

Global assessment of three *Rumex* species reveals inconsistent climatic niche shifts across introduced ranges

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2 **introduced ranges**

3

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12

13 **Abstract**

14 Climatic niche shifts occur when species occupy different climates in the introduced range than in
15 their native range. Climatic niche shifts are known to occur across a range of taxa, however we do
16 not currently understand whether climatic niche shifts can consistently be predicted across multiple
17 introduced ranges. Using three congeneric weed species, we investigate whether climatic niche
18 shifts in one introduced range are consistent in other ranges where the species has been introduced.
19 We compared the climatic conditions occupied by *Rumex conglomeratus*, *R. crispus*, and *R.*
20 *obtusifolius* between their native range (Eurasia) and three different introduced ranges (North
21 America, Australia, New Zealand). We considered metrics of niche overlap, expansion, unfilling,
22 pioneering, and similarity to determine whether climatic niche shifts were consistent across ranges
23 and congeners. We found that the presence and direction of climatic niche shifts was inconsistent
24 between introduced ranges for each species. Within an introduced range, however, niche shifts
25 were qualitatively similar among species. North America and New Zealand experienced diverging
26 niche expansion into drier and wetter climates respectively, whilst the niche was conserved in
27 Australia. This work highlights how unique characteristics of an introduced range and local
28 introduction history can drive different niche shifts, and that comparisons between only the native
29 and one introduced range may misrepresent a species' capacity for niche shifts. However,
30 predictions of climatic niche shifts could be improved by comparing related species in the introduced
31 range rather than relying on the occupied environments of the native range.

32

33 **Keywords:** alien species; biological invasions; climatic niche shift; macroecology; niche dynamics;
34 niche expansion.

35

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38 Bio-Protection Research Centre.

39

40 **Conflicts of interest**

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

42

43 **Availability of data and material**

44 The datasets generated and analysed during the current study are available in the Figshare
45 repository: DOI 10.6084/m9.figshare.17148317

46

47 **Code availability**

48 The code generated during the current study is available upon reasonable request.

49

50 **Authors' contributions**

51 All authors contributed to the study conception and design. Philip Hulme obtained the research
52 funding. Data collection and analysis were performed by Thomas Carlin and Jennifer Bufford. The
53 first draft of the manuscript was written by Thomas Carlin and all authors participated in revisions
54 and approved the final manuscript.

55 Introduction

56 Attempts to predict the establishment of plants introduced to new regions have commonly assumed
57 species inhabit similar environments across the globe, usually termed climatic niche conservatism
58 (Bradley et al., 2012; Bradley, Blumenthal, et al., 2010; Bradley, Wilcove, et al., 2010; Liu et al.,
59 2020). A species' realised climatic niche is the set of climates a species currently occupies and in
60 which it experiences stable or positive population growth (Atwater et al., 2018; Holt, 2009;
61 Hutchinson, 1957), and niche conservatism occurs when a species inhabits that same niche in both
62 the native and introduced range (Liu et al., 2020; Petitpierre et al., 2012). However, studies have
63 revealed shifts in the climatic niche between introduced and native ranges across many taxa and
64 environments (Atwater & Barney, 2021; Atwater et al., 2018; Bujan et al., 2020; Christina et al.,
65 2019; Comte et al., 2017; Liu et al., 2016; Silva et al., 2016; Tingley et al., 2014). Niche shifts can
66 occur when species occupy climates in the introduced range that are either available but unoccupied
67 in the native range (expansion), unavailable in the native range (pioneering), or by failing to occupy
68 climates in the introduced range that are occupied in the native range (unfilling; Atwater et al., 2018;
69 Guisan et al., 2014). A better understanding of niche shifts is essential to predict the establishment
70 and future range dynamics of introduced species under ongoing spread and global climate change.

71 While it is well-documented that climatic niche shifts can occur between the native range and an
72 introduced range, the question remains whether such shifts are predictable and consistent in both
73 direction and magnitude across multiple introduced ranges for a given species. Hundreds of species
74 across different taxa and continents have been compared to date as part of the ongoing debate
75 around the frequency of niche shifts (Atwater et al., 2018; Atwater & Barney, 2021; Liu et al., 2020;
76 Petitpierre et al., 2012; Webber et al., 2012), however these studies provide little insight into
77 whether information on niche shifts is transferable between regions or species. To date, most
78 studies have focussed on pairwise comparisons of plant distributions between the native and one
79 introduced range (Early & Sax, 2014; Fernández & Hamilton, 2015; Gallagher et al., 2010; Randin et
80 al., 2006) and comparisons across studies are challenging, since studies have used different
81 underlying variables to define the environmental space (Liu et al., 2020). Whilst these comparisons
82 provide useful information on how often niche shifts occur, approaches that consider several
83 introduced ranges are required to determine if niche shifts are consistent within a species across
84 introduced ranges. Currently the transferability of plant species distributions between different
85 introduced ranges has been little explored (Datta et al., 2019; Petitpierre et al., 2012), however it
86 has been assessed for some animal species (Hill et al., 2017; Pili et al., 2020; Silva et al., 2016).
87 Understanding whether niche shifts are consistent between ranges will provide insight into how

88 species adapt to these new climates, what environmental factors limit species distributions and
89 predictions of future invasion risk.

90 When comparing niche shifts across several introduced ranges there are a number of potential
91 outcomes (Figure 1). Firstly, a species may consistently shift into certain climates across all observed
92 ranges (Figure 1A). Consistent niche shifts across ranges may be expected in species where the
93 native range does not fully encapsulate their fundamental environmental tolerances. This would
94 suggest that the species is either pre-adapted to, or able to rapidly adapt to, a specific subset of
95 climates. Silva et al. (2016) showed that independent invasions of a dung beetle, *Onthophagus*
96 *taurus*, into different introduced regions all experienced niche shifts towards more humid climates
97 than those occupied in the native range. Alternatively, we may see idiosyncratic patterns in the
98 direction of niche shifts, with the species shifting in different directions across ranges (Figure 1B), or
99 experiencing niche shifts in some ranges but niche conservatism in others (Figure 1C). This could
100 indicate that non-climatic factors in the introduced range are facilitating a niche shift, or that a niche
101 shift represents an escape from non-climatic factors which restrict the species distribution in some
102 ranges (Bulleri et al., 2016). For example gorse, *Ulex europaeus*, occupies warmer areas in Australia
103 and South America than in its native range, yet cooler areas in North America, but the mechanisms
104 behind these niche shifts are unknown (Christina et al., 2019). Inconsistent niche shifts across ranges
105 could also be explained due to differences in genetic diversity, where founder effects result in
106 phenotypic differences between populations (Flanagan et al., 2021; Liao et al., 2020; Ribas et al.,
107 2018). Additionally, niche shifts may be inconsistent in magnitude, where niche shifts in two
108 independent ranges could both be towards similar climates but more extreme in one introduced
109 region than the other. Variations in magnitude of a niche shift would amplify the difficulty in
110 predicting the climatic thresholds a species may be able to tolerate, and subsequently which areas
111 are susceptible to establishment.

112 As well as understanding how niche shifts occur it is also important to know whether they occur
113 under analogue or non-analogue climates. Analogue climates are climates available to a species in
114 both the native and introduced ranges, whereas non-analogue climates are present in only one
115 range (Figure 1D). Liu et al. (2020), as well as other earlier work (Petitpierre et al., 2012; Tingley et
116 al., 2016), chose not to investigate niche dynamics under non-analogue climates because shifts due
117 to rapid evolution cannot be distinguished from shifts due to an underestimation of the fundamental
118 niche. Whilst it is important to distinguish between these two types of niche shifts, shifts into non-
119 analogue climates still represent realised niche shifts that can affect the accuracy of environmental
120 niche models (Atwater et al., 2018; D'Amen & Azzurro, 2020; Pili et al., 2020; Webber et al., 2012)

121 and the impact of invasions. When considering niche shifts across several introduced ranges, shifts
122 into non-analogue climates may become important as each range will have novel combinations of
123 climates. Determining whether species experience shifts into non-analogue climates that are similar
124 across their ranges is an important step in determining the likelihood of shifts into non-analogue
125 climates.

126 It is currently not well understood whether closely related species show consistent niche shifts.
127 Previous studies of niche shifts in multiple ranges have mostly looked at a single species (Christina et
128 al., 2019; Datta et al., 2019; Silva et al., 2016; Tingley et al., 2014), but comparisons of closely related
129 species would provide new insights into whether they experience consistent niche shifts across
130 ranges. If closely related species share a similar climatic niche and shift niches consistently, we may
131 conclude that common factors, such as climate availability, in the introduced range may be a larger
132 driver of niche shifts than individual species attributes. If this is the case then data from related
133 species could be used to supplement our knowledge of the species niche, and aid in predicting shifts
134 (Smith et al., 2019). We could then use the presence of a known species to make strong inferences
135 about where a related species could spread.

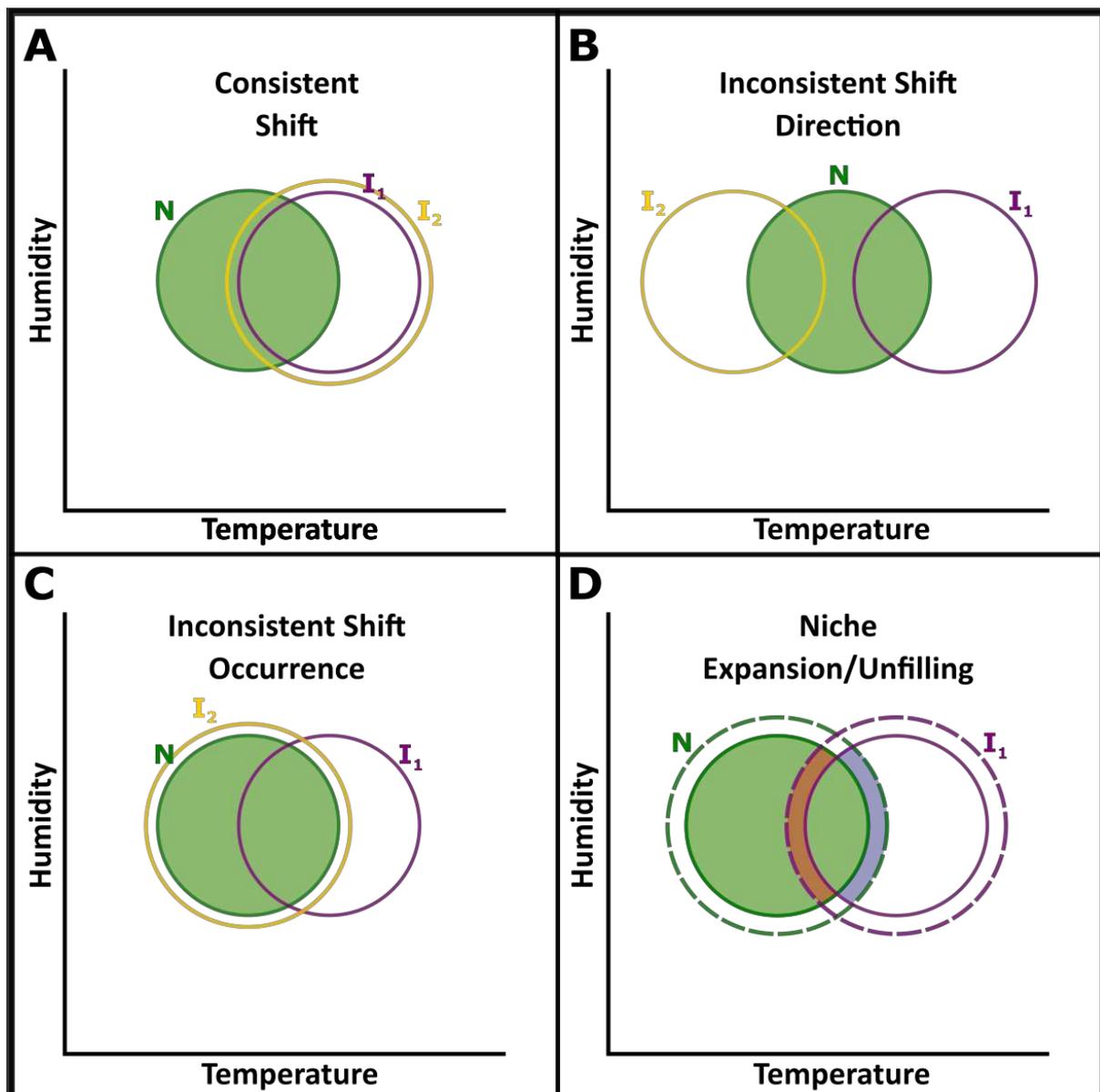


Figure 1 Possible niche shift scenarios between regions. Axes represent two different example environmental gradients across which a niche shift could be observed. Areas occupied in a species' native range (N) are shown by the green shaded circle; areas occupied in two different introduced ranges (I_1 , 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 can 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).

136

137 Here we assess the consistency of climatic niche shifts across multiple introduced ranges for three
 138 closely related, globally invasive, herbaceous species. Combining climatic information across both

139 ranges and species allows us to make previously unseen direct comparisons of niche occupancy in
140 shared environmental space to ask:

- 141 1. Do species shift their niches in the same direction across introduced ranges?
- 142 2. Are climatic niche shifts consistent across closely related species?

143

144 Where species undergo climatic niche shifts, we expect to find shifts into similar climates in all
145 introduced ranges (Figure 1A) unless the species' distribution in the introduced range is constrained
146 by non-climatic factors. Similarly, we expect that such shifts would be consistent across closely
147 related species, allowing information from the distribution of one species to help inform the
148 likelihood of other species undergoing climatic niche shifts. With this analysis we hope to shed light
149 on when and where niche shifts occur, and whether the direction of niche shifts can be forecasted.
150

151 **Methods**

152 ***Study Area and Species***

153 We studied three common dock species: *Rumex obtusifolius* L., *R. crispus* L., and *R. conglomeratus*
154 Murray. These species are all ruderals, typically colonising open, disturbed environments associated
155 with human activity, including pasture (Cavers & Harper, 1964, 1966; Grime et al., 2007; Holm et al.,
156 1997; Lousley & Kent, 1981). *Rumex* spp. are short lived and tend to reproduce annually if conditions
157 are favourable but are capable of biennial or perennial life strategies (Cavers & Harper, 1964; Grime
158 et al., 2007). These congeners all prefer open environments with minimal shading, nitrogen rich
159 soils, and can tolerate either weakly acidic or basic soils. They are capable of hybridising with one
160 another (Cavers & Harper, 1964; Holm et al., 1979; Lousley & Kent, 1981) and share broad
161 environmental tolerances (Grime et al., 2007; Hill et al., 1999; Lousley & Kent, 1981). Despite this,
162 small differences in environmental tolerances are observed between species, with *R. obtusifolius* in
163 particular able to tolerate extremely nutrient rich or polluted soils and waterways (Grime et al.,
164 2007). *Rumex conglomeratus* has a smaller global range size and is restricted to more mild
165 temperatures and wetter habitats, such as along waterways (Hill et al., 1999; Lousley & Kent, 1981).
166 In comparison, *R. obtusifolius* and *R. crispus* can tolerate cooler, drier climates, with their native
167 distributions extending to the Arctic Circle (Hultén, 1950).

168 All three species are of Eurasian origin yet over the last five hundred years have been introduced and
169 established across the globe as agricultural seed contaminants (Table 1; Figure S.1; Holm et al., 1979;
170 Holm et al., 1997; Vibrans, 1998). Furthermore, occurrence data for these species are numerous in
171 both the native and several introduced ranges, making them ideal candidates for assessing global
172 niche shifts. Despite the wide variety of ecoregions *Rumex* spp. inhabit (Olson et al., 2001) they
173 generally occupy similar habitats across the globe, indicating that any possible niche shifts would
174 likely be driven by climate rather than habitat limitations (Figure 2; Cavers & Harper, 1964; Grime et
175 al., 2007; Holm et al., 1997; Lousley & Kent, 1981). Their long invasion history suggests they are likely
176 to have reached climatic equilibrium in their introduced ranges, and that sufficient generations have
177 passed for adaptations to new climates to develop (Table 1; Vibrans, 1998). As such, *Rumex* spp.
178 have had ample opportunities for niche shifts to occur. *Rumex* spp. were not deliberately introduced
179 for agricultural or horticultural purposes and have not been subjected to artificial selection which
180 may affect their invasiveness or climatic tolerances (Kitajima et al., 2006). Therefore, any niche shifts
181 observed are likely due to natural processes.

182

183 **Table 1** Number of usable records and earliest known record obtained for each range. Usable
 184 records were identified to species level, had coordinate precision ≤ 10 km, and were
 185 counted prior to 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 & Niezgodna, 2019)
	<i>R. crispus</i>	2014	1822	(Gall, 2019)
	<i>R. obtusifolius</i>	435	1550	(Vibrans, 1998)

186 We modelled these species' niches across the native range, predominantly in Europe, and three
 187 regions where the species are recorded as naturalised in the Global Invasive Species Database
 188 (Invasive Species Specialist Group, 2019) as well as regional floras: western North America (USDA &
 189 NRCS, 2019), south-eastern Australia (*Atlas of Living Australia*, 2019), and New Zealand (New
 190 Zealand Plant Conservation Network, 2019a). These regions were selected because they have an
 191 abundance of occurrence records for all three species, a wide variety of climates, and a long history
 192 since the species were first introduced (Table 1). Additional information on ranges not included in
 193 this study is presented in Figure S.1.

194

195 *Defining the Native range*

196 We define the native range for each of these species as spanning Europe, the Middle East, and
 197 Northern Africa (Figure 2). Multiple databases, including the Global Biodiversity Information Facility
 198 (GBIF; GBIF.org, 2019) the Atlas Florae Europaea (AFE, 1979), the Flora of Japan (FOJ; Flora of
 199 Japan, 2019), Calflora (Calflora, 2019), Centre for Agriculture and Bioscience International (CABI,
 200 2019), U.S. Germplasm Resources Information Network (USDA, 2019), and the Global Weed
 201 Compendium (Randall, 2017), were consulted to determine where these species were classified as
 202 native (Table S1). Areas of continuous species occurrence contiguous with these regions were

203 likewise considered native, unless otherwise stated as a known introduction, as these occurrences
204 were considered likely to be naturally distributed from the same range. A literature search (Table S2)
205 was conducted to determine whether historical records indicated known introductions. Table S1
206 displays a full list of the countries considered in this study and whether we classified these *Rumex*
207 species as native or introduced in that country.

208 There is no consensus on whether Japan is part of the native or introduced range for *R. obtusifolius*
209 and *R. crispus*. Some sources include eastern Asia and Japan as part of the native range for *R.*
210 *obtusifolius* and *R. crispus* (Flora of Japan, 2019; USDA, 2019), while other sources consider the
211 species as introduced (Grossrieder & Keary, 2004; Makuchi & Sakai, 1984; Miyagi et al., 2010;
212 Nishida, 2002). Additionally, the available data for these species in Asia show a large geographic
213 distance between the closest European and Asian populations suggesting that they are likely to be
214 genetically isolated, or that there are large gaps in sampling. As a result, our analyses did not include
215 Japan as part of the native range for *R. obtusifolius* and *R. crispus*. The analyses were repeated with
216 Japan included as part of the native range of *R. obtusifolius* and *R. crispus*, and this had minimal
217 effect on our results (Table S5). *Rumex conglomeratus* is not considered native to eastern Asia by
218 any of the sources we assessed.

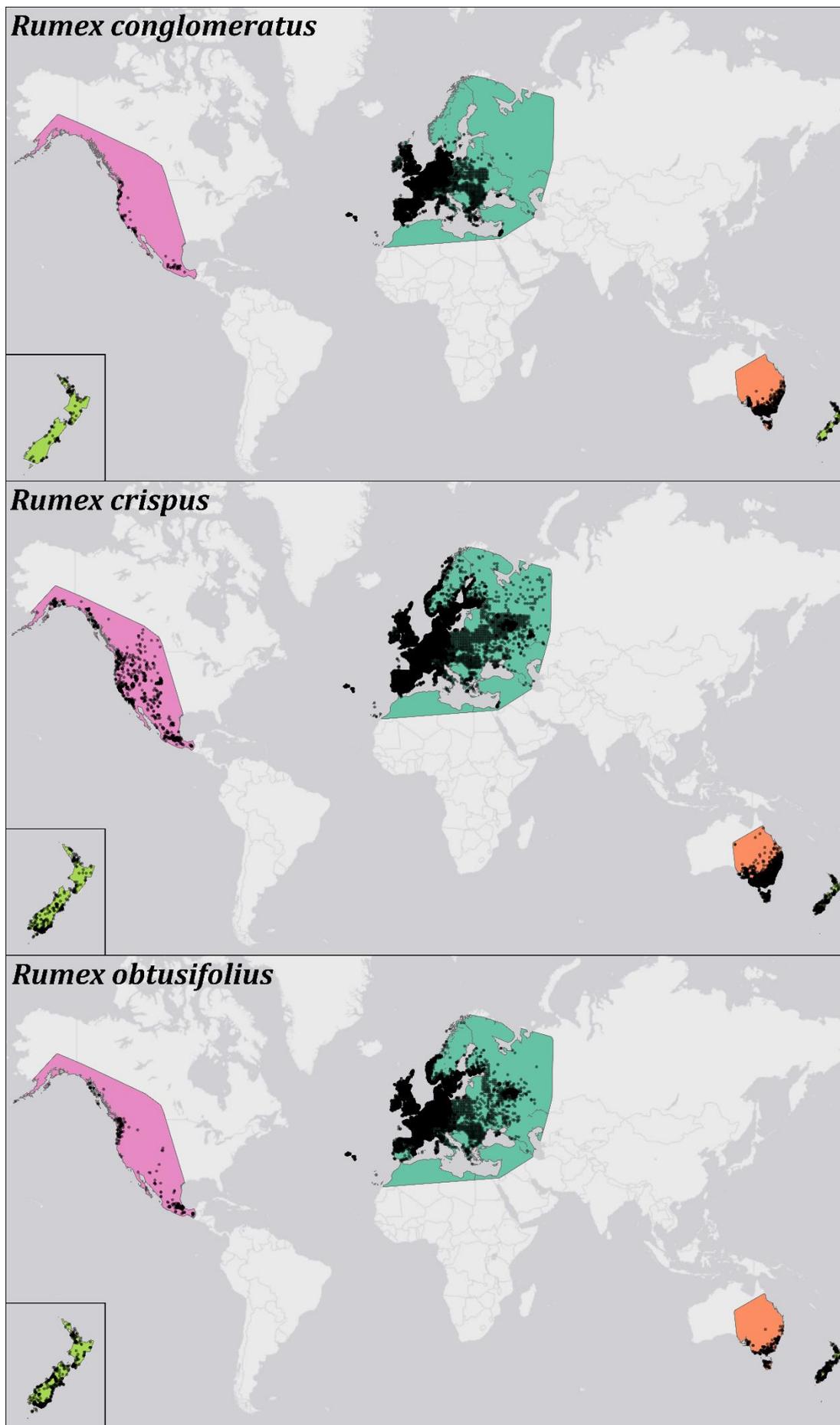


Figure 2 Distribution of *Rumex conglomeratus* (top), *Rumex crispus* (middle) and *Rumex obtusifolius* (bottom) records included in our study, plotted as black points at 50% opacity. Records span temperate and tropical zones. The background climates used are displayed by shaded minimum convex polygons and are consistent between species for direct comparison: Native range – Teal; Western North America – Magenta; Eastern Australia – Orange; New Zealand – Green. New Zealand is also displayed in the inset of each distribution map for better visualization.

220 **Data Collection**

221 *Species' occurrence data*

222 Occurrence records were collected for the three *Rumex* spp. from: GBIF, AFE, the Atlas of Living
223 Australia (ALA), the Early Detection and Distribution Mapping System (EDDMapS; University of
224 Georgia, 2019), Calflora, records georeferenced from targeted journals (Table S2; Table S3), and our
225 own surveys in the UK and NZ. Due to the underreporting of *Rumex* spp. distribution records in New
226 Zealand, we examined New Zealand journals that commonly publish floristic inventories, using the
227 search term "*Rumex*" and checked all results for occurrence records. Records were georeferenced at
228 the highest possible resolution using Google Maps (google.com/maps) and details are provided in
229 Table S4. Occurrence records were cleaned by removing records with missing or inaccurate
230 coordinates and records with coordinate uncertainties of over 10 km. Records were separated into
231 the native range and three introduced ranges and thinned by applying a 2.5 arc minute (~5 km at the
232 equator) grid over the occurrence points, and selecting one random point per grid cell using the R
233 package GSIF (Hengl, Kempen, Heuvelink, & Malone, 2014). Thinning the occurrence records reduces
234 geographic sampling bias and removes duplicate results.

235

236 *Climate data*

237 To improve predictability and interpretability of our models we used six bioclimatic variables
238 commonly used to best represent constraints on plant ecology (Alexander, 2013; Dullinger et al.,
239 2017; Fourcade et al., 2018; Keller et al., 2009; Root et al., 2003): temperature seasonality (BIO4),
240 maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month
241 (BIO6), precipitation seasonality (BIO15), precipitation of the wettest quarter (BIO16), and
242 precipitation of the driest quarter (BIO17). Both temperature (Benvenuti et al., 2001; Cavers &
243 Harper, 1964, 1966) and precipitation, through soil moisture (Cavers & Harper, 1964), are important
244 in determining plant species distributions at local scales and using fewer, more biologically relevant
245 variables makes results more interpretable. These six variables were obtained from the WorldClim
246 dataset (Booth et al., 2014; Fick & Hijmans, 2017; worldclim.org) at 2.5 arc minute (~5 km at the
247 equator) resolution.

248

249 **Niche Analysis**

250 In order to assess climatic niche shifts in the introduced ranges we utilised the environmental
251 principal component analysis (PCA-env) approach proposed by Broennimann et al. (2012), and later
252 improved by Petitpierre et al. (2012) and Guisan et al. (2014) which standardises the environment

253 across ranges. This method corrects for sampling biases by applying a kernel density smoother to
254 estimate the density of occurrences and is considered the “gold standard” for assessing niche
255 conservatism (Liu et al., 2020). We adapted the standard approach by extracting climatic data from
256 minimum convex polygons (MCPs) fitted around all three species’ occurrence points combined, for
257 each region, as opposed to extracting data for each species individually. This allowed us to compare
258 niches and niche shifts for all three species within the same climatic boundaries. Following methods
259 developed by Silva et al. (2016), a buffer zone of 1 decimal degree (~111 km at the equator) was
260 added around species’ presences and MCPs were fitted around this area for each region (Figure S1).
261 In order to reduce the number of variables to two, which the PCA-env approach requires, a principal
262 component analysis (PCA) was performed on the climates available to *Rumex* spp. and we used
263 values of the PCA axes at the species’ known occurrence points to calculate the occupied climate
264 conditions for each species in each range. Following guidelines from Guisan et al. (2014) and
265 amended by Silva et al. (2016), pairwise comparisons were performed between all ranges.

266 In order to determine whether climatic niche shifts occurred, we compared the available
267 environmental conditions of each of the three introduced ranges and the native range, following
268 metrics suggested by Guisan et al. (2014). We followed a framework based on centroid shift,
269 overlap, unfilling, and expansion (COUE; Liu et al. 2020) however, given the known issues related to
270 centroid shift methods (Godsoe, 2010; Guisan et al., 2014) we characterised shifts based only on
271 overlap (*D*), unfilling (*U*), and expansion (*E*). We also assessed niche shifts into non-analogue space
272 by measuring niche pioneering (*P*), the proportion of occupied environmental space in the
273 introduced range which is only present in the introduced range (Atwater et al., 2018; Guisan et al.,
274 2014; Petitpierre et al., 2012; Webber et al., 2012). Niche overlap in each comparison was
275 calculated using Schoener’s *D* (Broennimann et al., 2012; Schoener, 1970; Warren et al., 2008), a
276 metric which varies from 0, indicating the greatest possible distance between predicted occurrences
277 in each range (no niche overlap), to 1, indicating no differences (complete niche overlap). Niche
278 similarity was calculated to determine whether niches in the native and introduced ranges are more
279 or less similar than expected by chance given the available climates (Aguirre-Gutiérrez et al., 2015;
280 Warren et al., 2008, 2010). Significant niche similarity indicates the niches are more similar than
281 expected by chance, whereas non-significant niche similarity indicates a niche shift. The PCA output
282 was also used to determine the direction, and hence consistency, of the shifts in climate space
283 across regions for each species. The same methods were then applied to measure the degree of
284 niche overlap and similarity between species within each introduced range. All metrics were
285 calculated using the *ecospat* package (Di Cola et al., 2017) in the statistical software R version 3.5.1
286 (R Core Team, 2013).

287 **Results**

288 ***Principal Component Analysis***

289 The first two principal components explained 76.6% of the variation in the original six climate
290 variables (44.0% and 32.6% for PC1 and PC2 respectively) and therefore adequately represented the
291 available environmental space. Increasing values of PC1 corresponded to colder areas with more
292 seasonal variation in their temperatures, and less seasonal variation in precipitation. Increasing
293 values of PC2 indicated areas with higher precipitation and less seasonality in their temperatures
294 (Figure 3).

295

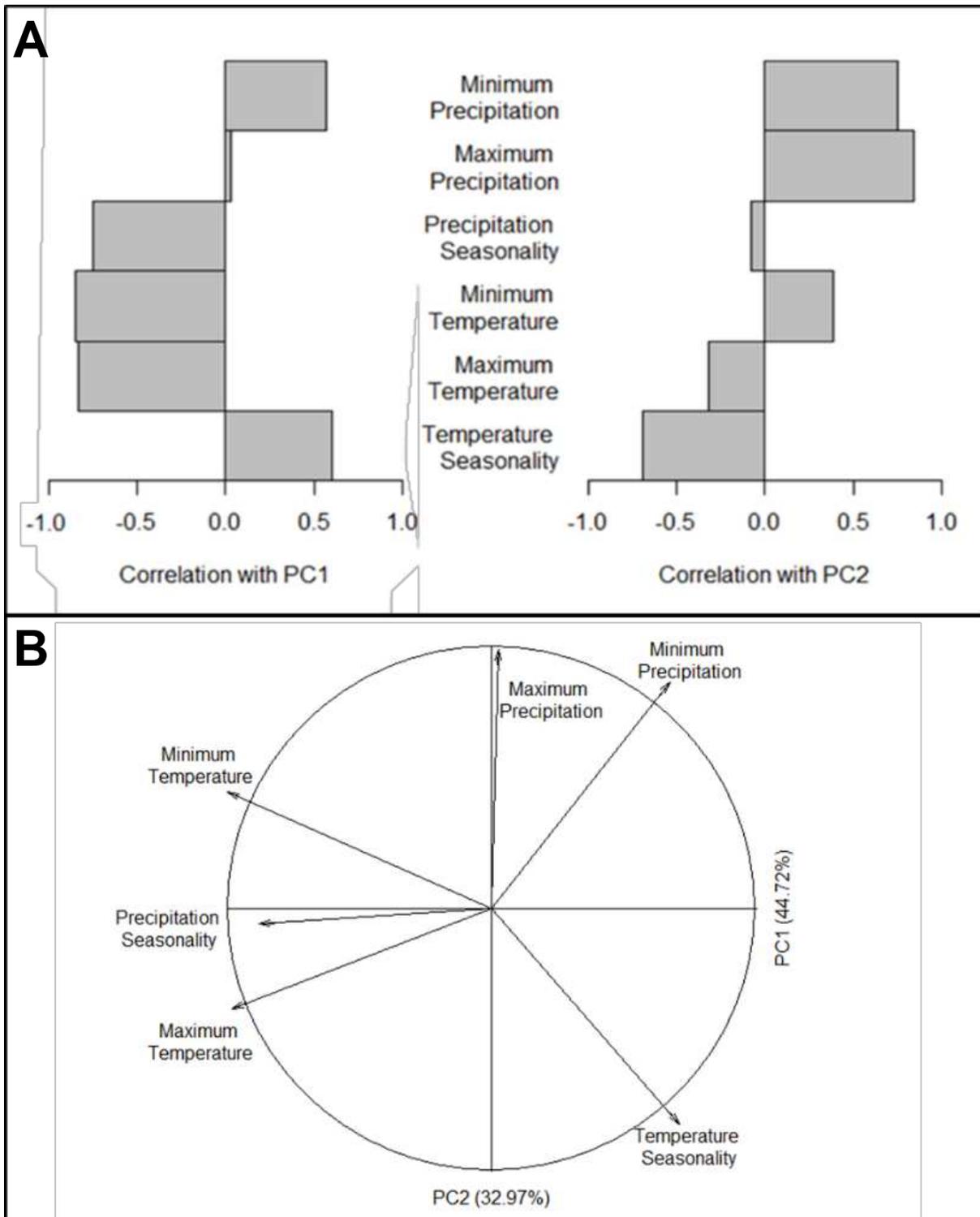


Figure 3 A) Contributions of variables to the first two axes of the principal component analysis. B) Direction of variables with respect to the first two principal components. Direction of arrows indicates increasing values of that variable. The first two principal components represent the environmental 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).

297 **Niche shifts are inconsistent across regions**

298 Climatic niche shifts were idiosyncratic between introduced regions for all species, with one region
299 characterised by niche conservatism (Figure 4; Australia) and two regions characterised by large
300 niche shifts (Figure 4; New Zealand and North America).

301 Australia is the only region in which *Rumex* spp. largely conserved their climatic niche (Figure 4), and
302 it was the region with the highest level of niche overlap with the native range ($0.20 \leq D \leq 0.34$; Table
303 2). Furthermore, Australia is the only region that had niche similarity values that were significantly
304 similar to the native range for all three species ($p = 0.01$; Table 2). *Rumex* spp. in Australia
305 experienced low levels of niche expansion, in both analogue and non-analogue climates ($0.01 \leq E \leq$
306 0.07 ; $0.01 \leq P \leq 0.06$), and high levels of niche unfilling ($0.39 \leq U \leq 0.60$; Table 2). Niche unfilling in
307 Australia occurred in wet areas with highly seasonal temperatures and drier areas with less seasonal
308 temperatures (both higher and lower values of PC2; Figure 4).

309 In New Zealand all three species expanded into warmer, wetter areas with more variable
310 precipitation (lower values of PC1 and higher values of PC2; Figure 4). The climatic niche shifts in NZ
311 were primarily into non-analogue climate space ($0.30 \leq P \leq 0.37$), however niche expansion into
312 analogue climate was also prevalent ($0.24 \leq E \leq 0.33$; Table 2; Figure 4). New Zealand was the only
313 introduced range where the occupied niche in analogue climates was not significantly similar to the
314 native range for any species ($p \leq 0.05$; Table 2). Niche overlap and unfilling between the occupied
315 climates in NZ and the native range were low ($D \leq 0.16$; $U \leq 0.07$; Table 2).

316 In North America the climatic niche expanded predominantly into warmer, drier climates (lower
317 values of PC1 and PC2), but also into cooler climates with less stable temperatures (higher values of
318 PC1; Figure 4). Climatic niche shifts in North America were observed across both analogue and non-
319 analogue climate space ($0.40 \leq E \leq 0.69$; $0.32 \leq P \leq 0.57$; Table 2; Figure 4). The niche in North
320 America was significantly similar to the niche in the native range for both *R. crispus* and *R.*
321 *conglomeratus* ($p = 0.04$ & $p = 0.01$ respectively). However, low levels of niche overlap ($D = 0.15$ & D
322 $= 0.17$ respectively) suggest the species have largely expanded into non-analogue climates (Table 2).
323 Two species, *R. obtusifolius* and *R. conglomeratus*, showed high levels of niche unfilling in North
324 America ($U = 0.52$ & $U = 0.91$ respectively) where available wetter, cooler areas remained
325 unoccupied in the introduced range (high values of both PC1 and PC2; Figure 4).

326 **Congeners display similar niche shift directions but low overlap**

327 Both the direction and presence of climatic niche shifts were consistent across *Rumex* species
328 (Figure 4). In all but one instance niche overlap between species within a range was higher than
329 overlap between the native range and the introduced ranges (Table 2; Table 3). The only exception
330 was the overlap between *R. crispus* and *R. conglomeratus* in North America, where overlap between

331 niche space in North America and the native range was higher for both species than the overlap
332 between species in North America. Nevertheless, niche overlap between species in each introduced
333 range was lower than between species in the native range (Table 3).

334 Comparisons of niche overlap among the three *Rumex* spp. show little consistency across introduced
335 regions (Table 3). In New Zealand, *Rumex* spp. were significantly similar to one another ($p < 0.05$)
336 and displayed high levels of niche overlap ($0.59 \leq D \leq 0.76$). In North America, *R. obtusifolius*
337 occupied significantly similar niche space to both *R. crispus* and *R. conglomeratus* ($p < 0.05$) with
338 moderate values of niche overlap ($0.391 \leq D \leq 0.448$), whilst *R. crispus* and *R. conglomeratus*
339 occupied dissimilar niche space ($p = 0.42$). In contrast, occupied niche space in Australia was only
340 significantly similar between *R. conglomeratus* and *R. crispus* ($p < 0.04$), despite moderate values of
341 niche overlap for all comparisons ($0.442 \leq D \leq 0.630$).

342

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 expected by chance alone. Note that niche metrics are weighted according to the density of occurrences in climate space.

Species	Region	N	Niche Overlap (<i>D</i>)	Niche Similarity (p-value)	Niche Expansion (<i>E</i>)	Niche Unfilling (<i>U</i>)	Niche Pioneering (<i>P</i>)
<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

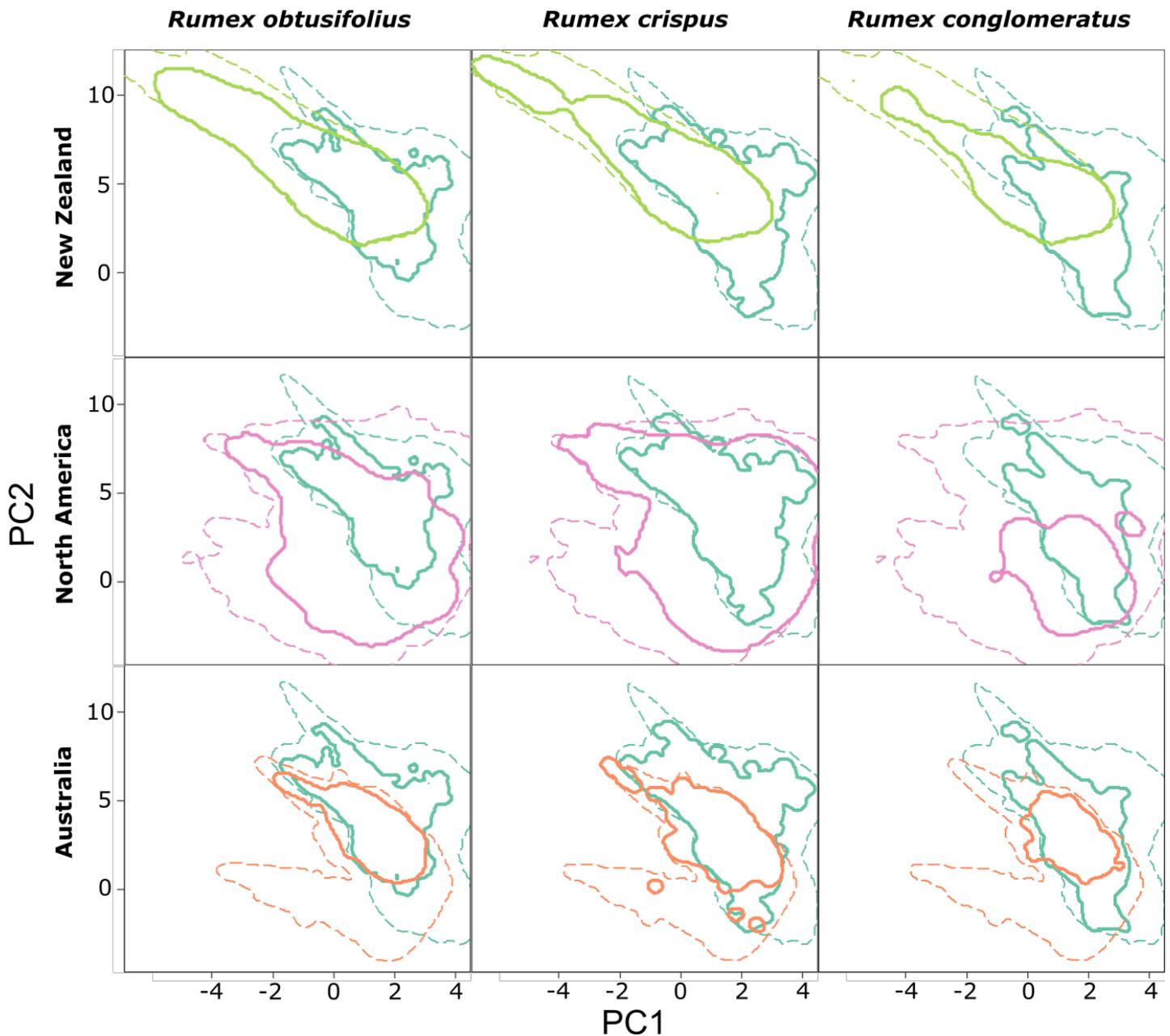


Figure 4 Comparisons of niche overlap in environmental space. Each panel shows a comparison between the native range (Teal) and one of the introduced ranges (New Zealand – Green; North America – Pink; Australia – Orange). The climate space occupied by the species is shown in solid lines and the total available climate space of the respective range is shown with dashed lines. 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 more stable precipitation. Increasing values of PC2 broadly correspond to increased precipitation, and more stable temperatures. Variable correlations with PC1 and PC2 can be seen in full in Figure 3.

Table 3 Pairwise comparisons of niche overlap (*D*) and niche similarity between the three species within each region. High values of *D* indicate that there is large overlap in the occupied niche space between that pair of species. Niche similarity is displayed as a p-value which, if <0.05, indicates regions are more similar than expected by chance alone.

Schoener's <i>D</i>	<i>R. obtusifolius</i> vs <i>R. crispus</i>	<i>R. obtusifolius</i> vs <i>R. conglomeratus</i>	<i>R. crispus</i> vs <i>R. conglomeratus</i>
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	0.01	0.01	0.01
Australia (East)	0.06	0.21	0.04
North America (West)	0.05	0.03	0.42
New Zealand	0.02	0.03	0.03

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350 Discussion

351 By comparing climatic niches between multiple introduced ranges and species, we found that
352 independent introductions of *Rumex* spp. have resulted in different niche shifts across geographically
353 distinct ranges into both analogue and non-analogue climates. We have shown that even superficially
354 similar invasions by closely-related species can lead to examples of every niche change proposed by
355 Guisan et al. (2014). We found evidence that the direction of climatic niche shifts was similar between
356 close relatives, although the resulting occupied climates did not always overlap. Our work suggests that
357 the dynamics driving niche shifts differ between ranges and that information from closely related
358 species may offer greater insight into likely niche occupancy in the introduced range than assumptions
359 of niche conservatism.

360 Our results highlight how niche shifts can vary dramatically from one range to another. This lack of
361 consistency in niche shifts between ranges suggests that one cannot easily extrapolate the likelihood of
362 a climatic niche shift from one range to another range and that whether species conserve their niche
363 depends on both the species and the range considered. Work on *Ulex europaeus* (Christina et al., 2019),
364 similarly found inconsistency in niche shifts across introduced ranges. This limits the utility of
365 approaches that classify species as either undergoing niche shifts or conserving their niche (Atwater et
366 al., 2018; Bates & Bertelsmeier, 2021; Early & Sax, 2014; Liu et al., 2020; Petitpierre et al., 2012) or
367 which consider all geographically distinct introduced ranges together, as this may obscure differences
368 between ranges and lead to ambiguous results (e.g. Guo et al., 2013). To determine how common
369 inconsistent niche shifts are across regions and taxa further studies must standardise the environmental
370 space between multiple introduced ranges as suggested by Liu et al. (2020). However, as more ranges or
371 species are included in the standardised environmental space the environmental space is likely to
372 become less representative for any one range or species. As such, these methods would be unsuitable
373 for simultaneously comparing large numbers of taxa as other studies have done (Atwater & Barney,
374 2021; Atwater et al., 2018; Early & Sax, 2014; Liu et al., 2020; Petitpierre et al., 2012)

375 In both North America and New Zealand, niche pioneering into non-analogue climates was a large
376 contributor to overall niche shifts (Figure 4), consistent with other studies (Atwater et al., 2018; D'Amen
377 & Azzurro, 2020; Pili et al., 2020; Webber et al., 2012). Ignoring non-analogue space, as some authors
378 have (e.g. Kolanowska & Konowalik, 2014; Liu et al., 2020; Petitpierre et al., 2012), is likely to produce
379 environmental niche models that under-predict species distributions. Given the aim of quantifying niche
380 conservatism is to estimate the validity of transferring environmental niche models (Guisan et al., 2012;
381 Liu et al., 2020; Petitpierre et al., 2012), information on non-analogue niche dynamics should be
382 included to prevent the under-prediction of species distributions (Atwater et al., 2018; Webber et al.,

383 2012). Furthermore, while Liu et al. (2020) concluded that the extinction risk of introduced terrestrial
384 plants may be higher than other taxa as they experience lower niche expansion, we demonstrate that
385 accounting for non-analogue climates indicates *Rumex* spp. can tolerate warmer, cooler, wetter, or drier
386 climates than those found in the native range (Figure 4). This not only reduces the risk of extinction, but
387 also increases the risk that invasive species will persist and spread.

388 Given that our results show *Rumex* spp. experienced dramatic climatic niche shifts in some ranges whilst
389 conserving their niche in others, it begs the question what is driving these niche shifts. If *Rumex* spp. are
390 pre-adapted to all of the climates they occupy in each range we would expect those climates to be
391 occupied in every range. Alternatively, it is possible that *Rumex* spp. have rapidly adapted to tolerate
392 the climates available in both North America and New Zealand (Bates & Bertelsmeier, 2021; Boheemen
393 et al., 2019; Clements & Jones, 2021; Hulme & Barrett, 2013; Luo et al., 2019), though *Rumex* spp.
394 conserved their niche in Australia. Given that some unoccupied climates in Australia are occupied in
395 North America, it is possible that a genetic bottleneck in Australia reduced the species' adaptative
396 capacity. Alternatively, factors other than climate may limit or facilitate *Rumex* spp. distributions in their
397 introduced ranges. Whilst climate typically determines species' distributions at broad scales (Bello et al.,
398 2013), recent work has highlighted the importance of non-climatic factors, such as human disturbance,
399 in introduced plant species distributions (Essl et al., 2020; Kołodziejek & Patykowski, 2015; Mairal et al.,
400 2021; Pysek et al., 2010; Redpath & Rapson, 2015; Seebens et al., 2018). Biotic interactions can both
401 restrict (Alexander et al., 2018; Bello et al., 2013; William Godsoe et al., 2018) and facilitate (Stephan et
402 al., 2021) changes in niche shifts, but this is less likely to influence *Rumex* species as they do not rely
403 upon pollinators, seed dispersers, or mycorrhiza (Cavers & Harper, 1964; Grime et al., 2007). Although
404 they have escaped specialised herbivores in New Zealand this has not led to fitness differences or
405 increased competitive ability (Costan, 2021). Changes in *Rumex* species' occupied niche space are more
406 likely due to the prevalence of anthropogenic land use (e.g. disturbed roadsides, irrigated land or
407 pasture margins) which can facilitate niche shifts into climates that otherwise would be unsuitable
408 (Dainese et al., 2017; Koide et al., 2017). Understanding whether non-climatic factors or species' traits
409 affect the consistency of climatic niche shifts may help predict whether consistent niche shifts would be
410 observed for different ranges or species.

411 Compared to a recent synthesis by Liu et al. (2020), our values of niche expansion for *Rumex* spp. are
412 larger than average for invasive plants whereas our values for niche unfilling vary more between ranges.
413 *Rumex* species in New Zealand have occupied almost all the available analogue climate space and have
414 experienced a large niche expansion towards warmer, wetter climates. In contrast, *Rumex* spp. in North
415 America have expanded into a wide variety of climates, but their large values of unfilling suggest that

416 they have not reached climatic equilibrium or have been under sampled. *Rumex* spp. are often not
417 recorded officially at the species level, in part due to the difficulty of identifying them (Baskin & Baskin,
418 1978; Cavers & Harper, 1964; Grime et al., 2007; Holm et al., 1977, 1997), creating taxonomic bias
419 (Troudet et al., 2017). Additional occurrence records from introduced ranges would likely increase the
420 magnitude of shifts observed or reduce the incidence of niche unfilling, depending on where the records
421 occurred in climate space, and therefore would not substantially affect our conclusions. Furthermore,
422 niche shifts in climate space observed through ordination based analyses, such as ours, do not always
423 correlate with large geographic range shifts (Atwater & Barney, 2021; Guo et al., 2013; Liu et al., 2020).

424 Our results indicate that qualitative similarities between congeneric species niche shifts can be used to
425 predict whether a species is likely to experience climatic niche shifts when introduced to new ranges.
426 Niche overlap between species within a range was almost always greater than niche overlap between a
427 species' introduced range and its native range. This suggests that environmental niche models (ENMs)
428 predicting species niche shifts would be more accurate if based on congener data rather than assuming
429 niche conservatism. Nevertheless, these ENMs would miss important niche divergence between species
430 after invasions, as we found there was greater overlap between species in the native range than in any
431 introduced range (Table 3). This suggests that while these species occupy similar climates in the native
432 range, either pre-adaptation or rapid adaptations to new environments can cause even similar species
433 to occupy different environments post invasion. Whilst this could be due to differences in intraspecific
434 genetic diversity, it could also reflect differing non-climatic environmental preferences such as in soil
435 nutrient richness, pH, and moisture (Cavers & Harper, 1964; Hill et al., 1999; Lousley & Kent, 1981).
436 These results suggest that pooling data between related species (Smith et al., 2019; but see: Mota-
437 Vargas & Rojas-Soto, 2016) or across introduced ranges is unlikely to completely predict species
438 resulting distributions after a climatic niche shift occurs, but may be more accurate than only including
439 species data from the native range.

440 We examined climatic niche shifts in three congeners across three introduced ranges and demonstrated
441 that not only do the species occupy different niches in the introduced range than in the native range,
442 but that the direction and magnitude of these niche shifts differs between ranges. Though there were
443 qualitative similarities within a range between congeners, the degree of niche overlap was generally
444 moderate or low. This indicates that the processes that drive niche shifts, including pre-adaptation to
445 climates outside the native range, biotic interactions, founder effects or genetic admixture, and rapid
446 evolution are not consistent across invasions even within a species. Understanding which processes are
447 driving these shifts and how they are influenced by their environmental context will improve our ability
448 to predict and manage invasions, including through more accurate modelling of species' expected

449 distributions. In the meantime, data from closely related species may provide some qualitative
450 indications of likely niche shifts, which can be used to guide monitoring efforts, and supplement
451 individual species distribution models.

452

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