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). 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 climes (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.

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**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       | *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 L, 2019)                                   |
|                    | *R. obtusifolius* | 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 ($D$) | 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           |

**Schoener's $D$**

| Region                | $R. obtusifolius$ vs $R. crispus$ | $R. obtusifolius$ vs $R. conglomeratus$ | $R. crispus$ vs $R. conglomeratus$ |
|-----------------------|------------------------------------|----------------------------------------|-------------------------------------|
| 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                               |

**Niche similarity**

*(p-value)*

| Region                | $R. obtusifolius$ vs $R. crispus$ | $R. obtusifolius$ vs $R. conglomeratus$ | $R. crispus$ vs $R. conglomeratus$ |
|-----------------------|------------------------------------|----------------------------------------|-------------------------------------|
| Native Range          | 0.010                              | 0.010                                  | 0.010                               |
| Eastern Australia     | 0.059                              | 0.208                                  | 0.040                               |
| Western North America | 0.050                              | 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).
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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