Do geographic, climatic, or historical ranges differentiate performance of central vs. peripheral populations?

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ABSTRACT

Aim

The “centre-periphery hypothesis” (CPH) predicts species performance (genetics, physiology, morphology, demography) will decline gradually from the centre towards the periphery of the geographic range. This hypothesis has been subjected to continuous debate since the 1980’s, essentially because empirical studies showed contrasting patterns. Moreover, it has been proposed that species performance might not be higher at the geographic range centre, but rather at the environmental optimum, or at sites presenting greater environmental stability in time. In this paper we reevaluate the CPH by disentangling the effects of geographic, climatic and historical centrality/marginality on the demography of three widely distributed plant species, and genetic diversity of one of them.

Location

Europe and North America

Methods

Based on a species distribution modeling approach, we test whether demographic parameters (vital rates, stochastic population growth rates, density) of three plant species of contrasting life forms, and genetic diversity of one of them, are higher at their geographic range centres, climatic optima, or projected glacial refugia.

Results

While geographic, climatic and historical centre-periphery gradients are often not concordant, overall, none of them explain well the distribution of species’ demographic performance, whereas genetic diversity responds positively only to a historical centrality, related to post-glacial range dynamics.

Main conclusions

73 To our knowledge, this is the first assessment of the response of species performance to
74 three centrality gradients, considering all the components of different species' life
75 cycles and genetic diversity information across continental distributions. Our results
76 support previous studies challenging the idea that geographically, climatically or
77 historically marginal populations always perform worse than central ones. We
78 particularly emphasize the importance of adopting an interdisciplinary approach in
79 order to understand the relative effects of contemporary vs. historical and geographic
80 vs. ecological factors on the distribution of species performance.

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98 INTRODUCTION

99 Ongoing global change raises the need to understand and forecast the responses of the
100 Earth's organisms to climate and land use changes. Disentangling the mechanistic
101 processes and ecological factors that drive species' range limits and ultimately
102 coexistence, speciation and extinction is therefore of central importance (Gaston, 2009;
103 Sexton *et al.*, 2009; Buckley & Kingsolver, 2012). In this context, one of the most
104 invoked biogeographical paradigms explaining the variation in performance across a
105 species range is the "centre-periphery" hypothesis (hereafter CPH), also known as the
106 "abundant-centre" (Sagarin & Gaines, 2002) or the "central-marginal" hypothesis
107 (Eckert *et al.*, 2008). Originally, the CPH focused on species abundance and population
108 genetic structure (Carson, 1959; Soulé, 1973; Hengeveld & Haeck, 1982; Brown, 1984).
109 Indeed, it posits that species abundance declines from the centre towards the edge of the
110 range and that, due to their supposed higher population size, connectivity and gene
111 flow, central populations exhibit higher genetic diversity and lower genetic
112 differentiation (Eckert *et al.*, 2008). Over time, this hypothesis has been generalized to
113 other components of species performance (genetics, physiology, morphology,
114 demography) predicting them to be higher and more constant at central locations
115 (Sexton *et al.*, 2009; Abeli *et al.*, 2014). Although simplistic, the CPH is based upon
116 some sensible premises, and if confirmed, would have important consequences in
117 ecology, evolution and conservation biology (Sagarin *et al.*, 2006). However, numerous
118 empirical studies have cast doubt on its reliability (Sagarin & Gaines, 2002; Eckert *et al.*,
119 2008; Sexton *et al.*, 2009; Abeli *et al.*, 2014), though only a few have been able to
120 test it considering different components of species' life cycles across multiple years, and
121 spanning substantial parts of species' ranges (Purves, 2009; García *et al.*, 2010). Sagarin
122 & Gaines, 2002 found that only 39% of the studies supported the CPH for species

123 abundance, whereas Eckert *et al.*, 2008 showed that 64% supported it for genetic
124 diversity, although pointing out several methodological flaws in the papers reviewed.
125 The main assumption of the CPH is that geographic and environmental spaces are
126 concordant, so that conditions are more favorable and stable at the centre of the species
127 range and become gradually harsher towards the periphery (Brown, 1984). However,
128 this assumption might not always be true, since not all marginal populations are
129 peripherally located and not all peripheral populations are ecologically marginal (Soulé,
130 1973). Although many studies use a geographic framework, by considering ranges of
131 latitude, longitude, or altitude (Angert, 2009; Eckhart *et al.*, 2011; Villellas *et al.*,
132 2013a), and assuming these are good proxies for environmental gradients, many others
133 consider a clear dichotomy between geography and environment by focusing rather on
134 central and marginal habitats, regardless of geographic position (Kawecki, 2008). More
135 recently, three studies compared the response of the performance of different species
136 according to geographic and climatic centre-periphery gradients. While Martínez-Meyer
137 *et al.*, 2013 and Lira-Noriega & Manthey, 2014 found that abundance and genetic
138 diversity decreased from the climatic (but not geographic) centre towards marginal
139 conditions, Gerst *et al.*, 2011 did not find such a clear pattern for different plants' vital
140 rates.
141 Additionally, as environmental conditions and species ranges change over time, a
142 population currently considered to be central from a geographic or environmental point
143 of view might have been marginal in the past, or vice-versa. As argued by Eckert *et al.*,
144 2008 and Lira-Noriega & Manthey, 2014, although they might be correlated,
145 contemporary geography and environment probably do not affect directly species
146 genetic variation. Rather, considering shifts in species distributions driven by
147 environmental changes over time might be more appropriate. In this context, the post-

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3 148 glacial dynamics of species ranges is of particular interest, as refugia (i.e. areas with
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5 149 high stability in environmental suitability over time) might represent hotspots of genetic
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7 150 diversity (Cain, 1944; Carnaval *et al.*, 2009). Moreover, we can expect species
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9 151 demography or traits to differ significantly at the rear and leading edges (older vs.
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11 152 recolonizing populations) (Hampe & Petit, 2005; Moritz *et al.*, 2012). Several
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13 153 influential studies have called for unraveling the importance of this historical dimension
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15 154 from the CPH framework (Hampe & Petit, 2005; Eckert *et al.*, 2008).
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18 155 Here, we shed new light on the CPH by reanalyzing and synthesizing extensive
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20 156 ecological information gathered across large-scale latitudinal transects for three widely
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22 157 distributed species of contrasting biogeographic and life-history characteristics. Using
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24 158 demographic information for the three taxa, genetic diversity for one of them, and a
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26 159 species distribution modeling approach, we test whether demographic performance and
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28 160 genetic diversity decline gradually from the centre towards the periphery of the species'
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30 161 current geographic range (hereafter "geographic centre/periphery"), from the species'
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32 162 climatic optimum towards marginal conditions ("climatic centre/periphery"), or from
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34 163 the species' projected glacial refugium towards more recently colonized areas
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36 164 ("historical centre/periphery"). This study shows that (1) geographic, climatic, and
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38 165 historical centres/peripheries are not necessarily concordant; (2) species' performance is
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40 166 not consistently better (i.e. neither higher nor more stable demographic parameters) in
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42 167 any distribution centre and worse towards any periphery; (3) the temporal dynamics of
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44 168 species ranges, through historical climate changes, might have a stronger effect on the
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46 169 genetic structure of populations than contemporary climate and geography.
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173 MATERIAL AND METHODS

174 Study Species

175 *Plantago coronopus* (Plantaginaceae), also called “Buck’s-Horn Plantain”, naturally
176 spreads from the Mediterranean basin to southern Scandinavian coasts (Hultén & Fries,
177 1986). It is a short-lived plant (annual or perennial) occurring in different habitats such
178 as sand dunes, coastal prairies, or areas disturbed by human activities. Plants have one
179 or a few basal rosettes, and spikes of wind-pollinated flowers.

180 *Polygonum viviparum* (Polygonaceae), also known as “Alpine Bistort”, is a long-lived
181 herb occurring all over the high Arctic region, at all elevations in Scandinavia, and in
182 mountainous areas in the Northern Hemisphere (e.g. Pyrenees, Tibetan Plateau, Rocky
183 mountains). In North America, it is recorded from the mountain belt to the upper alpine
184 level on damp or rocky soil. Individuals reproduce asexually, through bulbils produced
185 on reproductive spikes (Diggle *et al.*, 1998).

186 *Silene acaulis* (Caryophyllaceae), also called “Moss Campion”, is an extremely long-
187 lived cushion plant (Morris & Doak, 1998). It also occurs in the arctic-alpine regions of
188 the Northern Hemisphere. However it is more restricted to mountain summits and rocky
189 soils than *P. viviparum*. Each cushion has a single taproot, and presents insect-
190 pollinated flowers which produce seeds that are dispersed to very short distances.

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192 Study Populations: geographic, demographic, and genetic data

193 We individually monitored hundreds to thousands of plants for several years in each of
194 11 populations of *P. coronopus* in six European regions, from southern Spain to
195 southern Sweden (four years of data from Villellas *et al.*, 2013a, 2014) and 18
196 populations of *P. viviparum* and 19 of *S. acaulis* in five North American regions, from
197 New Mexico to northern Alaska (six years of data from Doak & Morris, 2010, plus five

198 more years from populations in Colorado and Alaska, U.S.A., plus four years from two
199 new populations of each species in New Mexico, U.S.A.) (see Fig.1, Table S1, Fig.S1 in
200 Supporting Information). Although the monitored populations encompass a large part of
201 the climatic variability across most of the species' continental ranges, we note that
202 sampling them evenly over their entire global distributions/climatic niches was not
203 feasible for this study.

204 To assess the CPH through demographic performance, we use the mean annual vital
205 rates (survival, growth, fecundity, and recruitment) of each population. Since vital rates
206 were obtained for different size classes, we restrict our analysis to those of small plants
207 for *P. coronopus* and large plants for *P. viviparum* and *S. acaulis* which, according to
208 Doak & Morris, 2010 and Villellas *et al.*, 2013b, have the strongest impact on the
209 stochastic population growth rates (highest elasticities). Survival represents the
210 proportion of plants that remains alive from one year to the next. Growth is the
211 proportional change in square-root plant leaf area from one year to the next for *P.*
212 *viviparum*, whereas, for *S. acaulis* and *P. coronopus*, it is the proportion of plants
213 advancing from one size class to the next larger one, over one year. Fecundity is the
214 number of seeds produced per reproductive plant for each size class for *P. coronopus*,
215 the number of bulbils per square-root leaf area for *P. viviparum*, and the number of
216 fruits per cm² of cushion area for *S. acaulis*. For *P. viviparum* and *S. acaulis*, we only
217 consider fecundity of the largest individuals, as propagule production of the small plants
218 is negligible (Doak & Morris, 2010). Recruitment of *P. coronopus* and *P. viviparum*
219 corresponds respectively, to the number of new seedlings or "bulblings" in a given year
220 divided by the number of seeds or bulbils dispersed the previous year in the sampling
221 area. *S. acaulis* recruitment is an estimate of the average fraction of seeds that emerged
222 as seedlings after having spent one winter in the soil (see Doak & Morris, 2010 for

223 details). We also estimated the inter-annual variability of all these vital rates except for
224 *S. acaulis* recruitment for which our estimation method provided only a single mean
225 value. For rates that represent probabilities (e.g. survival), we calculated inter-annual
226 variability as the standard deviation divided by the maximum possible standard
227 deviation given the mean (Morris & Doak, 2004). For all continuous rates (e.g.
228 fecundity), inter-annual variability is calculated as the coefficient of variation. For each
229 population of each species, plant density was also estimated.
230 Based on matrix projection models (Caswell, 2001), stochastic population growth rates
231 (λ_S) were computed, accounting for temporal variability and correlations in vital rates
232 (see Doak & Morris, 2010; Villellas *et al.*, 2013b). For *P. viviparum* and *S. acaulis*, λ_S
233 was calculated using only vital rates measured between 2001 and 2006.
234 In 10 of the 11 populations of *P. coronopus*, genetic diversity (H_D) was also calculated
235 and averaged for 461 polymorphic bands, using Amplified Fragment Length
236 Polymorphism (AFLP) (see Villellas *et al.*, 2014 for methodological details). To
237 increase sample size, we also used, in parallel analysis, genetic diversity information for
238 eight additional populations whose demography has not been monitored (from Villellas
239 *et al.*, 2014).

241 **Species distribution modeling**

242 To arrive at non-arbitrary classifications of species' ranges limits, we modeled the
243 distributions of the three species by coupling occurrence data extracted from the Global
244 Biodiversity Information Facility (GBIF, <http://data.gbif.org/welcome.htm>) and the
245 Anthos database (<http://www.anthos.es/>) with different sets of bioclimatic variables
246 from the Worldclim database (Hijmans *et al.*, 2005). For the Euro-Mediterranean
247 species (*P. coronopus*), we used annual mean temperature, temperature seasonality,

mean temperature of the wettest quarter, precipitation of the wettest month, and precipitation seasonality. For the two species studied in North America (*P. viviparum* and *S. acaulis*), we used temperature seasonality, maximum temperature of the warmest month, precipitation of the wettest month, and precipitation seasonality. We employed climatic and occurrence data at a resolution of 10 arc-minutes (~20 km). As the accuracy of species distribution models can vary depending on their type and the quality of the input data (Elith & Leathwick, 2009), we modeled species distributions using five different modeling techniques implemented in the BIOMOD package in R (Thuiller *et al.*, 2009; R Development Core Team, 2010). Finally, we evaluated each model's predictive accuracy using a repeated split sampling approach, with two different metrics: the True Skill Statistics (TSS, Allouche *et al.*, 2006) and the area under the Receiver Operating Characteristic curve (ROC, Hanley & McNeil, 1982). In total, for each species, we ran 1,000 models by using five different statistical models, 10 repeated selections of pseudo-absences, two evaluation metrics, and 10 repetitions of the random-splitting strategy.

We projected these species distributions at the current time, as well as at the Last Glacial Maximum (LGM; ~ 21,000 years ago), which allows identifying species refuges. Climatic conditions at the LGM were projected by the Palaeoclimate Modelling Intercomparison Project (Braconnot *et al.*, 2007), and provided by Worldclim. To account for variability in the LGM climate projections in our species distribution modeling, we used two different global circulation models outputs: MIROC3.2 and CCSM. Based on Marmion *et al.*, 2009, we computed a mean of the different ensembles of projections weighed by their respective model predictive accuracy. As LGM climate conditions over part of the North American ice sheet might have been suitable for the two boreoalpine species, we lowered their probabilities of presence to zero at the ice

273 sheet location, according to the 10-minutes resolution map provided by Peltier, 2004.
274 We also transformed the resulting current distributions maps (probabilities of species
275 presence) into a binary format (species presence/absence) applying a threshold that
276 optimizes the TSS score.
277 More details about our species distribution modeling procedure are given in the
278 Appendix S1.

280 **Statistical Analyses**

281 The geographic centre corresponds to the centre of the current continental range of the
282 species. The climatic centre is calculated from the climatic space defined by the
283 different climatic variables used to model species distributions (see above). Finally, the
284 historical centre is also a geographic centre but projected at the LGM. For the
285 geographic and historical centres, we projected each pixel of our study area in a space
286 represented by the two variables: latitude and longitude. We weighed each of these
287 pixels' values by either the current probability of presence of the species at this pixel, or
288 its presence probability at the LGM. Finally, we calculated the Euclidean distance to the
289 centre of each scatter plot to obtain distances to, respectively, the geographic and
290 historical centres. For the climatic centre, we used the same technique but projecting
291 each pixel in climatic spaces defined by the climatic variables collected for each
292 species. We also weighed them by their current probabilities of presence of the species,
293 and calculated their Euclidean distance to the scatter plots centres. For projecting each
294 pixel's values in the different spaces, we performed Principal Components Analysis
295 (PCA) with mean-centered data. Although using probabilities of presence obtained from
296 species distribution models to compute both climatic and geographical distances might
297 induce a slight circularity, we consider the effect of this procedure to be negligible as

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3 298 climatic and geographical spaces are clearly different. Using an independent map (e.g.
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5 299 from Hultén & Fries, 1986) or a different technique (e.g. minimum convex polygon,
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7 300 such as in Gerst *et al.*, 2011) could be alternatives to identify geographical centres
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9 301 independently, however, they would provide poorer estimates of the three species'
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11 302 current distributions.

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14 303 Additionally, as we wanted to test for the effects of single variables, and not only
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16 304 combinations of variables, we also decomposed our three definitions of centre/periphery
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18 305 into different sub-levels (i.e. distances to the mean latitude, mean longitude, range edge,
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20 306 mean of each bioclimatic variable) (more details in Appendix S2).

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23 307 For each species, we therefore extracted the different distance-to-centre values at the
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25 308 locations of the different monitored populations and standardized them (Table S2). We
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27 309 then used simple linear regressions to examine the relationships between response
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29 310 variables (demographic rates, genetic diversity) and explanatory variables (distances to
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31 311 the different centres). When the homoscedasticity assumption was not fulfilled, we
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33 312 applied a Box-Cox transformation to the response variable by using the *BoxCox*
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35 313 function of the *car* package in R (R Development Core Team, 2010).

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38 314 For examining the dynamics of the species ranges from the past 21,000 years, we also
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40 315 subtracted the LGM probabilities of occurrence of the species from the current ones.
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42 316 We obtained therefore a map representing how much the environmental suitability for
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44 317 each species has potentially changed since the LGM. This analysis was repeated for the
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46 318 two past climate scenarios (MIROC, CCSM). We finally compared the different genetic
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48 319 and demographic characteristics of the current populations that were predicted to be
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50 320 present at the LGM (refugial populations) and the ones predicted to be absent
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52 321 (recolonizing populations), using Wilcoxon's two-sample test. Although this
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54 322 comparison is limited by the relatively low number of populations considered in each
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323 category, it allows a better representation of the effect of species range temporal
324 dynamics than the distance to the past centroid, which is a static image of the species
325 past distribution.
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RESULTS

Species distribution modeling

Our species distribution models performed fairly well according to criteria from Swets, 1988 and Thuiller *et al.*, 2009 (mean ROC and TSS scores: 0.977 ± 0.048 and 0.876 ± 0.102 , respectively, for *P. coronopus*; 0.788 ± 0.081 and 0.462 ± 0.131 for *P. viviparum*; and 0.794 ± 0.077 and 0.468 ± 0.122 for *S. acaulis*). According to the binary maps obtained, our models correctly predicted the current occurrences of all the monitored populations of the three species. Moreover, the projected distributions match quite well the ones given by Hultén & Fries, 1986. For *P. coronopus*, the predicted distribution even seems to improve the distribution estimate given by the 27-year-old map of Hultén & Fries, 1986, as it shows the recent expansion of the species into new areas of northern Europe (GBIF, <http://data.gbif.org/welcome.htm>).

Geographic centre/periphery

Regarding the estimated current geographic distribution of *P. coronopus*, the French population is considered as the most central, whereas the Scottish and Swedish ones are considered the most peripheral (Fig.1, Table S2). For *P. viviparum* and *S. acaulis*, the Canadian populations are considered the most central, whereas the ones from northern Alaska and New Mexico are considered the most peripheral (Fig.1, Fig.S2, Table S2). We observed very few significant relationships between the different genetic and/or demographic characteristics of the three species and the distances of their populations to the geographic centre (Table1). In contrast to the predictions of the CPH, at the geographic periphery, *P. coronopus* showed a significantly higher recruitment, *P. viviparum* had a significantly higher fecundity, and *S. acaulis* showed significantly higher λ_s , fecundity and growth of large plants. Other significant relationships were

373 observed when looking at distances to latitudinal and longitudinal centres individually,
374 or distances to the range edge, but no clear pattern emerged across species (Table S3).

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376 **Climatic centre/periphery**

377 Climatic conditions encountered at the two Danish populations' sites are considered
378 central for *P. coronopus* (Fig.1, Table S2). Wetter conditions occurring at the western
379 Scottish population's site represent marginal conditions for this species. The climate of
380 south-central Alaska represents central conditions for *P. viviparum* and *S. acaulis*,
381 whereas the higher temperatures of Colorado and New Mexico are considered as
382 marginal conditions for the two species (Fig.1, Fig.S2, Table S2).

383 Again, we found very few significant relationships between the species genetic and
384 demographic characteristics and the distances to their climatic niche centres (Table1).
385 For *P. coronopus*, the inter-annual variability in survival of small plants was found to be
386 higher at its climatic centre. For *P. viviparum*, growth of large plants was observed to be
387 significantly higher at the climatic margin. Finally, *S. acaulis* recruitment was observed
388 to be higher at the climatic centre, whereas its fecundity was found to be higher at
389 marginal conditions. We found other significant relationships when looking at each
390 climatic variable individually, but we did not encounter any clear pattern across species
391 (Table S3).

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393 **Historical centre/periphery**

394 Regarding the projected distribution of the three species at the Last Glacial Maximum,
395 southern-most populations are always considered as the most central (i.e. older refugial
396 populations at the current rear edge), whereas the northernmost ones are considered the

most peripheral (i.e. younger recolonizing populations at the current leading edge) (Fig.1, Fig.S2-S3, Table S2).

Again, overall, demographic characteristics of all species do not seem to be consistently related to distances to historical centres (Table1). We observed a significantly higher recruitment and population density at the *P. coronopus* historical margin, whereas the fecundity was found to be higher at the centre. Genetic diversity was also significantly higher at the historical centre, both when using 10 and 18 populations (Table S3). For *P. viviparum*, the fecundity and the inter-annual variability of large plant survival were found to be significantly higher at the historical periphery. Finally, *S. acaulis* λ_S was found to be higher at the historical margin, and its variability in fecundity was observed to be higher at the centre. Overall, these results were independent of which of the two past climate scenarios we used (Table S3). We found other significant relationships when focusing on the particular effects of latitude and longitude individually or the distance to the range edge, but no clear pattern emerged across species (Table S3).

When examining the temporal dynamics of species ranges, we observed that some of our monitored populations were projected to be absent at the LGM (Fig.2, Figs S4-S5-S6). For *P. coronopus*, according to the MIROC and CCSM scenarios, respectively, the six and five northern-most populations were found to be absent at the LGM, the French population being considered stable over time only by the MIROC scenario. For *P. viviparum* and *S. acaulis*, respectively, the twelve and thirteen northern-most populations were predicted to be located within the ice sheet at the LGM.

We found no consistent pattern among species between refugial and recolonizing populations. According to both scenarios (i.e. MIROC and CCSM), for *P. coronopus*, genetic diversity (considering 10 or 18 populations (Table S3)) and fecundity of refugial populations were found to be higher than of recolonizing ones ($P < 0.05$). For *P.*

422 *viviparum*, growth ($P < 0.01$), and its inter-annual variability ($P < 0.05$) were observed
423 to be higher in stable areas, whereas recruitment ($P < 0.05$) was higher in unstable ones.
424 For *S. acaulis*, fecundity ($P < 0.01$) was found to be higher in refugial populations,
425 whereas recruitment ($P < 0.001$) is higher in recolonizing ones. All the other
426 demographic characteristics of the three species (9 out of 11 for *P. coronopus*, 7 out of
427 10 for *P. viviparum*, 7 out of 9 for *S. acaulis*) did not present significant differences
428 among populations located in persistent and newly colonized areas.

DISCUSSION

“[The Universe] is an infinite sphere, the centre of which is everywhere, the circumference nowhere” (Pascal, 1669)

The multi-dimensionality of the notions of centre and periphery has been pointed out as early as the seventeenth-century (Pascal, 1669) and discussed later in the context of ecology and evolution (Cain, 1944; Soulé, 1973). Introducing the CPH, Brown, 1984 explicitly assumed a high correlation between geographical centrality/marginality and environmental conditions. Although they can be closely associated, their relationship is not perfect and a few recent studies showed that demographic performance and genetic diversity were not responding the same way to geographic and climatic centre-periphery patterns (Gerst *et al.*, 2011; Martínez-Meyer *et al.*, 2013; Lira-Noriega & Manthey, 2014). Our results agree with these previous observations as only fecundity of *Silene acaulis* was found to respond negatively to both geographic and climatic central-marginal gradients (Table 1). Moreover, environment itself is in fact composed of different aspects (abiotic, biotic), as is geography (latitude, longitude, altitude), which are obviously not all perfectly concordant with each other.

Another common assumption is that current geographic trends follow the directions of glacial/post-glacial species range shifts (especially in temperate areas), but relatively few studies unraveled the relative effects of contemporary and historical range position on species performance. For instance, Hoban *et al.*, 2010 showed that the genetic structure of the North American butternut was not explained by a contemporary centre-periphery pattern, nor by recent population losses, but rather by its postglacial recolonization history. Our demographic results showed more concordance with the geographic and historical centrality patterns than with the climatic one (Table 1). As our “geographic” and “historical” distances are both computed in the same geographic

space, they might be obviously more correlated. However, as for Hoban *et al.*, 2010, our approach still allowed highlighting different responses of species' features (e.g. *P. coronopus*' genetic diversity) to contemporary and historical factors. These dichotomies between geographic vs. ecological, and contemporary vs. historical gradients therefore highlight the importance of avoiding simplistic assumptions, and call for more interdisciplinary research (e.g. molecular ecology, population biology, biogeography) to better understand the distribution of species performance and the relative importance of the different factors shaping range boundaries.

480

481 **Plant demography along the three centre-periphery gradients**

None of our three study species present consistently higher vital rates or population density at any centre (geographic, climatic, or historical) (Table 1). One of the key vital rates, survival, never follows a trend in relation to any of the centre/periphery gradients. Fecundity and recruitment are the most frequent vital rates showing some relation with the different measures of centrality/peripherality in the two species dependent on sexual reproduction (*P. coronopus* and *S. acaulis*), but results are not consistent across these measures. Moreover, no pattern emerges across biogeographical or longevity groups (the mediterranean short-lived *P. coronopus* vs. the boreoalpine long-lived *P. viviparum* and *S. acaulis*). Our results do not show a lower inter-annual variability of vital rates at any centre either. Species demographic performance is therefore neither higher, nor more stable at the geographic range centre, the inferred climatic optimum, or the glacial refugium. This conclusion is consistent with the few other analyses considering geographical centrality/marginality and empirical demographic data collected for different components of the species life cycle across continental distributions (Purves, 2009; García *et al.*, 2010). Moreover, the fact that every vital rate can present either a

positive, negative, or neutral response to any centre-periphery pattern explains well the inconsistency of the results obtained by other studies considering only part of the species life history or geographic range (Sexton *et al.*, 2009; Gerst *et al.*, 2011; Abeli *et al.*, 2014).

In spite of its intuitiveness, the theoretical basis of the CPH oversimplifies the reality of spatial demographic variation by assuming that all components of population performance are higher at one geographic or environmental centre. Should that be true, species ranges would be continuously retracting towards this centre (Channell & Lomolino, 2000). Demographic compensation between the different vital rates across the whole species' geographic and environmental ranges is a reasonable alternative to this hypothesis (Doak & Morris, 2010; Villellas *et al.*, 2013b). Indeed, different demographic rates might change in opposite directions over the species' ranges, the highest ones compensating for the lowest ones and resulting in stable population growth rates, as a way to buffer populations against extreme environmental conditions. Consequently, species performance would not decrease gradually from one centre towards one periphery but rather dramatically once an environmental tipping point is exceeded (e.g. abrupt changes in climate, land use, and/or biotic interactions) (Doak & Morris, 2010).

Plant genetic diversity along the three centre-periphery gradients

Our results show a higher genetic diversity of *P. coronopus* in persistent populations (i.e. unglaciated sites that remained climatically suitable at the LGM) than in younger recolonizing populations (i.e. unsuitable, most probably glaciated sites at the LGM). These results follow the commonly accepted genetic models that predict a higher genetic diversity in glacial refugia (Eidesen *et al.*, 2013; Griffin & Willi, 2014, but see

Petit *et al.*, 2003). Coupled to previous work, our study suggests therefore that postglacial range dynamics is the clearest determinant of the large-scale distribution of genetic diversity, over contemporary ecological and geographic marginality (Hoban *et al.*, 2010; Eidesen *et al.*, 2013). For *S. acaulis* and *P. viviparum*, we would therefore expect a higher genetic diversity in southern populations, declining towards areas glaciated at the LGM (Fig.2), but the latter deviates from this prediction due most probably to its asexual mode of reproduction (Diggle *et al.*, 1998; Marr *et al.*, 2013). The presence of nunataks within the ice sheet at the LGM could also potentially act as refugia for boreoalpine plants and therefore alter this prediction.

The lack of relationship between *P. coronopus*' genetic diversity and the distances to its geographic centre and climatic optimum is surprising according to the general patterns found by previous studies (Eckert *et al.*, 2008; Lira-Noriega & Manthey, 2014). Indeed, Eckert *et al.*, 2008 found that genetic diversity was often correlated positively with the distance from the range centre. However, these authors pointed out numerous conceptual and methodological issues in the supporting studies, and recommended the use of a historical approach. As mentioned previously, current geography (e.g. latitude) often follows the directions of post-glacial range dynamics, which might ultimately confound the historical effects with the contemporary ones and explain the results from Eckert *et al.*, 2008. Besides, Lira-Noriega & Manthey, 2014 did not find a strong geographic pattern but rather a better correlation with the distance from the species' climatic optima. However, the authors argue that the historical dynamics of species ranges might have a more direct effect on genetic diversity than current geography and climate. It would therefore be interesting to test this hypothesis with such an extensive dataset as Lira-Noriega & Manthey's using the historical approach proposed in this study.

547

548 **Conclusion**

549 Our study is the first assessment of the CPH based on empirical genetic and
550 demographic data collected across different life stages and whole continental
551 distributions of species of contrasted life histories, comparing the geographic, climatic
552 and historical concepts of centrality. Our findings challenge the main basis of this
553 hypothesis, which assumes that ecological and/or historical processes systematically
554 follow geographic patterns. Moreover, they support previous observations reporting that
555 species ranges do not systematically contract from their periphery to their centre
556 (Channell & Lomolino, 2000), and call for further evaluation of the relative effects of
557 spatial, temporal and environmental (abiotic and biotic) factors on the distribution of
558 species performance. Understanding what drives species to local extinction/expansion
559 and how these factors shape their range limits would ultimately help to improve
560 forecasts of distributional change, as well as to prioritize global conservation efforts,
561 without discarding *a priori* geographically, ecologically, or historically central or
562 peripheral populations.

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597 REFERENCES

- 598 Abeli, T., Gentili, R., Mondoni, A., Orsenigo, S. & Rossi, G. (2014) Effects of
599 marginality on plant population performance. *Journal of Biogeography*, **41**,
600 239–249.
- 601 Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species
602 distribution models: prevalence, kappa and the true skill statistic (TSS).
603 *Journal of Applied Ecology*, **43**, 1223–1232.
- 604 Angert, A.L. (2009) Colloquium Papers: The niche, limits to species' distributions,
605 and spatiotemporal variation in demography across the elevation ranges of
606 two monkeyflowers. *Proceedings of the National Academy of Sciences*, **106**,
607 19693–19698.
- 608 Braconnot, P., Otto-Bliesner, B., Harrison, S., Joussaume, S., Peterchmitt, J.-Y., Abe-
609 Ouchi, A., Crucifix, M., Driesschaert, E., Fichefet, T., Hewitt, C.D., Kageyama,
610 M., Kitoh, A., Laîné, A., Loutre, M.-F., Marti, O., Merkel, U., Ramstein, G.,
611 Valdes, P., Weber, S.L., Yu, Y. & Zhao, Y. (2007) Results of PMIP2 coupled
612 simulations of the Mid-Holocene and Last Glacial Maximum – Part 1:
613 experiments and large-scale features. *Clim. Past*, **3**, 261–277.
- 614 Brown, J.H. (1984) On the relationship between abundance and distribution of
615 species. *The American Naturalist*, **124**, 255–279.
- 616 Buckley, L.B. & Kingsolver, J.G. (2012) Functional and Phylogenetic Approaches to
617 Forecasting Species' Responses to Climate Change. *Annual Review of*
618 *Ecology, Evolution, and Systematics*, **43**, 205–226.
- 619 Cain, S.A. (1944) *Foundations of plant geography*, Harper & Brothers, New York and
620 London.
- 621 Carnaval, A.C., Hickerson, M.J., Haddad, C.F.B., Rodrigues, M.T. & Moritz, C. (2009)
622 Stability Predicts Genetic Diversity in the Brazilian Atlantic Forest Hotspot.
623 *Science*, **323**, 785–789.
- 624 Carson, H.L. (1959) Genetic Conditions Which Promote or Retard the Formation of
625 Species. *Cold Spring Harbor Symposia on Quantitative Biology*, **24**, 87–105.
- 626 Caswell, H. (2001) *Matrix population models: construction, analysis, and*
627 *interpretation*, Sinauer Associates.
- 628 Channell, R. & Lomolino, M.V. (2000) Dynamic biogeography and conservation of
629 endangered species. *Nature*, **403**, 84–86.
- 630 Diggle, P.K., Lower, S. & Ranker, T.A. (1998) Clonal diversity in alpine populations
631 of *Polygonum viviparum* (Polygonaceae). *International Journal Of Plant*
632 *Sciences*, **159**, 606–615.
- 633 Doak, D.F. & Morris, W.F. (2010) Demographic compensation and tipping points in
634 climate-induced range shifts. *Nature*, **467**, 959–962.
- 635 Eckert, C.G., Samis, K.E. & Loughheed, S.C. (2008) Genetic variation across species'
636 geographical ranges: the central-marginal hypothesis and beyond.
637 *Molecular Ecology*, **17**, 1170–1188.
- 638 Eckhart, V.M., Geber, M.A., Morris, W.F., Fabio, E.S., Tiffin, P. & Moeller, D.A. (2011)
639 The Geography of Demography: Long-Term Demographic Studies and
640 Species Distribution Models Reveal a Species Border Limited by Adaptation.
641 *The American Naturalist*, **178**, S26–S43.
- 642 Eidesen, P.B., Ehrich, D., Bakkestuen, V., Alsos, I.G., Gilg, O., Taberlet, P. &
643 Brochmann, C. (2013) Genetic roadmap of the Arctic: plant dispersal
644 highways, traffic barriers and capitals of diversity. *New Phytologist*, **200**,

898–910.

Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology Evolution and Systematics*, **40**, 677–697.

García, M.B., Goñi, D. & Guzmán, D. (2010) Living at the Edge: Local versus Positional Factors in the Long-Term Population Dynamics of an Endangered Orchid. *Conservation Biology*, **24**, 1219–1229.

Gaston, K. (2009) Geographic range limits of species. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1391–1393.

Gerst, K.L., Angert, A.L. & Venable, D.L. (2011) The effect of geographic range position on demographic variability in annual plants. *Journal of Ecology*, **99**, 591–599.

Griffin, P.C. & Willi, Y. (2014) Evolutionary shifts to self-fertilisation restricted to geographic range margins in North American *Arabidopsis lyrata*. *Ecology Letters*, **17**, 484–490.

Hampe, A. & Petit, R.J. (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.

Hanley, J.A. & McNeil, B.J. (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, **143**, 29–36.

Hengeveld, R. & Haack, J. (1982) The Distribution of Abundance. I. Measurements. *Journal of Biogeography*, **9**, 303.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hoban, S.M., Borkowski, D.S., Brosi, S.L., McCleary, T.S., Thompson, L.M., McLachlan, J.S., Pereira, M.A., Schlarbaum, S.E. & Romero-Severson, J. (2010) Range-wide distribution of genetic diversity in the North American tree *Juglans cinerea*: a product of range shifts, not ecological marginality or recent population decline. *Molecular Ecology*, **19**, 4876–4891.

Hultén, E. & Fries, M. (1986) *Atlas of North European vascular plants (North of the Tropic of Cancer)*, Vols. I–III.

Kawecki, T.J. (2008) Adaptation to Marginal Habitats. *Annual Review of Ecology Evolution and Systematics*, **39**, 321–342.

Lira-Noriega, A. & Manthey, J.D. (2014) Relationship of Genetic Diversity and Niche Centrality: A Survey and Analysis. *Evolution*, **68**, 1082–1093.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. & Thuiller, W. (2009) Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*, **15**, 59–69.

Marr, K.L., Allen, G.A., Hebda, R.J. & McCormick, L.J. (2013) Phylogeographical patterns in the widespread arctic-alpine plant *Bistorta vivipara* (Polygonaceae) with emphasis on western North America. *Journal of Biogeography*, **40**, 847–856.

Martínez-Meyer, E., Díaz-Porras, D., Peterson, A.T. & Yáñez-Arenas, C. (2013) Ecological niche structure and rangewide abundance patterns of species. *Biology Letters*, **9**.

Moritz, C., Langham, G., Kearney, M., Krockenberger, A., VanDerWal, J. & Williams, S. (2012) Integrating phylogeography and physiology reveals divergence of thermal traits between central and peripheral lineages of tropical rainforest lizards. *Philosophical Transactions of the Royal Society B: Biological Sciences*,

- 694 **367**, 1680–1687.
- 695 Morris, W.F. & Doak, D.F. (2004) Buffering of Life Histories against Environmental
696 Stochasticity: Accounting for a Spurious Correlation between the
697 Variabilities of Vital Rates and Their Contributions to Fitness. *The American*
698 *Naturalist*, **163**, 579–590.
- 699 Morris, W.F. & Doak, D.F. (1998) Life history of the long-lived gynodioecious
700 cushion plant *Silene acaulis* (Caryophyllaceae), inferred from size-based
701 population projection matrices. *American Journal of Botany*, **85**, 784–793.
- 702 Pascal, B. (1669) *Pensées de M. Pascal sur la religion, et sur quelques autres sujets,*
703 *qui ont esté trouvées après sa mort parmy ses papiers [publiées avec une*
704 *préface par Étienne Perier]*, G. Desprez (Paris).
- 705 Peltier, W.R. (2004) Global glacial isostasy and the surface of the Ice-Age Earth:
706 The ICE-5G (VM2) Model and GRACE. *Annual Review of Earth and Planetary*
707 *Sciences*, **32**, 111–149.
- 708 Petit, R.J., Aguinagalde, I., Beaulieu, J.-L., Bittkau, C., Brewer, B., Cheddadi, R., Ennos,
709 R., Fineschi, S., Grivet, D., Lascoux, M., Mohanty, A., Muller-Starck, G.,
710 Demesure-Musch, B., Palme, A., Martin, J.P., Rendell, S. & Vendramin, G.G.
711 (2003) Glacial refugia: hotspots but not melting pots of genetic diversity.
712 *Nature*, **300**, 1563–1565.
- 713 Purves, D.W. (2009) The demography of range boundaries versus range cores in
714 eastern US tree species. *Proceedings of the Royal Society B-Biological*
715 *Sciences*, **276**, 1477–1484.
- 716 R Development Core Team (2010) *R: A Language and Environment for Statistical*
717 *Computing*, R Foundation for Statistical Computing, Vienna, Austria.
718 Available online at <http://www.R-project.org>, Vienna, Austria.
- 719 Sagarin, R.D. & Gaines, S.D. (2002) The “abundant centre” distribution: to what
720 extent is it a biogeographical rule? *Ecology Letters*, **5**, 137–147.
- 721 Sagarin, R.D., Gaines, S.D. & Gaylord, B. (2006) Moving beyond assumptions to
722 understand abundance distributions across the ranges of species. *Trends in*
723 *Ecology & Evolution*, **21**, 524–530.
- 724 Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009) Evolution and ecology of
725 species range limits. *Annual Review of Ecology, Evolution, and Systematics*,
726 **40**, 415–436.
- 727 Soulé, M. (1973) The epistasis cycle: a theory of marginal populations. *Annual*
728 *Review of Ecology and Systematics*.
- 729 Swets, J.A. (1988) Measuring the accuracy of diagnostic systems. *Science*, **240**,
730 1285–1293.
- 731 Thuiller, W., Lafourcade, B., Engler, R. & Araujo, M.B. (2009) BIOMOD – A platform
732 for ensemble forecasting of species distributions. *Ecography*, **32**, 369–373.
- 733 Villellas, J., Berjano, R., Terrab, A. & García, M.B. (2014) Divergence between
734 phenotypic and genetic variation within populations of a common herb
735 across Europe. *Ecosphere*, **5**, art56.
- 736 Villellas, J., Ehrlén, J., Olesen, J.M., Braza, R. & García, M.B. (2013a) Plant
737 performance in central and northern peripheral populations of the
738 widespread *Plantago coronopus*. *Ecography*, **36**, 136–145.
- 739 Villellas, J., Morris, W.F. & García, M.B. (2013b) Variation in stochastic demography
740 between and within central and peripheral regions in a widespread short-
741 lived herb. *Ecology*, **94**, 1378–1388.
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743 Additional references about the methods used in this study are found at the end of
744 Appendix S1 at {URL}.
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For Peer Review

BIOSKETCH

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770 Samuel Pironon is currently a PhD candidate at the Pyrenean Institute of Ecology
771 (CSIC) in Zaragoza, Spain. His research aims to investigate the spatial, environmental
772 and historical determinants of species range limits, focusing especially on the spatial
773 structure of species demographic performance.

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793 **FIGURE CAPTIONS**

794

795 **Figure 1.** Distances from all parts of the current ranges of *Plantago coronopus* and
796 *Silene acaulis* to the three different range centres considered. Maps of *Polygonum*
797 *viviparum* are omitted here for clarity as they look very similar to those for *S. acaulis*
798 (shown in Fig.S2). The geographic centre is the centroid of the current distribution of
799 the species. The climatic centre is the centroid of the climatic niche of the species,
800 inferred from species distribution models. The historical centre is the centroid of the
801 distribution of the species projected at the Last Glacial Maximum, according to the
802 MIROC scenario. Regions in red are considered central, whereas regions in blue are
803 considered peripheral. Regions in grey represent currently unsuitable areas. Green dots
804 represent regions where we monitored populations. One dot might indicate multiple
805 nearby populations. All populations' coordinates are given in Table S1 and presented in
806 Fig.S1.

807

808 **Figure 2.** Changes in environmental suitability for *Plantago coronopus* and *Silene*
809 *acaulis* between the Last Glacial Maximum (LGM) and the current time. Values were
810 obtained by subtracting the projected probabilities of occurrence of the species at the
811 LGM (MIROC scenario) from the ones at the present time. Regions in red represent
812 areas of high stability in environmental suitability over time, whereas regions in blue
813 represent areas of low stability. Green dots represent monitored populations projected to
814 be present both in the past and the current climatic conditions. Orange dots represent
815 monitored populations projected to be currently present, and absent at the LGM.
816 According to the CCSM scenario, the French population of *P. coronopus* is projected to

be absent at the LGM (Fig.S6), whereas both scenarios agree on the other populations.

Maps of *Polygonum viviparum* are given in Fig.S5.

TABLE CAPTION

Table 1. Linear regression statistics for relationships between the distances to the three different centres (geographic, climatic, and historical (MIROC scenario)) and the genetic and demographic characteristics of the three species. Adjusted R-squared are shown. Asterisks represent significant relationships ($***P \leq 0.001$, $**P \leq 0.01$, $*P \leq 0.05$). Red and bold values highlight significant relationships consistent with the Centre-Periphery Hypothesis (CPH), i.e. negative relationships for means of genetic diversity, population density, λ_S , and vital rates, and positive relationships for variances. Blue values highlight significant relationships contrary to the CPH, i.e. positive relationships for means and negative relationships for variances. We use vital rates from individuals from the smallest (*Plantago coronopus*) and largest (*Polygonum viviparum* and *Silene acaulis*) size classes. See Material and Methods for details about size classes.

† A Box-Cox transformation has been applied to the response variable

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842 **SUPPORTING INFORMATION**

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844 **Appendix S1.** Supplementary methods: species distribution modeling

845 **Appendix S2.** Supplementary methods: centre/periphery sub-definitions

846

847 **Table S1.** Locations of monitored populations

848 **Table S2.** Distances to the different centres

849 **Table S3.** Relationships between demography/genetics and distances to centres

850

851 **Figure S1.** Modeled current distributions

852 **Figure S2.** *Polygonum viviparum* distances to 3 main centres

853 **Figure S3.** Distances to the historical centre (CCSM scenario)

854 **Figure S4.** Modeled distributions at the Last Glacial Maximum

855 **Figure S5.** Temporal changes in environmental suitability for *Polygonum viviparum*

856 **Figure S6.** Temporal changes in environmental suitability (CCSM scenario)

P. coronopus

	Geography	Climate	History
Genetic diversity	0.094	0.267 †	0.671 **
Population density	0.247	-0.105	0.545 **
λ_s	0.024	0.154	-0.102
Fecundity	0.076	-0.007	0.570 **
Growth	0.057	-0.108	0.215
Survival	0.091	-0.104	0.044
Recruitment	0.359 *	0.953 †	0.984 ** †
Fecundity variance	0.602 †	-0.030	0.209
Growth variance	-0.015	0.281	-0.105
Survival variance	-0.005	0.315 *	-0.095
Recruitment variance	-0.008	-0.111	-0.111

P. viviparum

Geography	Climate	History
-	-	-
-0.072	-0.065	-0.074
-0.058	-0.032	-0.071
0.207 *	-0.041	0.544 ***
0.146	0.215 *	0.041
-0.061	0.116	0.099
0.034	0.658 †	0.029
-0.062	0.025	0.144
0.102	0.041	0.005
-0.025	0.038	0.211 *
0.307 †	0.350 †	0.025

S. acaulis

Geography	Climate	History
-	-	-
0.127	0.134	-0.056
0.554 ***	-0.018	0.278 *
0.317 **	0.252 *	-0.030
0.333 **	0.076	0.131
0.076	0.039	0.013
0.151	0.458 ***	0.122
-0.046	0.031	0.356 **
0.134	-0.059	-0.026
-0.050	-0.053	-0.059
-	-	-