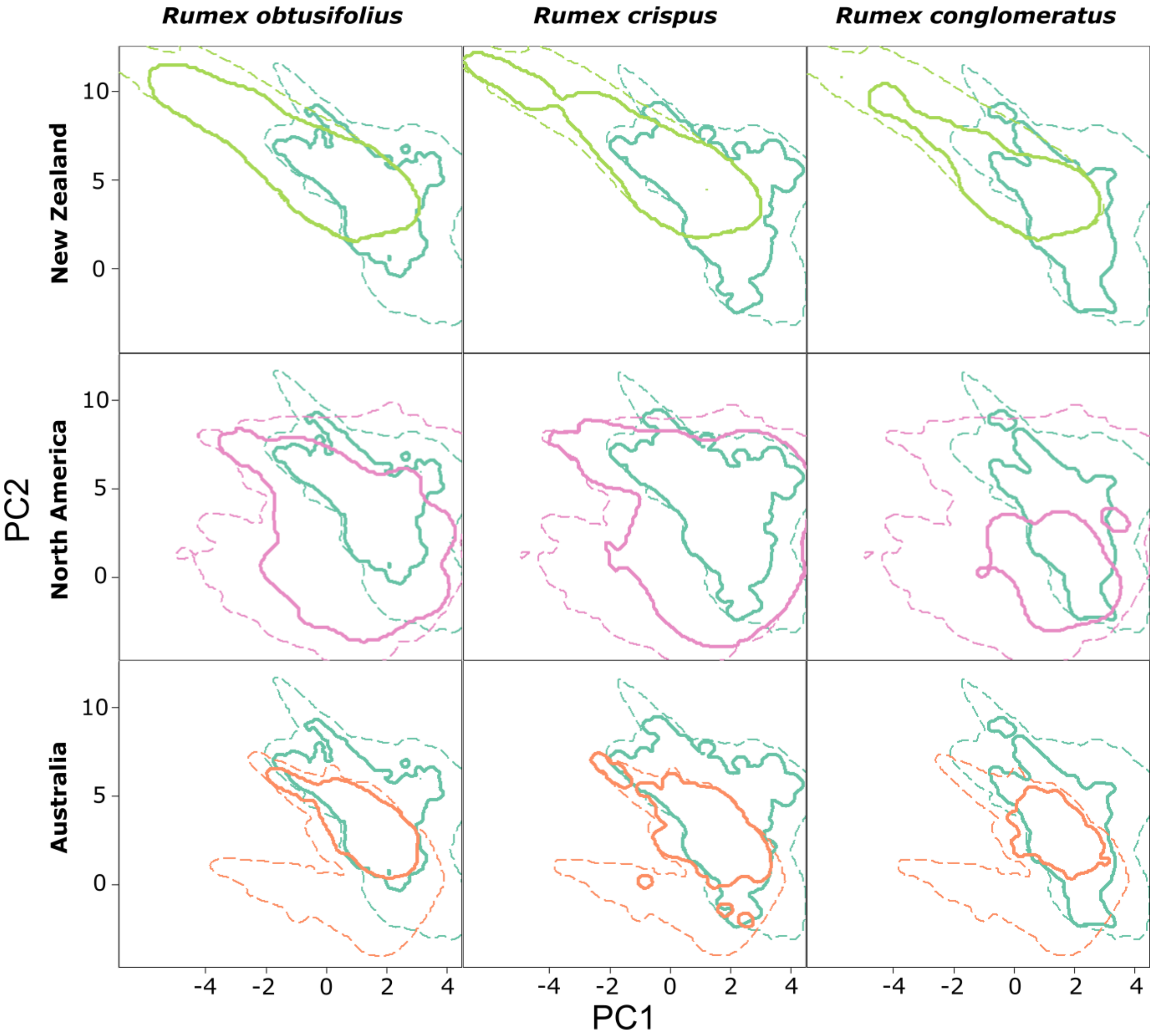

Figure 2.4 Comparisons of niche overlap in environmental space. Each panel shows the climate space occupied by the species (solid lines) and the total available climate space of the respective range (dashed lines). Each panel shows a comparison between the native range (Teal) and one of the introduced ranges (New Zealand – Green; North America – Pink; Australia – Orange). Comparing down columns shows differences between regions whereas comparing across rows shows differences between species in the same region. Increasing values of PC1 broadly correspond to cooler, more variable temperatures, and wetter, more stable precipitation. Increasing values of PC2 broadly correspond to cooler, more variable temperatures, and wetter, more stable precipitation. Variable correlations with PC1 and PC2 can be seen in full in Figure 2.3.

Table 2.3 Pairwise comparisons of niche overlap (*D*) and niche similarity between the three species within each region.

Schoener's D	*R.obtusifolius vs R. crispus*	*R. obtusifolius vs R. conglomeratus*	*R. crispus vs R. conglomeratus*
Native Range	0.914	0.709	0.682
Australia (East)	0.478	0.442	0.630
North America (West)	0.391	0.448	0.129
New Zealand	0.758	0.589	0.643
Niche similarity			
Native Range	0.010	0.010	0.010
Australia (East)	0.059	0.208	0.040
North America (West)	0.050	0.030	0.416
New Zealand	0.02	0.03	0.03

2.4 Discussion

Our results show that independent introductions of *Rumex* spp. have resulted in different realised climatic niches across geographically distinct ranges. In North America, *Rumex* spp. mostly shifted their niche towards drier climates, in contrast to New Zealand, where *Rumex* spp. shifted their niche towards much wetter climes (Figure 2.4). Whether *Rumex* spp. predominantly shifted their climatic niche into analogue or non-analogue climates also varied by region. Furthermore, I found little evidence that climatic niche shifts are consistent across closely related species, with only the distribution of *Rumex* spp. in New Zealand showing some consistency between species after climatic niche shifts. We are able to show that even superficially similar invasions by similar species can lead to examples of every theoretical niche change proposed by Guisan, Petitpierre, Broennimann, Daehler, & Kueffer (2014). This work suggests that the presence of a climatic niche shift in one region offers little assistance in forecasting climatic niche shifts in other regions.

Rumex spp. experienced climatic niche shifts in both North America and New Zealand, but conserved their niche in Australia. *Rumex* spp. in NZ have undergone dramatic niche expansion towards predominantly wetter climates. In NZ, *Rumex* spp. seem to occupy the majority of available climates, but have access to less variable climates than the other regions. Australia, on the other hand, has a large amount of hot, dry, non-analogue climate space (low values of PC1 and PC2) which is likely unsuitable for *Rumex* species, yet I found it still had unoccupied suitable analogue climates. Hence, Australia experienced high levels of niche unfilling, suggesting that factors other than climate are likely limiting *Rumex* spp. distributions in Australia. North America also experienced high levels of niche unfilling, but similarly high levels of niche expansion. This may indicate that *Rumex* populations in North America have rapidly adapted to novel climates, but may have lost adaptations to climates which are more common in the native range than in North America. Alternatively, factors other than climate are limiting or facilitating *Rumex* spp. distributions in North America. Whilst climate typically determines species' distributions at broad scales (Bello et al., 2013), it may be that these inconsistent climatic niche shifts are driven by non-climatic factors. Human disturbance is a strong driver of introduced species' distributions (Essl et al., 2020; Kołodziejek & Patykowski, 2015; Pysek et al., 2010; Redpath & Rapson, 2015; Seebens et al., 2018), and may facilitate species' climatic niche shifts into climates which otherwise would be unsuitable. Understanding whether non-climatic factors or species' traits affect the consistency of climatic niche shifts may help predict whether consistent niche shifts would be observed for different areas or species. I will return to this topic in chapter 3.

The lack of consistency in niche shifts between regions suggests that one cannot easily extrapolate the likelihood of a climatic niche shift in one region even if a species undergoes a climatic niche shift in another region. Our results broadly agree with Christina, Limbada, & Atlan (2019) who found that introductions of *Ulex europaeus* across five regions showed idiosyncratic climatic niche shifts between introduced ranges (Figure 2.1C). Furthermore, this study adds to the body of literature which suggests niche shifts are more common than previously thought (Atwater et al., 2018; Early & Sax, 2014). My study extends this work by demonstrating idiosyncrasy across multiple species, including climatic niche shifts in opposing directions (Figure 2.1B). In North America, all three species shifted into warmer, drier areas, and these populations expanded into a broader range of climates than New Zealand populations. Only a few other studies have compared shifts across multiple introduced regions (Christina et al., 2019; Silva et al., 2016), and they do not explicitly consider the direction of the observed shifts. My finding highlights the need to better understand the underlying causes of niche shifts to determine if we can predict whether species will undergo climatic niche shifts (Lantschner et al., 2019; Williams et al., 2019).

Despite the three *Rumex* spp. experiencing independent climatic niche shifts in a similar direction across all ranges, there were low levels of niche overlap between closely related *Rumex* species (Table 2.3). Whilst the distribution of *Rumex* spp. under analogue climates in NZ showed significant niche similarity, this was not the case in other regions. Furthermore, the distribution of *Rumex* spp. in their introduced ranges overlapped to a lesser degree than in their native range. Whilst this could indicate these species are still expanding into suitable climates in the introduced range, it could also show that climatic niche shifts are facilitating climatic niche divergence among these closely related species. These three *Rumex* spp. display differing environmental preferences in soil nutrient richness, pH, and moisture (Cavers & Harper, 1964; Hill et al., 1999; Lousley & Kent, 1981). Given these differences, and their long introduction histories allowing time for new adaptations to occur (Table 2.1; Vibrans, 1998), climatic niche divergence seems plausible as an explanation for why niche overlap in low. These results indicate that closely related species do not undergo similar climatic niche shifts, suggesting that pooling data between related species (Smith et al., 2019; but see: Mota-Vargas & Rojas-Soto, 2016) will have limited applications when predicting the distributions of species undergoing climatic niche shifts.

It is worth considering how sampling bias may have affected these results, as sampling bias can be common in the datasets I used. By sampling bias I mean that records are biased geographically, often around population centres or regular surveying sites. If records are highly biased they may influence values of niche overlap by increasing the density of presences in certain climates. To mitigate these problems I removed low quality data presences and spatially rarefied the remaining data. In addition to these steps the biology of *Rumex* spp. makes them less susceptible to sampling biases than other species. Sampling bias is most common when working with species that occur in inaccessible habitats (Beck et al., 2014), however our study species often occupy urban and other anthropogenic areas (Cavers & Harper, 1964). Furthermore, these species are common and well recorded across their native range. It is also worth considering whether taxonomic bias may have affected these results (Troudet et al., 2017). By taxonomic bias I mean that these species are often recognised but not recorded officially at the species level, as I found to be the case in NZ (Table A2). This may be in part due to the difficulty of identifying *Rumex* spp. before fruiting, and that hybridisation between *Rumex* spp. is common (Baskin & Baskin, 1978; Cavers & Harper, 1964; Grime et al., 2007; Holm et al., 1977, 1997). However, given that this study has relatively high levels of species' occurrences for this type of analysis, issues relating to taxonomic bias seem unlikely. Furthermore, additional occurrence records from the introduced ranges would most likely only increase the magnitude of shifts observed or reduce the incidence of niche unfilling, depending on where the records occurred in climate space. As such, I don't think these results would be strongly impacted by sampling or taxonomic biases in the data.

My results demonstrate that when species undergo climatic niche shifts, information from current introduced ranges may not provide useful information into the likelihood of climatic niche shifts occurring in a new region. For example, if we used data on climatic niche shifts between the native range and Australia to inform predictions of distributions in North America, we would dramatically underestimate the species' true distribution. It is however interesting to note that all three species had similar shifts in NZ, suggesting that niche shifts may be more predictable in some regions than others, however sampling of more species would be needed to test this possibility.

Expanding upon this work by using methods to quantify the magnitude of climatic niche shifts would aid in determining whether the magnitude of climatic niche shifts is predictable given species 'environmental tolerances. Modellers should however be careful and not simply rely on niche centroid methods which are unable to accurately discriminate between multiple niche dynamics, such as niche unfilling and expansion (Petitpierre et al., 2012). Improving methodologies to predict climatic niche shifts in the future is imperative to help stakeholders make informed management decisions.

As part of the major debate in ecology of how often species' niches are conserved, this study offers new insight by demonstrating inconsistency in niche shifts across multiple species and ranges. The occurrence and direction of climatic niche shifts lacked consistency when considered across different ranges, which weakens our ability to accurately predict the threat of introduced species to uninvaded ranges. These results agree with other studies which indicate niche dynamics are more difficult to predict than previously thought (Atwater et al., 2018; Christina et al., 2019). This study highlights that numerous niche dynamics can be experienced by a species depending on the range examined, and that these dynamics are not necessarily consistent between congeners.

Chapter 3

The importance of climatic vs non-climatic variables in predicting *Rumex* species distributions

3.1 Introduction

One of the main uses of species' distribution models (SDMs) is to predict the suitability of environments where a species could potentially establish outside of its native range (Lantschner et al., 2019; Parry et al., 2013; Pecchi et al., 2019; Vivek Srivastava et al., 2018). While climate is typically the largest determinant of distributions over large (i.e. continental) scales (Ashcroft et al., 2011; Petitpierre et al., 2017), non-climatic variables tend to dictate the distribution of species at smaller, local, scales (Bello et al., 2013; Collingham et al., 2000). Despite this, studies modelling non-native plant distributions rely primarily on climatic variables (Atwater et al., 2018; Bradie & Leung, 2017; Bradley et al., 2008; Broennimann et al., 2007; Chapman et al., 2019; Early & Sax, 2014; Gallagher et al., 2010; Petitpierre et al., 2012, 2017; Srivastava et al., 2019). However when non-climatic variables are included they are often important (Bello et al., 2013; Gallien et al., 2015; Gardner et al., 2019; Iturrate-Garcia et al., 2016). Bradie & Leung (2017) compared variable importance for roughly 1900 species and concluded that, for terrestrial plant species, resource variables such as distance to water and habitat characteristics were often the dominant predictor of their distributions when included in models. Soil (Mahgoub, 2019), disturbance (González-Moreno et al., 2015), topographical (Bello et al., 2013), geological, anthropogenic, hydrological (Bradie & Leung, 2017), and biotic (Jones & Gilbert, 2016) variables have also been considered important for plant species' distributions.

There are reasons to think that non-climatic variables could be quite important when predicting the suitability of environments beyond the native range. Human mediated dispersal along trade routes is the predominant driver of non-native plant species introductions (Essl et al., 2020; Seebens et al., 2018), either as seed contaminants in cargo (Gervilla et al., 2019; Lehan et al., 2013; Oseland et al., 2020), or direct introductions as ornamentals (Dehnen-Schmutz et al., 2007; Frick et al., 2011; van Kleunen, Essl, et al., 2018). These effects can be captured using non-climatic variables such as indices of human footprint (Venter et al., 2018). Furthermore, areas already disturbed by human activity are more susceptible to the establishment of non-native weeds than undisturbed areas (Kołodziejek & Patykowski, 2015; Pysek et al., 2010; Redpath & Rapson, 2015). As such, variables reflecting human influence rather than climate may be more reflective of non-native plant distributions in the introduced range and may be better predictors of their potential distributions than climatic variables.

Including non-climatic variables, such as land use or human footprint, in model projections could provide more accurate predictions in areas of non-analogue climate. Some regions where species have been introduced contain climates which are not present in the native range, otherwise known as non-analogue climates (Atwater et al., 2018). Model projections based on climatic data are not capable of making accurate predictions in these areas of non-analogue climates (Boiffin et al., 2017; Maguire et al., 2016; Sobek-Swant et al., 2012; Srivastava et al., 2019; Veloz et al., 2012). Non-climatic variables may however be analogous between regions in areas of non-analogue climates. For example, regions may show similar levels of human influence, such as infrastructure and population density, regardless of climate. In this case including non-climatic variables could lead to improved predictions.

In this study I utilise SDMs to predict the probability of presence across different environments for three ruderal weed species that have established outside of their native range: *Rumex obtusifolius*, *R. crispus*, and *R. conglomeratus*. These species have been spread worldwide as agricultural seed contaminants (Grossrieder & Keary, 2004; Halsted, 1889; Zaller, 2004) from as early as the 16th century (Vibrans, 1998). Chapter 2 established that in NZ these *Rumex* spp. undergo climatic niche shifts into warmer, wetter climates than the climates occupied in the native range. Given this climatic niche shift, we can now consider whether climatic variables are good predictors of *Rumex* spp. distributions in NZ or whether non-climatic variables may confer stronger predictive power. *Rumex* spp. are ruderals, typically colonising open, disturbed environments associated with human activity (Cavers & Harper, 1964, 1966; Grime et al., 2007; Holm et al., 1997; Lousley & Kent, 1981), suggesting human disturbance may be a good predictor of their distributions. Furthermore, *Rumex* are generally considered unpalatable to sheep, cattle, and rabbits (Cavers & Harper, 1964), allowing them to grow well in pasture systems as livestock preferentially graze on potential competitors. As the inclusion of biologically irrelevant variables can strongly impact the accuracy of model predictions (Austin & Van Niel, 2011; Brun et al., 2020; Fourcade et al., 2018; Merow et al., 2014) I consider only climatic and non-climatic variables that I expect to be important in predicting *Rumex* spp. distributions. Specifically, I investigate whether land use, human disturbance, hydrology, and livestock densities can improve on models made using only climate variables.

I compare models created for all three species in one of their introduced regions, New Zealand (NZ), and part of their native range, Great Britain (GB). I investigate whether utilising non-climatic variables in SDMs can better predict their distribution in the introduced range. I compare models computed using only climatic variables, only non-climatic variables, and a combination of both (hereafter combined model) to determine if utilising non-climatic variables can increase the accuracy of model predictions. With these analyses I aim to answer the following questions:

- Are climatic variables more important than non-climatic variables when predicting *Rumex* spp. distributions?
- Can models trained in the native range predict *Rumex* spp. distributions in the introduced range more accurately when utilising non-climatic variables?

Insights gained from answering these questions will shed light on which variables are most important for predicting the distributions of these species, and whether the variables that determine these species' distributions are consistent across species and regions.

3.2 Methods

3.2.1 Species and Study Area

For this analysis I selected three *Rumex* species: *R. obtusifolius* L., *R. crispus* L., and *R. conglomeratus* Murray. All three species grow well near water but *R. conglomeratus* specifically has higher soil moisture requirements than the other two species, typically only growing near water bodies or areas of high precipitation (Cavers & Harper, 1964; Hill et al., 1999; Lousley & Kent, 1981). These species are shade intolerant, with both germination and and flowering inhibited by low light levels (Cavers & Harper, 1964). *Rumex* are generally considered unpalatable to most mammalian herbivores, but deer will readily consume them (Cavers & Harper, 1964). Furthermore, they can withstand significant grazing or mowing, and can regrow from small root fragments (Holm et al., 1997).

All three species are native to Europe, the Middle East, and Northern Africa (GBIF.org, 2019; Holm et al., 1979) and have established on every continent aside from Antarctica (Chapter 2). New Zealand (NZ) is one of the many regions across the world where these *Rumex* spp. were introduced as agricultural seed contaminants and have subsequently established and spread (Grossrieder & Keary, 2004; Halsted, 1889; Zaller, 2004). Historical trade routes and observations indicate that Great Britain (GB) is likely the initial source of *Rumex* spp. contaminants in NZ (Darwin & Keynes, 1835). As such, I selected GB to represent the species' native range. Both countries have similar land areas and climate, but differ in levels of human density and land uses which may be important determinants of species' distributions (Table B.3). Additionally, GB also contains the majority of analogue climates found between the native range and NZ (Chapter 4). Furthermore, Chapter 2 showed that occurrence records are available for both countries across the majority of available climates.

I collected records for each country using a combination of data from the Global Biodiversity Information Facility (GBIF; GBIF.org, 2019) and personal records from the research team, excluding records from overseas depedencies of both countries (Table 3.1). Due to the large number of islands around both regions I included any island within 100km of the mainland and greater than 1km^2 as part of the region (Figure B.1). In NZ, a substantial number of records were added for each species through personal data collection by the research team and a review of the available online literature. Due to the undersampling or underreporting of *Rumex* spp. distribution records in NZ I examined New Zealand journals that commonly publish floristic inventories, searching for articles using the search term "Rumex" and checked all results for occurrence records. Records were georeferenced at the highest possible resolution using Google Maps (google.com/maps). Table B.1 shows a breakdown of the number of records obtained from each data source. For greater accuracy, occurrence records with a coordinate uncertainty greater than 1km were excluded. Records older than 1981 were also excluded to ensure the occurrence data matched the climate and land use variables.

Table 3.1 Number of occurrences for each species in the native (GB) and introduced (NZ) ranges used in species' distribution models. Occurrences were collated from GBIF, literature records, and personal records (Table B.1). Numbers shown are remaining records after filtering for quality and year, and subsequent spatial rarefication (Table B.1).

Species	Great Britain	New Zealand
Rumex obtusifolius	11484	271
Rumex crispus	6540	220
Rumex conglomeratus	1462	44

3.2.2 Environmental Layers

Only environmental variables that I expected to be of biological relevance to *Rumex* species were included in SDMs. These variables fall into 4 general categories: climate, land use, human impact, and hydrology. To ensure an accurate comparison between countries, environmental variables were only included if they were consistent between countries in years recorded, scale, and coverage. For this reason soil type was not included, as 63.4% of NZ has not currently been assessed (Manaaki Whenua - Landcare Research, 2020), and soil categories between the two countries are not uniform.

Climate

Cavers & Harper (1964) suggest that *R. obutisfolius* and *R. crispus* are unlikely to be limited by climate in GB. *Rumex conglomeratus* is absent from much of northern GB, and it is known to be less tolerant of cold climates than the other two species (Hill et al., 1999), suggesting that climate limits its distribution in GB. As *Rumex* spp. are shade intolerant and depend on exposure to light to germinate (Cavers & Harper, 1964) differences in light availability may affect their distribution and growth (Bradie & Leung, 2017; Mason, 2009; Monteith, 1977). Furthermore, due to the differences in UV intensity in NZ and GB one might expect the importance of light availability on distributions to vary between these regions (Hock et al., 2019). I used four climate variables I suspect would affect *Rumex* spp. distributions: mean temperature of the warmest month, mean temperature of the coldest month, mean precipitation of the wettest month, and median sunshine hours. For GB, data were downloaded from the Met Office HadUK-Grid datasets at a 1km^2 spatial resolution from 1981-2010 (Met Office et al., 2018). For NZ, data was acquired from the National Institute of Water and

Atmospheric Research (NIWA, 2019b) at a 500m^2 spatial resolution from 1981-2010, and subsequently aggregated into a 1km^2 grid over NZ.

Land use

Global land use data were downloaded from the European Space Agency (ESA, 2019a). Global data were converted from netcdf format and subsetted into separate datasets for GB and NZ using SNAP software (ESA, 2019b). The initial thirty-eight land use categories were grouped into seven land class types (Table B.2) using ArcGIS Pro v2.4.2 (ESRI, 2019). Hydrological data was included as a separate variable and therefore I excluded water bodies as a land use category (Table B.2). Data were extracted onto a 1km^2 grid in R v3.5.1 (R Core Team, 2013) where the value of each cell represented the proportion of that cell covered by the land cover type. This resulted in six separate continuous land cover variables for each region. Pasture, which is a land use type considered important for the distribution of *Rumex* species (Cavers & Harper, 1964; Grime et al., 2007; Holm et al., 1997), falls within the "Grassland" land use category. The proportion of each country associated with the different land cover types can be seen in Table B.3.

Human

Three human-related variables were included: sheep density, cattle density, and human footprint index. I chose to include data on livestock densities as the target *Rumex* spp. are all agricultural weeds which establish well in grazing pastures (Cavers & Harper, 1964; Grime et al., 2007; Holm et al., 1977, 1997). Global livestock density data were downloaded as a 0.00833333^o decimal degree grid, collected in 2006. These grids were then converted from netcdf formats in SNAP, and adapted into a 1km^2 grid using the raster package in R (Robert J. Hijmans, 2019).

To measure human disturbance I used the human footprint index downloaded from the Center for International Earth Science Information Network (CIESIN; https://sedac.ciesin.columbia.edu/data/set/wildareas-v3-2009-human-footprint). This index aggregates information from 2009 on built-up environments, population density, electric power infrastructure, crop lands, pasture lands, roads, railways, and navigable waterways (Venter et al., 2018). It is thought to be a good approximation of human disturbance which is known to affect the distribution of weed species (Lantschner et al., 2019; Maskell et al., 2020; Pysek et al., 2010). Data was downloaded as 1km^2 grids.

Hydrology

Bradie & Leung (2017) indicated that distance to water was the most important variable, aside from climate, in predicting the distributions of land plants. Gardner et al., (2019) similarly demonstrated that the typical climatic variables included in SDMs such as seasonal or annual rainfall are poor proxies of water availability. Accordingly, I created a separate hydrological variable from global river data downloaded from the WWF HydroRIVERS dataset (Lehner & Grill, 2013). Total length of rivers within a grid was used as a proxy for distance to water and to generalise the variable onto the same spatial scale as other variables. The total length of rivers within each 1km^2 grid cell was calculated using ArcGIS Pro.

3.2.3 Sample Bias

Species' presences show strong spatial biases due to geographic differences in recording effort (Aikio et al., 2012). For common, widespread, species such as *Rumex* these biases may also reflect underreporting in areas where the species may actually be common, as widespread species may be considered less important and hence not targeted by botanists (Kramer-Schadt et al. (2013). To correct for biases I used two complementary strategies. Presence data were spatially filtered to reduce clumping by thinning data to one point per 1km grid cell using the R package spThin (Aiello-Lammens et al., 2015). I also included a sample bias layer in the models to reduce the influence of areas where bias occurred (Kramer-Schadt et al. 2013). I produced an estimate of bias for each country by pooling data from all three *Rumex* spp. together to create a raster in ArcGIS Pro. Total number of presences was counted within in each grid cell and subsequently converted to a proportion of the maximum number of presences in a single cell, hence values ranged from 0-1. Grid cells which initially contained 0s were given a value of 0.01, representing that these cells had 1% survey effort compared to the cells that had maximum survey effort (1.00) in each country. Initially I created bias files using data from all plant species available on GBIF in GB and NZ, however the resulting sample bias layer did not adequately capture the sampling bias for *Rumex* spp. in NZ (Figure B.1). This is likely due the large number of presences derived from targeted Rumex surveys undertaken by the research team in areas of low survey effort for NZ plants. Including a sample bias layer produced from all plants does not adequately account for the authors' surveys.

3.2.4 MaxEnt Modelling and Evaluation

To estimate the suitability of environments across each country I ran SDMs using MaxEnt version 3.4.1 (Phillips et al., 2020) for each *Rumex* species. MaxEnt compares a null model, where a species prefers all environmental conditions proportionally to their prevalence in the landscape, to an alternative model where a species' distribution is constrained by information from the observed presences (Elith et al., 2011; Phillips et al., 2006; Phillips & Dudík, 2008). Parameter estimates in MaxEnt are designed to minimises the distance between these two models subject to constraints imposed by the background information from presence locations (Elith et al., 2011). These constraints ensure that the final predictions reflect the original presences by ensuring that, for example, the predictions of environmental variables from the final model have the same mean values as given by the species' presence locations. Minimising the distance between both models with constraints is the equivalent of maximising the entropy of the null model (Elith et al., 2011).

MaxEnt often matches or outperforms other modelling methods in terms of predictive power, especially in studies such as ours which use presence-only data (Gastón & García-Viñas, 2011; Merow et al., 2013; Merow & Silander, 2014; Mousazade et al., 2019; Shabani et al., 2017; Vivek Srivastava et al., 2020; West et al., 2016). MaxEnt can have model accuracy and predictions similar to ensemble models, which combine multiple algorithms to predict species' distributions (Kaky et al., 2020; Vivek Srivastava et al., 2018). It also performs well with small sample sizes (Barry & Elith, 2006), as is the case for *R. conglomeratus* in NZ. MaxEnt provides an intuitive and accurate way to measure variable importance (Smith & Santos, 2020) using a jackknife approach to systematically remove one variable at a time and measure the subsequent change in model performance. Variable importance can also be measured by fitting a model with only one variable at a time, and measuring the changes in model performance. The iterative model fitting approaches implemented in MaxEnt are also robust to strongly correlated variables (Braunisch et al., 2013; Synes & Osborne, 2011), as is often the case with climate variables. The increase in performance from including these correlated variables within the model tends to outweigh possible collinearity issues (Braunisch et al., 2013; Dormann et al., 2013). Nonetheless, I tested for multicollinearity among all variables to look for unexpected relationships between variables (Table B.4).

Models were run using: i) only climatic variables, ii) only non-climatic variables, and iii) both climatic and non-climatic variables. All models were run using MaxEnt version 3.4.1 (Phillips et al., 2020) with the following settings: random test percentage = 30; regularization multiplier = 1; maximum number of background points = 10,000. Individual models were run for each species in both GB and NZ. Number of training and testing records are presented for each model in Table B.5. All models were replicated 100 times utilising non-parametric bootstrapping and the results from the average model are presented. We present predictions as the probability of presence, derived by using the cloglog option, which is more easily interpretable and offers more robust results than the raw output (Phillips et al., 2017). The main effect of using cloglog transformed data as opposed to other output formats is that areas of moderately high output are more strongly predicted (Phillips et al., 2017). To determine whether the models were suitable at predicting *Rumex* spp. distributions I used two measures of SDM accuracy: the area under the receiver operating curve (AUC) and the true skill statistic (TSS). Values of AUC range from 0-1, where models with values greater than 0.7 are generally considered to have good discriminatory power (Hosner & Lemeshow, 1989). TSS is calculated as follows:

$$\text{TSS} = \text{sensitivity} + \text{specificity} - 1$$

Sensitivity is the proportion of presences accurately predicted and specificity is the proportion of absences accurately predicted. Values range from -1 to 1, where values approaching 1 show a model with accurate predictions, values approaching -1 show a model with inaccurate predictions, and values close to 0 show an indiscriminate model (Allouche et al., 2006). The TSS relies on a user-selected threshold to differentiate between true presence/absences and predicted presence/absences to calculate its values of sensitivity and specificity. To select an appropriate threshold I followed the suggestion of Liu, White, & Newell (2013) who concluded that an objective and accurate threshold value should be based on maximising the sum of sensitivity and specificity (SSS). AUC and TSS scores are unaffected by the choice to present MaxEnt output on the cloglog scale (Phillips et al., 2017).

I used permutation importance values to assess variable importance alongside the response curves associated with each variable. Permutation importance values indicate which variables contributed most to the final model by calculating any change in performance when the variable's values are randomized (Phillips et al., 2006). Response curves are produced for each variable which indicate how the probability of occurrence is affected at a variables different values. I also compared maps of species' habitat suitability predictions to determine whether using different variables significantly affected the interpretation of suitable habitats.

To understand whether non-climatic variables could aid in predicting *Rumex* spp. distributions beyond the native range I projected all models for each species from GB to NZ. I assessed the accuracy of model projections by comparing them to existing species' data in the introduced range (Journé et al., 2020; Pannell et al., 2019; Sobek-Swant et al., 2012). TSS scores for models and model projections were calculated using the available NZ occurrence data and pseudo-absences randomly generated across NZ using the dismo and pROC R packages (Hijmans et al., 2015; Robin et al., 2011). Pseudo-absences were equally weighted against presences in calculations of TSS scores. Random generation of pseudo-absences adds uncertainty to the TSS scores so I repeated the process one hundred times and calculated 95% confidence intervals. Models were considered statistically different from one another if their 95% confidence intervals did not overlap.

3.3 Results

3.3.1 Are models good at predicting *Rumex* spp. distributions?

All three NZ models had AUC scores >0.7 which indicate good predictive power and the TSS scores ranged from 0.48-0.78 indicating good discrimination of true presences and absences compared to a null model (Figure 3.2; Figure B.2). Models for GB generally had lower AUC and TSS values than NZ models (Figure 3.2; Figure B.2), with AUC ranging from 0.52-0.76 and TSS ranging from 0.09-0.45 for the combined model. Values of AUC between 0.5-0.6, and TSS scores close to 0, suggest models are not much better than chance at predicting distributions (Figure 3.1). As such, all models for *R. crispus* and *R. obtusifolius* in GB performed poorly. Models of *R. conglomeratus* in both regions had consistently higher AUC and TSS scores compared to the other two species, aside from the climate model for NZ in which it scored lowest. The combined model generally performed better than the non-climate models and always performed better than the climate models (Table 3.2).

3.3.2 Are climatic variables more important than non-climatic variables?

In all cases non-climate models either significantly outperformed or matched the performance of climate models (Figure 3.2). The actual differences between climate only and non-climate models in AUC and TSS scores were typically small (AUC within 0.05; TSS within 0.1), indicating similar accuracy in predictions. However, the non-climate model substantially outperformed the climate model for *R. conglomeratus* in NZ (Figure 3.2). Despite similarities in model performance, predictions of presence vary between the two model types (Figure 3.3).

Human related variables were generally the most important contributors to models, regardless of species or country, when considering the grouped average permutation importance of variables in combined models (Table 3.2). The two exceptions were the models for *R. crispus* in NZ and *R. conglomeratus* in GB where climate was on average the greatest contributor to the models. According to permutation importance, human footprint was the greatest contributor to every model aside from the combined model of *R. conglomeratus* in GB which relied heavily on climatic variables. However, permutation importance values may be lower for climatic variables due to higher multicollinearity compared to non-climatic variables (Table B.4). Suitability was high for habitats with moderate values of human footprint compared to habitats with low values (Figure B.3). Beyond a certain point increasing values of human footprint either reduced the probability of presence (*R.*

conglomeratus) or showed little difference in probability of presence (*R. obtusifolius* and *R. crispus*) (Figure B.3).

Between countries and species there were marked differences in which individual variables were important in predicting their distributions. Models of all species for GB showed herb and shrubland to be a predominant contributor to model predictions, but this contribution was low for all NZ models (Table 3.2). Herb and shrubland is forty-five times more prevalent in the UK than in NZ as a proportion of total land cover (Table B.3). Similarly, forest cover was more important in all NZ models compared to UK models, even if the overall contribution was low (Table 3.2), and is three times more prominent in NZ than in GB (Table B.3). Cropland is five times more prevalent in NZ than in GB, but was never a strong contributor to models. Median sunshine hours was shown to be important for *R. obtusifolius* in both regions, however never contributed highly for models of *R. conglomeratus*.

3.3.3 Can models trained in the native range accurately predict *Rumex* spp. distributions in the introduced range?

All model projections from GB onto NZ performed better than expected by chance alone when considering TSS (Figure 3.4). Non-climate models for all species had the highest TSS when projected from GB onto NZ. Projections using only climatic variables consistently showed the poorest performance with a TSS at least 0.1 lower compared to projections using non-climatic variables for all species. Models trained in NZ outperformed model projections from GB in all but one comparison. Projections based on non-climate models of *R. conglomeratus* performed similarly to models trained in NZ, whereas projections of both combined and climate models showed poorer performance (Figure 3.4).

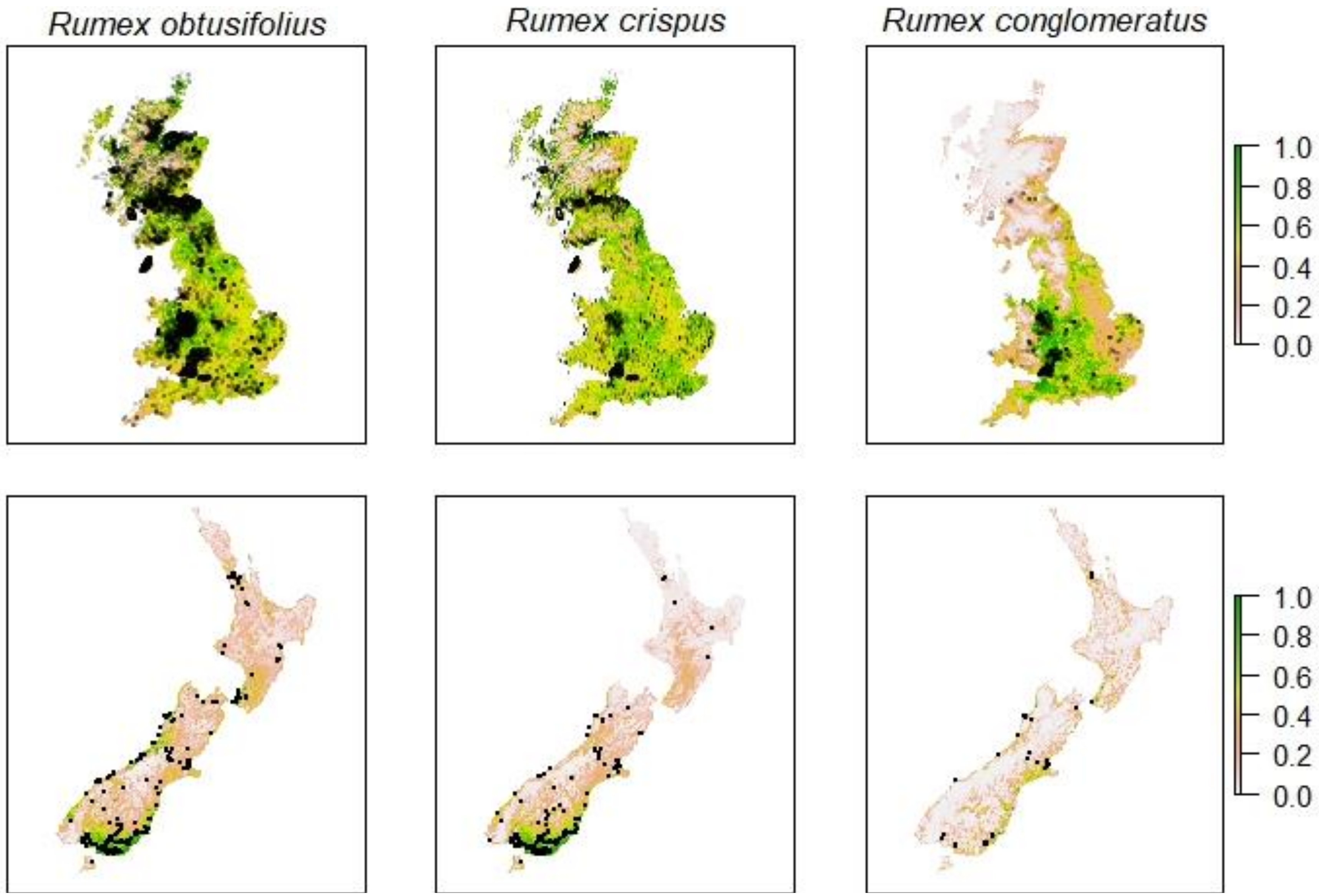

Figure 3.1 Species' occurrence points (black) plotted over average MaxEnt predictions of suitable environments for GB (top row) and NZ (bottom row) based on the 100 replications of the combined model utilising bootstrapping. Points in GB are plotted at a 10% opacity to give an indication of the density across the country. Values range from 0-1 where 0 (white) indicates a low and 1 (green) indicates a high probability of occurrence.

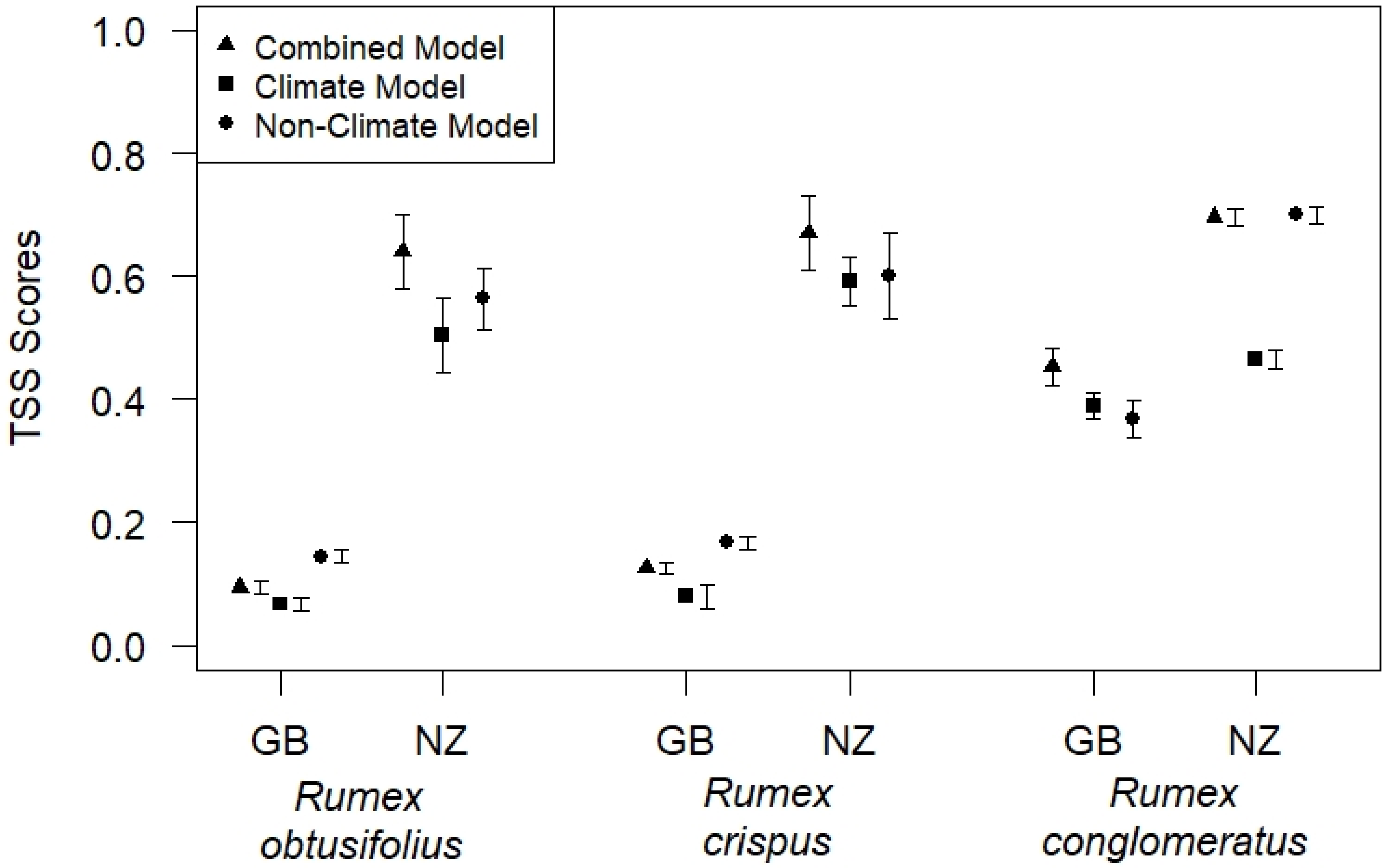

Figure 3.2 **True skill statistic (TSS) scores for species' distribution models of *Rumex* spp. in both GB and NZ. TSS varies from -1 – 1, where 1 represents completely accurate predictions, -1 represents completely inaccurate predictions, and 0 indicates model predictions are no better than chance alone. Models were run using a combination of either only climate or non-climate variables, or a combination of both climate non-climate variables. Error bars represent 95% confidence intervals. Note that some error bars are jittered for better visualisation.**

Table 3.2 **Permutation importance values of each variable included in the average combined model for each region and species. Top 3 variables for each model are indicated by bold values. Values add up to 100. The average value of all permutation importance values in variable groupings are also provided as a rough comparison of variable importance between groupings. These averages of variable groups are not equivalent to the value that would be obtained if all variables in that group were randomly permuted simultaneously.**

Groupings	Variable	*Rumex obtusifolius*		*Rumex crispus*		*Rumex conglomeratus*	
		NZ	GB	NZ	GB	NZ	GB
Land Use	Bare	4.8	0.5	5.2	0.1	1.5	0.1
	Cropland	3	0.7	1.9	0.0	1.6	0.0
	Forest	7.8	4.2	**7.9**	2.6	9.3	1.4
	Grassland	7.8	1.1	7.7	5.3	10.2	1.0
	Herb/Shrub	5.3	**17.6**	2	**21.6**	3.1	**14.2**
	Urban	4.4	0.1	4	0.0	0.7	0.0
	Average	5.5	4.0	4.8	4.9	4.4	2.8
Human	Cattle	**8.5**	0.4	4.8	**13.1**	**10.3**	2.9
	Human	**19.3**	**46.8**	**23.7**	**36.3**	**30.4**	0.0
	Sheep	4.3	0.0	4.1	0.0	9.6	2.4
	Average	10.7	15.7	10.9	16.5	16.7	1.8
Hydrology	Hydrology	4.4	0.0	1.2	0.6	**10.7**	1.3
Climate	Max Temp	6.6	0.8	13	9.7	1.9	**42.6**
	Min Temp	6.5	0.1	7.2	5.4	2.2	4.9
	Precipitation	5.5	11.3	6.8	4.6	6.7	**25.4**
	Sun Hours	**11.8**	**16.4**	**10.6**	0.5	1.8	4.7
	Average	7.6	7.15	9.4	5.1	3.2	19.2

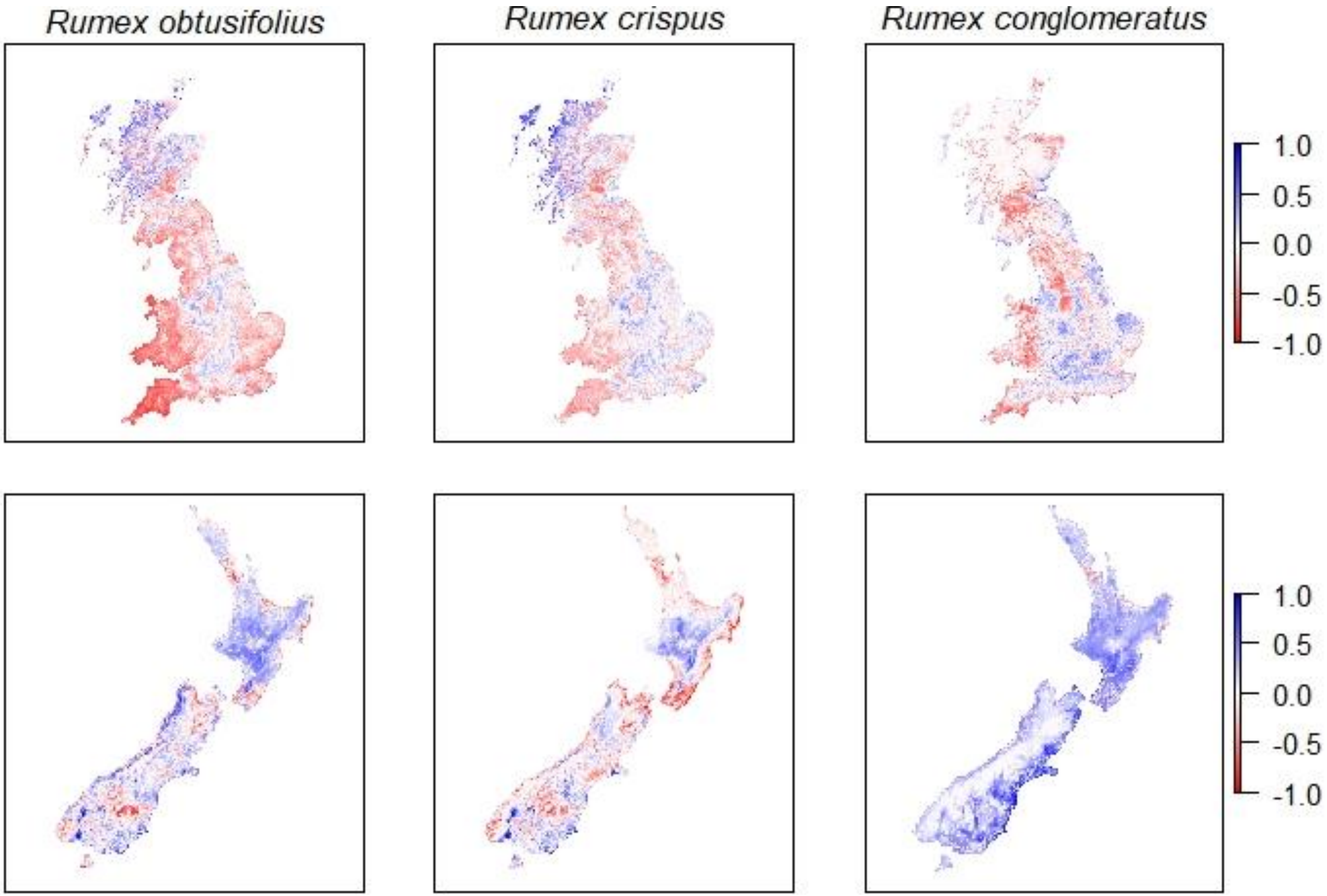

Figure 3.3 Differences between MaxEnt predictions from a model using only climatic variables and a model using only non-climatic variables. Values above 0 (blue) indicate the climate model predicted higher probability of presence than the non-climatic model and values below 0 (red) show areas which the climate model predicted lower probability of presence. Values close to 0 (white) indicate areas of agreement between the two model types.

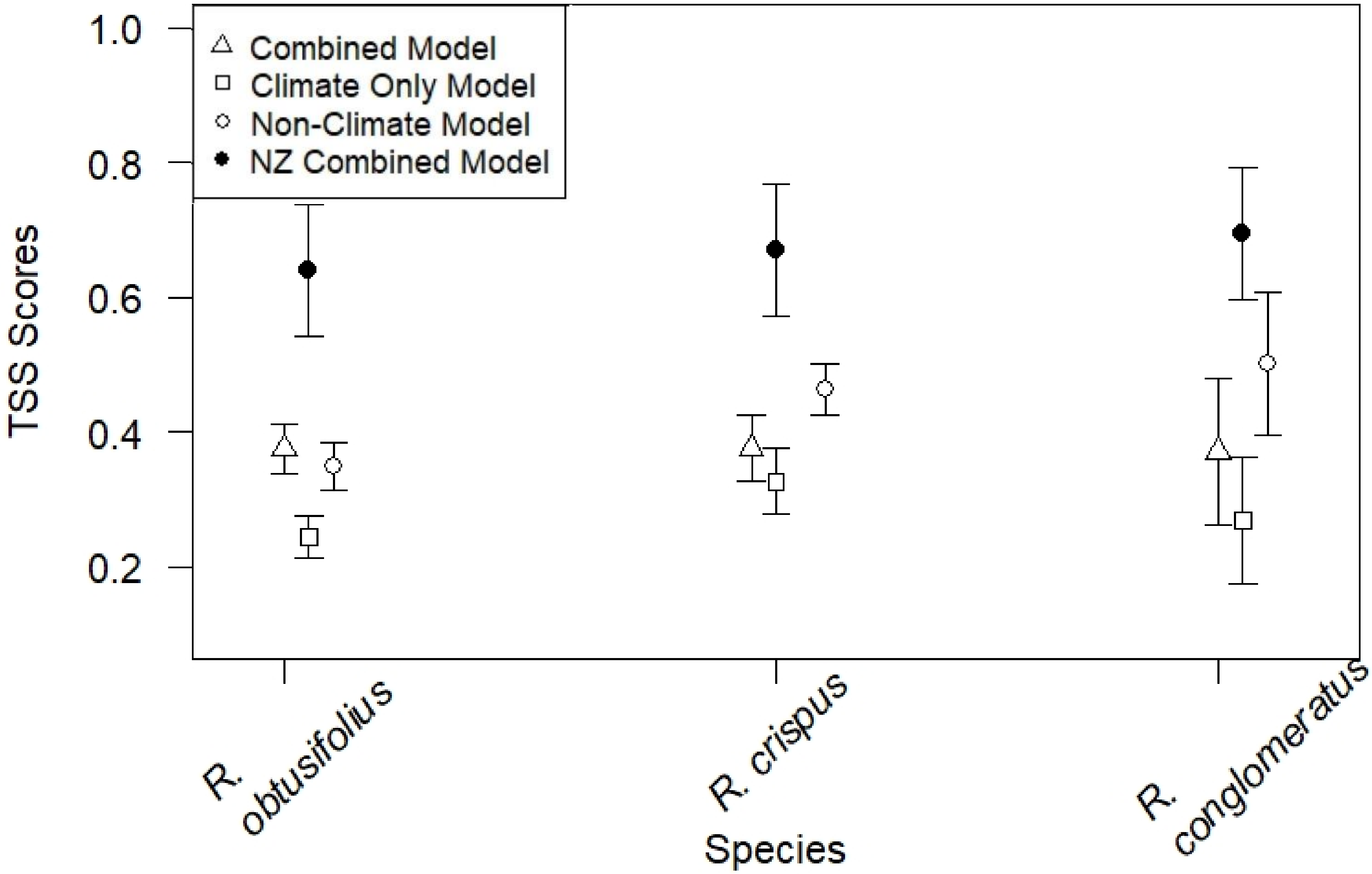

Figure 3.4 Comparison of TSS scores between model projections from GB onto NZ for climate only (square), non-climatic only (circle), and combined models (triangle). Combined models trained and tested in NZ were shown as a comparison of performance. TSS scores were calculated by comparing predictions to known presences in NZ and randomly generated pseudo-absences. Points represent mean TSS score of a particular species' model with error bars displaying 95% confidence intervals. Random generation of pseudo-absences was conducted 100 times to get both mean values and 95% confidence intervals. TSS values range from -1-1 where values close to 0 indicate a model is no better than chance.

3.4 Discussion

The importance of non-climatic variables to SDMs is currently unclear (Journé et al., 2020; Lantschner et al., 2019; Stanton et al., 2012). The results of this study show that including non-climatic variables in SDMs almost always improved the accuracy of predictions. The only exception was *R. crispus* models in NZ, for which climate only models performed best (Figure 3.2). Despite this, the contribution of most non-climatic variables to models was relatively small. Non-climatic variables were particularly important when projecting SDMs between ranges, with the most accurate projections excluding climate data entirely. This result is important because many model projections are based solely on climatic data (Journé et al., 2020; Lantschner et al., 2019). This work suggests that including non-climatic variables in SDMs would often lead to improvements in predicting distributions of introduced species.

The utility of a climate model seems to depend on the *Rumex* spp. examined. For the two broadly distributed generalists, *R. obtusifolius* and *R. crispus*, climate models performed similarly to the combined models. For *R. conglomeratus* however, the combined and non-climate models were a considerable improvement over climate only models in the introduced range (Figure 3.2). Including non-climatic variables in models never reduced the AUC or TSS of a model, suggesting that drawbacks in model performance when they are included are uncommon. Whilst I was working at large spatial scales, across countries, I considered variables at a relatively fine grain, 1km^2. As such, these results agree with other studies that non-climatic variables are good at predicting species' distributions at a fine grain however these results may be less applicable at coarser scales (Bello et al., 2013; Cherrill et al., 1995; Gogol-Prokurat, 2011; Guisan & Thuiller, 2005; Reinhardt et al., 2020; Shabani et al., 2020; Sobek-Swant et al., 2012; Wang et al., 2019).

Non-climatic variables were often the most important variables in the combined models. In particular, human footprint was generally the largest predictor of *Rumex* spp. distributions. This finding is in agreement with other studies suggesting that human disturbance is a driver of non-native plant species' establishment at large scales (Lantschner et al., 2019; Maskell et al., 2020; Pysek et al., 2010; Venter et al., 2018). Climatic variables nonetheless had large contributions to the majority of models. Interestingly, combined, climate only, and non-climate only models all performed similarly for models in GB. This suggests that, even though multicollinearity between climatic and non-climatic variables is low (Table B.4), climatic and non-climatic variables explain much of the same variation in how species are distributed. Despite their similar performance, interpretations from models can differ drastically (Figure 3.3). Including non-climatic variables in models seems to reduce predicted suitability across the majority of the distribution (Figure B.2).

Land use and livestock density were generally less important in *Rumex* models. This was surprising given that *Rumex* spp. are readily found in pastures (Cavers & Harper, 1964; Grime et al., 2007; Holm et al., 1997). For *R. conglomeratus* cattle density was an important contributor to the combined model in NZ, however the variable response curves suggest that the presence or absence of cattle may be a stronger determinant of its distributions than density (Figure B.4D,J). This may be the case as the presence or absence of livestock corresponds to where land is irrigated in NZ. As *R. conglomeratus* has strict water reliance, it may be that irrigation allows this species to establish in area that would otherwise be unsuitable (Hill et al., 1999; Lousley & Kent, 1981). Alternatively, effects of livestock density on *Rumex* spp. distribution could be better explained by the proportion of grassland, included as a land use category in the models, which were somewhat correlated (Table B.4). As Bradie & Leung (2017) suggested distance to water was an important variable, I thought the hydrology variable would be important to the models, however it had little effect in any model aside from a moderate contribution to the model of *R. conglomeratus* in NZ. Given that at least one of the species, *R. conglomeratus*, relies on moist habitats to grow (Hill et al., 1999), it seems likely that the hydrology variable did not adequately represent the hydrological conditions around the occurrence data. The HydroRivers dataset I utilised does not capture small streams, drainage ditches, or many ephemeral systems for which these species may rely upon. As such, the hydrological variable likely was not as biologically relevant as I had hoped.

The importance of individual land use variables was likely related to their prevalence in each country. The proportion of herb and shrubland in GB was a significant contributor to all models, most likely as this was a dominant land cover type in GB (Table B.3). Similarly, contributions from the proportion of cropland and forest cover seemed in line with the proportion of those land cover types in each country. Interestingly, although the proportion of grassland was similar between countries, the proportion of grassland contributed more to models of NZ distributions than UK distributions. This discrepancy may be due to some unexpected bias in our sampling efforts. On the South Island of NZ, where most of our occurrence data come from, grasslands are often irrigated to improve pasture yield, particularly around Canterbury (Quinn et al., 2009; Stats NZ, 2021). Irrigation is far less common in the UK (Doyle, 1981). If our data were more representative of the grasslands of the North Island, which undergo less irrigation (Stats NZ, 2021), the contribution of grasslands to NZ models would likely be more similar to that of UK models.

Projections of habitat suitability from GB to NZ were stronger when non-climatic variables were included (Figure 3.4). Although projections including non-climatic variables are rare (Lantschner et al., 2019), this finding agrees with the current literature on species' temporal shifts due to climate change (Journé et al., 2020). These results indicate that model projections using only non-climatic variables were always significantly better than any model projection including climatic variables (Figure 3.4). Both spatial and temporal projections of climatic models are common in the literature (Early & Sax, 2014; Reinhardt, Russell, Senay, & Lazarus, 2020; Shabani et al., 2020; Sobek-Swant et al., 2012), but model projections including non-climatic variables seem to be rare (Journé et al., 2020; Lantschner et al., 2019). Typically, models with non-climatic variables are performed only within the assessed region (Blach-Overgaard et al., 2010; Padalia et al., 2014) or combine data from multiple ranges to assess the invasion potential within an introduced range. These results indicate that non-climatic variables play an important role in predicting introduced plant species' distributions. When no data in the introduced range are available, non-climatic model projections seem to provide the most accurate means to assess potential of introduced species' distributions. However, non-climate model projections only performed as well as models trained in the introduced range for one species, *R. conglomeratus* (Figure 3.4). Hence, models based off of existing data in the introduced range are preferable.

The addition of non-climatic variables to models did not increase the accuracy of predictions in areas of non-analogue climate. This is surprising as, although climate model projections are known to be strongly negatively affected by areas of non-analogue climate (Boiffin et al., 2017; Sobek-Swant et al., 2012; Srivastava et al., 2019), I expected predictions based on non-climatic variables to be unaffected in these areas. New Zealand has large areas of non-analogue climate space when compared with GB, largely driven by mountain ranges and high precipitation on the west coast of the South Island of NZ (Chapter 2; Chapter 4). By comparing model projections both with and without non-climatic variables, I can see that the addition of non-climatic variables does not change predictions in these non-analogue areas (Figure B.5). This may be because predictions from non-climatic variables similarly suffer from areas of non-analogue environments, such as differing land uses. I likely have large areas of non-analogue land use between these regions in moorland in GB, which is forty-five times more prevalent in GB than in NZ, different forest types, and different use of pasture and grasslands as previously mentioned. Alternatively, the enhanced AUC and TSS scores seen in projections of non-climate models may be due to the correct predictions of absences across much of NZ. In contrast, the climate model projections predict high suitability along mountain ranges (*R. obtusifolius*), the entire North Island (*R. crispus*), and the far south of NZ (*R. conglomeratus*) which is inconsistent with the observed distribution.

Including non-climatic variables in models seems to produce predictions at a finer grain (Figure B.3). Predictions of habitat suitability from the climate models change gradually along environmental gradients, for example, with probability of presence declining with increasing temperatures moving north on the North Island of NZ (Figure B.2A). When non-climate variables are included, predictions often differ between adjacent cells (Figure 3.1). This allows for a greater resolution when distinguishing suitable from unsuitable areas, which can be more useful when assessing impacts or the extent of introduced species' ranges at a fine scale. This finding agrees with other studies that suggest models including non-climatic variables are more useful when finer detailed predictions are required to assess areas at risk (Kriticos et al., 2015; Lantschner et al., 2019), and that non-climatic variables are larger determinants of species' distribution at a local scale (Bello et al., 2013). Although micro-climates can change over small scales and have large effects on species' distributions (Pannell et al., 2019) the climatic data I used in this study is unlikely to capture these effects. Shabani, Tehrany, Solhjouy-fard, & Kumar (2018) compared the accuracy of projections into the future between climatic models and non-climatic models for the Asian tiger mosquito, *Aedes albopictus*. Similar to my models, they concluded that while both sets of predictions were largely in agreement the non-climatic models were ultimately more useful as they better discriminated unsuitable areas. From this they were better able to predict areas at risk in the future and could recommend where to focus future eradication efforts.

Models for *R. conglomeratus* consistently had higher AUC and TSS scores when compared with *R. obtusifolius* and *R. crispus*. This could be due to *R. conglomeratus* having stricter habitat requirements than the other two species (Cavers & Harper, 1964, 1966; Grime et al., 2007; Grossrieder & Keary, 2004; Hill et al., 1999; Monaco & Cumbo, 1972; Pino et al., 1998; Rechinger & Akeroyd, 1993; Zaller, 2004), and hence being more sensitive to changes in environmental variables (Figure B.3). Alternatively, the lower AUC scores seen for *R. obtusifolius* and *R. crispus* models could be due to the high number of occurrence records of these species in the GB. When species occupy a large proportion of environments it can be difficult to predict where absences would occur, and subsequently reduce AUC scores (Lobo et al., 2008).

There are many problems associated with selecting variables for SDMs. Including biologically irrelevant variables can lead to models which are too flexible and overfit relationships to noise in the data rather than meaningful interactions (Merow et al., 2014). Understanding the ecology of the species is paramount for selecting biologically relevant variables (Austin & Van Niel, 2011; Brun et al., 2020; Fourcade et al., 2018; Merow et al., 2014). We know that *Rumex* species grow poorly on acidic soils (Cavers & Harper, 1964; Grime et al., 2007), and including soil type in models can lead to more accurate models of plant distributions (Bradie & Leung, 2017; Buri et al., 2020; Zuquim et al., 2020). I unfortunately could not account for soil type in the models due to a lack of reliable soil data in NZ which, if included, would have made it difficult to compare between regions. Currently only 36.6% of soil types have been assessed (Manaaki Whenua - Landcare Research, 2020), and soil categories included in these assessments are not consistent between GB and NZ. Similarly, many studies have demonstrated the effects that biotic interactions can have on species' distributions at both fine scales (Guisan & Thuiller, 2005; le Roux et al., 2013; Meineri et al., 2012) and coarse scales (Araújo & Luoto, 2007; Giannini et al., 2013; Godsoe et al., 2015; Godsoe & Harmon, 2012; Palacio & Girini, 2018). Though I did not assess biotic variables explicitly, related work shows that differences in some important biotic interactions have limited consequences for the performance of *Rumex* spp. in NZ. Costan (2021) investigated the effects that biotic interactions, namely differences in biomass, plant chemistry, competitive ability, and level of herbivory, have on *Rumex* spp. in GB and NZ. Despite significantly higher herbivory in GB, largely due to a greater herbivore biodiversity and the presence of a root borer, there was little change in plant performance between provenances compared in glasshouse experiments. I am therefore confident that including biological interactions in the models would not significantly change the results.

Understanding which variables model species' distributions best is critical if we intend to use model predictions in pest species management. Here I have demonstrated the utility of adding non-climatic variables to SDMs both within and between ranges. Including non-climatic variables in models generally improved the models, particularly when projecting between ranges. I found no evidence that non-analogue environments were better predicted by including non-climatic variables, however further study is needed. Non-climatic variables may also provide useful information on habitat restrictions for species with strict habitat requirements which are often missed when only considering climate. This study provides further evidence that non-climatic variables should be considered when modelling species' distributions, and I agree with other studies that modellers need to consider which variables are most relevant to their species' ecology before producing models (Srivastava et al., 2019; Thuiller et al., 2019).

Chapter 4

Rumex species are pre-adapted to non-analogue climates: a common garden approach

4.1 Introduction

Species introduced to regions outside of their native range have been known to establish and thrive in climates different from those they occupy in their native range, a process known as a niche shift (Atwater, Ervine, & Barney, 2018; Christina, Limbada, & Atlan, 2019; Comte, Cucherousset, & Olden, 2017; Liu et al., 2017; Silva, Vilela, Buzatto, Moczek, & Hortal, 2016; Sotka et al., 2018; Tingley, Vallinoto, Sequeira, & Kearney, 2014). The niche is defined as the subset of available environments in which a species experiences a stable or positive population growth rate (Godsoe, 2010; Hutchinson, 1957). We know that niche shifts into non-analogue climates, i.e. climates that are unique to the introduced range, are common (Atwater et al., 2018) hence there is a need to understand how and why populations can grow under non-analogue climates.

The causes of niche shifts into non-analogue climates are currently unclear. Some have argued that species are preadapted to these non-analogue climates, suggesting that these climates are within the species' environmental tolerances but are inaccessible in their native range (Bocsi et al., 2016; Cadotte et al., 2018; Early & Sax, 2014; González-Moreno et al., 2015). Preadaptation to a wide range of environments has been observed in species which are often described as having general-purpose genotypes such as *Verbascum Thapsus* L. (Dlugosch & Parker, 2008b; Parker et al., 2003). Furthermore, species which have major range restrictions, such as those that are endemic to islands, are more likely to be preadapted environments beyond their native range limits (Alexander & Edwards, 2010). Others have argued that these niche shifts are due to rapid evolution of species to non-analogue climates (Boheemen et al., 2019; Hulme & Barrett, 2013; Luo et al., 2019; Maron et al., 2004). Rapid evolution has been observed in species such as *Hypericum canariense* L. which, despite suffering a severe genetic bottleneck, has established and spread aggressively across different climates in the US in less than 50 years (Dlugosch & Parker, 2008b). Populations of this species have adapted to have greater growth, survival, and reproduction than plants from the native range, as well as developing a latitudinal cline in flowering times.

Current analytical methods cannot distinguish between preadaptation or rapid evolution as the cause for niche shifts as they rely on correlative species' distribution models (SDMs) (Lantschner et al., 2019; Williams et al., 2019). Utilising SDMs to analyse niche shifts is common in the climate change literature where niche shifts into non-analogue climates occur through time rather than space (Boiffin et al., 2017; Maguire et al., 2016; Veloz et al., 2012; Williams & Jackson, 2007). However, SDMs are known to perform poorly when species undergo niche shifts (Lake et al., 2020; Larson et al., 2014; Smith et al., 2019; Zurell et al., 2009), particularly into non-analogue climates (Fitzpatrick & Hargrove, 2009; Guisan et al., 2014; Mandle et al., 2010). Therefore, while comparing SDMs between countries can show when niche shifts occur (Chapter 2), field experiments are required to explain the underlying causes of these niche shifts (Alexander & Edwards, 2010; Escobar et al., 2016; Guisan et al., 2014; Hill et al., 2017; Lantschner et al., 2019). Transplant experiments comparing the performance of individuals from both the native and introduced range can help fill this gap (Hierro et al., 2005). Many experiments have compared the fitness of genotypes within and beyond a species' native range limit (Bayly & Angert, 2019; Block et al., 2020; Hargreaves et al., 2014; Pannell et al., 2019) and performance between ranges (Genton et al., 2005; Poll et al., 2009; Williams et al., 2008), but none have tested for adaptation to non-analogue climates in the introduced range (Pannell et al., 2019). Whilst experiments show fitness typically declines beyond range limits, less than half of these range limits occur at niche limits (Hargreaves et al., 2014). This suggests that either previous analyses have misidentified species' climatic niches, or that factors other than climate such as geographic barriers or biotic interactions are limiting their distributions (Bello et al., 2013; Hargreaves et al., 2014).

With transplant experiments we can distinguish a number of possibilities that are obscured in SDM-based analyses of niche conservatism, and help determine whether niche shifts are in the fundamental or realised niche. The fundamental niche represents the range of abiotic environments in which a species can exist indefinitely, whereas the realised niche is a subset of the fundamental niche constrained by biotic variables or accessibility and represents where the species is actually present (Soberón, 2007). If individuals from the introduced range outperform those from the native range when grown in a common garden under non-analogue climates (Figure 4.1A) it would suggest species have adapted to these environments since introduction. This could indicate that species are undergoing a shift in their fundamental niche. However if individuals from the native range perform similarly to those from the introduced range when grown in common gardens under non-analogue climates (Figure 4.1B) it would suggest that the species are preadapted to those environments. This would indicate that species are undergoing realised niche shifts. If individuals from the introduced range outperform those from the native range across a series of common gardens encompassing a wider range of climates (Figure 4.1C) it would suggest that individuals from the introduced range have adapted to have increased performance across the entire introduced range (Grant & Kalisz, 2020; Wan et al., 2020). If individuals from the native range outperform those from the introduced range in a series of common gardens encompassing a wider range of climates in the introduced range (Figure 4.1D) it would suggest that the populations that established in the introduced range are maladapted, possibly due to genetic bottlenecks during introductions (Boheemen et al., 2019; Bossdorf et al., 2005; Brandenburger et al., 2019; Dlugosch & Parker, 2008b).

Understanding the factors underlying niche shifts, and whether shifts are the result of preadaptation or rapid adaptation, would improve our risk assessments of introduced non-native plants. If species are preadapted to climates beyond those found in their native range it would suggest we should focus efforts on better understanding the species niche to then produce better predictions when projecting the species niche to new regions. However, if species are rapidly evolving to new climates when introduced to new ranges we may focus efforts towards species more likely to rapidly evolve, such as those with short generation times (Barraclough, 2015; Bradley, Blumenthal, et al., 2010; Friedman, 2020; Grant & Kalisz, 2020; van Kleunen, Bossdorf, et al., 2018).

In this chapter I aim to understand whether climatic niche shifts into non-analogue climates are the result of preadaptation or rapid adaptation using three closely related, globally invasive, herbaceous non-native plants. To accomplish this I established two common gardens, one in analogue climate space and the other in non-analogue climate space in the introduced range in New Zealand. I planted three widely distributed *Rumex* species known to have exhibited climatic niche shifts into warmer and wetter non-analogue climates in New Zealand (Chapter 2): *Rumex obtusifolius* L., *R. crispus* L., and *R. conglomeratus* Murray. These species are ideal candidates for this experiment as they produce seed within 1-2 years (Cavers & Harper, 1964; Foster, 1989) and have been established in NZ for over 150 years (Darwin & Keynes, 1835; Rechinger & Akeroyd, 1993; Thompson, 1922) which is likely sufficient time for climate adaptations to develop (Atwood & Meyerson, 2011). By comparing the performance of *Rumex* plants sampled from the native and introduced range in common gardens in New Zealand, I aim to provide evidence for the underlying causes of niche shifts in non-analogue climates by answering the following questions:

1. Have individuals from the introduced (New Zealand) provenance adapted to have increased fitness in non-analogue climates (Figure 4.1A)?
2. Do plants from both provenances perform better in analogue rather than non-analogue climates (Figure 4.1B)?
3. Do individuals from the introduced provenance consistently outperform individuals from the native (United Kingdom) provenance in the introduced range (Figure 4.1C)?

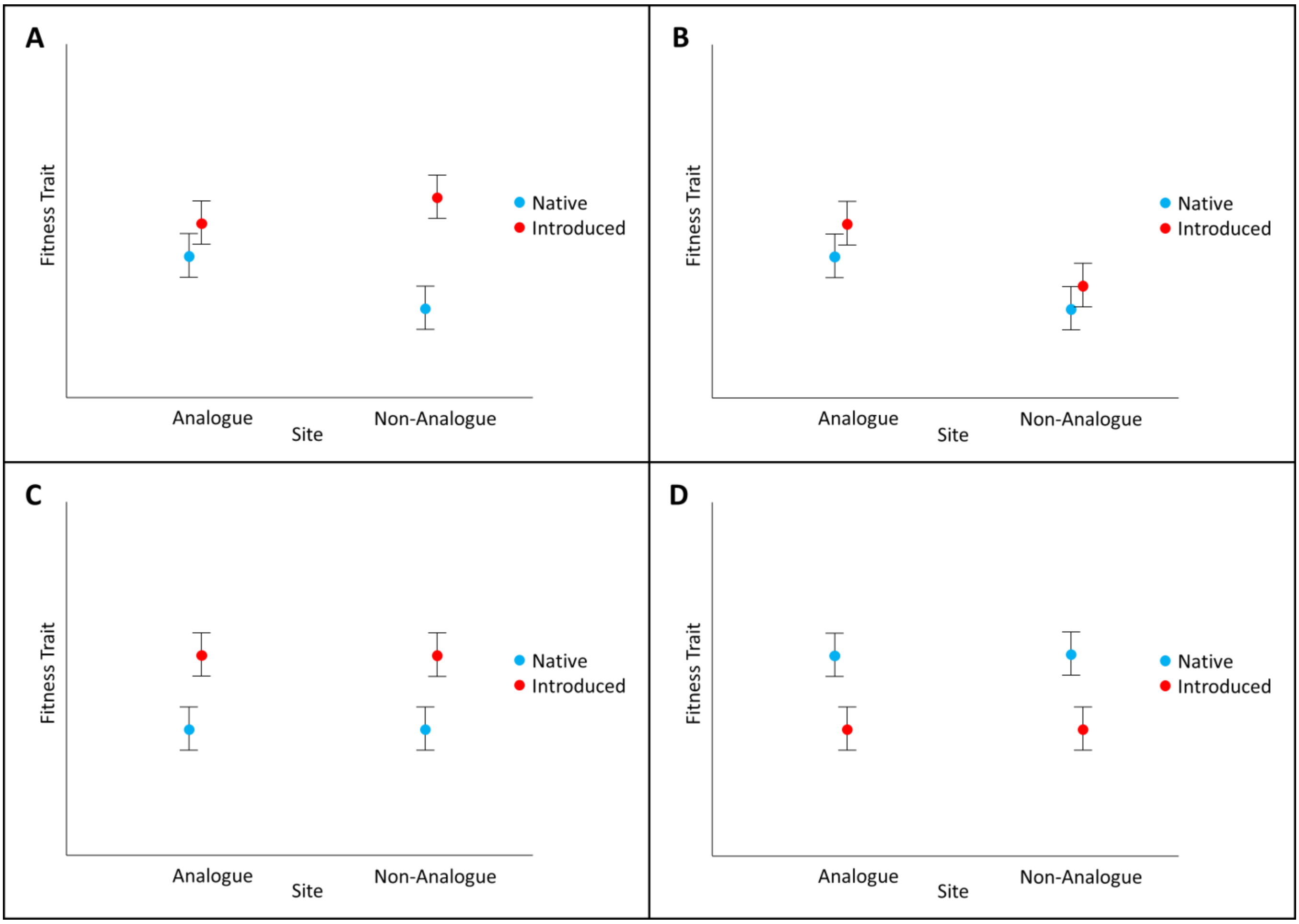

Figure 4.1 Examples of possible differences in performance between individuals from the native and introduced ranges, when grown in the introduced range in climates both analogous and non-analogous to those found in the native range. A) Individuals from the introduced range have rapidly adapted to climates not found in the native range, leading to greater performance in non-analogue climates. B) The species is pre-adapted to both analogous and non-analogous climates resulting in no differences in performance between individuals from the native and introduced ranges. C) Individuals from the introduced range have adapted to increase performance across all occupied climate space in the introduced range. D) Individuals from the introduced range are maladapted to the introduced range, reducing performance across all occupied climate space.

4.2 Methods

4.2.1 Species

All three *Rumex* species selected in this study are ruderals, typically colonising open, disturbed environments associated with human activity, including pastures (Cavers & Harper, 1964, 1966; Grime et al., 2007; Holm et al., 1997; Lousley & Kent, 1981). It is imporant to clarify the species' native range, as this may affect which climates are considered analogous or non-analogous to the introduced range. Therefore, I classify the native range for these species as Europe, the Middle East, and Northern Africa (GBIF.org, 2019; Holm, Pancho, Herberger, & Plucknett, 1979; Chapter 2). *Rumex* spp. have been spread across the world at least as early as the 16th century (Vibrans, 1998). All three species were introduced to New Zealand (NZ) as agricultural seed contaminants and have subsequently established and spread (Grossrieder & Keary, 2004; Halsted, 1889; Zaller, 2004). The UK is likely the initial source of *Rumex* spp. in NZ via at least two routes 1) contaminants in NZ due to historic trade between the UK and NZ in the 19th century and 2) the sale of *Rumex* spp. seeds to the indigenous Māori populations by UK settlers claiming they were tobacco seeds (Darwin & Keynes, 1835). These three species have since experienced a climatic niche shift between their native range and NZ and occupy warmer, wetter climates in NZ than they do in the native range (Chapter 2).

I considered differences in the species' relative fitness within both analogue and non-analogue space to determine the mechanism for these shifts. Relative fitness measures successful reproduction relative to other genotypes in a population, and is notoriously difficult to measure in plants (Alexander et al., 2015; Laughlin et al., 2020; Primack & Kang, 1989; Younginger et al., 2017). For *Rumex* spp. in particular relative fitness is difficult to measure because: (1) they are hermaphroditic so both male and female reproductive success must be measured; (2) cross-fertilisation, self-fertilisation (sexual), and fragmentation (asexual) reproduction are common; (3) different seeds from the same plant may be fertilised by multiple individuals making tracking paternity difficult; (4) they are primarily wind dispersed so pollen and seeds can travel far from parent plants, making their success difficult to track; and (5) they can grow as either annuals or perennials, making lifetime reproduction difficult to track over the course of an experiment (Cavers & Harper, 1964; Grime et al., 2007; Holm et al., 1977, 1997). I therefore considered three measurements as a proxy for relative fitness which represent the most important life stages for a plant: germination rate, survival probability, and fecundity (Laughlin et al., 2020). In particular, both germination (Kaur et al., 2017) and seed production are strong proxies of fitness when assessing plants of the same age (Younginger et al., 2017).

I extend the assessment of relative fitness by considering differences in integrative fitness, i.e. their combined fitness across multiple life stages, which was assessed as the number of potential offspring for individuals from each provenance at each site. Integrative fitness was calculated by multiplying germination rate, survival rate, and total number of seeds produced averaged within each maternal line. Total number of seeds produced was estimated by determining mean individual seed mass from a subsample, then considering the total mass of the seeds once cleaned. 95% confidence intervals were calculated to assess differences in the integrated fitness of each provenance. This does not represent true lifetime fitness as, had they not been destroyed, the plants may have continued reproducing after the end of the experiment.

4.2.2 Seed collection

Seeds were collected in autumn from the United Kingdom (UK, native range, September to October 2016) and New Zealand (NZ, introduced range, February to April 2017). Seeds from the UK were collected from South West England, the East of England, and two locations in the Scottish Lowland regions. In NZ, seeds were collected from the Southland, Westland, and Canterbury regions. These regions were chosen to capture a range of temperature and precipitation regimes that occur in both ranges. Four populations were sampled in each region, and five individuals from each population. Populations within a region were generally at least 5km apart (mean = 30 km, range = 3.5 to 99 km). Clean seeds from the UK were imported into NZ (MPI permit 2016061142) and stored in darkness at room temperature until used (7-12 months).

4.2.3 Sites

To compare climates between ranges and delimit analogue and non-analogue climates I used the WorldClim dataset (Fick & Hijmans, 2017). Climatic variables were compared between New Zealand and the native range (Chapter 2). Of the 19 available climatic variables I excluded “Mean Temperature of the Wettest Quarter” and “Mean Temperature of the Driest Quarter” as these variables aggregate information on precipitation and temperature in a way that can lead to artefacts at large spatial scales. I conducted a principal components analysis (PCA) with the remaining 17 bioclimatic variables and used the first two principal components to plot the available climate space for both the native range and NZ (Figure C.1). Analogue climate space was defined where the available climate space for Europe and NZ overlapped. The range of climates found in the UK encompasses the majority of the analogue climate space between Europe and NZ (Figure C.1). This confirms that UK specimens are sourced from the relevant native range habitats. From this, I identified an analogue site (Southland) and a non-analogue site (Westland) for the common garden experiment (Figure C.1).

Located in analogue climate space, the Southland field site was situated on managed pasture at the AgResearch research station at Woodlands, NZ (46.364S, 168.578E). The Southland field site is situated roughly 41m above sea level, with soils classified as loamy with a low stone content (Manaaki Whenua - Landcare Research, 2020). The climate of Southland is characterised by cool coastal breezes and with rainfall averages over 1000mm annually near the coast (Grant, 2008; Macara, 2013). The Southland site is located roughly 15km from Invercargill where median hourly air temperatures vary from ~4°C-~17°C across the year (Macara, 2013). Located in non-analogue climate space, the Westland field site was situated on managed pasture on a private farm near Atarau in the Grey Valley region, NZ (42.335S, 171.488E). The Westland field site is situated roughly 115m above sea level with soils classified as loamy with a high stone content (Manaaki Whenua - Landcare Research, 2020). The climate of the West Coast is characterised by high rainfall averages with the Grey Valley receiving over 2100mm annually on average (Macara, 2016; Nathan, 2009), evenly distributed throughout the year. This level of rainfall far exceeds levels of precipitation found in most of the native range (Fick & Hijmans, 2017). Median hourly air temperatures of the Grey Valley vary from ~4°C-~16°C across the year (Macara, 2016).

Climate data throughout the duration of the experiment was collected from nearby weather stations and aggregated to assess whether the climates experienced at the field sites matched my initial expectations (NIWA, 2017c, 2017a, 2018b, 2018m, 2018l, 2018k, 2018c, 2019c, 2019e, 2017b, 2018e, 2018d, 2018h, 2018a, 2018i, 2018g, 2018f). Data were collected from Invercargill (Invercargill Aero AWS) and Greymouth (Greymouth Aero EWS) airports, which, as well as being the closest weather stations to the field sites, are known to experience similar climates to our field sites (Macara, 2013, 2016). These data were transformed into the 17 relevant bioclimatic variables using the “dismo” R package (Hijmans et al., 2020),

To study the direct effect of climate, as opposed to indirect effects mediated by competition, competition was suppressed with the existing pasture species. Both sites were sprayed with glyphosate three weeks prior to planting and were subsequently covered in weed cloth. The weed cloth allows water to pass through but blocks light to the soil surface and provides a physical barrier to competing plants trying to grow underneath (Jabran & Chauhan, 2018). At both sites a fence was erected around the plots to exclude sheep, cows, hares and rabbits.

4.2.4 Field Experiment

Three blocks were established at each field site, with room for transplanted plants to grow in the centre and germination trays around the perimeter (Figure C.2). Each germination tray contained 10 seeds from each of five individuals from each of two populations, separated by weed cloth in the centre. Seeds were planted at Westland on the 4th-6th October 2017 and at Southland on the 12th-13th October 2017. The soil used in the germination trays was from the local site, with large plant matter and stones removed. Where available, one seedling from each maternal line that germinated was transplanted into the block, with each block able to hold 120 plants per species. In cases where no seedling germinated for a maternal line in one block, a matching seedling was transplanted from a different block if one was available. The number of seeds which germinated for each maternal line was recorded at both sites during November 2017, as a proportion of the total seeds planted. To improve identification, seedlings were left in germination trays until at least one true leaf had developed, at this stage seedlings could be identified to at least genus level. Transplanting occurred throughout November 2017, after germination counts were complete. Individuals were watered directly after planting to help avoid transplant shock (Doust, 1981). After transplanting, site visits were conducted approximately every 2-3 months where survival and life stage status were recorded.

At the end of each growing season, all seeds were harvested. Harvesting occurred at Westland in March 2018 and January 2019, and at Southland in March 2018 and February 2019. After seeds were harvested in early 2019, plants were destroyed and the land was returned to pasture. As seeds are wind dispersed (Cavers & Harper, 1964) some individuals had lost considerable seed mass prior to harvesting. Individuals that were estimated to have lost >30% of their seed mass prior to harvest were excluded from analyses. Air-dried seeds from 2019 were cleaned of large debris and weighed to measure fecundity.

4.2.5 Analysis

Each species was analysed separately using linear (LMMs) or generalised linear mixed effects models (GLMMs). A mixed effects model approach was used to quantify the variation among units in our experimental design, namely the effects created by the block design and the inclusion of multiple individuals from individual maternal lines (Bolker et al., 2009). To account for this variation, block and maternal line were included as random effects in all models. Population was initially included as a random effect in all models, but was removed to reduce model complexity as it did not account for any additional variation when maternal line was also included (Bolker et al., 2009).

Germination and survival were analysed using GLMMs with binomial distributions and a logit link function. The effect of plant country of origin (UK or NZ) on the germination rate under different climates (analogue or non-analogue) was examined by modelling germination rate as a function of site and provenance and their interaction. Similarly, the effect of plant origin on the survival rate under different climates was examined by modelling survival rate (from transplantation until harvest) as a function of site, provenance and their interaction.

As our measurements of total seed mass for all species spanned several orders of magnitude, a log transformation was applied to this response variable. As such, log-transformed seed mass was analysed using LMMs with a Gaussian distribution and identity link function. The effect of plant origin on seed production under different climates was examined by modelling log-transformed seed mass as a function of site, provenance and their interaction.

In order to better understand the contribution of main effects in the models, where interactions between provenance and site were not significant, the model was refit without them. To determine whether the interaction between provenance and site was significant, I conducted Wald's chi squared tests on the initial models (Fahrmeir et al., 2013). All models were conducted using the package 'lme4' (Bates et al., 2015). Models were checked by examining the residuals (Bufford, 2020), and testing for influential data points using Cook's Distance (Cook, 1977). Where influential data points were found to affect model results, the data points were removed and a summary of the difference in model output is provided in Figure C.5. The significance of fixed predictor variables in the model was then assessed by using a parametric bootstrap with 1000 simulations, where significance was determined if the bootstrapped 95% confidence interval did not overlap zero. *p*-values from Wald chi-squared tests are also presented. Both conditional and marginal R^2 values are given for all models (Nakagawa & Schielzeth, 2013). Data exploration and analyses followed methods employed by Bufford, Lurie, & Daehler (2016) in R (version 4.0.2; R Core Team, 2013). Linear mixed models were selected over alternatives, such as generalised additive mixed models or Bayesian methods, to reduce model complexity which can lead to better model fit and increase interpretability (Bolker et al., 2009; Dormann et al., 2018; Merow et al., 2014).

4.3 Results

The climates experienced at both field sites were as expected, with Southland and Westland being located under analogue and non-analogue climates respectively (Figure C.3). A total of 180 measurements of germination were taken per provenance, per species, per site. Full details of the number of measurements recorded for each life stage are displayed in Table C.1. In total, 226 *R. conglomeratus*, 184 *R. crispus*, and 232 *R. obtusifolius* plants were transplanted at the analogue field site, and 205, 222, and 272 at the non-analogue field site respectively. Of those, 60 *R. conglomeratus*, 36 *R. crispus*, and 31 *R. obtusifolius* plants had their seed harvested at the analogue field site, and 103, 82, and 73 plants were harvested at the non-analogue field site respectively.

4.3.1 Model Results

The introduced provenance underperformed or performed no different than the native provenance for all but one assessed components of fitness (Figure 4.2). The contribution of the random effect of block was much smaller than the contribution of maternal lines in all cases. R^2 values were low in all cases aside from *R. conglomeratus* fecundity (Table C.2). Assessing integrated fitness showed no significant differences between provenances for any species, but some significant differences in performance between sites (Figure 4.3).

Germination data tended to support the hypothesis that the introduced provenance is maladapted in the introduced range (Figure 4.1D). I found no evidence that the introduced provenance outperformed the native provenance (Figure 4.2A-C; Figure C.4A-C). Individuals of *R. crispus* and *R. conglomeratus* from the native provenance had higher germination at both sites than individuals from the introduced provenance ($p < 0.001$). However, the performance of each provenance depended on the site examined for *R. conglomeratus* (Site x Provenance interaction: $p < 0.001$; Figure C.4A). Individuals of *R. conglomeratus* from the native provenance performed worse at the non-analogue site, but still better than individuals from the introduced provenance (Figure 4.2A). The performance of each provenance also depended on the site examined for *R. obtusifolius* (Site x Provenance interaction: $p < 0.001$; Figure C.4C), however this species performed better at the non-analogue site, matching performance of individuals from the native provenance at the non-analogue site (Figure 4.2C). Contrary to my initial hypothesis, the native provenance had higher germination rates than the introduced provenance at both sites ($p < 0.001$; Figure 4.2B; Figure C.4B).

Survival data tended to support the hypothesis that there are no differences in performance between either provenance (Figure 4.1B), however there were differences in performance between sites. Survival did not significantly differ between either provenance at either site for any species (*p*

> 0.08; Figure 4.2D-F; FigureS3D-F). The interaction of site and provenance was non-significant for all species ($p > 0.4$). Survival was significantly higher at Westland for *R. conglomeratus* and *R. crispus* ($p = 0.007$ & $p < 0.001$ respectively; Figure 4.2D-E; Figure C.4D-E), but not for *R. obtusifolius* ($p = 0.379$; Figure 4.2F; Figure C.4F). Analysis of residuals using Cook's D showed that significance for *R. crispus* was influenced by observations from three individuals from a single maternal line, collected in Canterbury NZ, all of which died. These individuals were therefore removed prior to analysis (Figure C.5A). A preliminary analysis including these *R. crispus* individuals indicated the native provenance had significantly greater survival than the introduced provenance ($p = 0.039$; Figure C.5B), and the interaction between site and provenance was still non-significant ($p = 0.257$). These outliers do not change the qualitative conclusion that introduced genotypes are pre-adapted to the introduced range. There were no other assumption violations.

Fecundity data suggested that either the introduced provenance was better adapted to non-analogue climates (Figure 4.1A) or that no differences in performance were present between provenances (Figure 4.1B), depending on which species was considered. There were no significant differences in total seed produced between provenances for *R. crispus* and *R. obtusifolius* ($p = 0.239$ & $p = 0.071$ respectively; Figure 4.2H-I; Figure C.4H-I). Individuals grown at the analogue site produced significantly more seed for both *R. conglomeratus* and *R. crispus* ($p < 0.001$ & $p = 0.049$ respectively; Figure 4.2G-H; Figure C.4G-H), but not *R. obtusifolius* ($p = 0.585$; Figure 4.2I; Figure C.4I). Individuals of *R. conglomeratus* from the introduced provenance produced significantly more seeds than individuals from the native range across sites ($p = 0.033$; Figure 4.2G; Figure C.4G). Provenance by site interactions for total seed production were non-significant for all species ($p > 0.43$).

Integrated fitness across all life stages was not significantly different between provenances (Figure 4.1B). Similarly, no significant differences in integrated fitness were observed between sites for *R. crispus* and *R. conglomeratus,* however there were differences in fitness between sites for *R. obtusifolius* (Figure 4.3). Individuals of *R. obtusifolius* from both provenances had significantly higher fitness at the non-analogue site. Interestingly, *Rumex conglomeratus* was the species with the greatest variability in potential offspring, UK 95% CI (12602, 25708) NZ 95% CI (1929, 16583) at the analogue site.

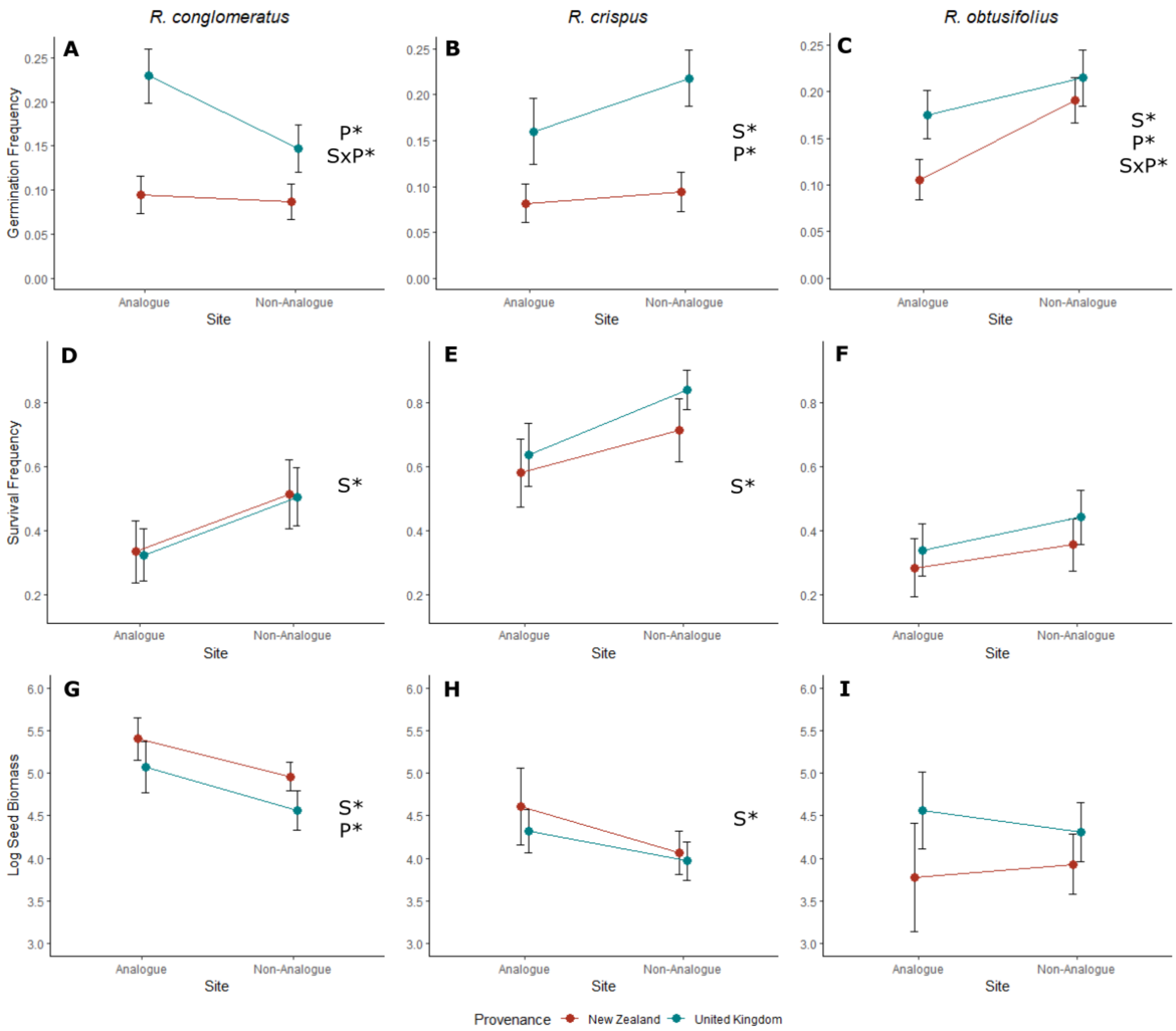

Figure 4.2 **Comparison of fitness between the native (blue) and introduced (red) provenances at each site, controlling for block and seedling maternal line. All comparisons display the mean and 95% confidence intervals. Germination (A-C) was measured as the proportion of seeds, out of 10, which germinated per individual. Survival (D-F) was measured until harvest at the end of the second growing season. Fecundity (G-I), measured using total seed mass collected from each plant, is displayed on a natural log scale. Significant differences (as shown in Figure C.4) are displayed here as: S* - significant site differences; P* - significant provenance differences; and SxP* - significant site by provenance interaction.**

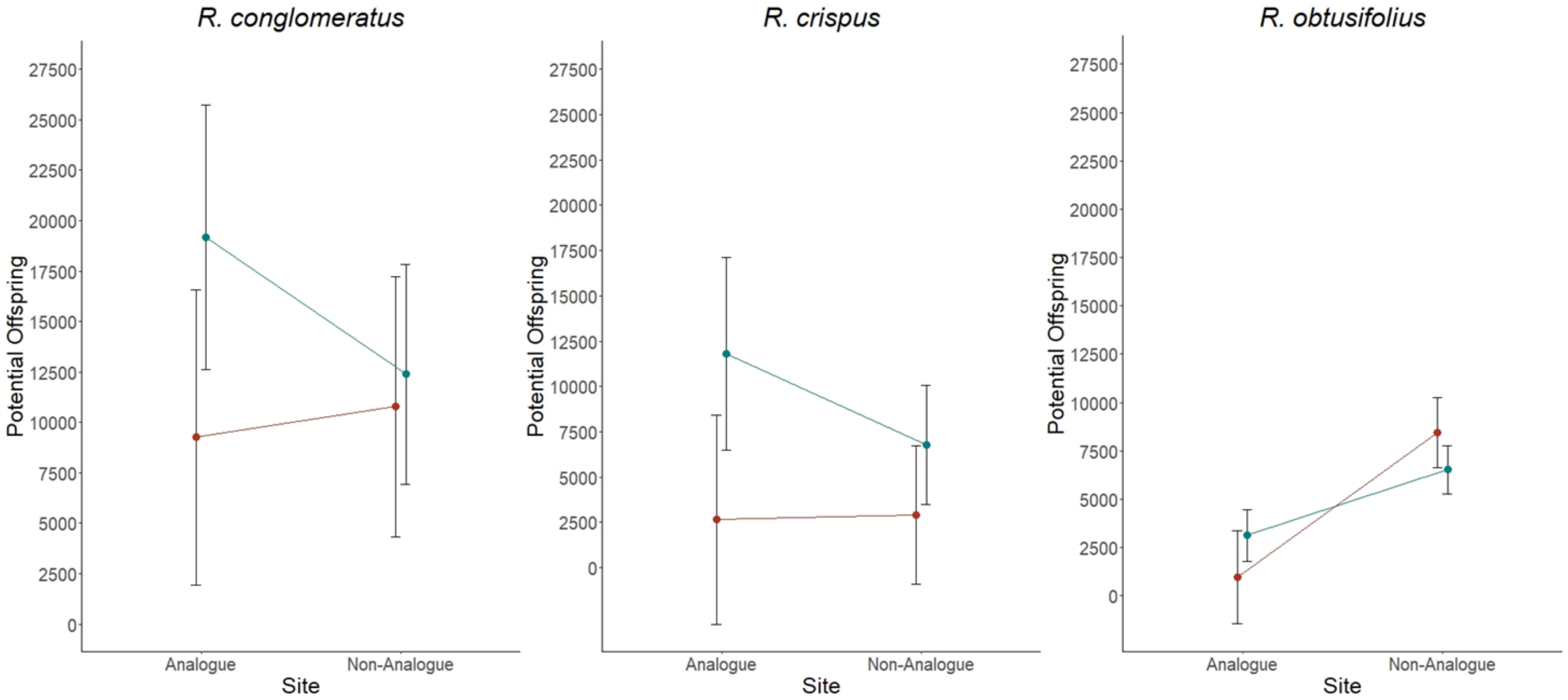

Figure 4.3 Integrated fitness of individuals from either the native (blue) or introduced (red) provenance. Points represent the mean absolute fitness at either the analogue (Southland) or non-analogue (Westland) field site, and error bars display 95% confidence intervals. Integrated fitness is measured by the predicted number of potential offspring per individual from either the native or introduced provenance at each site. Potential offspring was calculated as germination rate*survival rate*total number of seed produced, and was assessed for all sampled *Rumex* populations for any given provenance. The top left panel displays the absolute fitness of all *Rumex* species considered together, with the other panels showing results for individual species.

4.4 Discussion

The native provenance performed at least as well as the introduced provenance in the non-analogue climate indicating that these *Rumex* spp. are pre-adapted to climates found outside of their native range (Figure 4.1B). We found this to be generally true across all assessed measurements and species. This study is one of the first to complete a large scale common garden experiment comparing the performance of both the native and introduced provenances between analogue and non-analogue climates in the introduced range. This work suggests that niche expansion into non-analogue climates may be, more often than previously thought, the result of species' pre-adaptation. If this is the case, this study promisingly indicates that climatic niche shifts may be predictable, so long as the species niche is well understood. Therefore, I suggest that forecasts of niche expansion should focus on characterizing a species' fundamental niche rather than assuming species are rapidly evolving in the introduced range.

My results suggest that the success of *Rumex* is due to pre-adaptation rather than rapid evolution. For the majority of fitness measures, the introduced provenance did not have a significantly higher fitness than the native provenance in the non-analogue site (Figure C.4). The only exception is the amount of seed produced by *R. conglomeratus* which was significantly higher for individuals from the introduced provenance at the non-analogue site (Figure C.4), despite producing only slightly more seed biomass (Figure 4.2). It therefore seems plausible that *R. conglomeratus* may have locally adapted to wetter climates in NZ, developing higher seed production. Having higher seed set, while maintaining equivalent survival rates compared to individuals from the native provenance, could produce a net positive population growth rate for *R. conglomeratus* in the non-analogue climate. This would help explain why *R. conglomeratus* is so common in Westland, NZ, whilst difficult to find in other regions (Chapter 3). However, it should be noted that even at the non-analogue site individuals of *R. conglomeratus* from the introduced provenance had significantly lower germination than those from the native provenance (Figure 4.2A, S3A). The higher seed production is offset by the lower germination rate, resulting in no differences in integrated fitness of individuals in non-analogue climates (Figure 4.3).

The native provenance generally had significantly greater germination compared to the introduced provenance, which could suggest reduced performance for the introduced provenance. By contrast, other studies have shown species adapt under new environments, which should increase germination (Boheemen, Atwater, & Hodgins, 2019; Luo, Xu, Zheng, Guo, & Hu, 2019; Maron, Vilà, Bommarco, Elmendorf, & Beardsley, 2004; but see: Brandenburger et al., 2019). In the case of

Rumex spp, lower germination could be due to lower genotypic diversity expressed in NZ due to a genetic bottleneck upon introduction (Boheemen et al., 2019; Bossdorf et al., 2005). However, this seems unlikely as no other significant fitness differences were detected between provenances and it is likely that multiple introductions have occurred over two centuries of agricultural trade between NZ and the rest of the world (Brooking & Pawson, 2007; Wilson et al., 2016). Alternatively, the lower germination rate of individuals from the introduced provenance could be an artefact of my sampling protocol. As seeds ripen at opposite ends of the calendar year between the Northern and Southern Hemispheres, the seeds collected from the UK were stored for roughly six months longer than those from NZ. The length of time seeds are in dry storage may affect germination rate through changes in dormancy. Although previous studies have indicated *Rumex* spp. do not undergo strong dormancy periods, time in dry storage can increase germination success (Baskin & Baskin, 1985; Cavers & Harper, 1966). Similar work has indicated that seeds from both provenances had high viability (Bufford, J, [Local Adaptation of *Rumex* species]. Unpublished raw data).

Contrary to expectations, performance was significantly better overall at the non-analogue site for two species with regards to germination and survival rates, but better at the analogue site for two species with regards to total seed production (Figure C.4). Whilst total seed produced at the non-analogue site for both *R. conglomeratus* and *R. crispus* was significantly less than at the analogue site, this could be an artefact of greater density, and therefore competition, of plants at the non-analogue site. No differences in integrated fitness were detected between sites except for *R. obtusifolius* which has greater fitness at the non-analogue site. As neither provenance experienced significant detrimental effects at the non-analogue site compared to the analogue site (Figure 4.2; Figure 4.3) I conclude that *Rumex* spp. are pre-adapted to non-analogue climates found outside their native range.

However, the patterns shown by the response variables at each life stage are inconsistent between species. *Rumex conglomeratus* displayed greater survival at the non-analogue site, but reduced seed production and germination of individuals from the native provenance (Figure 4.2A,D,G; Figure C.4A,D,G). This is surprising as *R. conglomeratus* is the species most dependent on soil moisture (Cavers & Harper, 1964; Hill et al., 1999), so we would expect it to perform better at the non-analogue site. Whilst I previously mentioned there could have been potential issues with overcrowding at the non-analogue site, this was not an issue in germination trays. *Rumex obtusifolius* experienced greater germination at the non-analogue site. Survival rate and seed production were not significantly different for *R. obtusifolius* between sites, which is in line with my expectations as both *R. obtusifolius* along with *R. crispus* can both successfully occupy a wide range of environments (Chapter 2,3; Cavers & Harper, 1964, 1966; Grime, Hodgson, & Hunt, 2007; Holm, Doll, Holm, Pancho, & Herberger, 1997; Lousley & Kent, 1981). Finally, *R. crispus* experienced significantly higher germination, but significantly lower survival and seed production, at the non-analogue site compared to the analogue site. The lower survival and fecundity of *R. crispus* at the non-analogue site seems plausible as populations of *R. crispus* were difficult to find on the West Coast during the seed collection surveys (T Carlin, pers. obs., 2017). Even though closely related species showed differences in response variables at analogue and non-analogue sites, these results emphasise that I found little to no evidence supporting rapid adaptation as the method in which these species underwent climatic niche shifts.

Future efforts towards predicting the distribution of introduced plants should first consider better characterising the species' current niche rather than assuming species have adapted to new environments. This suggests that tools which can better characterise the species' niche may be more useful than forecasts of species' range responses to rapid evolution (Urban et al., 2016). Experiments which directly test species' physiological tolerances via manipulations can be used to produce SDMs with a better understanding of a species' fundamental niche (Benning & Moeller, 2019; Godsoe et al., 2017; Hargreaves et al., 2014; Lee-Yaw et al., 2016; Willi & Van Buskirk, 2019). Alternatively, mechanistic models of population growth may provide better predictions of where species can persist (Angilletta et al., 2019; Buckley et al., 2010; Kearney & Porter, 2009; Srivastava et al., 2019).

The results of this study rely on the accurate assessment of which climates are analogous between regions. This depends both on the reliability of the underlying climate data, and the specific weather conditions experienced during the experiment. For example, the WorldClim data I utilised indicates the maximum annual precipitation in the UK is 2600mm, whereas the Met Office suggests the maximum value can reach 4100mm around some mountain tops in Scotland (Hollis et al., 2019). However, it is unlikely that *Rumex* spp. occur in these areas, and therefore this difference would be unlikely to greatly influence what climates are considered analogous.

Whilst the results of this study demonstrated that *Rumex* spp. are likely preadapted to the non-analogue climates found on the West Coast of NZ, additional common gardens under other climates are needed to determine if this is the norm. New Zealand possesses a large amount of non-analogue climates (Figure C.1), and establishing common gardens across this spectrum would be highly informative as to whether fitness deteriorates as the climates become less similar to those experienced in the native range. Furthermore, my previous work has shown that *Rumex* spp. undergo niche pioneering into different non-analogue climates in other ranges such as North America (Chapter 2). It is possible that *Rumex* spp. may be preadapted to some non-analogue climates but that rapid adaptation is responsible for niche pioneering in other ranges. Experiments in other introduced ranges could elucidate this. Finally, this experiment would greatly benefit from the inclusion of sites in the native range to distinguish whether individuals from the introduced range have lost adaptations, such as loss of defences to native enemies, which may alter their performance in the native range (Colautti & Lau, 2015; Genton et al., 2005; Poll et al., 2009; Williams et al., 2008). If this is the case we would expect individuals from the introduced range to perform poorly when reintroduced to the native range.

Understanding what drives niche shifts into non-analogue climates is critical for predicting where species can establish. Using a common garden experiment I have shown that Individuals from the native range performed equally well, or better than, individuals from the introduced range in non-analogue climates. Surprisingly, I found little evidence that individuals from either provenance experienced reduced performance under non-analogue climates compared to climates found in the native range. I demonstrated that the native range of *Rumex* spp. does not adequately represent the range of climates the species are capable of tolerating, and note that this may have serious implications for species' distribution modelling efforts. I recommend that when producing SDMs modellers recognise that species' ranges may not represent all of the environments to which the species are preadapted. Modellers should try to better understand the species' niche, and hence the environments they can currently tolerate, rather than focussing on whether species will evolve adaptations to new environments. To the best of my knowledge, this study provides some of the first empirical evidence that species are pre-adapted to environments found outside the scope of their native range.

Chapter 5

General Discussion

5.1.1 Scope of the thesis

This thesis examined several aspects of a plant species' climatic niche, and situations in which the niche undergoes shifts between the native and introduced range. Although studies often use correlative methods to measure whether a niche shift has occurred between two regions (Atwater et al., 2018; Early & Sax, 2014; Gallagher et al., 2010; Lantschner et al., 2019; Petitpierre et al., 2012; Williams et al., 2019), few studies currently consider niche shifts across all of a species' ranges (Christina et al., 2019; Silva et al., 2016) or offer empirical evidence for why these shifts occur (Lantschner et al., 2019). At a global scale, I first considered whether *Rumex* spp. shift their niche when introduced into multiple new ranges across the world, finding that niche shifts are not always consistently towards similar environments. At a national scale, I then considered the types of variables that most accurately predict species' distributions when a realised niche shift has occurred, showing that non-climatic variables play an important role. Finally, at a regional scale I conducted one of the first large-scale field experiments to determine whether fitness differences exist between plants from the native and introduced ranges when grown in the introduced range. Strong performance of individuals from both ranges indicated that novel adaptations to the environments of the introduced range has probably not occurred in *Rumex* species, providing some of the first evidence for preadaptation to non-analogue environments as a cause of niche shifts.

5.1.2 Major Findings of the thesis

Niche shifts are inconsistent across introduced ranges (Chapter 2)

To determine whether climatic niche shifts occurred for *Rumex* spp. I considered three ranges each with wide environmental variation where the species had been independently introduced. Such comparisons are common between the native range and a single introduced range (Atwater et al., 2018; Early & Sax, 2014; Gallagher et al., 2010; Petitpierre et al., 2012) but assessments of whether climatic niche shifts in introduced plants are consistent across multiple ranges are lacking (Datta et al., 2019; Wang et al., 2017). It was therefore unclear whether the presence of a niche shift in one region could be used to predict the likelihood and direction of a niche shift in another region. We observed that *Rumex* spp. underwent niche shifts inconsistently across each of the three introduced ranges considered. Furthermore, the types of climates into which *Rumex* spp. shifted their niche in each range were idiosyncratic. This observation is only possible when considering multiple ranges across the globe, which few other studies have done (Christina et al., 2019; Silva et al., 2016). Also, in each introduced range we observed niche expansion into both analogue and non-analogue climate space, indicating that factors other than climate are restricting the species in their native range. Although these climatic niche shifts were in a similar direction between species, there was little overlap in the occupied climates of species in each range. This indicates that the use of closely related species in predicting species' distributions that undergo climatic niche shifts is limited. Aside from providing new evidence that the species' native range is a poor indicator for its potential distribution when introduced elsewhere, we provide strong evidence that the presence of a niche shift in one range may not predict niche shifts in other ranges.

Non-climatic variables can provide more accurate predictions of species' distributions (Chapter 3)

Since I found evidence that these species underwent climatic niche shifts between the native and introduced ranges, and that the direction of these shifts depended on both the species and region considered (Chapter 2), I sought to better understand the factors limiting the species' distribution in the native range and a single introduced range. Therefore, I considered which variables best predict the distribution of *Rumex* spp. in NZ and the UK. Studies typically only consider climatic variables when projecting species' distributions beyond the native range (Atwater et al., 2018; Bradie & Leung, 2017; Bradley et al., 2008; Broennimann et al., 2007; Chapman et al., 2019; Early & Sax, 2014; Gallagher et al., 2010; Petitpierre et al., 2012, 2017; Srivastava et al., 2019), however recent studies suggest non-climatic variables may be important (Bello et al., 2013; Bradie & Leung, 2017; Gallien et al., 2015; Gardner et al., 2019; Iturrate-Garcia et al., 2016). We found that climatic variables were poor predictors of the species' distribution compared to non-climatic variables when projecting from the native range to the introduced range. Species' distribution models based on non-climatic variables were either just as, or more, accurate than models based on climate data. In particular, SDMs produced using only non-climatic variables were the most accurate when projecting distribution information from the native range. Unfortunately, SDMs utilising non-climatic variables were still poor predictors of species' distributions in areas of non-analogue climate.

Surprisingly, including non-climatic variables in SDMs did not seem to improve the predictions of species' distributions under non-analogue climates (Figure 3.1). Species' distributions are notoriously difficult to predict under non-analogue climates as we have no prior information from the native range of how a species will respond to that particular climate (Boiffin et al., 2017; Maguire et al., 2016; Sobek-Swant et al., 2012; Srivastava et al., 2019; Veloz et al., 2012). I had predicted that non-climatic variables would fill this gap as areas of non-analogue climate in the introduced range may have areas of analogous non-climatic variables that could be used to better inform SDMs. For example, if human disturbance strongly affects where *Rumex* spp. occur under all climates, then including it in SDMs may correctly predict *Rumex* spp. distributions under non-analogue climates based on the level of human disturbance. However, this did not seem to be the case in our models. The lack of accuracy of predictions under non-analogue climates may indicate that I did not account for some important non-climatic variables that dictate the distribution of *Rumex* species. For example, we know that *Rumex* spp. have preferences towards both soil pH and nitrogen content (Cavers & Harper, 1964; Grime et al., 2007), both of which may account for where *Rumex* spp. occur at a local scale. Non-climatic variables that help predict distributions under non-analogue climates may also vary between introduced ranges. For instance, whilst hydrological variables are unlikely to be a good predictor under NZ non-analogue climates, as these are typified by high precipitation, hydrological variables may be a strong determining factor of where *Rumex* spp. occur under drier North American or Australian non-analogue climates (Figure 2.4). This would be especially important for *R. conglomeratus*, which relies on high moisture (Cavers & Harper, 1964; Hill et al., 1999; Lousley & Kent, 1981).

***Rumex* spp. are preadapted to non-analogue environments (Chapter 4)**

Having observed that *Rumex* spp. experienced niche expansion into non-analogue climates in NZ (Chapter 2), and that SDMs utilising non-climatic variables still struggled to predict distributions under non-analogue climates (Chapter 3), I wanted to discover whether this expansion was the result of preadaptation (Cadotte et al., 2018; Early & Sax, 2014; González-Moreno et al., 2015) or rapid evolution to climates in the introduced range (Boheemen et al., 2019; Hulme & Barrett, 2013; Luo et al., 2019; Maron et al., 2004). I conducted a large-scale common garden experiment, transplanting seeds from the native range into the introduced range. I compared the performance of native and introduced provenance plants at different life stages in both analogue and non-analogue climates. I found that plants from the native range are likely preadapted to both the analogue and non-analogue climates of the introduced range as no significant fitness differences were observed between individuals from the native or introduced provenances. This finding contradicts much of the current literature which suggests niche shifts are more likely to be the results of contemporary evolution (Boheemen et al., 2019; Hulme & Barrett, 2013; Luo et al., 2019; Maron et al., 2004).

5.1.3 Synthesis of findings from Chapters 2-4

As we determined that SDMs based on non-climatic variables lead to more accurate predictions of species' distributions when projected from the native range, this raises the question as to whether non-climatic variables would offer more accurate projections in all of the species' introduced ranges assessed in Chapter 2. If non-climatic variables had been included in this comparison of niche shifts in multiple introduced ranges more similarities may have been observed in the types of environments *Rumex* shifted into. Whilst this would not change the fact that *Rumex* spp. are experiencing niche expansion into different climates in different ranges, it may help explain why *Rumex* spp. have expanded their climatic niche in these ranges. For example, *Rumex* spp. may have shifted into environments where human disturbance is greater, as long as these regions are still within their overall climatic limitations. If this were the case then data on human disturbance would be a good indicator of where these species are likely to establish in the future, including as a result of niche shifts. Unfortunately availability of high quality environmental data for multiple regions is scarce, in particular as collection methods for the data need to be comparable. Furthermore, we know that climate dictate species' distributions at broad scales (Bello et al., 2013), and as such, it is possible that the analysis in Chapter 2 may have been at too broad a scale for the effects of non-climatic variables to be detected.

Having determined that *Rumex* spp. are preadapted to climates beyond those found in the native range (Chapter 4) one might think that these niche shifts could be due to a lack of suitable climates in the native range. However, Chapter 2 shows that *Rumex* spp. also experience niche shifts in introduced ranges into analogue climate space. This not only shows that the native range is not a good approximation of the species' fundamental niche, but also raises the question of what limits the range of these species in the native range and analogue niche space. As *Rumex* spp. can easily disperse their seeds via wind, water, agricultural machinery, endozoochory (Cavers & Harper, 1964; Grime et al., 2007), as well as the historical prevalence of contaminations in agricultural seed stock (Grossrieder & Keary, 2004; Halsted, 1889; Zaller, 2004), it seems likely that seed would be able to reach most suitable climates. The ease of dispersal combined with the broad range of available climates in the native range (Chapter 2; Olson et al., 2001) suggest that accessibility to climate space is unlikely to be limiting *Rumex* spp. distributions in the native range.

Given that non-climatic variables were better predictors of the species' distribution in the introduced range, non-climatic variables may be the limiting factor for *Rumex* spp. in their native range also (Bradie & Leung, 2017; Gallien et al., 2015; González-Moreno et al., 2015; Iturrate-Garcia et al., 2016). In Chapter 3 I highlighted that that human disturbance is a large driver of the species' distribution in both the native and introduced ranges, except for *R. conglomeratus* in the native range. This makes sense as *R. conglomeratus* has greater climatic restrictions than *R. obtusifolius* and *R. crispus* (Cavers & Harper, 1964; Grime et al., 2007; Hill et al., 1999), hence climate is a strong predictor of its distribution in the UK where it has a range margin. Furthermore, whilst other studies have shown that biotic interactions can impact range limits (Godsoe et al., 2015; Palacio & Girini, 2018; Urban et al., 2016), similar work by Costan (2021) suggests this is unlikely for *Rumex* species. Costan (2021) observed herbivory of *Rumex* spp. in the UK and NZ was low, and likely not strong enough to affect population dynamics.

More work will be needed to determine if this result generalises to other systems. It is possible that the generalist nature of *Rumex* spp. allows them to be preadapted to a broader range of environments than other species. Many invasive species exhibit generalist natures (Ainsworth & Drake, 2020; Clavel et al., 2011; Marvier et al., 2004), suggesting that preadaptation to a wide range of climates may be common. However, as rapid adaptation to analogue climates has been observed in other introduced plants (Dlugosch & Parker, 2008b), it is clear that not all range expansions are the result of preadaptation. Whether introduced plants will undergo rapid adaptation to undergo climatic niche shifts into non-analogue climates has yet to be empirically tested, however seems likely.

5.1.4 Contribution to the SDM literature

This study showed that the accuracy of models projecting the species' native distribution based only on non-climatic variables were superior to those using only climatic in all instances at a 1km^2 spatial resolution. Furthermore, including climatic variables in combination with non-climatic variables in models projecting species' distributions from the native range onto the introduced range often decreased their accuracy. When predicting the potential distribution within a region rather than between regions, models based on only non-climatic variables were either superior or were no different in accuracy than when using only climatic variables. Models based on only climatic variables never produced more accurate predictions of species' distributions compared to either non-climatic or combined models. This is particularly striking as using climatic variables in projections from the native range is commonplace, and often considered the standard approach. These results display the importance of utilising non-climatic variables in SDMs, even in the absence of climatic niche shifts.

Given that climate was a particularly poor predictor when projecting into non-analogue climates, this poses questions about the accuracy of projections into future climates. As projections into future climates simply represent range shifts temporally rather than spatially, the results of this study should still be applicable. This would suggest that the predicted distributions of plant populations under future climate scenarios likely underestimate the true possible distribution, as the climates species currently occupy likely do not correspond to all suitable climates they can tolerate. This is particularly relevant for species whose distributions, like *Rumex* spp., are largely determined by variables other than climate. Projections of species that show strong climatic limitations into future climate scenarios would likely be more accurate than those of *Rumex* species.

5.1.5 Contribution to the management of *Rumex* species

The results of this thesis can be used to inform the management of *Rumex* spp. populations. We now understand that current records of the environments *Rumex* spp. can tolerate likely underestimate their true potential distribution (Holm et al., 1979). Furthermore, as *Rumex* species are naturally preadapted to a broad range of climates there is no lag time between species entering a region and developing adaptations to those climates. Whilst *Rumex* spp. are likely close to their realising their full potential distribution in countries such as the UK and NZ where they do not have strong climatic limitations, other parts of the world will likely become susceptible to the establishment of *Rumex* spp. as climate changes progresses. As the climate warms, the distribution of *Rumex* spp. is likely to shift poleward with countries such as Canada, Argentina, Finland, and Russia susceptible to invasion due to their close proximity to existing populations. Therefore these regions should focus on prevention of seed contamination and managing nearby populations to reduce spread. Whilst both *R. obtusifolius* and *R. crispus* are already present in small numbers in these regions, populations are likely to expand. As the climate warms, *R. conglomeratus* will likely be recorded in these countries which are currently too cold for large populations to establish (Hill et al., 1999). Areas that are most at risk would be identified primarily by their level of human disturbance, as I have shown this to be one of the largest determinants of *Rumex* spp. distributions (Chapter 3). Unfortunately, areas which currently do not have *Rumex* spp. populations, unless under extreme climatic conditions, are likely not immune to establishment.

5.1.6 Future directions and thesis limitations

While this thesis observed that the species' niche can shift in different directions in different ranges it would be interesting to quantify and compare the magnitude of these niche shifts. By knowing the magnitude of niche shifts we may discover that some climates are more prone to or resilient to large niche shifts. This could help stakeholders decide where to distribute resources to prevent introduced species. I considered using centroid shift methods to test this as an extension to Chapter 2, however centroid shift methods are sensitive to the size of the species' realised niche in each range (Petitpierre et al., 2012). As a result, centroid shifts would be liable to over-predict the magnitude of shifts if niche unfilling occurs in the introduced range. Whilst one can argue that niche unfilling represents a niche shift, niche unfilling is commonly a function of time since establishment rather than indicating that these environments are unsuitable (Atwater et al., 2018; Petitpierre et al., 2012). As such, methodologies measuring the edge of the niche limits rather than the centre would be more informative.

Climatic variables may be sufficient to predict species' distributions at a coarse scale (Ashcroft et al., 2011; Bello et al., 2013; Petitpierre et al., 2017), however non-climatic variables are clearly important at a finer scale where management and impacts occur (Bello et al., 2013; Cherrill et al., 1995; Collingham et al., 2000; Gogol-Prokurat, 2011; Guisan & Thuiller, 2005; Reinhardt et al., 2020; Shabani et al., 2020; Sobek-Swant et al., 2012; Wang et al., 2019). Future work could consider modelling species' distributions, both within and projecting between ranges, at finer scales (less than 1km^2) to determine whether information derived from climatic variables becomes obsolete or even detrimental to model performance as scale decreases. Additionally, future work could investigate the importance of non-climatic variables for different species or across different environments. The distributions of *Rumex* species are not strongly limited by climate, however models of species that exhibit strong climatic limitations may show less improvement in accuracy through the inclusion of non-climatic variables.

Future work should also further investigate more accurate methods of predicting niche shifts into non-analogue climates. Such shifts are common, but correlative methods offer poor predictions of whether and where shifts occur. Whilst I hypothesised projections from non-climatic variables may better predict distributions in non-analogue climatic regions this did not prove to be true for *Rumex* species. Given that *Rumex* spp. are preadapted to these climates, by better quantifying the species' niche limits we should be able to predict its distribution in non-analogue climates. Quantifying the fundamental niche of species can be primarily achieved through two methods. Firstly, conducting experiments which directly test species' physiological tolerances via manipulations can be used to produce better estimates of a species' fundamental niche (Benning & Moeller, 2019; Godsoe et al., 2017; Hargreaves et al., 2014; Lee-Yaw et al., 2016; Willi & Van Buskirk, 2019). Alternatively, mechanistic models of population growth may provide better predictions of where species can persist than correlative methods (Angilletta et al., 2019; Buckley et al., 2010; Kearney & Porter, 2009; Srivastava et al., 2019).

Whilst further work needs to be completed on niche shifts into both analogue and non-analogue climates, modellers should be wary that what is classified as analogue can be influenced by their selection of variables. With fewer variables, more regions are likely to be classified as analogous, but the models may be missing crucial factors that determine the presence or absence of species. Including biologically relevant variables is most important (Austin & Van Niel, 2011; Brun et al., 2020;

Fourcade et al., 2018; Merow et al., 2014), however in many cases data on such variables can be lacking. For example, for *Rumex* spp. we lacked high quality soil data which could provide additional information on their distributions.

Further large-scale common garden experiments similar to ours would provide much needed insight into whether other introduced plant species are preadapted to climates beyond those in their native range and could help determine which traits preadapt species to these climates. Whilst logistically challenging, providing sites in the native range as well as the introduced range could determine whether plants from the introduced range have lost adaptations to the native range.

5.1.7 Conclusions

My thesis has demonstrated that species' realised niche shifts are more common than previously thought, highlights the underlying mechanisms of niche shifts, and provides guidance for how we can better predict introduced species' distributions in the future. By showing that niche shifts are inconsistent across the globe, I highlight new challenges for the niche shift literature. I then highlight a potential solution to this challenge: that non-climatic variables may be more useful than climatic variables. Furthermore, my work suggests that better understanding the characteristics of the species niche, by testing species' tolerances to climates beyond those in their native range, can predict niche shifts before they occur. Therefore, better measurements of a species' fundamental niche should be prioritised over assessments of rapid evolution in the introduced range to better improve forecast models in the future. These findings will thus alter the way in which niche shifts are predicted and studied across introduced ranges.

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Appendix A

Chapter 2 Supplementary Material

Table A.1 Full list of countries containing occurrences of *Rumex obtusifolius*, *R. crispus*, and *R. conglomeratus* considered in the analyses. Crosses indicate the species' presence in the particular country according to the available datasets.

Country	***Rumex obtusifolius***	***Rumex crispus***	***Rumex conglomeratus***
Native			
Albania	**X**	**X**	**X**
Andorra	**X**	**X**	-
Austria	**X**	**X**	**X**
Azerbaijan	**X**	**X**	**X**
Belarus	**X**	**X**	**X**
Belgium	**X**	**X**	**X**
Bosnia and Herzegovina	**X**	**X**	**X**
Bulgaria	**X**	**X**	**X**
Croatia	**X**	**X**	**X**
Czechia	**X**	**X**	**X**
Denmark	**X**	**X**	**X**
Estonia	**X**	**X**	-
Finland	**X**	**X**	**X**
France	**X**	**X**	**X**
Germany	**X**	**X**	**X**
Great Britain	**X**	**X**	**X**
Greece	**X**	**X**	**X**
Hungary	**X**	**X**	**X**
Ireland	**X**	**X**	**X**
Isle of Man	**X**	**X**	**X**
Israel	**X**	**X**	**X**
Italy	**X**	**X**	**X**
Jordan	**X**	**X**	-
Latvia	**X**	**X**	**X**
Lithuania	**X**	**X**	**X**
Luxembourg	**X**	**X**	**X**
Macedonia	**X**	**X**	**X**
Moldova	**X**	**X**	**X**
Montenegro	**X**	**X**	**X**
Morocco	**X**	**X**	**X**
Netherlands	**X**	**X**	**X**
Norway	**X**	**X**	**X**
Palestine	**X**	**X**	**X**

Poland	X	X	X
Portugal	X	X	X
Romania	X	X	X
Russia	X	X	X
Serbia	X	X	X
Slovakia	X	X	X
Slovenia	X	X	X
Spain	X	X	X
Sweden	X	X	X
Switzerland	X	X	X
Syria	X	X	X
Turkey	X	X	X
Ukraine	X	X	X
Introduced			
Australia	X	X	X
Canada	X	X	X
Mexico	X	X	X
New Zealand	X	X	X
United States of America	X	X	X
Japan	X	X	X

Table A.2 List of occurrence records georeferenced from journals expected to contain *Rumex* spp. records. Amount of records from each article is recorded.

Number of Records			
Rumex obtusifolius	*Rumex crispus*	*Rumex conglomeratus*	Reference
1	1	0	(Allan, 1925)
2	0	0	(Allan & Dalrymple, 1926)
0	1	0	(Allen et al., 1997)
1	0	0	(Allen et al., 1992)
1	1	0	(J. B. Armstrong, 1879)
1	1	0	(J. F. Armstrong, 1871)
0	1	0	(Aston, 1915)
0	1	0	(Aston, 1911)
0	0	1	(Bagnall, 1975)
1	1	1	(Bagnall & Ogle, 1981)
36	0	0	(Blackwell et al., 2011)
1	0	0	(Boerema et al., 1980)
1	0	0	(Bourdôt et al., 2019)
1	1	1	(Brownell, 2004)
1	1	0	(Buchanan, 1876)
1	1	0	(Burrows, 1986)
1	0	0	(Campbell, 1984)

1	1	0	(Carse, 1910)
1	1	0	(Thomas. F. Cheeseman, 1871)
1	0	0	(T. F. Cheeseman, 1879)
1	1	1	(T. F. Cheeseman, 1882)
1	1	0	(T. F. Cheeseman, 1896)
1	0	0	(Clark & Harris, 1985)
1	0	0	(Claydon et al., 2003)
0	1	0	(Copson & Leaman, 1981)
4	0	0	(Croker, 1955)
0	1	2	(Crumpton, 1978)
1	0	0	(Crush et al., 2006)
1	0	0	(Darwin & Keynes, 1835)
1	1	0	(Dickinson et al., 1998)
4	1	0	(Dingley, 1959)
1	1	0	(Druce & Williams, 1989)
1	1	1	(Duguid, 1990)
1	0	0	(Elliott & Lynch, 1958)
1	4	4	(Esler, 1978a)
1	0	0	(Esler, 1978b)
2	3	3	(Esler, 1980)
1	1	1	(Esler, 1987)
1	0	0	(Esler, 1988b)
1	0	0	(Esler, 1988a)
1	1	1	(Esler & Astridge, 1987)
5	3	0	(Fineran, 1973)
2	0	0	(Fletcher, 2001)
1	0	0	(Gerard et al., 2007)
0	1	0	(Gillham, 1960c)
1	1	0	(Gillham, 1960a)
0	1	0	(Gillham, 1960b)
1	1	1	(Healy, 1959)
1	1	1	(Heginbotham & Esler, 1985)
0	1	0	(Hubbard & Wilson, 1988)
1	0	0	(Hughes, 1985)
1	0	0	(Hutton, 1871)
0	0	1	(P. Johnson, 2004)
17	18	2	(P. N. Johnson, 1982)
4	6	2	(P. Johnson & Rogers, 2003)
2	0	0	(Kirk, 1868)
1	1	0	(Kirk, 1869)
2	2	2	(Kirk, 1870)
1	0	0	(Kirk, 1872)
1	0	0	(Kirk, 1877b)
1	0	0	(Kirk, 1877a)
1	0	0	(Kirk, 1895)
1	1	0	(W. G. Lee et al., 1986)

2	0	0	(William G. Lee et al., 1983)
2	0	0	(F. Y. Liu et al., 1997)
1	1	0	(Macmillan, 1979)
3	4	0	(Madden & Healy, 1959)
0	1	0	(Mark et al., 1989)
1	0	0	(Meurk, 1982)
1	1	1	(Miller et al., 1994)
1	1	0	(Morgan, 1915)
1	0	0	(Muller, 1970)
1	1	0	(Northcroft & Healy, 1975)
1	0	0	(Oliver, 1909)
0	1	0	(Partridge, 1989)
7	7	0	(Perrin, 1959)
1	0	1	(Popay et al., 1983)
1	0	0	(Rattray & Joyce, 1970)
0	1	0	(Redpath & Rapson, 2015)
0	1	0	(Scott, 2000)
1	0	0	(W. W. Smith, 1888)
1	1	0	(W. W. Smith, 1903)
1	0	0	(Suckling, 1975)
1	1	1	(Sykes, 1982)
1	0	0	(Townson, 1906)
0	1	1	(Walker & Lee, 2000)
0	0	1	(Wardle, 1980)
0	0	1	(A. E. Wright & Cameron, 1985)
1	1	0	(A. M. Wright, 1910)
152	89	31	**Total**

Table A.3 Journals involved in the New Zealand focussed literature search of occurrence records. All articles related to the term "*Rumex*" were searched. The number of articles containing useful records from each journal are below. 'Other' refers to 3 reports with records that were discovered whilst georeferencing other records.

Journal	Total Articles Searched	Articles Containing Records
New Zealand Journal of Crop and Horticultural Science	33	1
New Zealand Journal of Experiment Agriculture	33	2
New Zealand Journal of Botany	120	28
New Zealand Journal of Agricultural Research	92	16
Transactions and Proceedings of the Royal Society of New Zealand	113	31
Journal of the Royal Society of New Zealand	25	7
Other	3	3
Total	419	88

Table A.4 Number of occurrences and respective data sources for each species. GBIF: Global Biodiversity Information Facility; AFE: Atlas Florae Europaea; ALA: Atlas of Living Australia; EDDMapS: Early Detection and Distribution Mapping System; LIT: New Zealand records derived from literature (see Tables A.2 and A.3 for details); SELF: Records personally collected by the authors.

	Number of Records		
Database	*Rumex obtusifolius*	*Rumex crispus*	*Rumex conglomeratus*
GBIF	332376	317364	85931
AFE	1997	2649	1670
ALA	758	9401	3416
EDDMapS	1642	7294	37
LIT	152	89	31
SELF	227	214	46
Total	337152	337011	91131

Table A.5 Pairwise comparisons of niche overlap (*D*), niche similarity, niche expansion, and niche unfilling between the native range and three introduced ranges. This differs from the initial comparisons in Table 2.2 by including Japan in the native range of *Rumex obtusifolius* and *R. crispus*.

Species	Region	N	Niche Overlap (*D*)	Niche Similarity (p-value)	Niche Expansion	Niche Unfilling	Niche Pioneering
Rumex obtusifolius	Eastern Australia	275	0.260	0.01	0.066	0.400	0.052
	Western North America	242	0.163	0.01	0.265	0.504	0.554
	New Zealand	345	0.121	0.04	0.366	0.020	0.342
Rumex crispus	Eastern Australia	4035	0.336	0.01	0.018	0.470	0.009
	Western North America	823	0.103	0.04	0.248	0.291	0.369
	New Zealand	271	0.169	0.03	0.306	0.054	0.351

Table A.6 Results from pairwise comparisons between all assessed ranges of *Rumex* species, measuring overlap (*D*) and niche similarity. These values are only representative of niche dynamics in analogue climate space. Results in the upper right section of the table are the results from range 1 projected onto range 2, and result in the lower left section of the table are the opposite. Range 1 (columns) and range 2 (rows) are indicated by superscript numbers. Values of specified niche metrics are presented below, all metrics vary from 0-1; niche similarity is displayed as a p-value.

Rumex obtusifolius				
D	Native^{1}	Eastern Australia^{1}	Western North America^{1}	New Zealand^{1}
Native^{2}				
Eastern Australia^{2}	0.32			
Western North America^{2}	0.08	0.14		
New Zealand^{2}	0.11	0.13	0.14	
Similarity				
Native^{2}		0.01	0.07	0.06
Eastern Australia^{2}	0.01		0.01	0.03
Western North America^{2}	0.07	0.01		0.03
New Zealand^{2}	0.06	0.02	0.01	
Rumex crispus				
D	Native^{1}	Eastern Australia^{1}	Western North America^{1}	New Zealand^{1}
Native^{2}				
Eastern Australia^{2}	0.33			
Western North America^{2}	0.15	0.11		
New Zealand^{2}	0.16	0.31	0.15	
Similarity				
Native^{2}		0.01	0.01	0.07
Eastern Australia^{2}	0.01		0.04	0.01
Western North America^{2}	0.01	0.01		0.05
New Zealand^{2}	0.07	0.01	0.08	
Rumex conglomeratus				
D	Native^{1}	Eastern Australia^{1}	Western North America^{1}	New Zealand^{1}
Native^{2}				
Eastern Australia^{2}	0.20			
Western North America^{2}	0.17	0.21		
New Zealand^{2}	0.15	0.33	0.16	
Similarity				
Native^{2}		0.01	0.04	0.06

Eastern Australia[2]	0.01		0.04	0.01
Western North America[2]	0.04	0.01		0.08
New Zealand[2]	0.06	0.01	0.11	

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Appendix B

Chapter 3 Supplementary Material

Table B.1 Number of occurrence points from each source that were used in species distribution models. Figures in brackets are number of records prior to spatial rarefication. Record sources were classified as follows: GBIF – records downloaded from the Global Biodiversity Information Facility; Literature – records obtained from a literature search of floristic inventories in NZ; Personal – records collected by the research team across NZ. Note that a literature search was not conducted in GB as there was already an abundance of occurrence data.

Country	Species	Source		
		GBIF	Literature	Personal
GB	*R. obtusifolius*	11440 (19897)	-	44 (65)
	R. crispus	6513 (13056)	-	27 (49)
	R. conglomeratus	1446 (2108)	-	16 (21)
NZ	*R. obtusifolius*	50 (100)	5 (5)	216 (216)
	R. crispus	32 (32)	3 (5)	185 (193)
	R. conglomeratus	9 (9)	2 (2)	33 (40)

Table B.2 Key for the classification system of land classes used. The original 38 available land classes were aggregated into 7 land class types. Land classes with an asterisk do not have data for NZ.

New Land Class	Original land class
No Data	No land class data available
	Water bodies*
Forest	Tree cover, broadleaved, evergreen >15%
	Tree cover, broadleaved, deciduous >15%
	Tree cover, needle leaved, evergreen >15%
	Tree cover, needle leaved, deciduous >15%
	Tree cover mixed leaf type
	Tree cover, flooded, fresh or brackish water*
	Tree cover, flooded, saline water
	Tree or shrub cover
	Tree cover, needle leaved deciduous closed >40%
	Tree cover, needle leaved, deciduous, open 15-40%
	Tree cover, broadleaved, deciduous, closed >40%
	Mosaic tree and shrub >50% / herbaceous cover <50%
	Tree cover, broadleaved, deciduous, open 15-40%*
	Tree cover, needeleaved, evergreen, closed >40%*
	Tree cover, needleleaved, evergreen, open 15-40%*
Cropland	Cropland, rainfed
	Cropland, irrigated or post flooding*
	Mosaic cropland >50% / natural veg <50%
Grassland	Grassland
Herb/Shrub Cover	Herbaceous Cover
	Shrubland
	Mosaic natural vegetation >50% / cropland <50%
	Mosaic herbaceous cover >50% / tree and shrub <50%
	Shrub or herbaceous cover, flooded, fresh/saline/brackish water
	Shrubland deciduous
	Shrubland evergreen*
Urban	Urban areas
Bare/ Sparse Areas	Bare areas
	Permanent snow and ice
	Sparse vegetation (tree, shrub, herbaceous cover) <15%
	Lichens and mosses*
	Sparse Herbaceous cover <15%
	Unconsolidated bare areas
	Sparse Shrub
	Sparse tree*
	Consolidated bare areas*

Table B.3 **Comparisons of climate, land use, and human variables between the native (GB) and introduced (NZ) range. Land class groups were aggregated from the original 38 land class variables (Table B.2). Land class groups are presented as a proportion of total surface area for either the native or introduced range. “No Data” refers to areas within a region with no assessed land use type; this includes large water bodies. Climatic averages are based on data from 1981-2010. Some variable names were shortened: Mean Temp. Warm Month = Mean Temperature of the Warmest Month; Mean Temp Cold Month = Mean Temperature of the Coldest Month; Mean Precip. Wet Month = Mean Precipitation of the Wettest Month. Human related variables, which vary over shorter timescales than other variables, are primarily displayed from the years used in the analysis (2009 for human density, 2006 for livestock data). For human related variables, more up to date figures are displayed in brackets: human density in 2020 for GB (Park, 2020) and 2018 for NZ (Stats NZ, 2020); cattle densities in 2017 for NZ (Stats NZ, 2019) and 2018 for GB (NBA, 2018); and sheep densities in 2020 for NZ (Beef + Lamb New Zealand, 2020) and 2015 for GB (NSA, 2015).**

Land Class Group	Proportion of total Surface Area	
	GB	NZ
Bare/ Sparse Areas	0.03	0.04
Cropland	0.02	0.11
Forest	0.09	0.27
Grassland	0.35	0.42
Herb/Shrub Cover	0.45	0.01
Urban	0.06	0.01
No Data	0.06	0.14
Climate	Average 1981-2010	
	GB	NZ
Mean Temp. Warm Month	12.4°C	15.0°C
Mean Temp. Cold Month	5.2°C	6.2°C
Mean Precip. Wet Month	1167mm	1834mm
Median Sunshine Hours	1374	1825
Human	Population Density per km^2	
	GB	NZ
Human	256 (275)	16 (18)
Cattle	42 (40)	36 (38)
Sheep	144 (151)	150 (100)
Hydrology	Average Length of Waterways per km^2	
	GB	NZ
Hydrology	0.09km	0.15km

Table B.4 **Pearson correlation values between all variables included in models. Grey cells (top right of the table) show values of correlations between GB variables; white cells (bottom left of the table) show values of correlations between NZ variables. Values greater than |0.7| are highlighted. Variable names are abbreviated similar to other figures where: “Max Temp” = Mean temperature of the warmest month, “Min Temp” = Mean temperature of the coldest month, “Precip” = Mean precipitation of the wettest month, “Sun Hours” = Median sunshine hours, “Shrub/Herb” = Proportion of Herb or Shrubland, “Human” = Human Footprint, and “Hydro” = Hydrological.**

Variables	Max Temp	Min Temp	Precip	Sun Hours	Cropland	Shrub/ Herb	Forest	Bare	Grassland	Urban	Cattle	Sheep	Human	Hydro
Max Temp		**0.84**	**-0.71**	**0.88**	0.40	0.05	-0.23	-0.66	0.02	0.38	0.18	-0.02	0.14	0.07
Min Temp	**0.84**		-0.49	**0.81**	0.26	-0.09	-0.25	-0.58	0.05	0.40	0.16	0.01	0.18	-0.04
Precip	-0.52	-0.22		**-0.72**	-0.39	-0.22	0.28	0.57	0.10	-0.29	-0.12	0.08	-0.12	0.02
Sun Hours	0.65	0.40	-0.51		0.39	0.04	-0.25	-0.53	0.04	0.27	0.21	0.00	0.14	-0.06
Cropland	0.08	-0.02	-0.12	0.14		0.20	0.00	-0.02	0.11	0.04	0.25	-0.03	-0.23	0.19
Shrub/Herb	-0.12	-0.06	0.09	-0.04	-0.02		0.01	0.01	-0.05	-0.01	0.14	-0.37	-0.54	0.34
Forest	-0.13	-0.03	0.34	-0.07	-0.12	0.01		-0.01	0.01	-0.01	0.08	0.03	-0.28	0.19
Bare	-0.43	-0.36	0.24	-0.24	-0.04	-0.01	-0.15		-0.01	-0.01	-0.04	-0.19	-0.17	0.00
Grassland	0.14	-0.08	-0.38	0.17	0.10	-0.23	-0.54	-0.13		-0.01	0.69	0.63	-0.48	0.41
Urban	0.10	0.10	-0.07	0.08	0.01	-0.03	-0.07	-0.03	-0.03		-0.04	-0.19	-0.11	0.17
Cattle	0.36	0.30	-0.21	0.21	0.03	-0.05	-0.13	-0.10	0.14	0.07		0.38	-0.40	0.36
Sheep	0.07	-0.15	-0.47	0.10	0.11	-0.10	-0.40	-0.06	0.54	0.01	0.15		-0.07	0.12
Human	0.30	0.41	-0.19	0.01	-0.08	-0.21	-0.33	-0.15	-0.33	0.02	0.00	-0.10		-0.50
Hydro	-0.10	-0.23	0.24	0.01	0.07	0.15	0.24	0.04	0.26	-0.01	0.05	0.06	**-0.76**	

Table B.5 Prevalence of training and testing records in each model type. All models utilised a 30% random testing percentage, meaning that models were trained using 70% of available records.

Species	Country			
	GB		NZ	
	Training	Testing	Training	Testing
Rumex conglomeratus	1023	439	31	13
Rumex crispus	4578	1962	154	66
Rumex obtusifolius	8039	3445	190	81

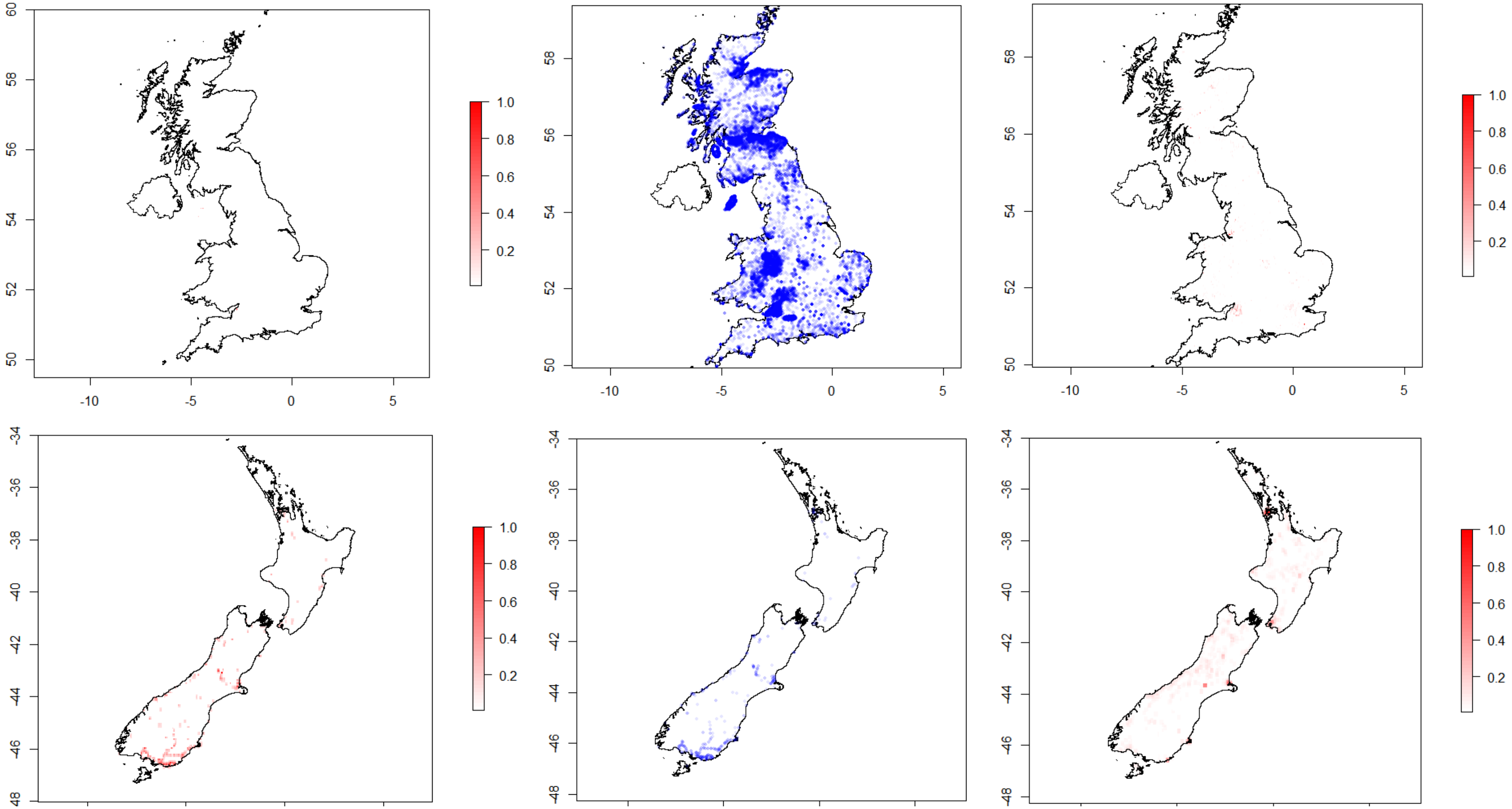


Figure B.1 Maps of GB (top row) and NZ (bottom row) displaying *Rumex* spp. occurrence data (centre column) and sample bias layers (left and right columns). Panels on the left side display the sample bias layer we used in our models which were made from combined occurrence data for *Rumex obtusifolius*, *R. crispus*, and *R. conglomeratus*. The central column displays the distribution of the occurrence data used to generate the sample bias layer in the left column. The right column displays sample bias layers calculated using data for all plants available on GBIF for GB and NZ. The sample bias layers shown on the left more accurately account for the sample bias shown in NZ. Note that areas of intense sample bias on the bottom right map occur around cities, namely Auckland, Christchurch, and Wellington, which are partially hidden behind the outline of the country. The scale varies from 0.01-1 where 1 (red) displays the most intensely sampled areas and 0.01 (white) indicates little to no sampling has occurred.

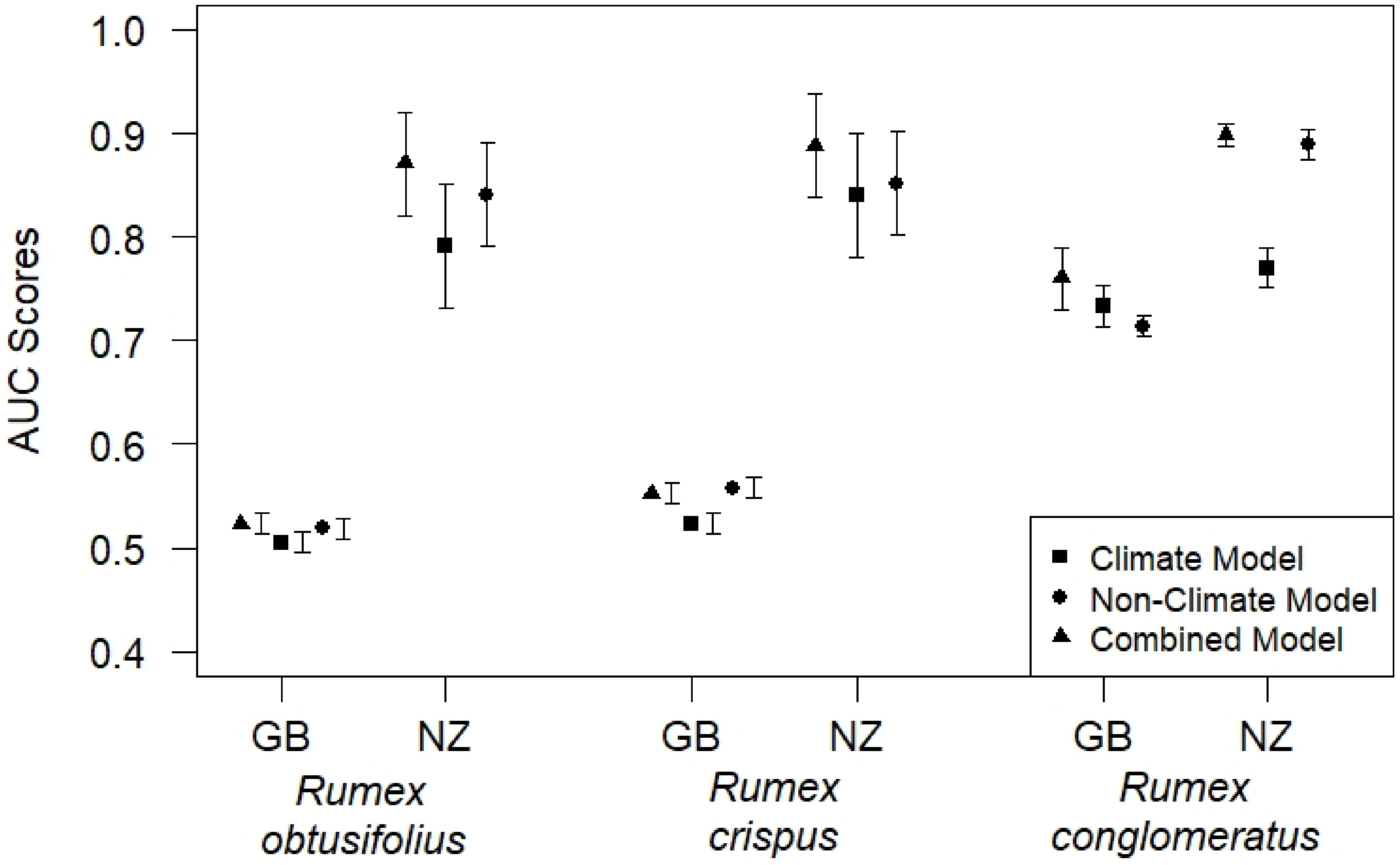
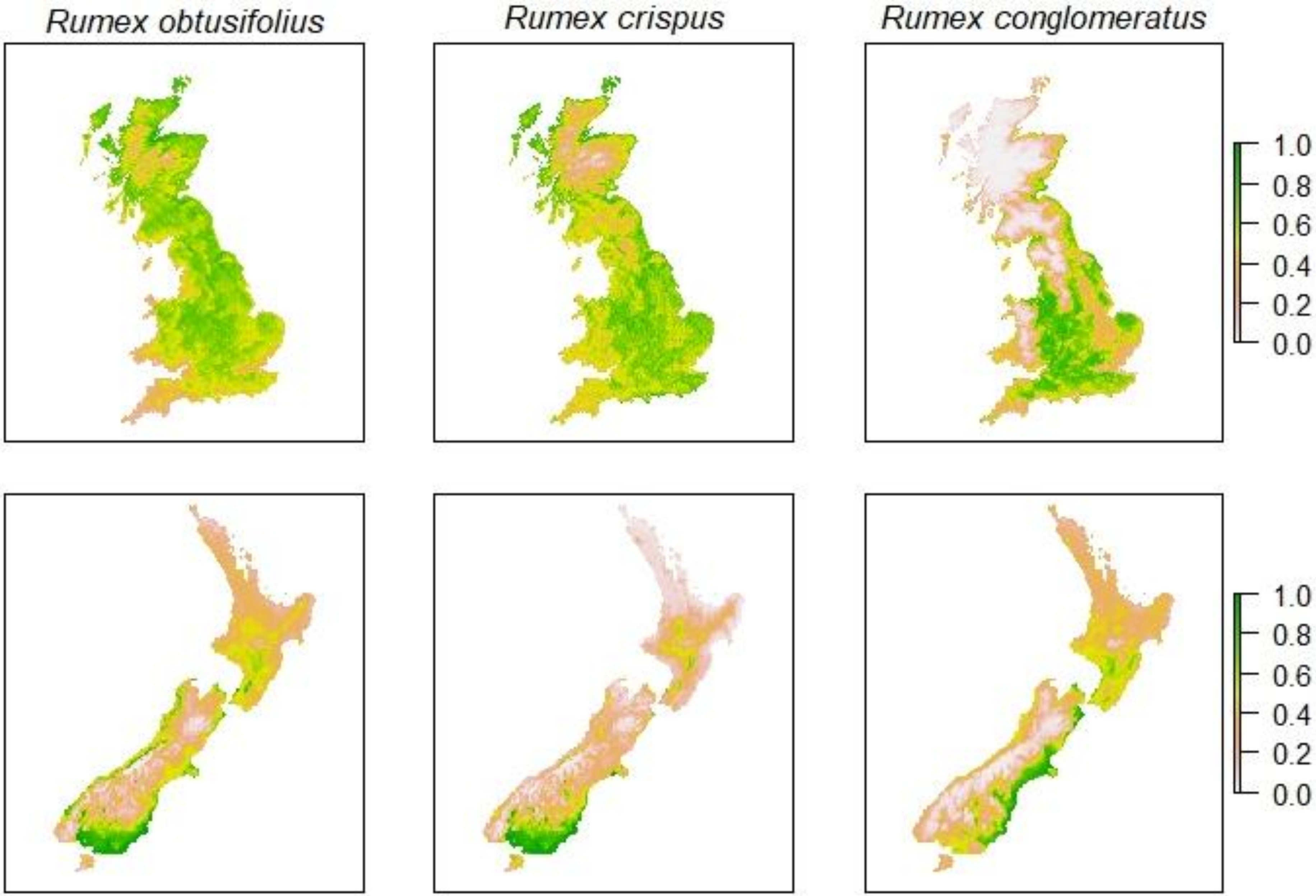
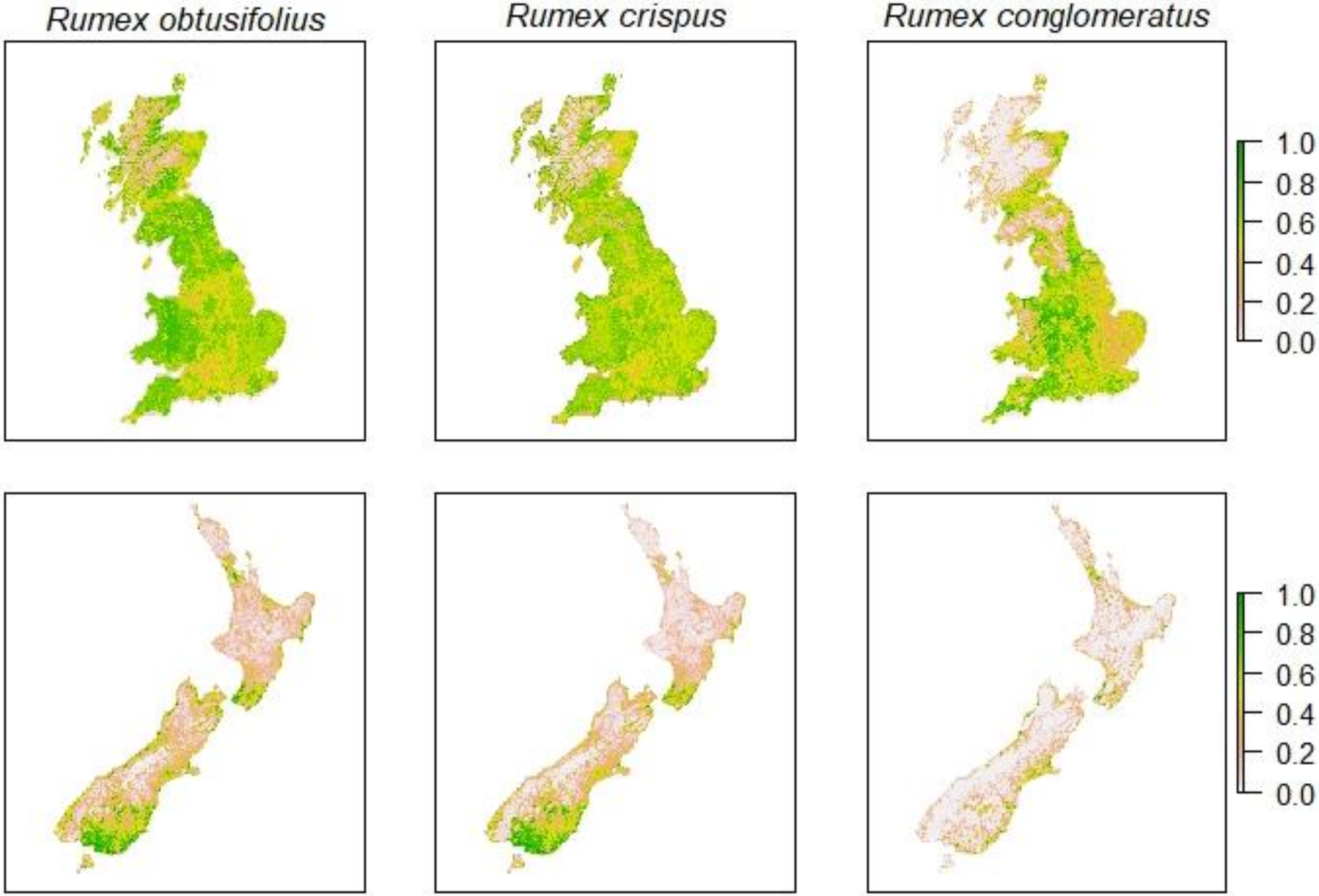


Figure B.2 Area under the receiver operating curve (AUC) scores for species' distribution models of *Rumex* spp. in both GB and NZ. AUC varies from 0-1, where 1 represents completely accurate predictions, 0 represents completely inaccurate predictions, and 0.5 indicates model predictions are no better than chance alone. Models were run using a combination of either only climate or non-climate variables, or a combination of both climate and non-climate variables. Error bars represent 95% confidence intervals. Note that some error bars are jittered for better visualisation.

A) Climate-Only Model



B) Non-Climate-Only Model



C) Combined Model

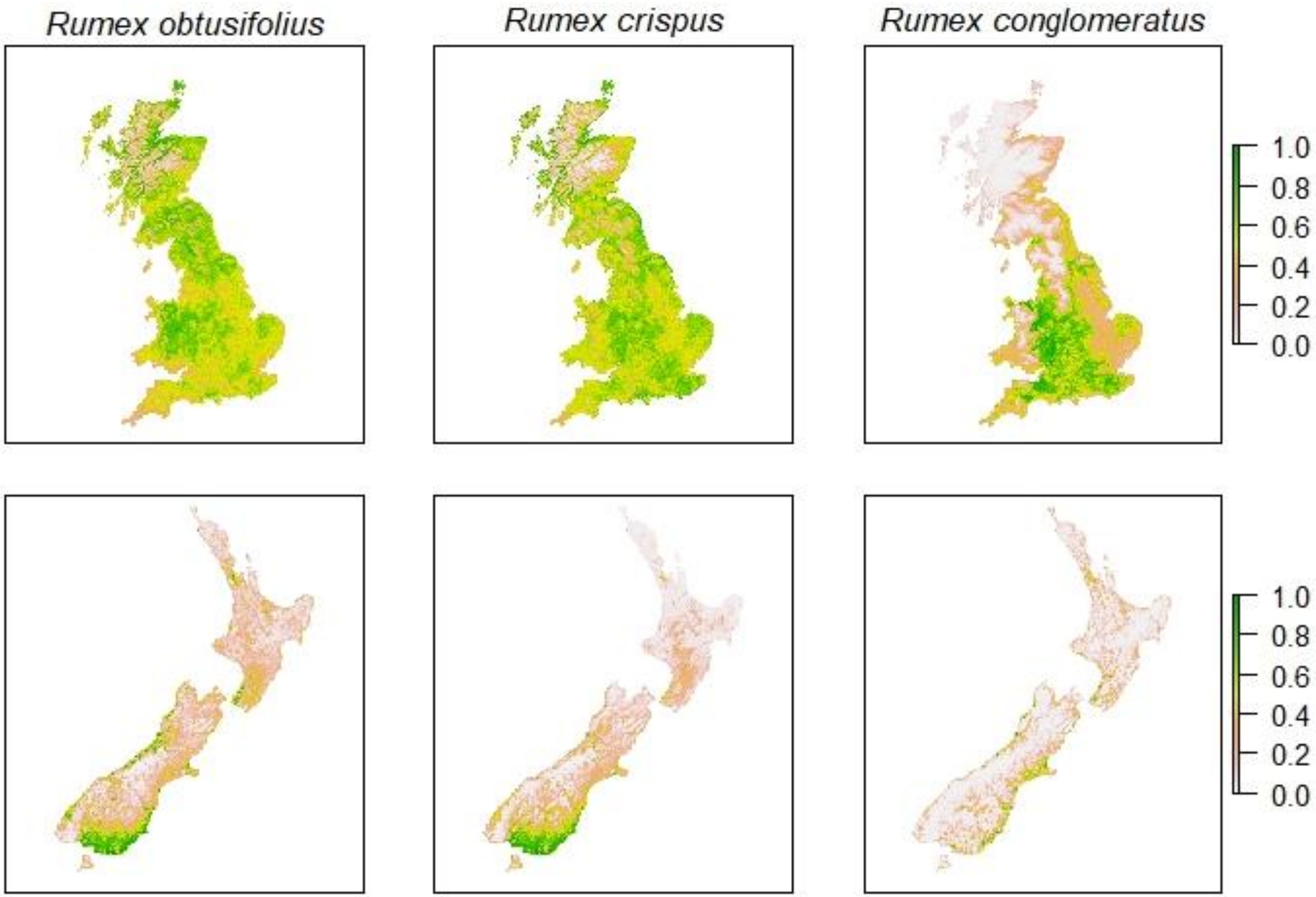
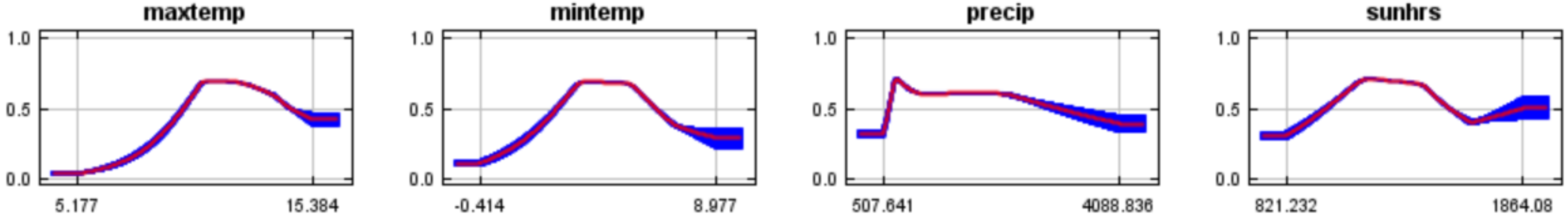


Figure B.3 **Average predictions of environmental suitability from 100 MaxEnt replicate runs for each species (columns) and country (rows). Models were run for both GB (top row) and NZ (bottom row). A) Predictions for models computed with only climatic variables. B) Predictions for models computed with only non-climatic variables. C) Predictions for models computed with both climatic and non-climatic variables.**

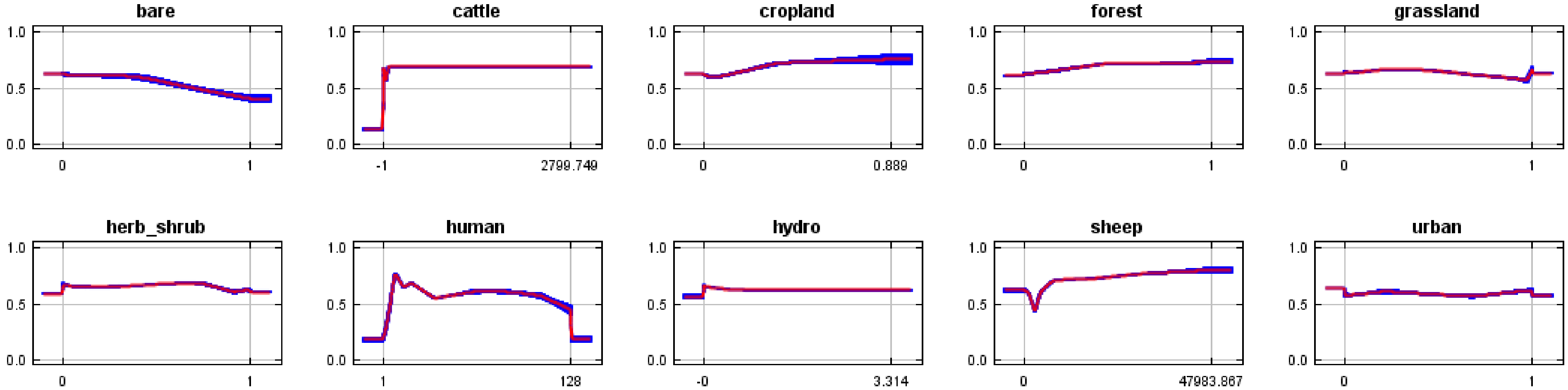
(A)

GB – *Rumex obtusifolius*

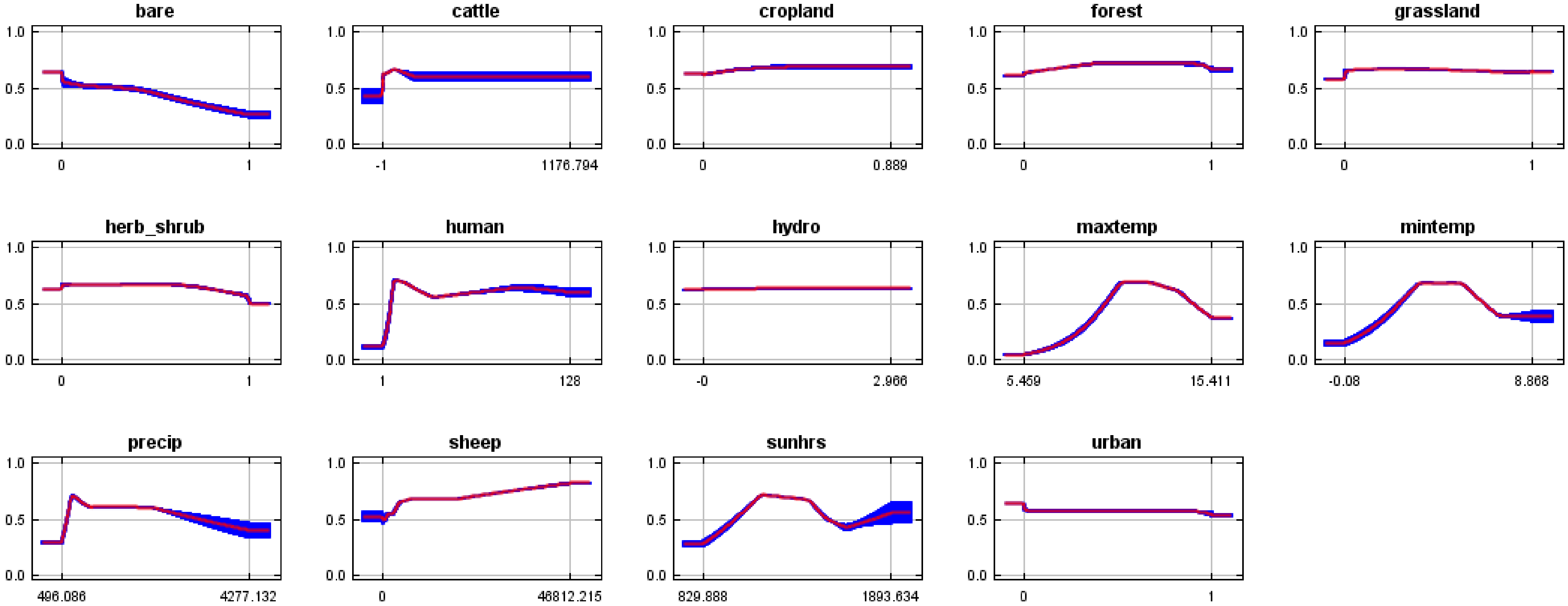
Climate Only



Non-Climate Only



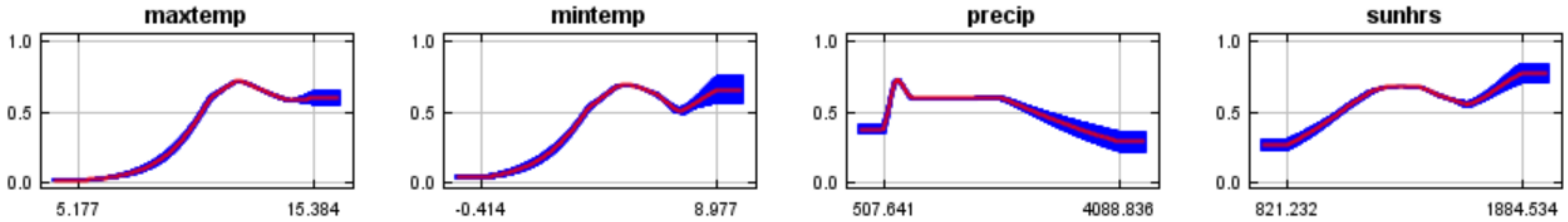
Combined Model



(B)

GB – *Rumex crispus*

Climate Only



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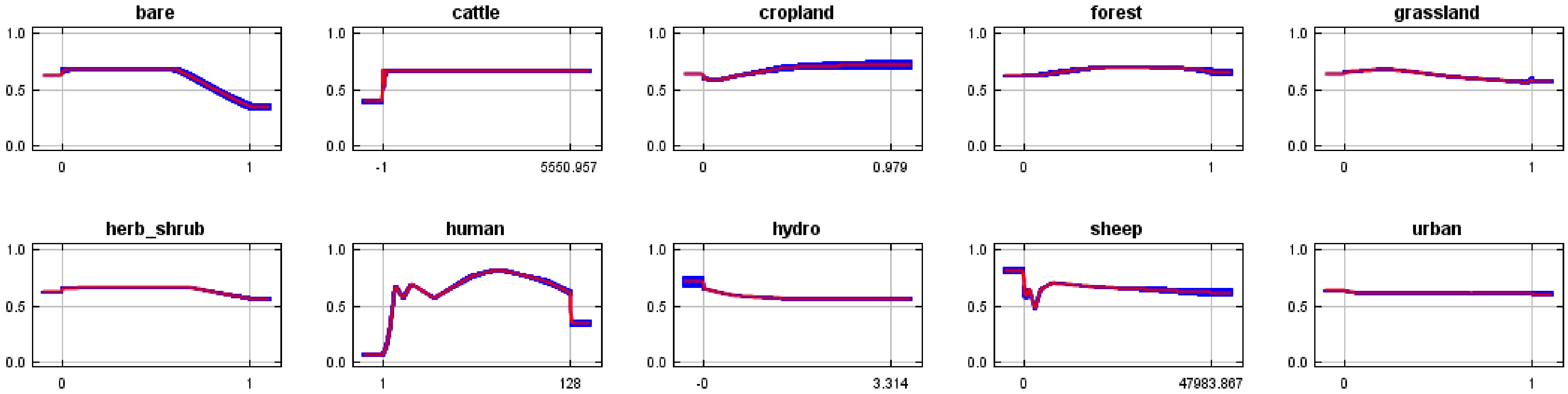
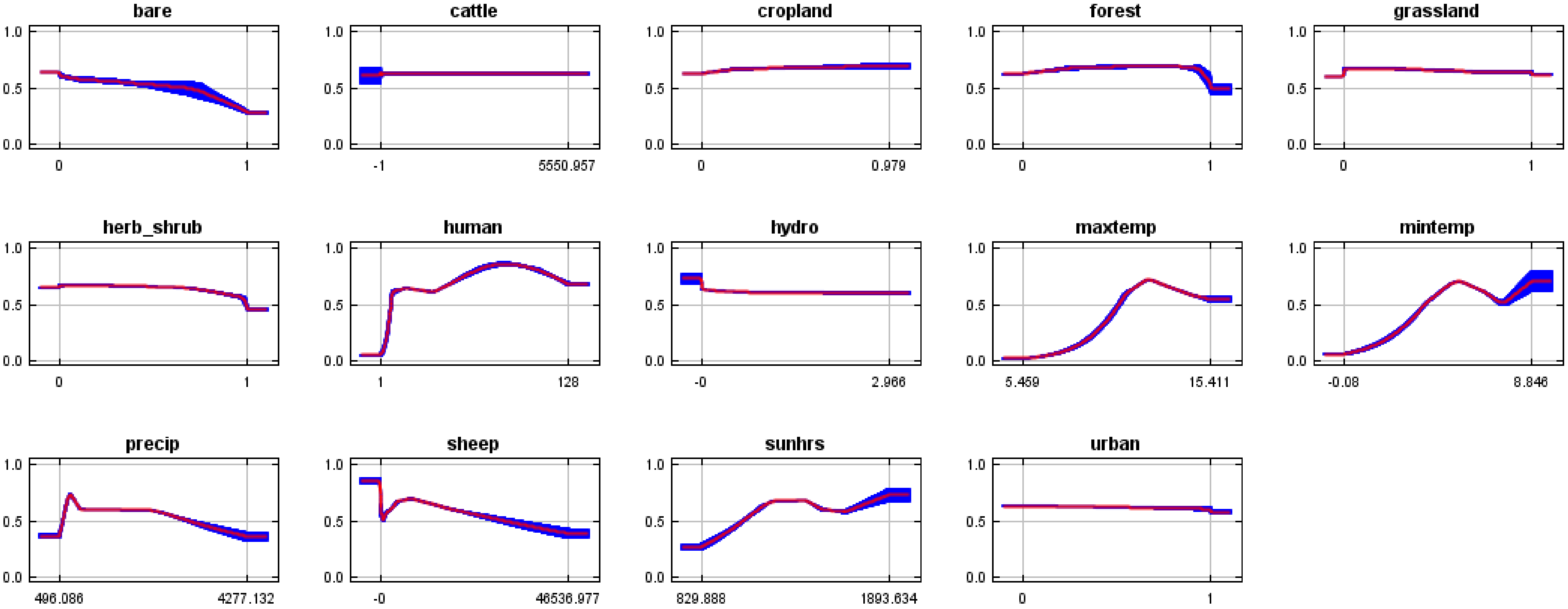


Combined Model


bare cattle cropland forest grassland

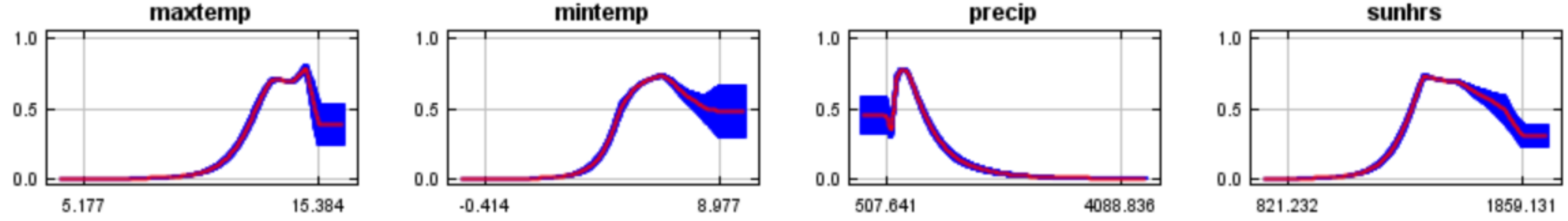
herb_shrub human hydro maxtemp mintemp

precip sheep sunhrs urban

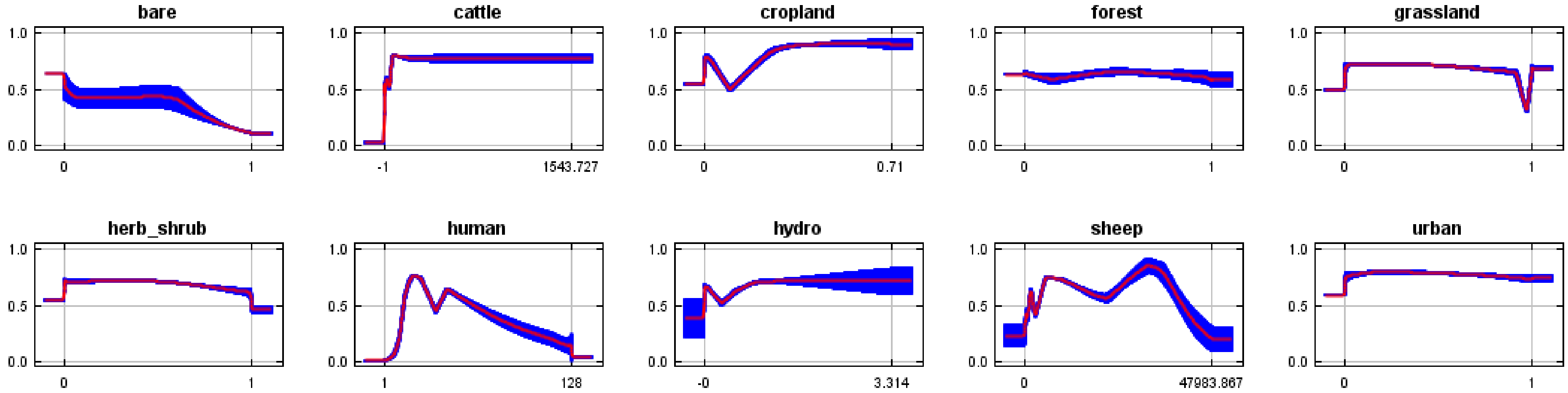
(C)

GB – *Rumex conglomeratus*

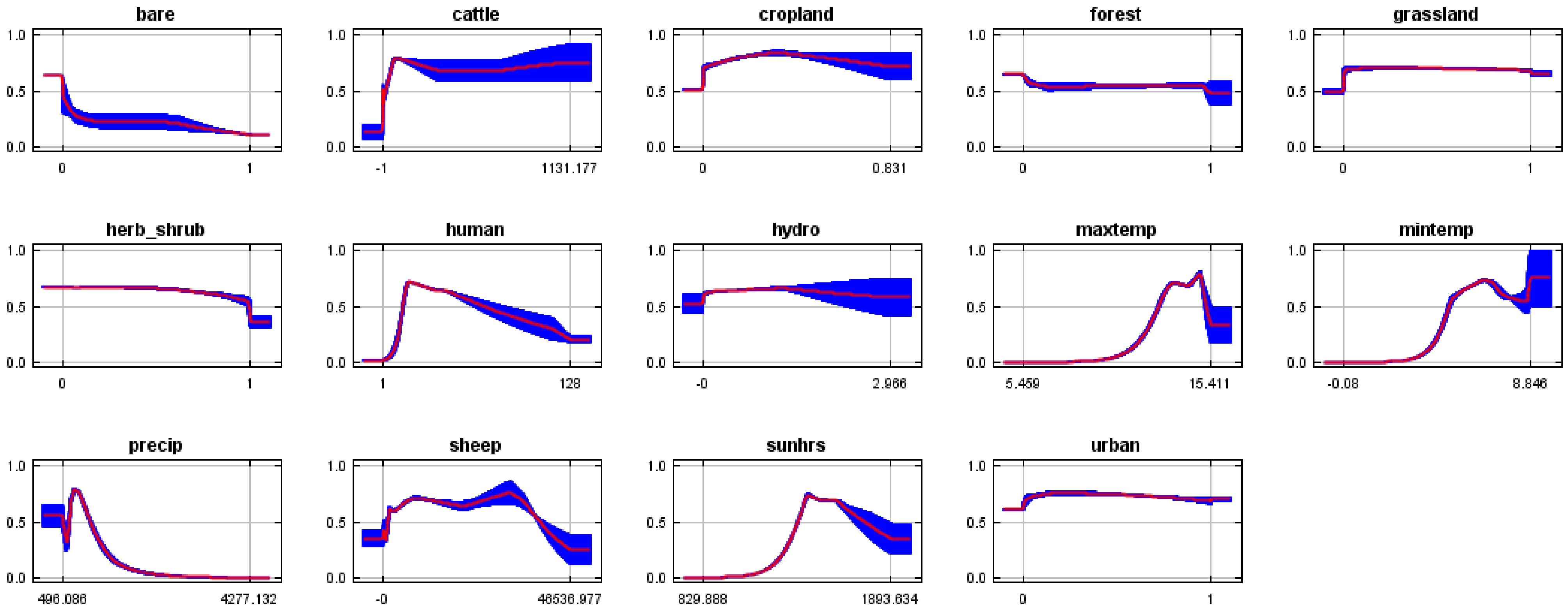
Climate Only



Non-Climate Only



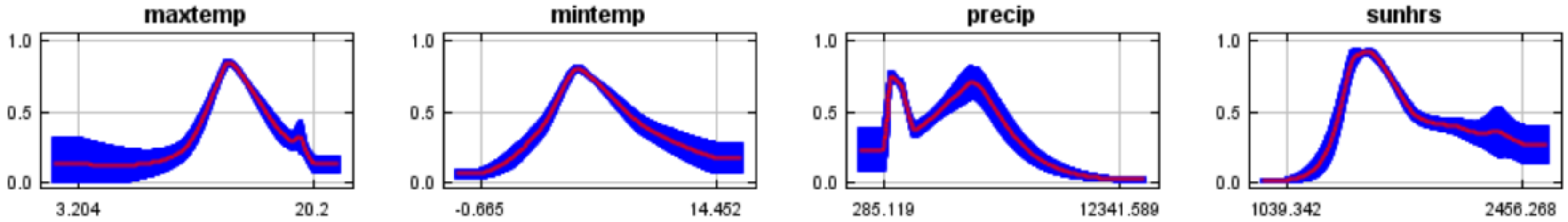
Combined Model



(D)

NZ – *Rumex obtusifolius*

Climate Only



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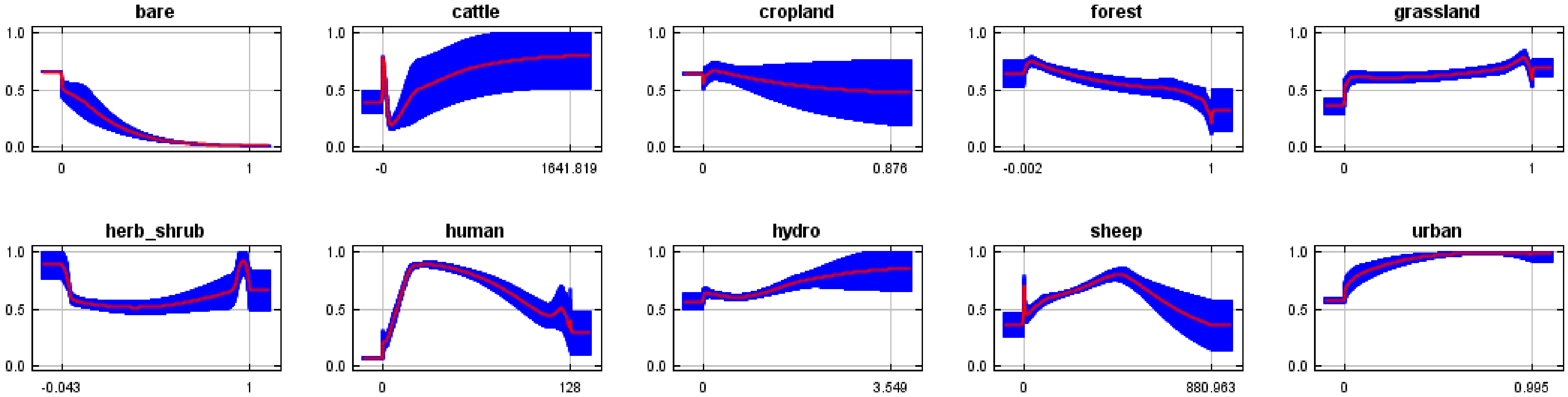
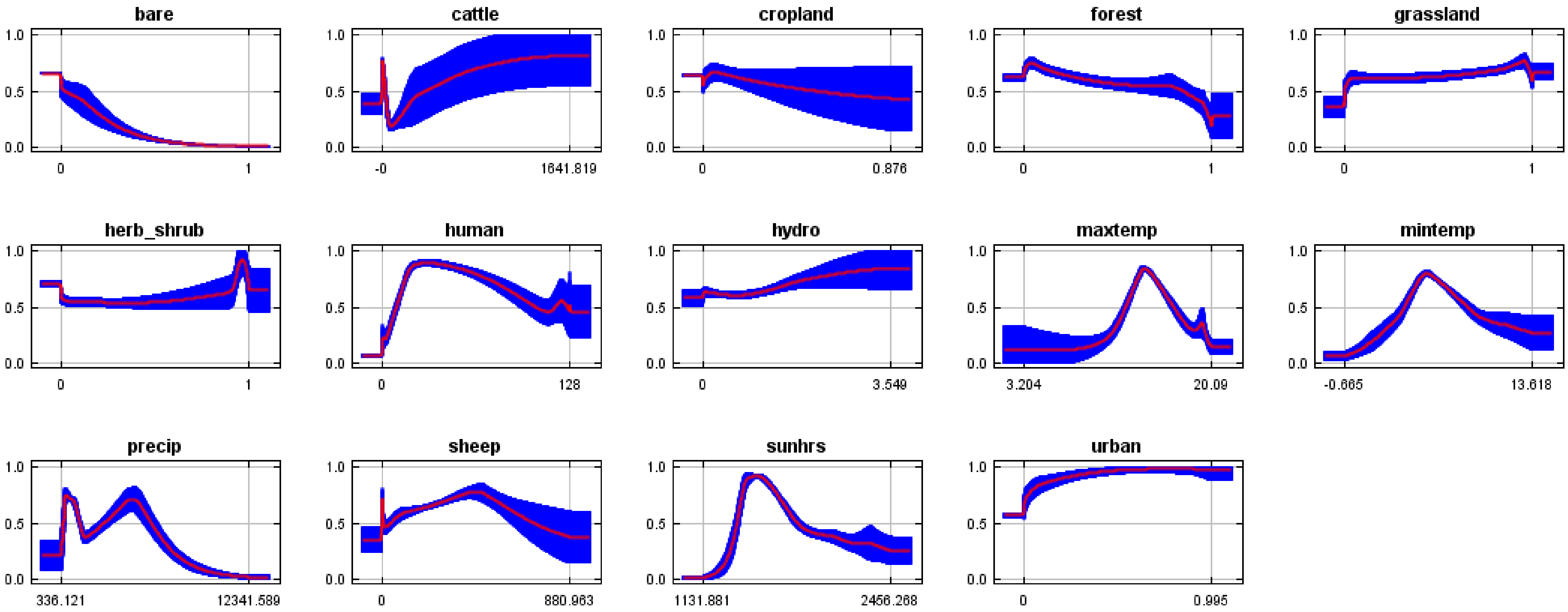
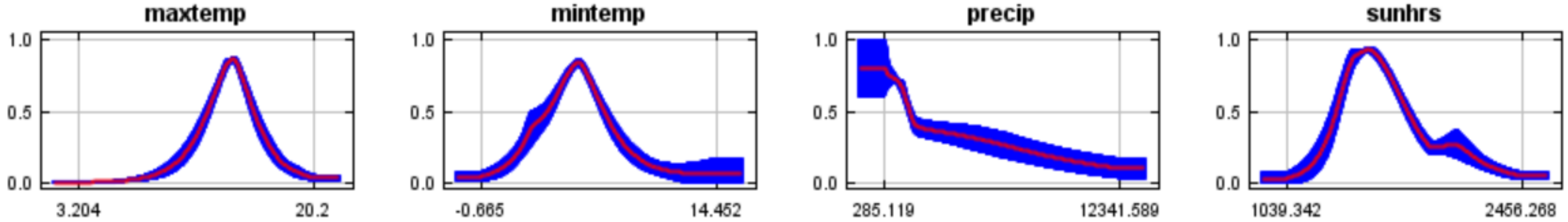


Combined Model



(E)
NZ – *Rumex crispus*

Climate Only



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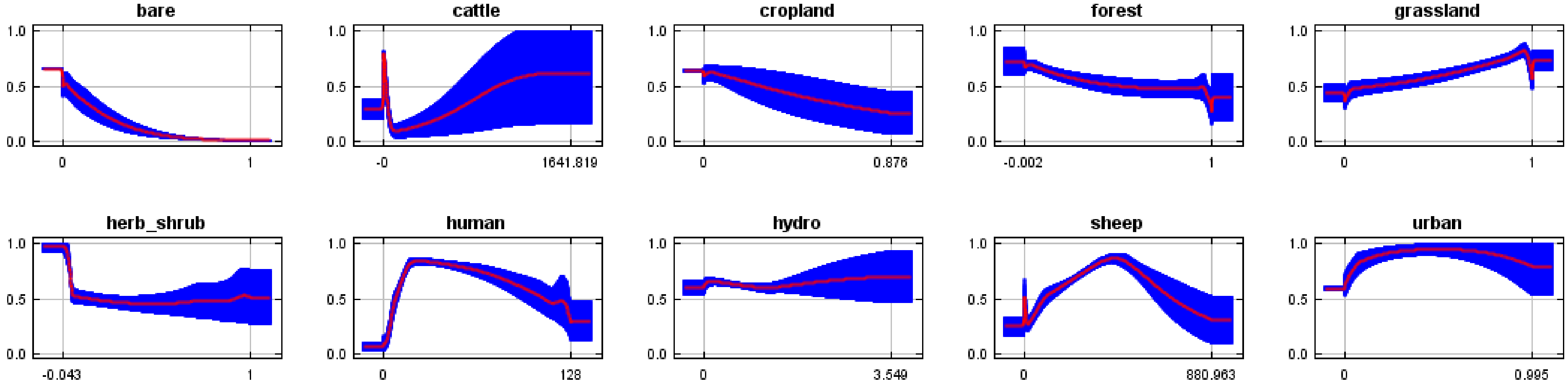
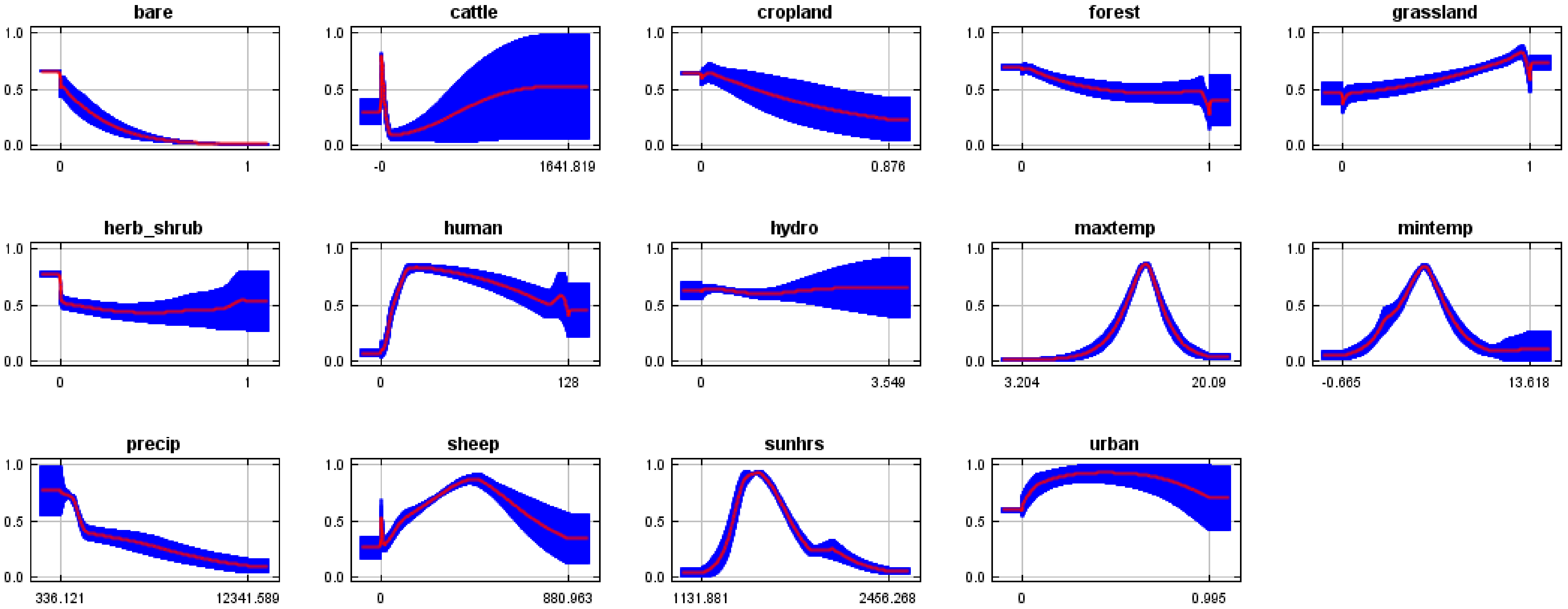


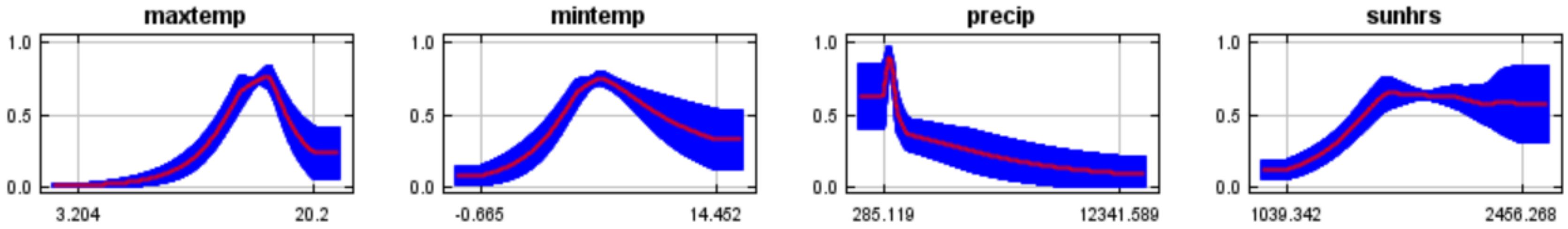
Combined Model



(F)

NZ – *Rumex conglomeratus*

Climate Only



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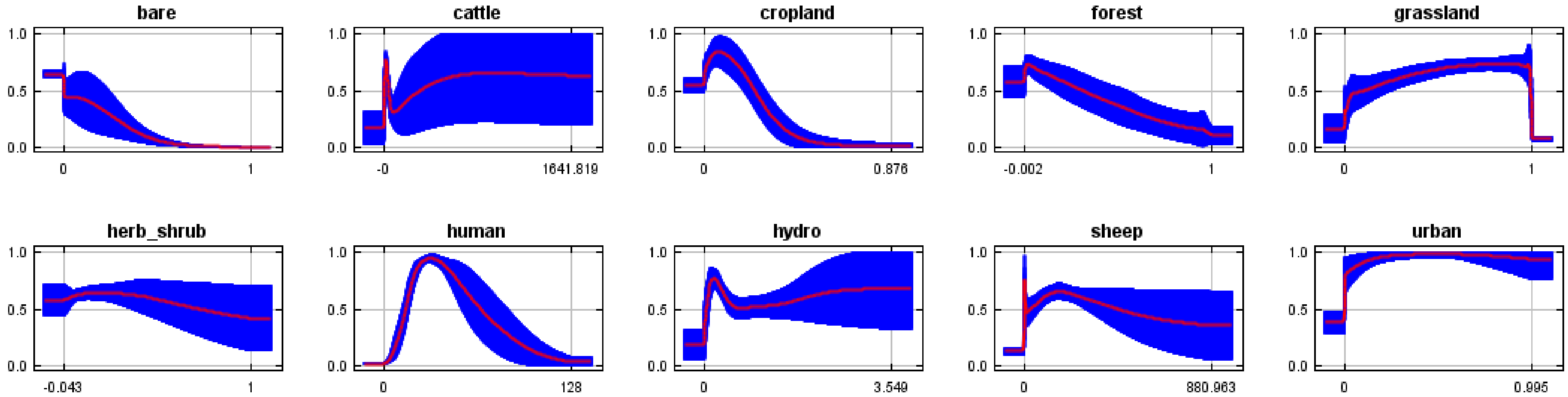


Combined Model

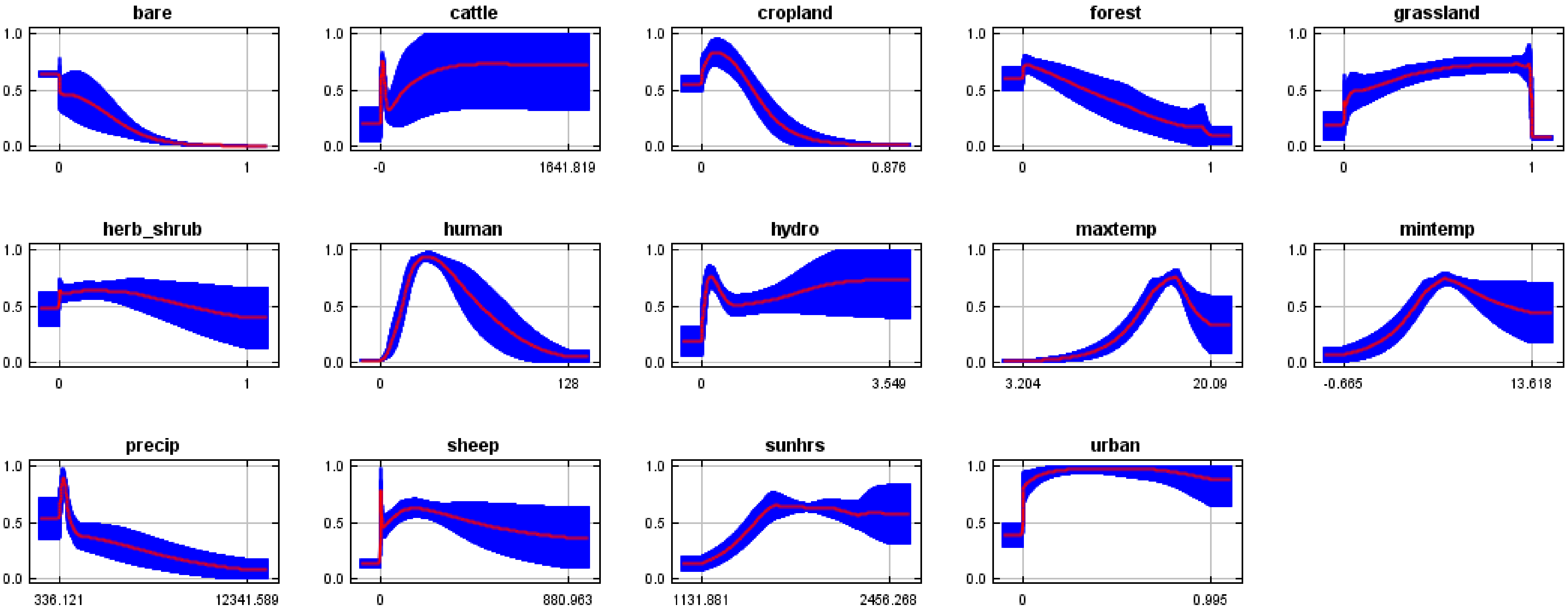
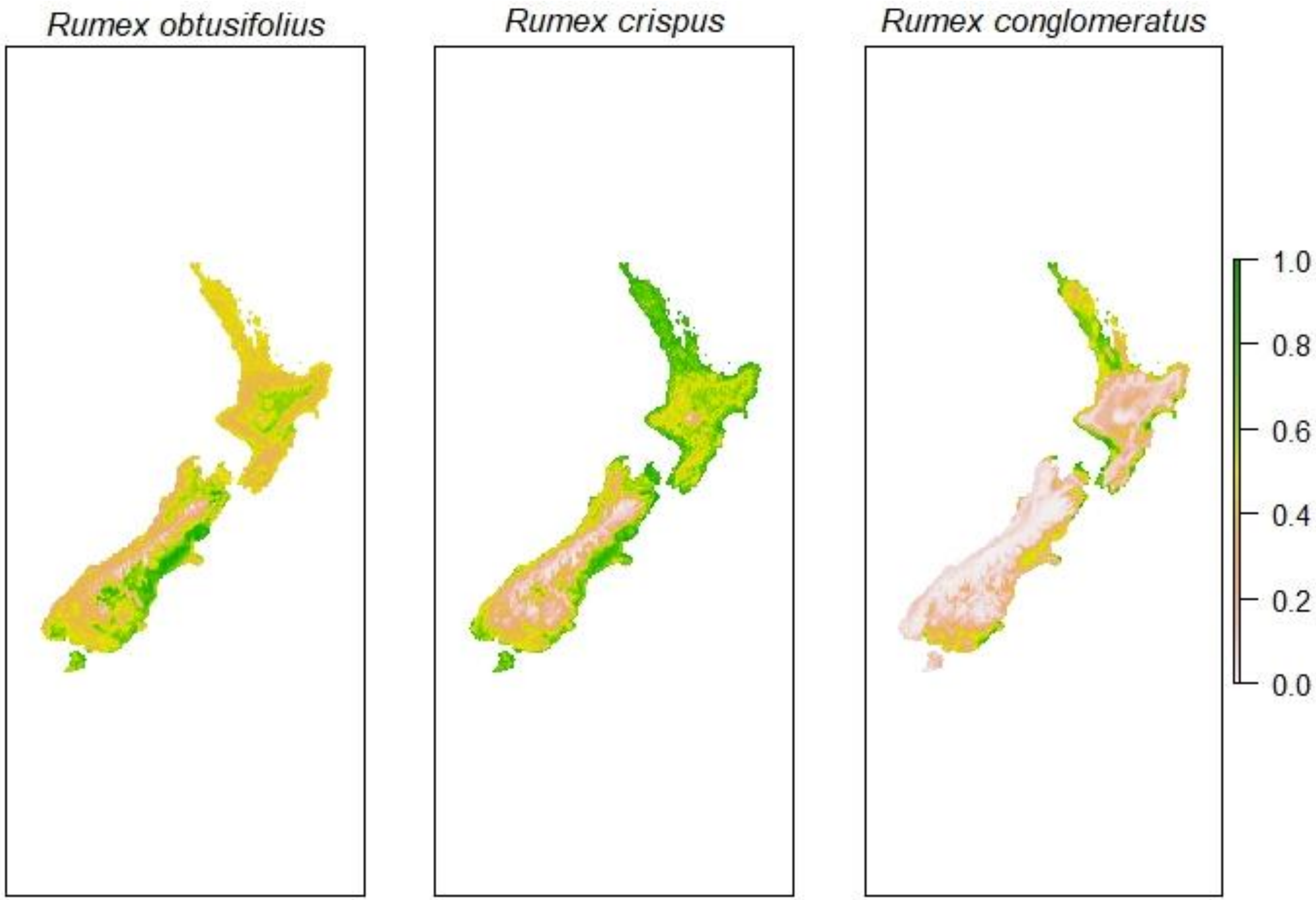
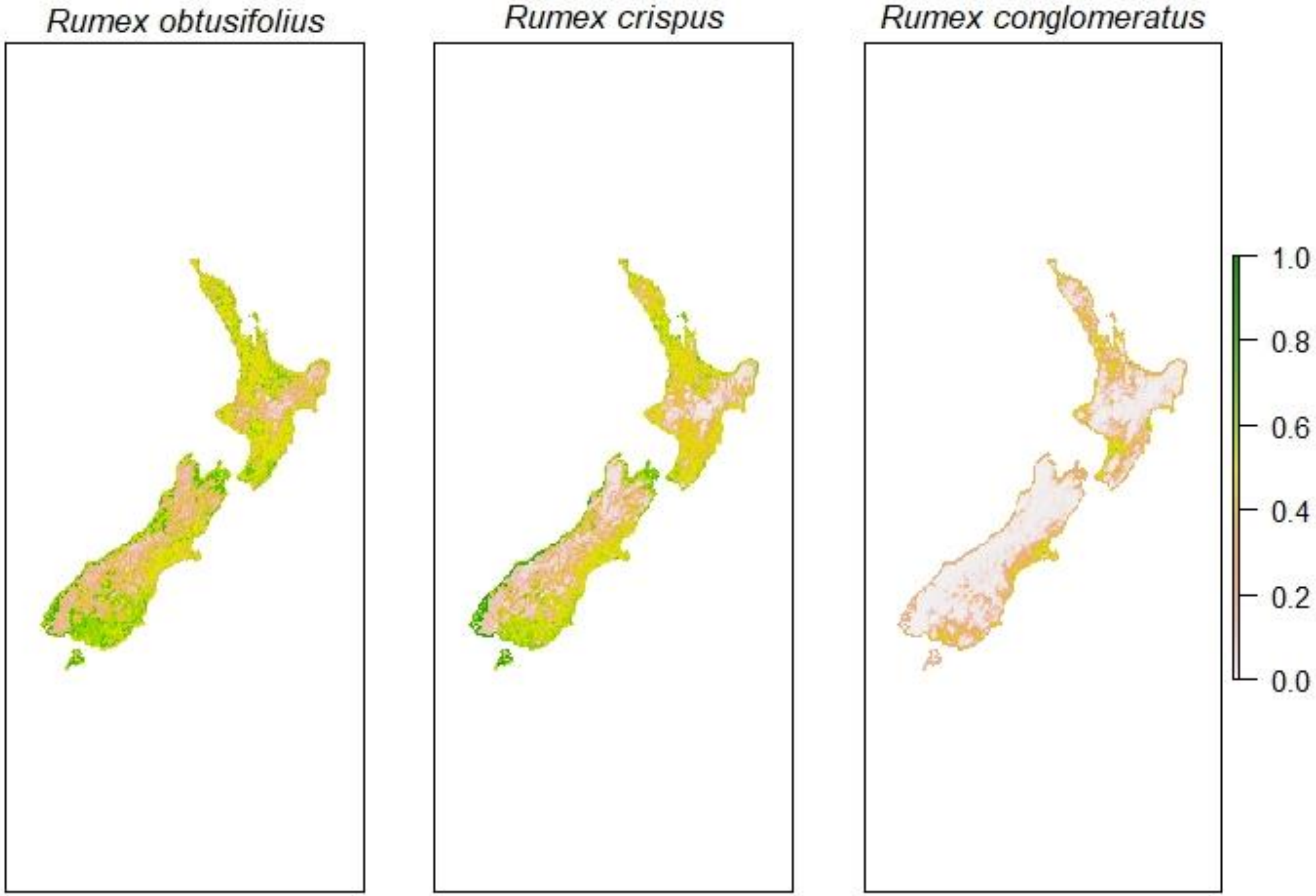


Figure B.4 Average response curves of MaxEnt models created using only the corresponding variables. These plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables. Response curves are shown for: *Rumex obtusifolius* GB (A) and NZ (D) models; *R. crispus* GB (B) and NZ (E) models; and *R. conglomeratus* GB (C) and NZ (F) models. The red line shows the response curve of the average model, and the blue error bars show the variation in response curves between the 100 replicate MaxEnt models. For all plots variable names are abbreviated where: "herb_shrub" = Proportion of Herb or Shrubland, "human" = Human Footprint, "hydro" = Hydrological, "maxtemp" = Mean temperature of the warmest month, "mintemp" = Mean temperature of the coldest month, "precip" = Mean precipitation of the wettest month, "sunhrs" = Median sunshine hours. Illogical values such as the lower bound of GB cattle density being "-1" represent an arbitrary value denoting no information was available for that cell.

A) Climate Only Model Projections



B) Non-Climate Only Model Projections



C) Combined Model Projections

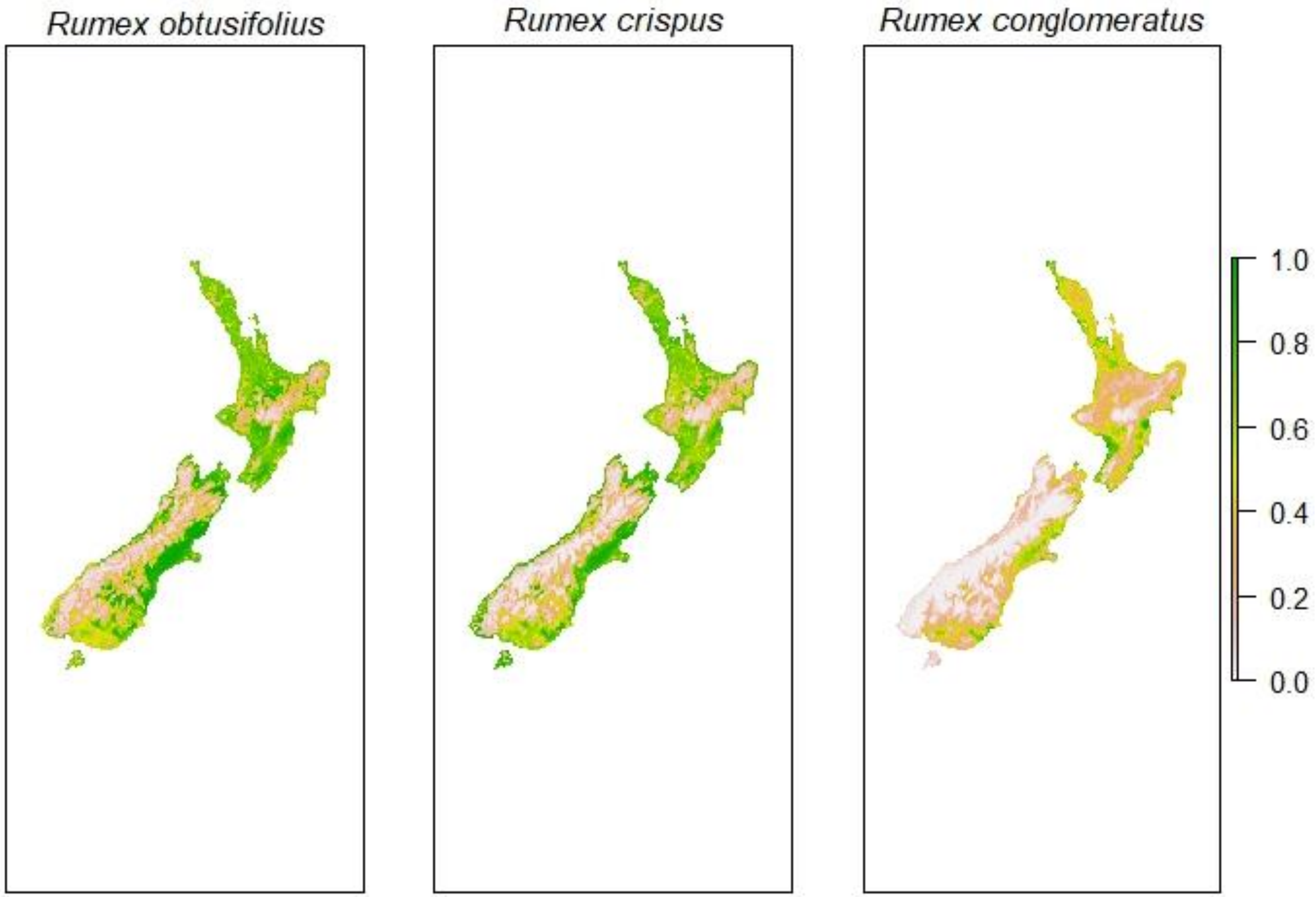


Figure B.5 Plots show projected predictions of habitat suitability for models trained in GB and projected onto NZ. These predictions are the average prediction of 100 replicated MaxEnt runs utilising bootstrapping. A) Models trained using only climatic variables. B) Models trained using only non-climatic variables. C) Models trained using both climatic and non-climatic variables.

B.1 References

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Appendix C

Chapter 4 Supplementary Material

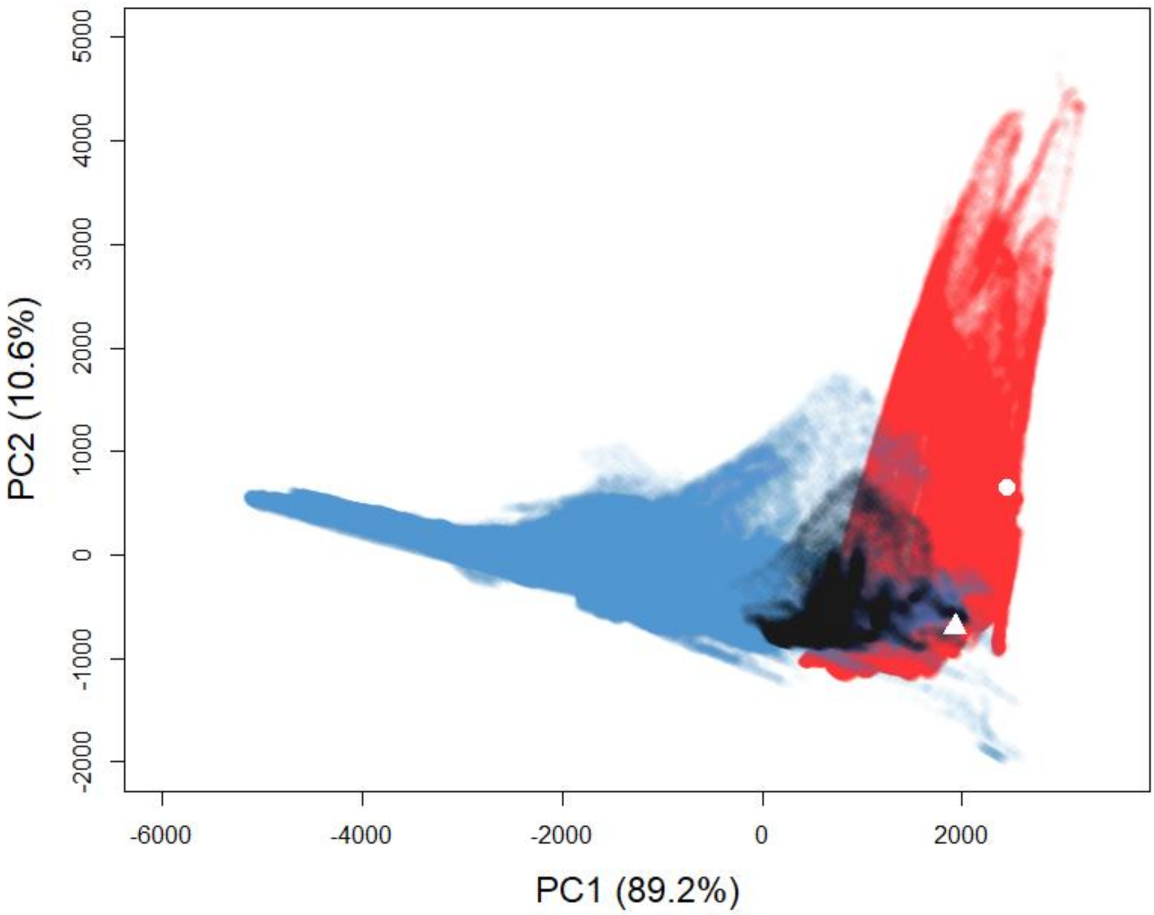

Figure C.1 Principal component analysis (PCA) showing available climates for all locations in the native range (blue), NZ (red), and the UK (black). The top two principal components explain >99% of the variation across 17 WorldClim variables for the native range and NZ. The white triangle denotes the location of our Southland field site in analogue space, i.e. where climates for the native range and NZ overlap. The white circle denotes the location of our Westland field site in non-analogue space. PC1 broadly corresponds to a temperature gradient, and PC2 to a precipitation gradient. The climates of the UK broadly overlap the available analogue climate space between the native range and NZ.

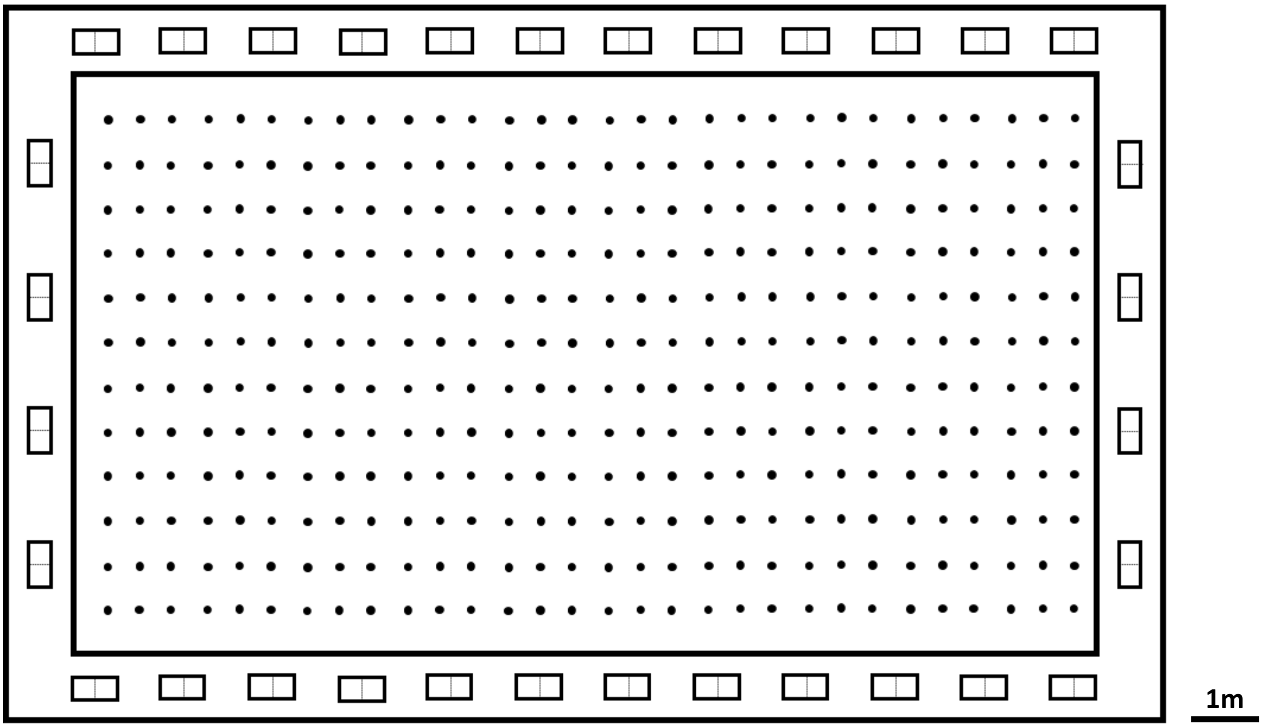

Figure C.2 Block design at each site. Each block was roughly 12m long and 9m wide, created using 18m rolls of weed cloth secured together by a combination of plastic and metal pegs. Each block had space for 360 individual plants, spaced 0.5m apart. 32 germination trays were arranged around the outside of the block, with 12 trays along each length and 4 trays along each width. Germination trays each contained seeds from 2 populations separated by weed cloth. Each population in a germination trays had seeds from 5 individuals, with 10 seeds from each individual, arranged along colour code sections of the tray for easy identification. The same colour codes were used for individual plants within the block by placing painted bamboo stakes at each potential plant location. To place trays and plants within the block, holes were cut into the weed cloth at the specific location. Holes for individual plants were only cut when transplanting the seedling to avoid reducing the integrity of the weed cloth and inviting unwanted weeds to germinate. Regular maintenance was required at blocks to repair stretches of weed cloth that were damaged.

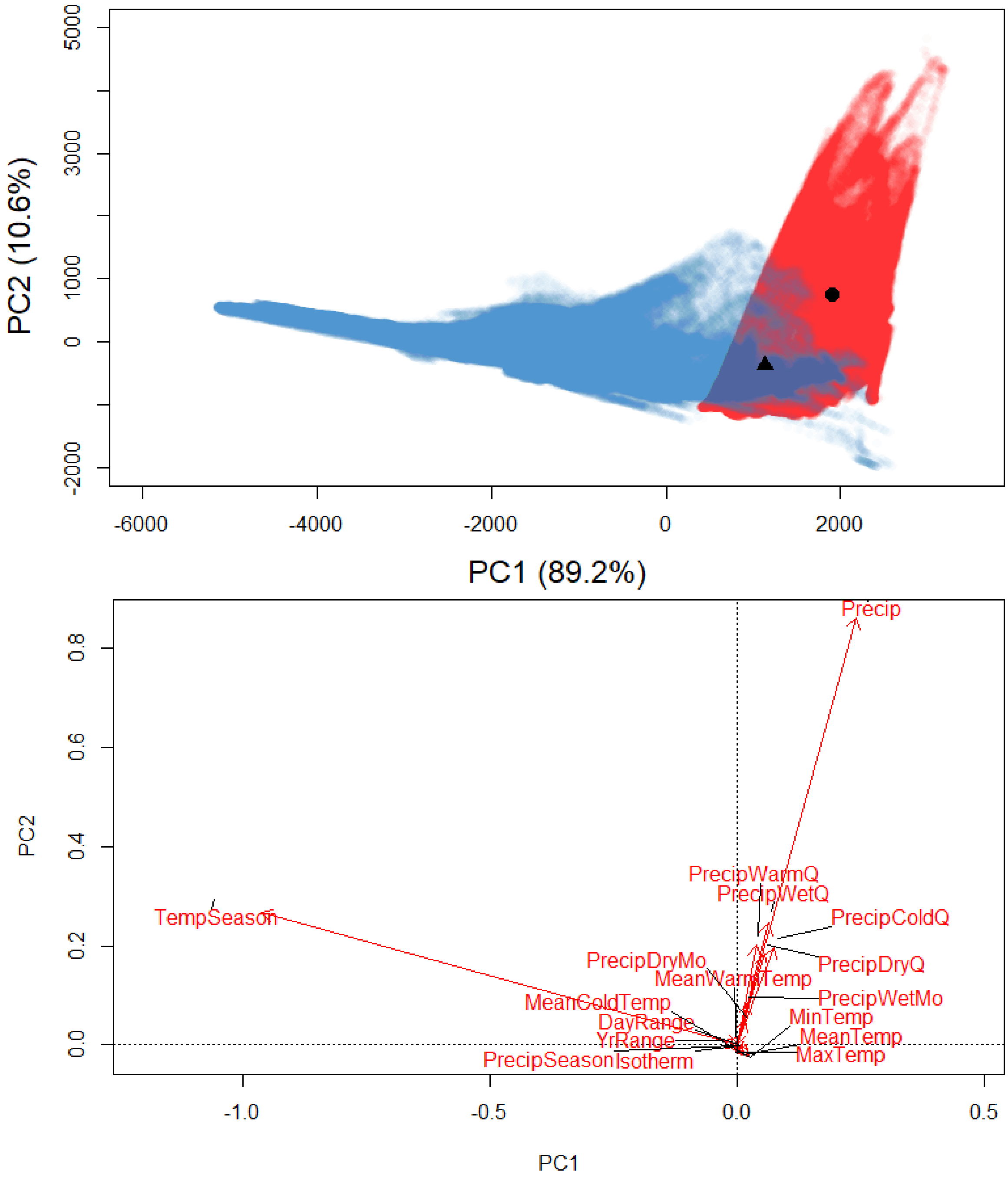

Figure C.3 **Top - Principal component analysis (PCA) showing available climates for all locations in the native range (blue), NZ (red). The top two principal components explain >99% of the variation across 17 WorldClim variables for the native range and NZ. The black triangle (Southland) and circle (Westland) indicate the climates experienced by our field sites during the years the experiment was conducted. The field sites experienced the expected climates with Southland being in analogue climate space and Westland being in non-analogue climate space. Bottom – PCA loadings indicate that this environmental space is driven primarily by two variables. PC1 is explained almost entirely by Temperature Seasonality, whereas PC2 is explained predominantly by precipitation.**

Table C.1 Number of plants at each life stage used in our analysis. Note that whilst a germination value was recorded for all germination trays, not all seeds germinated. Survival was recorded post transplantation, meaning that if an individual had a germinated rate of 0 it was not included in measurements of survival.

Germination	UK		NZ	
	Southland	Westland	Southland	Westland
R. conglomeratus	180	180	180	180
R. crispus	180	180	180	180
R. obtusifolius	180	180	180	180
Survival	UK		NZ	
	Southland	Westland	Southland	Westland
R. conglomeratus	130	119	96	86
R. crispus	96	138	88	84
R. obtusifolius	133	134	99	138
Fecundity	UK		NZ	
	Southland	Westland	Southland	Westland
R. conglomeratus	31	59	29	44
R. crispus	21	51	15	31
R. obtusifolius	20	40	11	33

Table C.2 Marginal and conditional are R^2 values for generalized mixed-effects models of *Rumex* spp. germination, survival, and total seed produced (Fecundity). Marginal R^2 ($R^2_{GLMM(m)}$) provides the variance explained only by fixed effects and conditional R^2 ($R^2_{GLMM(c)}$) provides the variance explained by the entire model.

	R. conglomeratus		*R. crispus*		*R. obtusifolius*	
	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
Germination	0.058	0.271	0.051	0.321	0.027	0.166
Survival	0.034	0.066	0.054	0.054	0.017	0.141
Fecundity	0.131	0.663	0.071	0.151	0.042	0.346

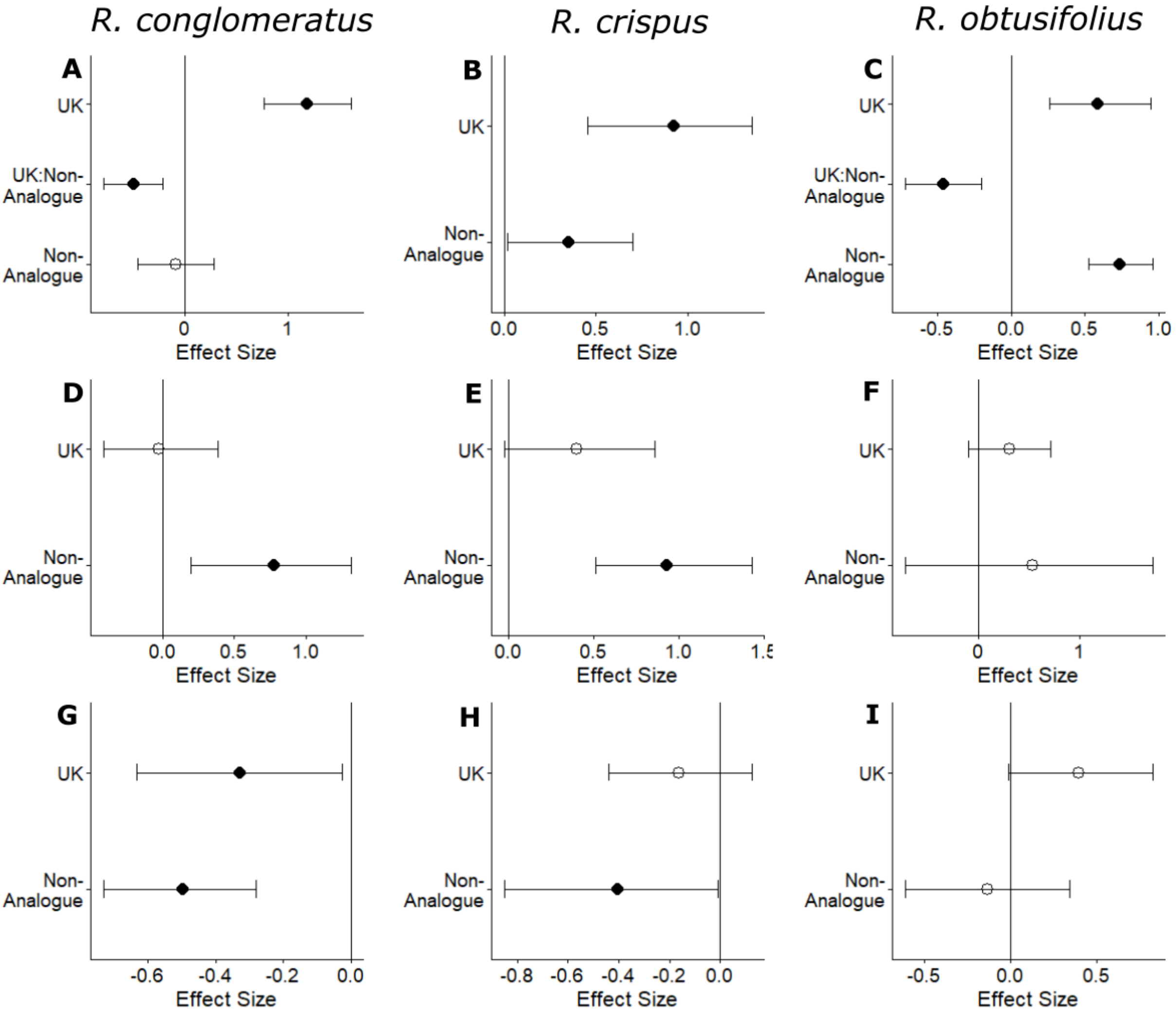

Figure C.4 Coefficient plots showing the effect size of differences between individuals from each site, provenance, and interaction between site and provenance (where applicable). When non-significant, the site by provenance interaction term was removed from models. Plots for germination (A-C), survival (D-F), and total seed produced (G-I) are shown for the three species *R. conglomeratus*, *R. crispus*, and *R. obtusifolius*. Empty dots show non-significant effects, i.e. where the 95% confidence interval overlaps 0, and filled dots show significant effects.

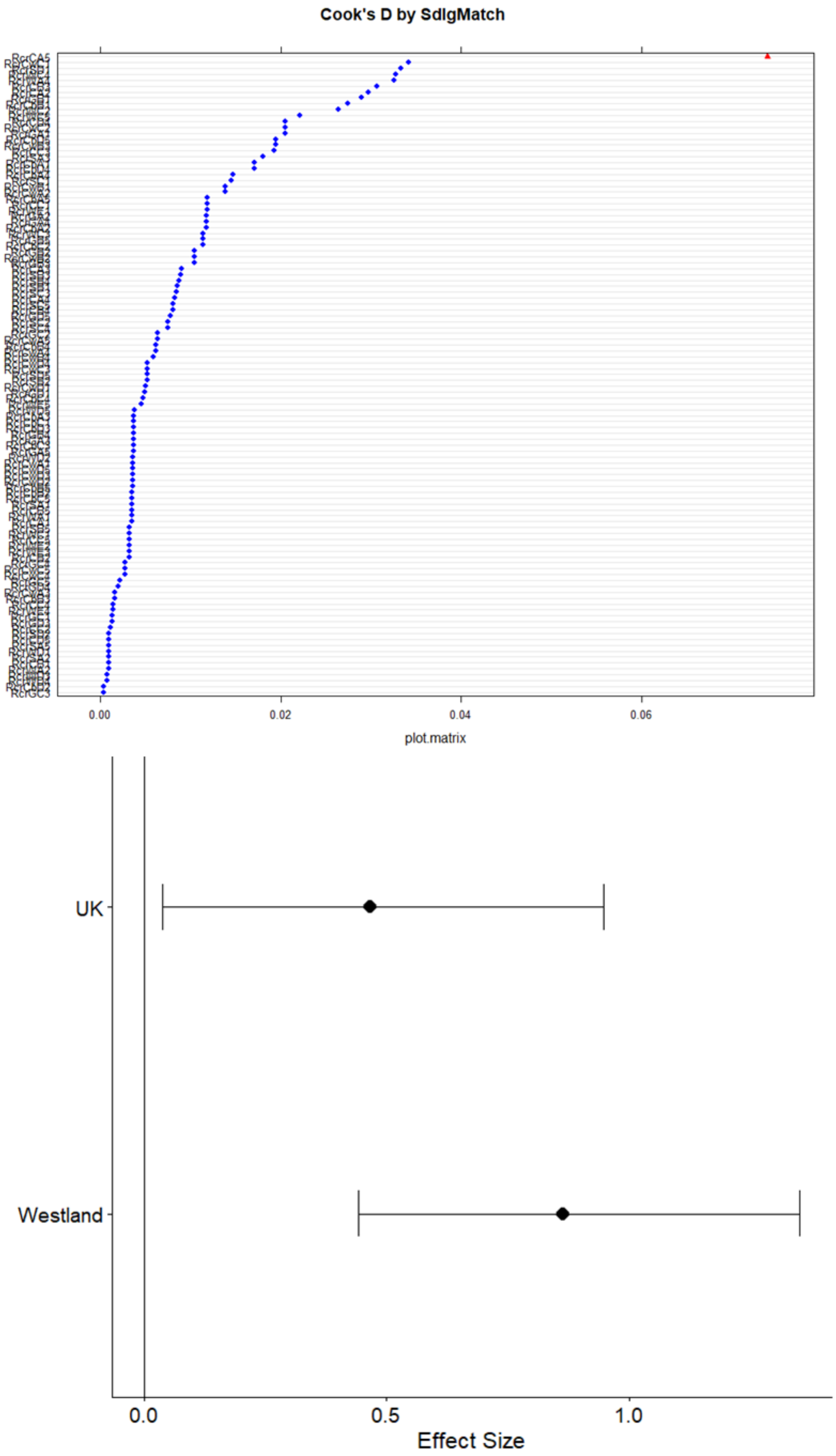

Figure C.5 Cook's D plot (top) showing the influential observations in *Rumex crispus* survival data. Coefficient plot (bottom) shows that both provenance and site are significant factors, i.e. the 95% confidence intervals do not overlap 0. When influential observations are removed (Figure 4.3E), differences attributed to provenance become non-significant. The influential observations are 3 data points attributed to a single maternal line, collected in Canterbury NZ. All seeds harvested from this individual that germinated died during the experiment.

Appendix D

Additional Experiments

Due to the nature of large-scale field experiments, there were additional aspects of the common garden experiment we presented in Chapter 4 which were not included in main text. This appendix is intended to lay out the reasons behind initiating these experiments, why they were not included in the main text, and whether our results would be changed if they were included. The additional experiments consist of:

1. An additional common garden which was removed from Chapter 4
2. A supplemental field germination experiment
3. An additional lab based germination experiment
4. An analysis of seed viability

Below we present the results of these additional experiments, and discuss some additional insights which were not included in the main text.

D.1 Lincoln Field Site

The large-scale common garden experiment we presented in Chapter 4 initially had a third field site located at Lincoln University, Canterbury. The Lincoln site was similar in set up to the other two sites, located in grazed pasture close by to known *Rumex* spp. populations that we collected seed from. The site was treated with glyphosate two weeks prior to laying down weed cloth and planting seeds. Lincoln is located closer to the analogue climate limit from the native range than the Southland field site (Figure D.1). The intention was to use these three field sites to see how *Rumex* spp. performed along a climatic gradient; from analogue (Southland), to the range limit between analogue and non-analogue (Lincoln), to non-analogue climate space (Westland). Unfortunately due to circumstances beyond our control the Lincoln field site failed to thrive, however we maintained the site for the full length of the experiment and still harvested the data at the end of the experiment.

Lincoln suffered through an extremely hot and dry summer during the first growing season (NIWA, 2018j, 2018n). This led to extremely low germination at Lincoln, particularly for *R. conglomeratus*. After transplanting in November 2017 plants received supplemental watering to reduce transplant shock (Doust, 1981). Despite this, survival after transplanting was low. We therefore decided to implement additional supplemental watering across the field site throughout the summer to alleviate the unusually dry conditions. On top of this, on 3/11/18 a flock of sheep was released onto the Lincoln field site after students unhooked a locked gate after hours and failed to re-secure it. The sheep decimated the germination experiment running at Lincoln (see section 2 below) by trampling all germination trays, and consumed all leaves of *Rumex* spp. inside the plots within browsing height (Figure D.2). All sheep damage was recorded on a subjective scale, from none, to minor, and major, as this would likely impact future survival and seed production of affected plants (Hendrix, 1990; McNaughton, 1983; Paige & Whitham, 1987; Turley et al., 2013). Additionally, the introduction of unwanted fertiliser to the experiment could also affect both survival and seed production (Fan & Harris, 1996; Harris, 1971; Kołodziejek, 2019). Due to the lack of initial data from Lincoln, and the uncertainty introduced to the remaining data through damage, we decided to exclude the Lincoln site from our analysis.

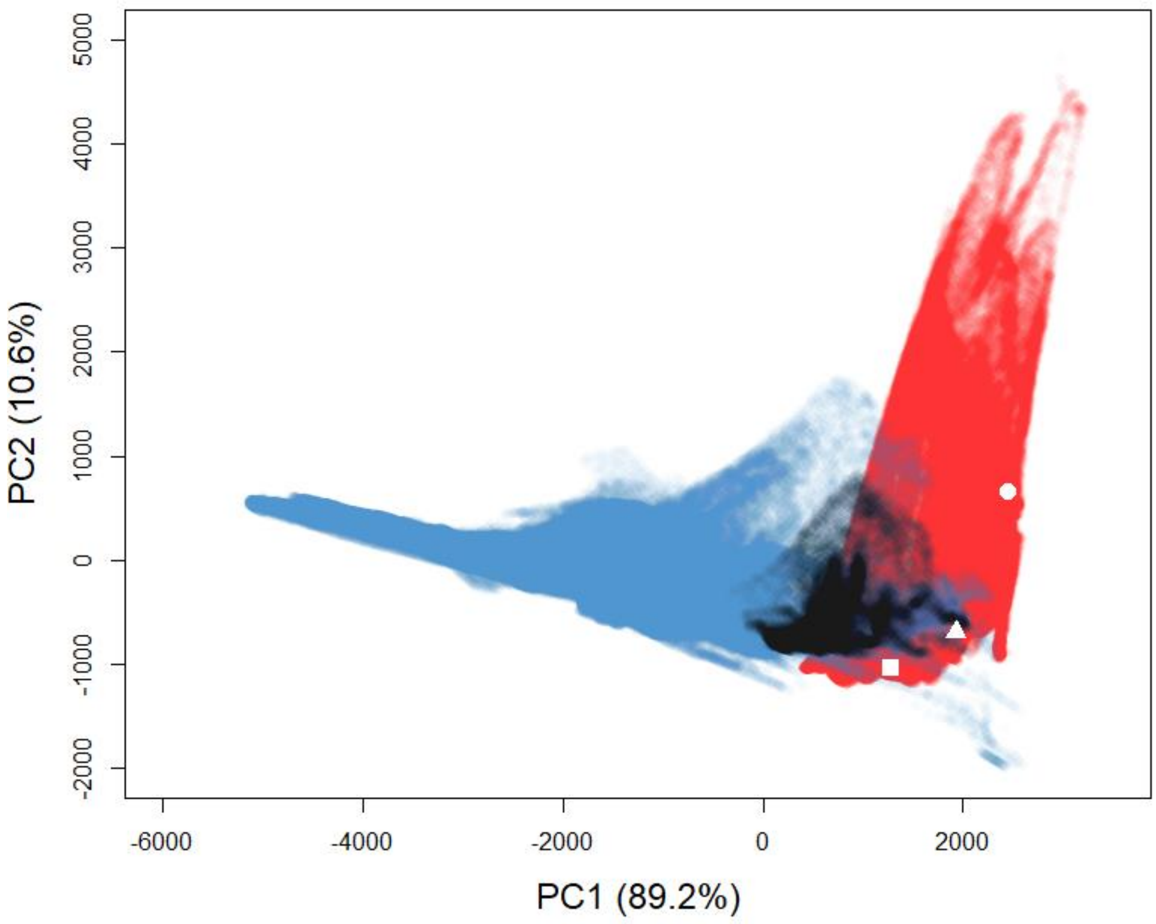

Figure D.1 Principal component analysis (PCA) showing available climates for all locations in the native range (blue), NZ (red), and the UK (black). The top two principal components explain >99% of the variation across 17 WorldClim variables for the native range and NZ. The white square and triangle denote the locations of our Lincoln and Southland field sites respectively, both in analogue space; i.e. where climates for the native range and NZ overlap. The white circle denotes the location of our Westland field site in non-analogue space. PC1 broadly corresponds to a temperature gradient, and PC2 to a precipitation gradient. The climates of the UK broadly overlap the available analogue climate space between the native range and NZ.

Figure D.2 A *Rumex crispus* individual with evidence of sheep browsing. The white line roughly shows the height at which browsing occurred. All foliage and flowers were removed from stems within browsing height of the sheep. The browsing height is estimated to be roughly 1.5m. This unexpected herbivory could affect plant survival and seed production thereby affecting the results of the experiment.

If we assume that the above issues do not significantly affect performance of the affected individuals and include the Lincoln site in our analysis we receive the following results. We still find little evidence that individuals from the NZ provenance have adapted to non-analogue climates (Figure D.3). Our results regarding germination were more heavily impacted by including Lincoln in the analysis than the other life stages due to the unusually low germination recorded at Lincoln. Patterns of germination provided no evidence that NZ individuals outperformed those from the UK (Figure D.3A-C). For all species, individuals from the UK provenance had significantly higher germination than those from the NZ provenance (*R. conglomeratus*: $p < 0.001$; *R. crispus*: $p < 0.001$;

R. obtusifolius: $p = 0.010$). The difference in germination rates from seeds from each provenance could be because the seeds from UK individuals were stored under dry conditions for 6 months longer than the seeds from NZ individuals. This could have led to a mismatch of seed dormancy leading to seeds from NZ individuals struggling to exit dormancy and germinate (Benvenuti et al., 2001). Whilst there is evidence that low temperature stratification of *Rumex* spp. seeds prior to planting may help match the dormancy cycles of seeds stored for different lengths of time (Fani et al., 2013; Totterdell & Roberts, 1979, 1980) the evidence is mixed (Cavers & Harper, 1966). An alternative explanation may be explained by Bufford & Hulme (unpublished) who investigated the effects of both seed size and local adaptation using the same field sites. Their preliminary results indicate that individuals from the UK provenance have a higher mean individual seed mass than individuals from the NZ provenance, which may give those individuals a higher probability of successfully germinating (Houssard & Escarré, 1991; Martinkova et al., 1999). Individuals of all species planted at Lincoln had significantly lower germination compared to both Westland and Southland (*R. conglomeratus*: $p < 0.001$; *R. crispus*: $p < 0.001$; *R. obtusifolius*: $p < 0.001$). This is unsurprising as the Lincoln site was disproportionately hotter and drier than normal compared to the other two field sites in late 2017 (NIWA, 2018j, 2018n). When including Lincoln, differences in germination rate between Westland and Southland for *R. crispus* are no longer significant (Figure D.3B), however patterns remain consistent with our results in Chapter 4 for the other two species (Figure D.3A,C). Interestingly, the performance of each provenance now depended on the site examined for *R. crispus* (Site x Provenance interaction: $p < 0.001$; Figure D.3B). This is likely due to the significantly greater performance of *R. crispus* individuals from the UK provenance compared to individuals from the NZ provenance at Lincoln (Figure D.3B).

Survival data also showed no evidence that individuals from NZ were better adapted to non-analogue climates. Patterns of survival were largely consistent with those presented in Chapter 4. There was no difference in survival between provenances for *R. conglomeratus* ($p = 0.985$; Figure D.3D), however individuals of *R. crispus* and *R. obtusifolius* from the UK provenance had significantly higher survival when data from Lincoln were included (*R. crispus*: $p = 0.033$; *R. obtusifolius*: $p = 0.028$; Figure D.3E,F). Again, higher survival after transplanting of individuals from the UK provenance could be explained by the increased mean individual seed mass of seeds from the UK (Houssard & Escarré, 1991; Martinkova et al., 1999). Differences in survival between sites were consistent with the results in Chapter 4. *Rumex conglomeratus* had significantly lower survival at Southland ($p = 0.018$), *R. crispus* had significantly greater survival at Westland ($p < 0.001$), and *R. obtusifolius* showed no difference in survival between sites ($p = 0.295$).

Similar to the results of Chapter 4, evidence that individuals from the introduced provenance were better adapted to non-analogue climates was mixed. *Rumex conglomeratus* individuals from the non-analogue provenance had significantly greater seed production than those from the native provenance. This could be a resource allocation trade-off in which the native provenance produces fewer but larger seeds (Houssard & Escarré, 1991; Maun & Cavers, 1971). When data from Lincoln are included in the analysis we see that the amount of seed produced by each provenance of *R. conglomeratus* now depends on the site examined (Site x Provenance interaction: $p = 0.026$; Figure D.3G). Individuals of *R. conglomeratus* from the native provenance produced significantly fewer seeds at Lincoln than at Southland and Westland, likely because *R. conglomeratus* struggled to thrive in the dry conditions at the Lincoln site. *Rumex crispus* and *R. obtusifolius* however showed no evidence that individuals from NZ were better adapted to climates in the introduced range, with no significant differences in seed production between provenances (*R. crispus*: $p = 0.198$; *R. obtusifolius*: $p = 0.067$). Interestingly, *R. crispus* showed significantly greater seed production at Lincoln than at Southland and Westland ($p < 0.001$; Figure D.3H), however *R. obtusifolius* showed no differences in seed production between sites ($p = 0.083$; Figure D.3I). This seems consistent with our results of Chapter 4 where we discussed the difficulty of finding wild *R. crispus* populations in non-analogue climates, which is a potential explanation for its reduced seed production in Westland (Figure D.3H).

Despite some results changing with the inclusion of data from the Lincoln field site our conclusion remains that we find little to no evidence that plants from the introduced range have adapted to have increased performance in non-analogue climates. This is in line with the conclusion we presented in Chapter 4. Individuals grown at Lincoln had the lowest chance of germinating and the greatest mass of seeds produced, but these patterns were consistent with our previous analysis indicating individuals from the native range typically outperformed, or performed similarly, to individuals from the introduced range. The one exception was the amount of seed produced by *R. conglomeratus*, which we noted in Chapter 4 as being the only case that could indicate adaptation to increased performance in individuals from the introduced range. Whilst the data from the Lincoln field site are understandably flawed, we are reassured by the fact that our conclusions remain consistent regardless of whether these data are included or not. Finally, the climates experienced at all field sites were as expected (Figure D.4)

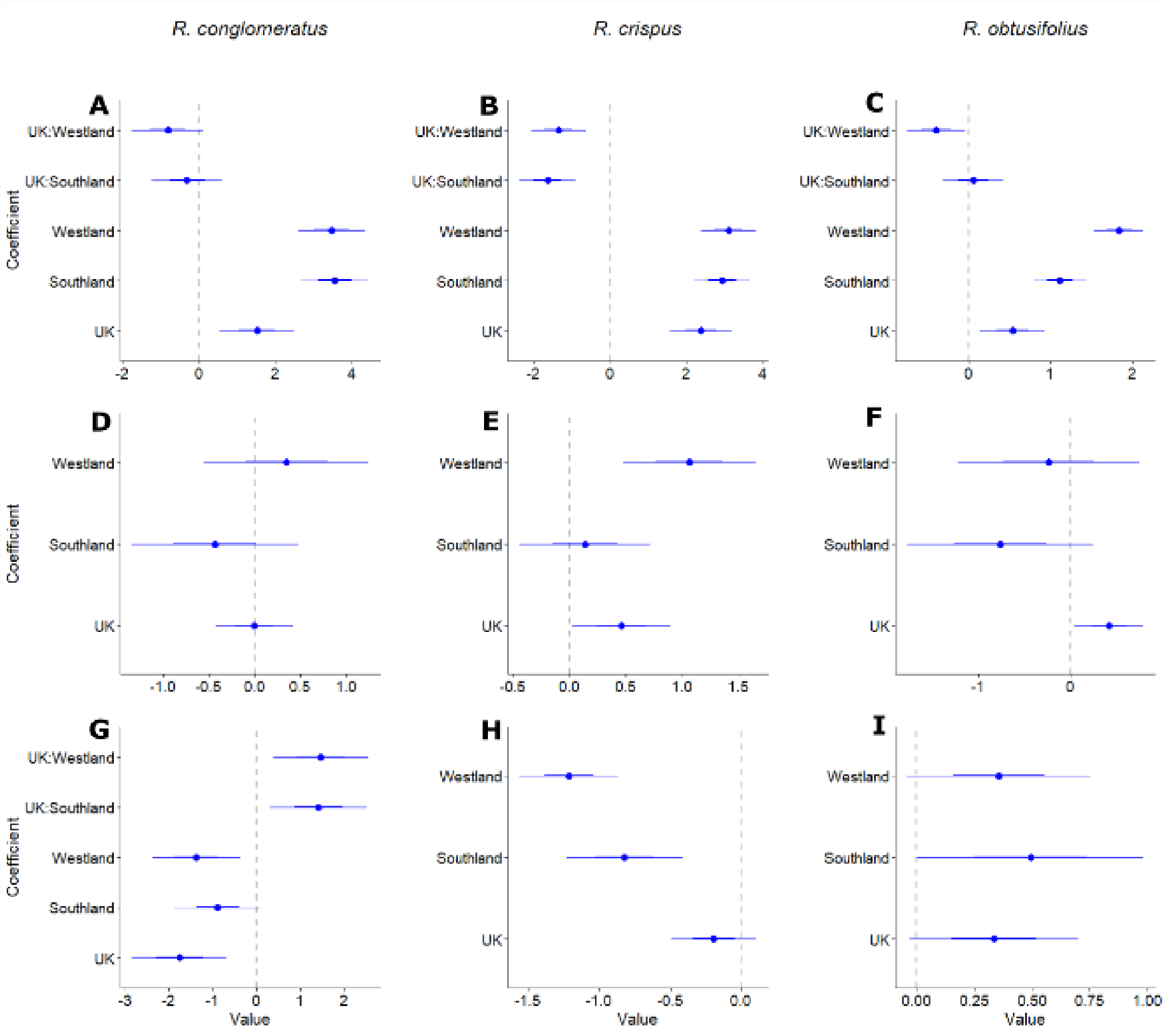

Figure D.3 **Coefficient plots showing the effect size of differences between individuals from each site, provenance, and interaction between site and provenance (where applicable). When non-significant, the site by provenance interaction term was removed from models. Plots for germination (A-C), survival (D-F), and total seed produced (G-I) are shown for the three species *R. conglomeratus*, *R. crispus*, and *R. obtusifolius*. Thick, inner, error bars show 1 standard deviation, and thinner, outer, error bars show 2 standard deviations from the mean. Significance is determined by Wald's Chi Squared tests, explained in the main text, but can be roughly assumed where error bars do not overlap 0.**

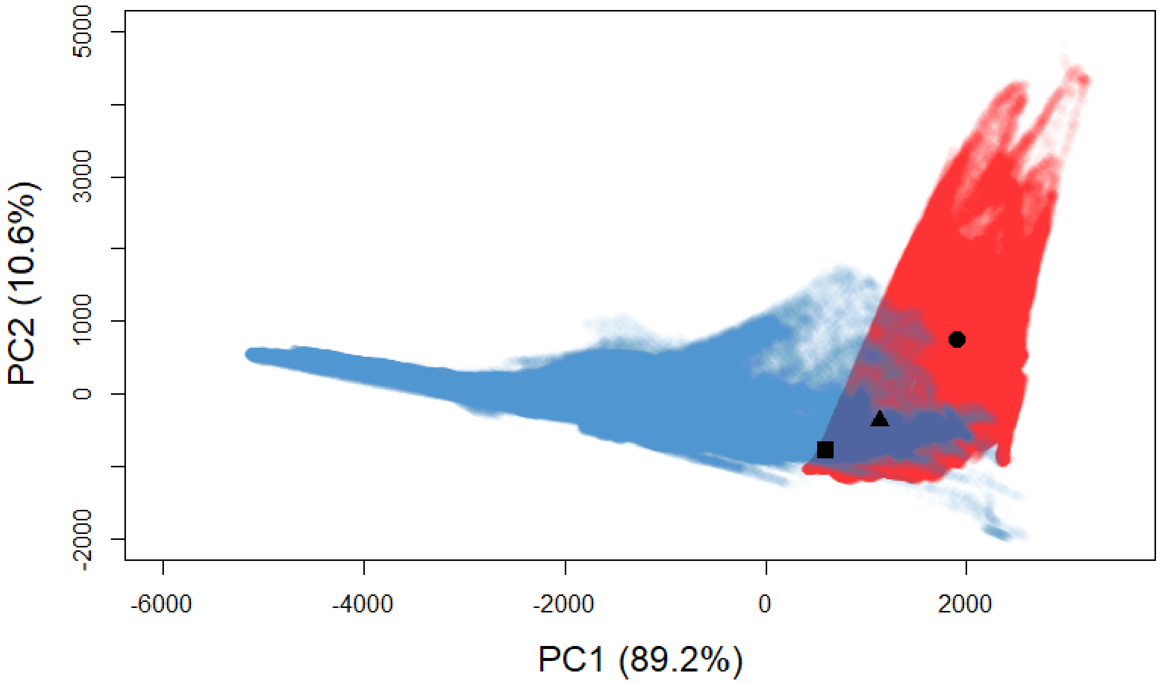

Figure D.4 Principal component analysis (PCA) showing available climates for all locations in the native range (blue) and NZ (red). The top two principal components explain >99% of the variation across 17 WorldClim variables for the native range and NZ. The black square and triangle denote the actual climates experienced over the course of the experiment at our Lincoln and Southland field sites respectively, both in analogue space; i.e. where climates for the native range and NZ overlap. The black circle denotes the climates experienced at our Westland field site in non-analogue space. PC1 broadly corresponds to a temperature gradient, and PC2 to a precipitation gradient.

D.2 Additional Field Germination Experiment

As overall germination from the field experiment was low it was decided that some additional steps should be undertaken to better capture the true germination rate of these species between analogue and non-analogue climate space. This decision was partly based on the poor germination seen at the Lincoln field site prior to our decision to exclude it from Chapter 4. One such step was to repeat the germination portion of the field experiment at two field sites, Lincoln and Westland. Furthermore, we decided to focus on the two species in which germination was lowest, *R. crispus* and *R. conglomeratus*. With this additional germination experiment, utilising information we gained from the initial plantings, we hoped to more accurately capture the germination rates of *Rumex* spp. within and beyond analogue climate space.

To better capture the effects of climate, rather than soil properties at each site, on germination we replaced the soil in germination trays with screened topsoil. Following the same methodology as in Chapter 4, we planted 10 seeds from each individual plant and recorded how many seedlings germinated. Planting took place at both sites in late May 2018.

Unfortunately, germination was again poor at both field sites and was heavily impacted to the point that the data was unusable. The year 2018 was again unusually hot and dry (NIWA, 2019a, 2019d), leading to poor germination at both field sites. On top of this, when sheep damaged the Lincoln field site (see section 1 above) all germination trays were significantly affected. Germination trays were trampled, both killing seedlings and displacing soil leading to the mixing of seeds from different individuals and populations. Due to the issues raised here, we were unable to determine germination rates based on this experiment.

D.3 Additional Lab Germination Experiment

Due to the poor germination experienced in the initial (Chapter 4) and additional (Appendix D Section 2) germination experiments we decided to investigate germination in an incubator setting. We again focussed on two species, *R. crispus* and *R. conglomeratus*. With this additional experiment we hoped to get a better estimation of germination potential under optimal conditions.
Twenty-five seeds were used from 2 individuals of each population of *R. crispus* and *R. conglomeratus*. Seeds were placed in sealed clear plastic containers in incubation chambers for 31 days. Watering occurred every 3 days until saturation, and any germinants were recorded and

removed. Incubation chambers were set to a 16/8 hour light/darkness cycle at 20^0C, which was determined to be the optimal conditions for germination of *Rumex* species (Benvenuti et al., 2001; Cavers & Harper, 1964).

For *R. crispus* the majority of seeds germinants emerged within 7 days, and no further germination occurred after 21 days. For *R. conglomeratus* the majority of germinants also emerged within 7 days, however germination continued until the end of the experiment (31 days). Unfortunately overall germination was low, with both species experiencing <50% germination on average. This was characterised by low germination for the majority of individuals, as well as 2 individuals of *R. crispus* and 8 individuals of *R. conglomeratus* showing no germinants at all.

We knew that these experiments were not accurate portrayals of the germination potential of our *Rumex* spp. seed stock as other experiments utilising the same seed stock informally reported much greater germination. At this stage I decided to informally test the germination from 30 individuals, split between each provenance. I collected 10-15 filled seeds from each individual in our dry storage. I planted ~5 in soil, and placed the remaining 10 in petri dishes on the windowsill of my office. I provided the seeds with ample water, similar to the incubator germination experiment. After 2 weeks, I noted almost 100% germination of each individual. This could potentially mean that some aspect of the incubation chamber was not conducive to germination of *Rumex* seeds, however we failed to specifically identify why germination was lower than expected.

D.4 Seed Viability Experiment

As some individuals of the incubator germination experiment (see section 3 above) experienced no germinants at all, we decided to specifically test the proportion of viable seeds used in this experiment. This would provide evidence that the seeds we planted were not only viable, but also determine whether differences in germination could be attributed to differences in dormancy between batches collected from the UK and batches from NZ.

Professor John Hampton suggested using the tetrazolium chloride test. Tetrazolium chloride (TTC) is a solution which can detect living tissue within seeds (Malone, 1967). The general process involved soaking seeds in water, cutting them in half, and exposing them to TTC for ~24 hours (Peters & Lanham, 2010). The TTC solution reacts with dehydrogenase enzymes in living tissue, which reduce the tetrazolium chloride to formazan, a reddish, water-insoluble compound (Dufour & Colon, 1992). This reaction only happens in or near living cells that are releasing hydrogen as they respire, so staining indicates the seed is likely alive and viable.

This test of seed viability is often thought of as a rapid evaluation of seed viability prior to conducting thorough germination tests (De Barros França-Neto & Krzyzanowski, 2019), however in practise often yields results very similar to the more thorough germination tests (Malone, 1967). Where it falls short however, is that it provides no information on seed dormancy which could affect germination (De Barros França-Neto & Krzyzanowski, 2019) and can give false positive readings by reacting to living tissue from fungal infections (Dufour & Colon, 1992). Furthermore, TTC is light sensitive and hence must be kept in the dark (Ghaly & Mahmoud, 2007). Whilst there are no standardised methods for performing TTC testing on *Rumex* spp. we followed guidance from Starfinger & Karrer (2016) who developed the protocol for testing the viability of ragweed species.

Seeds which did not germinate in the incubator germination experiment (see section 3 above) were tested for viability. We selected all seeds which did not germinate, or up to 10 seeds when >10 did not germinate from an individual. These seeds were imbibed in water for 24 hours. Seeds were then cut in half vertically using a scalpel and the largest portion was submerged in TTC solution. Seeds were left in TTC solution for a minimum of 24 hours under total darkness at room temperature. Seeds were then inspected under a microscope for signs of reddening. No *Rumex* spp. seeds were stained by the tetrazolium chloride solution, indicating either no viable seeds or an issue with the solution. After consulting Professor John Hampton, I attempted an assortment of treatments on remaining seed to determine whether TTC solution could affect *Rumex* spp. seeds. These treatments included: cutting seeds along different planes, scarification of the seed cuticle rather than cutting, and submersion in TTC for longer periods of time (up to a few weeks). None of these changes seemed to result in the staining of any seeds. I then germinated a subset of the remaining seeds in a petri dish to determine that the seeds were in fact viable, and determined that the TTC solution must be the issue.

As TTC appeared to have no effect on *Rumex* spp. I contacted the Chair of the Tetrazolium Committee of the International Seed Testing Association (ISTA), Stefanie Krämer (ISTA, 2020). Although none of the committee members initially had an explanation for the lack of staining of *Rumex* spp. seeds, they investigated this effect on my behalf by subjecting wild *Rumex* spp. seeds to different TTC treatments. They successfully received staining of *Rumex* spp. seeds when using a TTC solution prepared with a buffer rather than water (personal communication, October 22, 2020). When prepared using water it appears that *Rumex* spp. seeds cannot tolerate the pH of the TTC solution, killing the seeds and leaving no living tissue for the TTC solution to stain. Peters & Lanham (2010) provide a detailed set of instructions for preparing TTC with a buffer solution including which solutions to use and how to adjust the pH of the solution.

I am very grateful for the helpful responses from both Stefanie Krämer and Jose França-Neto in helping to resolve this conundrum. Unfortunately I did not have the opportunity to repeat this experiment using a buffered TTC solution, but this seems to be the only record of how to use this solution to effectively test the viability of *Rumex* spp. seeds.

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