

Global Assessment of Climatic Niche Shifts in Three *Rumex* Species

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Abstract

Climatic niche shifts occur when species occupy different climates in the introduced range than in their native range. We know that climatic niche shifts are common occurrences, however we do not currently understand whether climatic niche shifts can consistently be predicted across the globe. Using three congeneric weed species, we investigate whether the known presence of a climatic niche shift in one range can help predict a species' distribution in other ranges. We consider whether data either from other ranges or from closely related species can help predict whether climatic niche shifts will occur. We compared the climatic conditions occupied by *Rumex obtusifolius*, *R. crispus*, and *R. conglomeratus* between their native range (Eurasia) and three different introduced ranges (North America, Australia, New Zealand). We consider metrics of niche overlap, expansion, unfilling, pioneering, and similarity to determine whether i) climatic niche shifts have occurred and ii) climatic niche shifts were consistent across ranges and congeners. We found that the presence and direction of climatic niche shifts is inconsistent across ranges for all three species. Within an introduced range, however, niche shifts were similar between species. Despite this, species distributions outside of their native range could not be reliably predicted by the distributions of congeners in either their native or introduced ranges. This study is the first of its kind to consider niche shifts across multiple introduced ranges and species, highlighting new challenges in predicting species distributions when species undergo climatic niche shifts.

1.1 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 it currently occupies and in which it experiences stable or positive population growth (Atwater et al., 2018; Holt, 2009; Hutchinson, 1957). Climatic niche conservatism occurs when a species inhabits that same niche in both the native and introduced range (Petitpierre et al., 2012). However, many species shift their climatic niches when introduced to a new region (Atwater et al., 2018; Christina et al., 2019; Comte et al., 2017; Liu et al., 2017; Silva et al., 2016; Tingley et al., 2014). This leads to difficulties in predicting where introduced species may become problematic, or whether introduced species are likely to spread within a range (Atwater et al., 2018; Atwater & Barney, 2021; Petitpierre et al., 2012). 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). To date, most studies assessing climatic niche shifts have focused on comparisons between two regions (Atwater et al., 2018; Early & Sax, 2014; Gallagher et al., 2010; Petitpierre et al., 2012). However, species are often introduced to multiple new ranges and it is not clear whether niche shifts in one introduced range can be used to predict niche shifts in other ranges. Extrapolating from a single introduced range can be misleading if niche shifts are expressed differently across regions, hence an understanding of the consistency of niche shifts is needed.

The presence, magnitude and direction of niche shifts can vary across introduced ranges (Figure S.1). A species may consistently shift into certain climates across all observed ranges (Figure S.1A). This would suggest that the species is either pre-adapted to, or able to rapidly adapt to, specific climates. For example, when a set of climate conditions suitable for the species is absent from its native range, then in introduced ranges the species would be expected to show consistent shifts into this climate space. Silva et al. (2016) showed that the spread of a dung beetle, *Onthophagus taurus*, introduced into four different global regions expressed consistent niche shifts towards more humid climates than those occupied in its native range. Alternatively, species may shift in different directions across regions (Figure S.1B), or experience niche shifts in some regions but niche conservatism in others (Figure S.1C). This could indicate that non-climatic factors in the introduced range are either facilitating or constraining a niche shift in an introduced range (Bulleri et al., 2016), or could reflect the effects of hybridisation in an introduced range (Pfennig 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 and/or broad climatic tolerances but are limited by available climates in the native range or whose distribution limits are shaped by non-climatic factors.

If closely related species experience similar climatic niche shifts across regions then niche shifts in a new introduction could be predicted from established congeners. 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 phylogeny (Atwater et al., 2018; Broennimann et al., 2012; Early & Sax, 2014), but closely related species, especially from the same functional group, may be more likely to demonstrate similar niche shifts. This may be particularly relevant where factors such as climate availability in the introduced region are 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).

Here we test whether climatic niche shifts are consistent across regions for three closely related, globally invasive, herbaceous species. Specifically, we ask: Do species shift their niches in multiple introduced ranges? Do species shift their niches in the same direction across ranges? Are climatic niche shifts consistent across closely related species? We expect that species with broad environmental tolerances or widespread distributions will be able to shift their niche into different climates across multiple ranges. Species with more specialised climatic tolerances will be less likely to exhibit niche shifts, however if niche shifts are observed they would be more likely to be consistent across the introduced ranges. Finally, we expect that closely related species that share similar climates would likely experience similar niche shifts, allowing information from the distribution of one species to help inform others. With this analysis

we hope to shed light on when and where niche shifts occur and whether the direction of niche shifts can be predicted.

1.2 Methods

1.2.1 Study Area and Species

Three common dock species were studied: *Rumex obtusifolius* L., *R. crispus* L., and *R. conglomeratus* Murray. These species are all ruderal weeds, typically colonising open, disturbed environments associated with human activity, including pasture (Cavers & Harper, 1964, 1966, Grime et al., 2007, L. G. Holm et al., 1997, Lousley & Kent, 1981). All three species are of Eurasian origin yet have been introduced across the globe as agricultural seed contaminants (L. G. Holm et al., 1997, L. Holm et al., 1979). *Rumex* spp. have been unintentionally spread for over five hundred years (Table 1, Vibrans, 1998). Furthermore, the geographic distribution of these species in both the native and introduced ranges is well documented, making them ideal candidates for large scale climatic niche analyses.

The long history of introductions around the world suggests *Rumex* spp. are likely to have reached climatic equilibrium in their introduced ranges, and that a sufficient number of generations has passed for adaptations to new climates to develop (Table 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 have not been subjected to artificial selection for invasiveness or climatic tolerances (Kitajima et al., 2006). Therefore any niche shifts observed are likely due to natural processes.

We modelled the species' niches across the native range, predominantly in Europe, and 3 regions where the species are recorded as naturalised by national organisations and the Global Invasive Species Database (Invasive Species Specialist Group, 2019): Western North America (USDA & NRCS, 2019), 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 the species were first introduced before 1900 (Table 1). For consistency with other studies we separately considered observations in analogue climates, shared between the native and introduced ranges, and non-analogue climates, exclusive to either the native or introduced range (Atwater et al., 2018, Guisan et al., 2014, Petitpierre et al., 2012).

Defining the Native range

We define the native range for each of these species as spanning Europe, the Middle East, and Northern Africa (Figure 1). Multiple databases, including the Global Biodiversity Information Facility (GBIF, GBIF.org, 2019) the Atlas Florae Europaeae (AFE, 1979), the Flora of Japan (FOJ, Flora of Japan, 2019), Calflora (Calflora, 2019), the Invasive Species Compendium (CABI, 2019), U.S. Germplasm Resources Information Network (USDA, 2019), and the Global Compendium of Weeds (Randall, 2017), were consulted to determine where these species were classified as native and naturalised (Table S.1). In the

absence of specific data for a region, areas of continuous species occurrence contiguous with regions where the species was recorded as native, were also classed as part of the native range unless otherwise stated as a known introduction. A literature search was conducted to determine whether historical records indicated known introductions (Table S.2). As a result of these data screening procedures, three regions with high quality data and unambiguously naturalised populations of all three *Rumex* species were selected: Western North America, Eastern Australia and New Zealand. Sources are conflicting on whether eastern Asia, Japan in particular, is part of the native range of *R. obtusifolius* and *R. crispus*, as such we classify them as introduced but explore this possibility in supplementary information (Figure S.5).

1.2.2 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 S.2, Table S.3), and personal collections in the United Kingdom and New Zealand. Due to the underreporting of *Rumex* spp. distribution records in New Zealand, we 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](https://www.google.com/maps)). Table S.4 shows a breakdown of the number of records obtained for each species, and their sources.

One source of uncertainty in our approach is our use of publicly available records which could lead to records that are biased geographically, often around population centres or regular surveying sites (Beck et al., 2014). To mitigate these problems we removed records with missing or inaccurate coordinates and records with coordinate uncertainties over 10,000m, and then spatially rarefied the remaining data. Records in the native range and three introduced ranges were 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, T., Kempen, B., Heuvelink, G. B. M., & Malone, 2014). Thinning the occurrence records was necessary to reduce geographic sampling bias and remove duplicate results. 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). As a result, these species are well recorded across their native range.

Climate data

To encompass variation in temperature and precipitation six of the nineteen 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 effects on soil moisture (Cavers & Harper, 1964), are of importance in determining *Rumex* species distributions at local scales.

Niche Analysis

In order to assess whether the climatic niche of these species changed in their introduced range we utilised the environmental principal component analysis (PCA-env) approach proposed by Olivier Broennimann et al. (2012). In order to reduce the number of variables to two, which the PCA-env approach requires, a principal component analysis (PCA) was performed on the climate data. The values of the PCA axes at the species' known occurrence points was then taken to represent the conditions that are occupied by the species in each range. PCA-env requires that the user specify the environments available in each region by defining and fitting minimum convex polygons (MCPs). To facilitate comparisons among species, MCPs were 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. Given the similar introduction methods of *Rumex* species it is reasonable to assume all three species could reach all environments within these combined MCPs. 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 1). Following guidelines from Guisan et al. (2014) and amended by Silva et al. (2016), pairwise comparisons were performed between the native range and all 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 (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 between ranges (complete niche overlap). Niche similarity was calculated 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.

Niche shifts were further divided into the proportion due to niche expansion, niche unfilling and niche pioneering (Guisan et al., 2014). Using the values of these niche metrics we determined whether a species niche shifted between the native and introduced ranges. We 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 to compare the climate niches of species within each range. All metrics were calculated using the *ecospat* package (Di Cola et al., 2017) in the statistical software R version 4.0.4 (R Core Team, 2013).

1.3 Results

1.3.1 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 these were taken to represent the available environmental space adequately. Increasing values of PC1 correspond to colder, wetter areas with more seasonal variation in temperature, 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).

1.3.2 Niche shifts are inconsistent across regions

Climatic niche shifts were idiosyncratic across three regions for all species, with one region characterised by niche conservatism (Figure 3, Eastern Australia) and two regions characterised by large niche shifts (Figure 3, New Zealand and Western North America). *Rumex* spp. exhibited climatic niche shifts into both analogue and non-analogue climate space (Table 2). Both the direction and presence of climatic niche shifts was broadly consistent across *Rumex* species (Figure 3), however, niche overlap between species was low in all introduced ranges compared to the native range (Table 2). The occupied niche was significantly similar between all species in New Zealand, between *R. obtusifolius* and *R. conglomeratus* in Western North America, and between *R. crispus* and *R. conglomeratus* in Eastern Australia (Table 3). Despite being more similar than chance alone, niche overlap between species in each introduced region was lower than in the native range (Table 3).

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 3). Levels of niche overlap and unfilling between the occupied climates in New Zealand and the native range were low (Table 2). The climatic niche shifts in New Zealand were primarily into non-analogue climate space, however niche expansion into analogue climate was also present (Table 2, Figure 3). New Zealand was the only introduced range that was not significantly similar to the native range for any species (Table 2).

Climatic niche shifts in Western North America were observed across analogue and non-analogue climate space (Table 2, Figure 3). In Western North America the climatic niche expanded 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 3). Western 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 in analogue climates (Table 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 3).

In Eastern Australia *Rumex* spp. largely conserved their climatic niches (Figure 3, Table 2). *Rumex* spp. in Eastern Australia experienced low levels of niche expansion, in both analogue and non-analogue climates, and high levels of niche unfilling. Niche unfilling in Eastern Australia occurred in wet areas with highly seasonal temperatures and drier areas with less seasonal temperatures (both higher and lower values of PC2, Figure 3).

Comparisons of niche overlap between *Rumex* spp. within each range show little consistency across introduced ranges (Table 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. Although the highest niche overlap was between *R. obtusifolius* and *R. crispus* in the native range, this was not necessarily true in the introduced ranges (Table 3).

1.4 Discussion

Following independent introductions across geographically distinct ranges, *Rumex* spp. have undergone inconsistent climatic niche shifts. In Western 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 climates (Fig. 3). Furthermore, climatic niche shifts were only sometimes consistent across closely related species, with consistent distribution across all three *Rumex* spp. only in New Zealand. Thus we showed that even invasions by similar species introduced in similar ways can lead to examples of every niche change proposed by Guisan et al. (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 niches in Eastern Australia. In New Zealand, *Rumex* spp. seem to occupy the majority of available climates, including climates wetter than their native range, but have less access to seasonal climates than in other regions. Eastern Australia, on the other hand, is dominated by hot, dry, non-analogue climate space which is unoccupied by and is likely unsuitable for *Rumex* species. However, we also found unoccupied suitable analogue climates leading to high levels of niche unfilling and suggesting that factors other than climate limit *Rumex* spp. distributions in Eastern Australia. Western North America experienced high levels of both niche unfilling and niche expansion. This may indicate that factors other than climate may limit or facilitate *Rumex* spp. distributions in North America. Whilst climate typically determines species distributions at broad scales (Bello et al., 2013; Collingham et al., 2000), 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 when consistent niche shifts would be observed.

The lack of consistency in niche shifts between ranges suggests that one cannot easily extrapolate the likelihood of a climatic niche shift from one range to another. 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. 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 S.1C). Furthermore, results presented here add to the body of literature which suggests niche shifts are more common than previously thought (Atwater et al., 2018; Early & Sax, 2014). The present study extends this work by demonstrating idiosyncrasy across multiple species, including climatic niche shifts in opposing directions (Figure S.1B). Only a few other studies have compared shifts across multiple introduced ranges (Christina et al., 2019; Silva et al., 2016), and they do not explicitly consider the direction of the observed shifts. This 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 climatic niche shifts in a similar direction within each range, there were low levels of niche overlap between them (Table 3). Whilst the distribution of *Rumex* spp. under analogue climates in New Zealand showed significant niche similarity, this was not the case in other regions. Furthermore, the distribution of the three *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. The three *Rumex* spp. display different environmental preferences in soil nutrient richness, pH, and moisture (Cavers & Harper, 1964; Hill et al., 1999; Lousley & Kent, 1981) and their long introduction histories have allowed time for new adaptations to occur (Table 1; Vibrans, 1998). For example, compared to plants from the native range, *R. obtusifolius* from New Zealand exhibited greater plasticity under drought suggesting that greater adaptive plasticity may have evolved in New Zealand (Bufford & Hulme, 2021). This was not true of *R. conglomeratus*, however, potentially leading to climatic niche divergence and explaining why niche overlap is low. These results indicate that while general patterns of climatic niche shifts may be predicted from closely related species, attempts at pooling data from closely 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.

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. We have shown that the presence of climatic niche shifts in one range offers little to help predict climatic niche shifts in other ranges. Ultimately, this weakens our ability to accurately predict the threat of introduced

species to uninvaded ranges until we better understand the factors driving climatic niche shifts. 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).

Declarations

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Conflicts of interest

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Availability of data and material

The datasets generated and analysed during the current study are available in the Dryad repository, <https://doi.org/10.5061/dryad.cz8w9gj3w>

Code availability

The code generated during the current study is available in the Dryad repository, <https://doi.org/10.5061/dryad.cz8w9gj3w>

Authors' contributions

All authors contributed to the study conception and design. Data collection and analysis were performed by Thomas Carlin, and Jennifer Bufford. The first draft of the manuscript was written by Thomas Carlin and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

References

1. AFE. (1979). Atlas Florae Europaeae. Distribution of Vascular Plants in Europe. 4. Polygonaceae. In J. Jalas & J. Suominen (Eds.), *Atlas Florae Europaeae* (p. maps 384–478). The Committee for Mapping the Flora of Europe & Societas Biologica Fennica Vanamo.
2. Aguirre-Gutiérrez, J., Serna-Chavez, H. M., Villalobos-Arambula, A. R., Pérez de la Rosa, J. A., & Raes, N. (2015). Similar but not equivalent: ecological niche comparison across closely-related Mexican white pines. *Diversity and Distributions*, 21(3), 245–257. <https://doi.org/10.1111/ddi.12268>
3. *Atlas of Living Australia*. (2019). <https://www.ala.org.au/>
4. Atwater, D. Z., & Barney, J. N. (2021). Climatic niche shifts in 815 introduced plant species affect their predicted distributions. *Global Ecology and Biogeography*, geb.13342.

<https://doi.org/10.1111/geb.13342>

5. Atwater, D. Z., Ervine, C., & Barney, J. N. (2018). Climatic niche shifts are common in introduced plants. *Nature Ecology & Evolution*, 2, 34–43. <https://doi.org/10.1038/s41559-017-0396-z>
6. Australia's Virtual Herbarium. (2019). MEL 0610742A. Council of Heads of Australasian Herbaria. <http://avh.ala.org.au/>
7. Beck, J., Böller, M., Erhardt, A., & Schwanghart, W. (2014). Spatial bias in the GBIF database and its effect on modeling species' geographic distributions. *Ecological Informatics*, 19, 10–15. <https://doi.org/10.1016/J.ECOINF.2013.11.002>
8. Bello, F. de, Lavorel, S., Lavergne, S., Albert, C. H., Boulangeat, I., Mazel, F., & Thuiller, W. (2013). Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. *Ecography*, 36(3), 393–402. <https://doi.org/10.1111/j.1600-0587.2012.07438.x>
9. Benvenuti, S., Macchia, M., & Miele, S. (2001). Light, temperature and burial depth effects on *Rumex obtusifolius* seed germination and emergence. *Weed Research*, 41(2), 177–186. <https://doi.org/10.1046/j.1365-3180.2001.00230.x>
10. Booth, T. H., Nix, H. A., Busby, J. R., & Hutchinson, M. F. (2014). Bioclim: The first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. In *Diversity and Distributions* (Vol. 20, Issue 1). <https://doi.org/10.1111/ddi.12144>
11. Bradley, B. A., Blumenthal, D. M., Early, R., Grosholz, E. D., Lawler, J. J., Miller, L. P., Sorte, C. J., D'Antonio, C. M., Diez, J. M., Dukes, J. S., Ibanez, I., & Olden, J. D. (2012). Global change, global trade, and the next wave of plant invasions. *Frontiers in Ecology and the Environment*, 10(1), 20–28. <https://doi.org/10.1890/110145>
12. Bradley, B. A., Blumenthal, D. M., Wilcove, D. S., & Ziska, L. H. (2010). Predicting plant invasions in an era of global change. *Trends in Ecology & Evolution*, 25(5), 310–318. <https://doi.org/10.1016/J.TREE.2009.12.003>
13. Bradley, B. A., Wilcove, D. S., & Oppenheimer, M. (2010). Climate change increases risk of plant invasion in the Eastern United States. *Biological Invasions*, 12(6), 1855–1872. <https://doi.org/10.1007/s10530-009-9597-y>
14. Broennimann, O., Fitzpatrick, M. C., Pearman, P. B., Petitpierre, B., Pellissier, L., Yoccoz, N. G., Thuiller, W., Fortin, M. J., Randin, C., Zimmermann, N. E., Graham, C. H., & Guisan, A. (2012). Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*. <https://doi.org/10.1111/j.1466-8238.2011.00698.x>
15. Bufford, J. L., & Hulme, P. E. (2021). Increased adaptive phenotypic plasticity in the introduced range in alien weeds under drought and flooding. *Biological Invasions*, 1–14. <https://doi.org/10.1007/s10530-021-02532-5>
16. Bulleri, F., Bruno, J. F., Silliman, B. R., & Stachowicz, J. J. (2016). Facilitation and the niche: implications for coexistence, range shifts and ecosystem functioning. *Functional Ecology*, 30(1), 70–78. <https://doi.org/10.1111/1365-2435.12528>

17. CABI. (2019). *Invasive Species Compendium*. CAB International. www.cabi.org/isc
18. Calflora. (2019). *Search for Plants*. <https://calflora.org/>
19. Cavers, P. B., & Harper, J. L. (1964). *Rumex Obtusifolius* L. and *R. Crispus* L. *Journal of Ecology* *Journal of Ecology This*, 52(325), 737–766. <http://www.jstor.org/stable/2257859>
20. Cavers, P. B., & Harper, J. L. (1966). Germination Polymorphism in *Rumex Crispus* and *Rumex Obtusifolius*. *The Journal of Ecology*, 54(2), 367. <https://doi.org/10.2307/2257955>
21. Christina, M., Limbada, F., & Atlan, A. (2019). *Climatic niche shift of an invasive shrub (gorse, Ulex europaeus): a world scale comparison in native and introduced regions*. <https://hal.archives-ouvertes.fr/hal-02146154/>
22. Collingham, Y. C., Wadsworth, R. A., Huntley, B., & Hulme, P. E. (2000). Predicting the spatial distribution of non-indigenous riparian weeds: Issues of spatial scale and extent. *Journal of Applied Ecology*, 37(SUPPL. 1), 13–27. <https://doi.org/10.1046/j.1365-2664.2000.00556.x>
23. Comte, L., Cucherousset, J., & Olden, J. D. (2017). Global test of Eltonian niche conservatism of nonnative freshwater fish species between their native and introduced ranges. *Ecography*, 40(3), 384–392. <https://doi.org/10.1111/ecog.02007>
24. Darwin, C., & Keynes, R. D. (1835). *Charles Darwin's Beagle diary*. Cambridge University Press.
25. Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F. T., D'Amen, M., Randin, C., Engler, R., Pottier, J., Pio, D., Dubuis, A., Pellissier, L., Mateo, R. G., Hordijk, W., Salamin, N., & Guisan, A. (2017). ecospat: an R package to support spatial analyses and modeling of species niches and distributions. *Ecography*, 40(6), 774–787. <https://doi.org/10.1111/ecog.02671>
26. Dullinger, I., Wessely, J., Bossdorf, O., Dawson, W., Essl, F., Gatttringer, A., Klöner, G., Kreft, H., Kuttner, M., Moser, D., Pergl, J., Pyšek, P., Thuiller, W., van Kleunen, M., Weigelt, P., Winter, M., & Dullinger, S. (2017). Climate change will increase the naturalization risk from garden plants in Europe. *Global Ecology and Biogeography*, 26(1), 43–53. <https://doi.org/10.1111/geb.12512>
27. Early, R., & Sax, D. F. (2014). Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. *Global Ecology and Biogeography*, 23(12), 1356–1365. <https://doi.org/10.1111/geb.12208>
28. Essl, F., Lenzner, B., Bacher, S., Bailey, S., Capinha, C., Daehler, C., Dullinger, S., Genovesi, P., Hui, C., Hulme, P. E., Jeschke, J. M., Katsanevakis, S., Kühn, I., Leung, B., Liebhold, A., Liu, C., MacIsaac, H. J., Meyerson, L. A., Nuñez, M. A., ... Roura-Pascual, N. (2020). Drivers of future alien species impacts: An expert-based assessment. *Global Change Biology*, 26(9), 4880–4893. <https://doi.org/10.1111/gcb.15199>
29. Flora of Japan. (2019). *Database of Japanese Flora*. <https://herbaria.plants.ox.ac.uk/bol/florajapan/Explore>
30. Gall L. (2019). *Occurrence dataset*. Botany Division, Yale Peabody Museum. Yale University Peabody Museum. <https://doi.org/https://doi.org/10.15468/hrztgn>
31. GBIF.org. (2019). *GBIF*. <https://www.gbif.org/>

32. Grant, S., & Niezgodna, C. (2019). *Occurrence dataset*. Field Museum of Natural History (Botany) Seed Plant Collection. Version 11.10. Field Museum. <https://doi.org/https://doi.org/10.15468/nxnqzf>
33. Grime, J. P., Hodgson, J. G., & Hunt, R. (2007). *Comparative Plant Ecology: a functional approach to common British species* (2nd ed.). Castlepoint Press.
34. Guisan, A., Petitpierre, B., Broennimann, O., Daehler, C., & Kueffer, C. (2014). Unifying niche shift studies: insights from biological invasions. *Trends in Ecology & Evolution*, *29*(5), 260–269. <https://doi.org/10.1016/J.TREE.2014.02.009>
35. Hengl, T., Kempen, B., Heuvelink, G. B. M., & Malone, B. (2014). *GSIF: Global Soil Information Facilities*. (R version: 0.4-1.).
36. Hill, M. O., Mountford, J. O., Roy, D. B., & Bunce, R. G. H. (1999). *Ellenberg's indicator values for British plants. ECOFACT Technical Annex*. (Vol. 2). Institute of Terrestrial Ecology.
37. Holm, L. G., Doll, J., Holm, E., Pancho, J. V., & Herberger, J. P. (1997). *World weeds: natural histories and distribution*. Wiley.
38. Holm, L., Pancho, J. V., Herberger, J. P., & Plucknett, D. L. (1979). *A geographical atlas of world weeds*. John Wiley and Sons. <https://www.cabi.org/isc/abstract/19802330214>
39. Holt, R. D. (2009). Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences*, *106*. <https://doi.org/10.1073/pnas.0905137106>
40. Hutchinson, G. E. (1957). Concluding remarks Cold Spring Harbour Symposia on Quantitative Biology. *Symposia on Quantitative Biology*, *22*, 415–427.
41. Invasive Species Specialist Group. (2019). *Global Invasive Species Database*. <http://issg.org/database/welcome/>
42. Kitajima, K., Fox, A. M., Sato, T., & Nagamatsu, D. (2006). Cultivar selection prior to introduction may increase invasiveness: evidence from *Ardisia crenata*. *Biological Invasions*, *8*(7), 1471–1482. <https://doi.org/10.1007/s10530-005-5839-9>
43. Kołodziejek, J., & Patykowski, J. (2015). Effect of Environmental Factors on Germination and Emergence of Invasive *Rumex confertus* in Central Europe. *TheScientificWorldJournal*, *2015*, 170176. <https://doi.org/10.1155/2015/170176>
44. Lantschner, M. V., de la Vega, G., & Corley, J. C. (2019). Predicting the distribution of harmful species and their natural enemies in agricultural, livestock and forestry systems: an overview. *International Journal of Pest Management*, *65*(3), 190–206. <https://doi.org/10.1080/09670874.2018.1533664>
45. Liu, X., Petitpierre, B., Broennimann, O., Li, X., Guisan, A., & Li, Y. (2017). Realized climatic niches are conserved along maximum temperatures among herpetofaunal invaders. *Journal of Biogeography*, *44*(1), 111–121. <https://doi.org/10.1111/jbi.12808>
46. Lousley, J. E., & Kent, D. H. (1981). *Docks and knotweeds of the British Isles*. Botanical Society of the British Isles.

47. Mota-Vargas, C., & Rojas-Soto, O. R. (2016). Taxonomy and ecological niche modeling: Implications for the conservation of wood partridges (genus *Dendrortyx*). *Journal for Nature Conservation*, 29, 1–13. <https://doi.org/10.1016/j.jnc.2015.10.003>
48. New Zealand Plant Conservation Network. (2019a). *New Zealand's Flora*. <http://www.nzpcn.org.nz/page.aspx?flora>
49. New Zealand Plant Conservation Network. (2019b). *Rumex conglomeratus*. http://www.nzpcn.org.nz/flora_details.aspx?ID=2937
50. New Zealand Plant Conservation Network. (2019c). *Rumex crispus*. http://www.nzpcn.org.nz/flora_details.aspx?ID=2948
51. Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C., & Guisan, A. (2012). Climatic niche shifts are rare among terrestrial plant invaders. *Science (New York, N.Y.)*, 335(6074), 1344–1348. <https://doi.org/10.1126/science.1215933>
52. Pfennig, K. S., Kelly, A. L., & Pierce, A. A. (2016). Hybridization as a facilitator of species range expansion. In *Proceedings. Biological sciences* (Vol. 283, Issue 1839). The Royal Society. <https://doi.org/10.1098/rspb.2016.1329>
53. Pysek, P., Jarosík, V., Hulme, P. E., Kühn, I., Wild, J., Arianoutsou, M., Bacher, S., Chiron, F., Didziulis, V., Essl, F., Genovesi, P., Gherardi, F., Hejda, M., Kark, S., Lambdon, P. W., Desprez-Loustau, M.-L., Nentwig, W., Pergl, J., Paboljsaj, K., ... Winter, M. (2010). Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 107(27), 12157–12162. <https://doi.org/10.1073/pnas.1002314107>
54. R Core Team. (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <http://www.r-project.org/>
55. Randall, R. P. (2017). *A Global Compendium of Weeds* (R. P. Randall (Ed.), 3rd ed.). CABI.
56. Redpath, D., & Rapson, G. (2015). An extreme flood event initiates a decade of stand collapse in *Beilschmiedia tawa* forest, Turakina Valley, Rangitikei, New Zealand. *New Zealand Journal of Botany*, 53(1), 38–59. <https://doi.org/10.1080/0028825X.2014.1000934>
57. Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, 421(6918), 57–60. <https://doi.org/10.1038/nature01333>
58. Schoener, T. W. (1970). Nonsynchronous Spatial Overlap of Lizards in Patchy Habitats. *Ecology*, 51(3), 408–418. <https://doi.org/10.2307/1935376>
59. Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., van Kleunen, M., Winter, M., Ansong, M., Arianoutsou, M., Bacher, S., Blasius, B., Brockerhoff, E. G., Brundu, G., Capinha, C., Causton, C. E., Celesti-Grapow, L., ... Essl, F. (2018). Global rise in emerging alien species results from increased accessibility of new source pools. *Proceedings of the National Academy of Sciences of the United States of America*, 115(10), E2264–E2273. <https://doi.org/10.1073/pnas.1719429115>

60. Silva, D. P., Vilela, B., Buzatto, B. A., Moczek, A. P., & Hortal, J. (2016). Contextualized niche shifts upon independent invasions by the dung beetle *Onthophagus taurus*. *Biological Invasions*, *18*(11), 3137–3148. <https://doi.org/10.1007/s10530-016-1204-4>
61. Smith, A. B., Godsoe, W., Rodríguez-Sánchez, F., Wang, H.-H., & Warren, D. (2019). Niche Estimation Above and Below the Species Level. *Trends in Ecology & Evolution*, *34*(3), 260–273. <https://doi.org/10.1016/J.TREE.2018.10.012>
62. Tingley, R., Vallinoto, M., Sequeira, F., & Kearney, M. R. (2014). Realized niche shift during a global biological invasion. *PNAS*, *111*(28), 10233–10238. <https://doi.org/10.1073/pnas.1405766111>
63. University of Georgia. (2019). *EDDMapS Species Distribution Maps*. Centre for Invasive Species and Ecosystem Health. <https://www.eddmaps.org/distribution/>
64. USDA. (2019). *Taxon: Rumex crispus L.* GRIN. <https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomydetail?id=32530>
65. USDA, & NRCS. (2019). *The PLANTS Database*. National Plant Data Team, Greensboro, NC 27401-4901 USA. <http://plants.usda.gov>
66. Vibrans, H. (1998). Native maize field weed communities in south-central Mexico. *Weed Research*, *38*(2), 153–166. <https://doi.org/10.1046/j.1365-3180.1998.00082.x>
67. Victorian Biodiversity Atlas. (2019a). *2447402.00*. The State of Victoria, Department of Environment, Land, Water & Planning.
68. Victorian Biodiversity Atlas. (2019b). *2448526.00*. The State of Victoria, Department of Environment, Land, Water & Planning.
69. Warren, D. L., Glor, R. E., & Turelli, M. (2008). Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution*, *62*(11), 2868–2883. <https://doi.org/10.1111/j.1558-5646.2008.00482.x>
70. Warren, D. L., Glor, R. E., & Turelli, M. (2010). ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography*, *33*(3), 607–611. <https://doi.org/10.1111/j.1600-0587.2009.06142.x>
71. Williams, J. L., Hufbauer, R. A., & Miller, T. E. X. (2019). How Evolution Modifies the Variability of Range Expansion. *Trends in Ecology & Evolution*, *34*(10). <https://doi.org/10.1016/j.tree.2019.05.012>

Tables

Table 1: Number of usable records obtained for each region of interest and earliest known date of record for three *Rumex* spp in their native range and three introduced ranges. Usable records were of sufficient identifying information, coordinate precision, and were counted after spatial thinning.

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

Table 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.

Table 3 Pairwise comparisons of climatic niche overlap (*D*) and niche similarity between three *Rumex* species within their native range (Eurasia) and three introduced ranges. *D* indicates the level of overlap on a scale of 0-1 (no overlap-complete overlap). Niche Similarity tests whether the occupied niche is more similar than expected by chance alone. Significant p-values are displayed in bold, with borderline significant values in italics.

Species	Region	N	Niche Overlap (<i>D</i>)	Niche Similarity (p-value)	Niche Expansion	Niche Unfilling	Niche Pioneering
<i>Rumex obtusifolius</i>	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
<i>Rumex crispus</i>	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
<i>Rumex conglomeratus</i>	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

<i>Schoener's D</i>	<i>R. obtusifolius vs R. crispus</i>	<i>R. obtusifolius vs R. conglomeratus</i>	<i>R. crispus vs R. conglomeratus</i>
Native Range	0.914	0.709	0.682
Eastern Australia	0.478	0.442	0.630
Western North America	0.391	0.448	0.129
New Zealand	0.758	0.589	0.643
<i>Niche similarity</i> <i>(p-value)</i>			
Native Range	0.010	0.010	0.010
Eastern Australia	0.059	0.208	0.040
Western North America	<i>0.050</i>	0.030	0.416
New Zealand	0.02	0.03	0.03

Figures

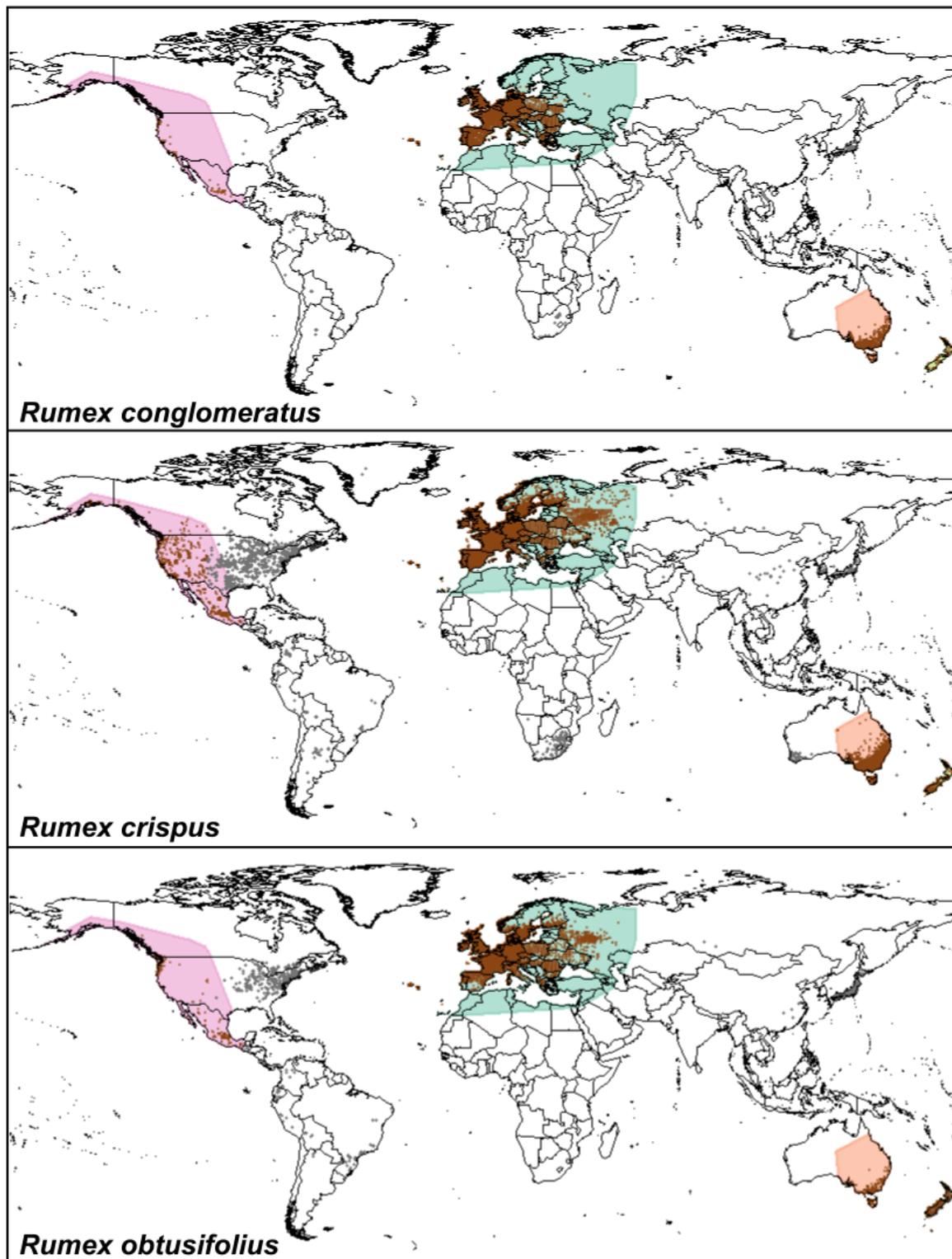


Figure 1

Worldwide distribution of *Rumex conglomeratus* (top), *Rumex crispus* (middle) and *Rumex obtusifolius* (bottom). Records span temperate and tropical zones. Records in brown were used in our analyses, records in grey are considered introduced but not used in our analyses. The native range and assessed

introduced ranges are shown via minimum convex polygons: Native range – Teal; Western North America – Magenta; Eastern Australia – Orange; New Zealand – Green.

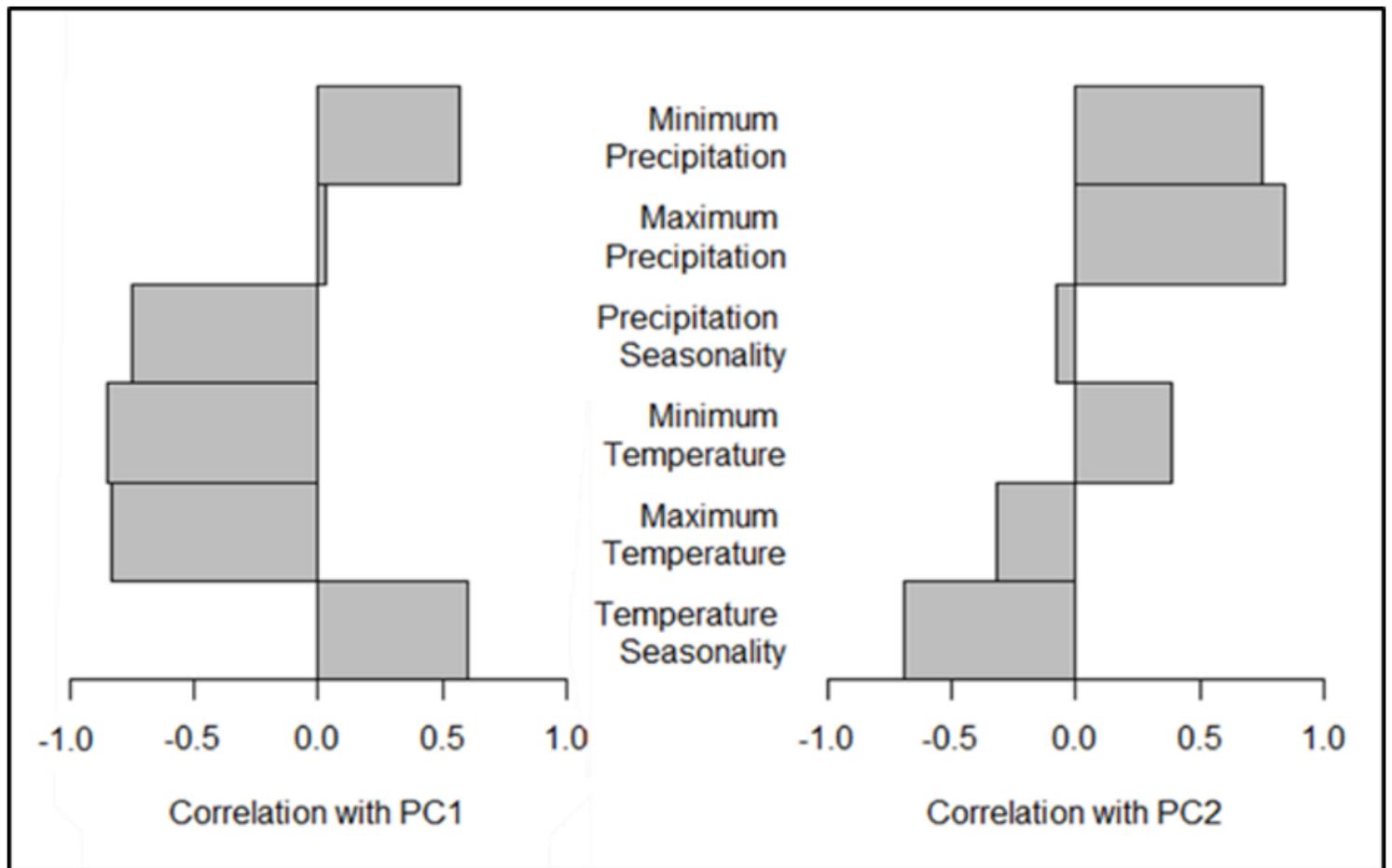


Figure 2

Contributions of variables to the first two axes of the principal component analysis. 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).

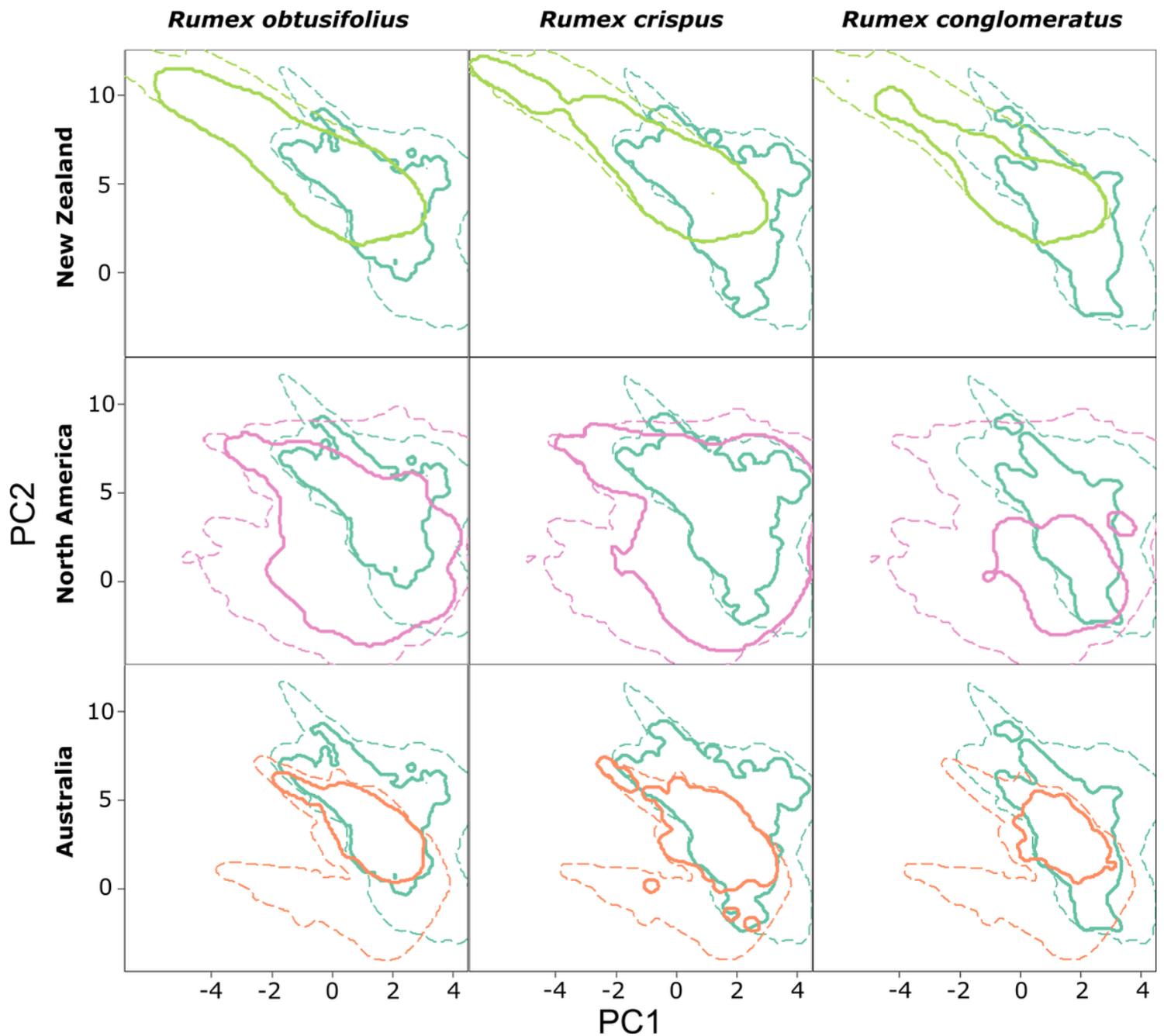


Figure 3

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; Western North America – Pink; Eastern 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

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