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1       **Running head:** Stochastic LTRE across spatial scales

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3       **Variation in stochastic demography between and within central and**

4 **peripheral regions in a widespread short-lived herb**

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26 **Abstract**

27 Analyzing intraspecific variation in population dynamics in relation to  
 28 environmental factors is crucial to understand the current and future distributions of  
 29 plant species. Across ranges, peripheral populations are often expected to show lower  
 30 and more temporally variable vital rates than central populations, although it remains  
 31 unclear how much any differences in vital rates actually contribute to differences in  
 32 population growth rates. Moreover, few demographic studies accounting for  
 33 environmental stochasticity have been carried out both at continental and regional  
 34 scales. In this study we calculated stochastic growth rates in five central and six  
 35 northern peripheral populations of the widespread short-lived herb *Plantago coronopus*  
 36 along the Atlantic Coast in Europe. To evaluate at two spatial scales how mean values  
 37 and variability of vital rates (*i.e.* fecundity, recruitment, survival, growth and shrinkage)  
 38 contributed to the differences in stochastic growth rates, we performed Stochastic Life  
 39 Table Response Experiment analyses between and within central and peripheral regions.  
 40 Additionally, we searched for correlations between vital rate contributions and local  
 41 environmental conditions. Lower mean values and greater variability for some vital  
 42 rates in peripheral than in central populations had an overall negative but non-  
 43 significant effect on the stochastic growth rates in the periphery. Different life cycle  
 44 components accounted for differences in population growth depending on spatial scale,  
 45 although recruitment was the vital rate with the highest influence both between and  
 46 within regions. Interestingly, the same pattern of differentiation among populations was  
 47 found within central and peripheral areas: in both regions, one group of populations  
 48 displayed positive contributions of growth and shrinkage and negative contributions of  
 49 recruitment and survival, the opposite pattern being found in the remaining populations.  
 50 These differences among populations within regions in vital rate contributions were

51 correlated with precipitation regime, whereas at the continental scale, differences in  
52 contribution patterns were related to temperature. Altogether, our results show how  
53 populations of *P. coronopus* exhibit life cycle differences that may enable it to persist in  
54 locations with widely varying environmental conditions. This demographic flexibility  
55 may help to explain the success of widespread plants across large and heterogeneous  
56 ranges.

57

58 **Key words**

59 Climatic conditions, comparative demography, compensatory shifts in vital rates,  
60 core and marginal populations, intraspecific variation, latitudinal gradient, matrix  
61 projection models, multiple spatial scales, *Plantago coronopus*, species distribution  
62 limits, Stochastic LTRE

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76 **Introduction**

77 Peripheral populations have been predicted to show lower densities, lower  
 78 population growth rates, or higher demographic fluctuations than central populations,  
 79 due to hypothetically less suitable conditions and higher isolation (Brown 1984, Lawton  
 80 1993, Vucetich and Waite 2003). Though some studies found declining performance of  
 81 plant populations towards range edges (Carey et al. 1995, Nantel and Gagnon 1999,  
 82 Eckhart et al. 2011), others did not (Angert 2009, Eckstein et al. 2009, García et al.  
 83 2010, Doak and Morris 2010), and recent reviews have seriously challenged the validity  
 84 of these widely accepted predictions (Sagarin and Gaines 2002, Gaston 2009, Sexton et  
 85 al. 2009). There is actually no reason to expect that population performance will always  
 86 decrease towards the periphery, as the locations where peripheral populations occur may  
 87 simply be the ones where the environment is locally favorable for the species, even if  
 88 such locations are less common near the range limits (Holt and Keitt 2000, Lennon et al.  
 89 2002). In addition, while some studies have assessed the means and temporal variability  
 90 in vital rates and the stochastic population growth rates in central and marginal areas of  
 91 species' distributions (Angert 2009, Doak and Morris 2010, Eckhart et al. 2011), the  
 92 relative contributions of differences in vital rate means *vs.* standard deviations to  
 93 population growth rates across ranges have never been quantified.

94 Another set of studies has explored spatial variability in population dynamics  
 95 within limited areas of species' distributions in relation to varying environmental  
 96 conditions (van Groenendael and Slim 1988, Horvitz and Schemske 1995, Jongejans  
 97 and de Kroon 2005). However, few studies have examined variability both between and  
 98 within distinct regions (but see Menges and Dolan 1998, Jongejans et al. 2010), even  
 99 though the relative importance of different vital rates for population growth may change  
 100 across spatial scales (Jongejans et al. 2010). Determining which life cycle components

101 have a higher influence on population performance is indeed one of the best ways to  
 102 analyze intraspecific demographic variation (Morris and Doak 2005). Unraveling the  
 103 spatial variability of the key processes shaping population dynamics and its possible  
 104 environmental drivers might help us to discern the causes of range limits (Eckhart et al.  
 105 2011), and may enable to project with greater precision the future distributions of  
 106 species (Keith et al. 2008, Lavergne et al. 2010).

107 Life Table Response Experiments (LTRE) are very useful in this context because  
 108 they allow us to evaluate how differences in vital rates contribute to differences in  
 109 growth rates among populations (Caswell 2001). In addition, this analysis can detect  
 110 differences in population dynamics even in situations of similar population growth  
 111 rates, if positive contributions of some life cycle components offset negative  
 112 contributions of other components. Indeed, compensatory changes in vital rates have  
 113 been already found among plant populations along environmental gradients (Jongejans  
 114 and de Kroon 2005, Elderd and Doak 2006, Doak and Morris 2010). Two  
 115 methodological advances have been incorporated into LTREs in recent studies: the  
 116 consideration of underlying vital rates, and the use of stochastic rather than  
 117 deterministic models (Caswell 2010, Davison et al. 2010, Jacquemyn et al. 2012). The  
 118 former provides more precise assessments of population dynamics because these rates  
 119 represent distinct biological processes better than projection matrix elements, which  
 120 may confound several of these processes (Franco and Silvertown 2004). In addition,  
 121 there is a growing recognition of the potential relevance of environmental stochasticity  
 122 for the fate of populations (Tuljapurkar et al. 2003; but see Buckley et al. 2010),  
 123 particularly for short-lived species (García et al. 2008, Morris et al. 2008), as temporal  
 124 variability generally leads to decreased long-term population growth (Lewontin and  
 125 Cohen 1969, Gillespie 1977). Stochastic LTREs (SLTRE), thus, constitute a valuable

126 tool to examine the contributions of both the average values and the variation in  
 127 underlying vital rates to the observed differences in stochastic growth rates (Davison et  
 128 al. 2010), a considerable advantage with respect to deterministic approaches when  
 129 analyzing strongly fluctuating vital rates. However, SLTREs have not yet been used to  
 130 compare stochastic demography between and within central and peripheral areas of  
 131 species' ranges.

132 In this study, we analyze intraspecific demographic variation in the widespread  
 133 short-lived herb *Plantago coronopus*, and apply SLTRE to assess the effects of  
 134 differences in vital rates between and within distinct regions of its distribution. Previous  
 135 studies have shown that populations of *P. coronopus* differ substantially in life history  
 136 and demography, both at local (Waite and Hutchings 1982, Braza et al. 2010, Braza and  
 137 García 2011) and continental scales (Villellas et al. 2012, Villellas and García 2012).  
 138 Across the species' latitudinal gradient, for example, central populations showed higher  
 139 fecundity, whereas northern peripheral populations presented higher recruitment  
 140 (Villellas et al. 2012). However, no clear pattern emerged between central and  
 141 peripheral regions in temporal variability of vital rates, and it remains untested whether  
 142 differences among populations in mean performance and demographic variability result  
 143 in differences in long-term population growth rates. Even within regions, *P. coronopus*  
 144 is exposed to a variety of environments, which may trigger demographic variation at  
 145 different spatial scales. Identifying the environmental factors associated with variation  
 146 in population dynamics over time and across ranges is indeed crucial for understanding  
 147 plant demography (Holt and Keitt 2005, Buckley et al. 2010, Eckhart et al. 2011).

148 Here we present an integrative analysis of population dynamics of the widespread  
 149 short-lived herb *P. coronopus*, using a 4-yr demographic dataset from five central and  
 150 six northern peripheral populations. To our knowledge, this is the first study that

151 performs a SLTRE at different spatial scales in a nested fashion (continental and  
 152 regional), analyzing central and peripheral populations of a plant, and accounting for  
 153 sampling variation in the estimation of temporal demographic variability. First, we  
 154 tested whether peripheral populations had lower stochastic growth rates than central  
 155 populations, and examined how differences in vital rates means and fluctuations  
 156 between the center and the periphery contributed to differences in stochastic population  
 157 growth. Second, we tested whether the same vital rates were responsible for  
 158 demographic variation between and within regions. Third, we analyzed the relationship  
 159 between variation in population dynamics and variation in environmental conditions,  
 160 *i.e.*, climate, soil fertility, and intraspecific competition.

161

162 **Methods**

163 **Study species and populations**

164 *Plantago coronopus* L. (Plantaginaceae) is a common, short-lived herb present  
 165 from North Africa and the Iberian Peninsula to SW Asia. It also extends to North  
 166 Europe in a narrow strip along the Atlantic coast and the Baltic Sea, and along the  
 167 coasts of the United Kingdom (Hultén and Fries 1986). We chose the subspecies  
 168 *coronopus* (hereafter *P. coronopus*), which is the most common one throughout the  
 169 species' distribution. Plants have one or a few basal rosettes, and produce spikes with  
 170 wind-pollinated flowers when they reach reproductive stage (which they sometimes do  
 171 in their first year).

172 *Plantago coronopus* occurs in a variety of environmental conditions, regarding  
 173 climate, vegetation cover and soil fertility. The species is present both in coastal and  
 174 inland locations in the range center, where it may grow in dunes, shrublands or human-  
 175 disturbed areas, and where populations present either annual or short-lived perennial



176 life-forms (Chater and Cartier 1976). Northern populations are rather restricted to the  
 177 coast, in seashore meadows and salt marshes, presenting a short-lived perennial life-  
 178 form. For this work we selected 11 perennial populations along the Atlantic coast to  
 179 minimize habitat differences, as our focus was on the latitudinal range rather than the  
 180 coastal-to-inland axis. We monitored five central populations in sand dunes in Spain  
 181 and France, and six northern peripheral populations in coastal meadows in Denmark,  
 182 Sweden and Scotland (Appendix A). Central populations were Tarifa (T), Camposoto  
 183 (CA), Corrubedo (C), Traba (TB) and Pen Bron (F). Northern peripheral populations  
 184 were Helnaes (DH), Skallingen (DS), Glommen (SG), Torekov (ST), Aberdeen (EA)  
 185 and Skye (ES). Our study did not include southern peripheral populations (*i.e.*, in North  
 186 Africa). All study populations contained thousands or tens of thousands of individuals,  
 187 and appeared to be relatively stable in the long term (J. Villellas and M. B. García,  
 188 *personal observation*). Further information of populations can be found in Villellas et  
 189 al. (2012).

190 Data collection

191 We surveyed populations annually for 4 yr, yielding three annual transitions. All  
 192 populations were sampled from 2007 to 2010, except for population F (period 2003-  
 193 2006). However, we verified that the average and the variance of climatic variables at  
 194 site F were similar in both sampling periods. In the first year, we established a number  
 195 of randomly distributed plots in each population. We censused and mapped all the  
 196 plants within plots each July (central populations) or August (peripheral populations),  
 197 when fruits had matured but before seed dispersal. In each population census, we  
 198 measured 100–400 individuals older than 1 yr that had been mapped in previous years.  
 199 For each plant, we recorded the number of leaves and inflorescences, and the length of  
 200 an average leaf and an average inflorescence. Plant size was later estimated as number

201 of leaves  $\times$  length of an average leaf, and seed production was estimated for  
 202 reproductive individuals as number of inflorescences  $\times$  length of an average  
 203 inflorescence  $\times$  number of seeds per unit of inflorescence length (calculated with a  
 204 regression equation for each population). We also mapped each year all the new  
 205 seedlings within plots (hereafter “yearlings”).

206 We collected 10-cm deep soil cores from all populations and measured the  
 207 percentage of organic matter content from the organic carbon (Heanes 1984).  
 208 Meteorological data were obtained from the Spanish National Meteorological Agency  
 209 (populations T and CA), MeteoGalicia (C and TB), MeteoFrance (F), Danish  
 210 Meteorological Institute (DH and DS), Swedish Meteorological and Hydrological  
 211 Institute (SG and ST) and Met Office (EA and ES). We used information from 10-20  
 212 years within the last four decades (depending on the availability) from the nearest  
 213 meteorological station to each population (between 1 and 35 km away). We calculated  
 214 mean annual temperature ( $^{\circ}\text{C}$ ), mean annual precipitation (mm), and coefficient of  
 215 variation (CV) in annual and monthly precipitation. The first year of this study we also  
 216 estimated mean above-ground available area per individual (yearlings excluded)  
 217 calculating Voronoi polygons on the scanned maps of plots (hereafter “resource area”;  
 218 see also Vilellas et al. 2012). We used resource area as an inverse proxy for  
 219 intraspecific competition.

220 Projection matrices and stochastic growth rates

221 Individuals were classified into four stages based on age and size: one stage of  
 222 yearlings (y) for plants younger than 1 yr, and three size stages (1, 2 and 3) for older  
 223 plants. We used the same thresholds for size stages across populations in order to  
 224 produce as even a distribution of individuals across stages as possible (see above for  
 225 details on calculation of plant size, estimated from total leaf length): size  $\leq$  32 cm (stage

226 1),  $32 < \text{size} \leq 50$  cm (stage 2), and  $\text{size} > 50$  cm (stage 3). For most populations and  
 227 years, sample sizes per size-based stage remained between 10 and 400 individuals, and  
 228 in the case of yearlings between 25 and 1500 individuals. To construct projection  
 229 matrices, we calculated 21 stage-specific vital rates for three annual transitions and  
 230 eleven populations, for a total of 33 matrices (Fig. 1; Appendix B). Vital rates were:  
 231 survival ( $s$ ); probability of growing to any larger size class conditional on surviving ( $g$ );  
 232 probability of growing two size classes conditional on surviving and growing ( $k$ );  
 233 probability of shrinking to any smaller size class conditional on surviving and not  
 234 growing ( $r$ ); probability of shrinking two size classes conditional on surviving and  
 235 shrinking ( $h$ ); probability of reproducing ( $p$ ); seed production conditional on  
 236 reproducing ( $f$ ); and recruitment, *i.e.* the proportion of seeds giving rise to yearlings the  
 237 following year ( $z$ ). Recruitment was estimated on each plot as the number of yearlings  
 238 divided by the number of seeds produced in the previous year, and then averaged across  
 239 plots, as recruitment from the seed bank is negligible in this species (Waite and  
 240 Hutchings 1979, R. Braza and M. B. García, *unpublished data*).

241         Raw estimates of vital rates vary annually due both to environmental variation and  
 242 to sampling variation (Gould and Nichols 1988). As our goal was to assess how much  
 243 true demographic variation due to environmental fluctuations contributes to population  
 244 differences in growth rates, we corrected the raw vital rate estimates for sampling error  
 245 with mixed models that contained only a random effect of year (cf. Altwegg et al. 2007,  
 246 Morris et al. 2011). Specifically, we corrected normally distributed vital rates (seed  
 247 production) using linear mixed models, and the other rates with generalized linear  
 248 mixed models, assuming binomial errors (*lme* and *lmer* procedures, packages *nlme* and  
 249 *lme4*, respectively; R Development Core Team 2011). This procedure produces annual  
 250 vital rate estimates that are “shrunk” toward the multi-year mean value in years with

251 low sample sizes. Accounting for sampling variation avoids overestimating the  
 252 contribution of the vital rates variabilities (Gould and Nichols 1988).

253 Following Caswell (2001), we calculated stochastic growth rates by projecting  
 254 each population 50000 yr using random draws from the set of three annual matrices,  
 255 assuming identical and independent distribution. To calculate 95% confidence intervals  
 256 (CI) on stochastic growth rates, we generated 5000 bootstrap replicates for each  
 257 population and identified the 2.5th and 97.5th percentiles of the distribution of growth  
 258 rates. To test for differences in stochastic growth rates between central and peripheral  
 259 populations, we performed a Mann-Whitney test (*wilcox.test* procedure, package *stats* in  
 260 R) because we could not assume a normal distribution.

261 SLTRE analyses

262 To evaluate the contributions of the differences among populations in vital rates to  
 263 the differences in stochastic growth, we carried out SLTRE analyses (Davison et al.  
 264 2010), but based on underlying vital rates rather than matrix elements (Jacquemyn et al.  
 265 2012). We performed SLTREs *between* central and peripheral regions of *P. coronopus*  
 266 (hereafter SLTRE<sup>b</sup>) and *within* both regions (hereafter SLTRE<sup>w</sup>). In the central  
 267 SLTRE<sup>w</sup>, we analyzed differences among the five central populations, comparing them  
 268 to a central reference population (CR); in the peripheral SLTRE<sup>w</sup>, we compared the six  
 269 peripheral populations to a peripheral reference population (PR); in the SLTRE<sup>b</sup>, we  
 270 compared CR and PR to a grand reference population (GR). To construct CR and PR  
 271 annual matrices, we averaged annual vital rates across central and peripheral  
 272 populations, respectively. To construct GR annual matrices, we averaged the mean  
 273 annual vital rates from CR and PR. For all the reference and study populations, we  
 274 calculated means and standard deviations of all vital rates across years (Davison et al.  
 275 2010). We then computed for each SLTRE the contribution of each vital rate's mean

276 ( $C_m$ ) and standard deviation ( $C_{sd}$ ). For each vital rate and study population,  $C_m$  was  
 277 calculated as  $C_m = (x^P - x^R) \times S_m$ , where  $x^P$  is the vital rate's mean in the study  
 278 population,  $x^R$  is the vital rate's mean in the corresponding reference population, and  $S_m$   
 279 is the sensitivity of the reference population's stochastic growth rate to changes in the  
 280 vital rate's mean. Similarly,  $C_{sd}$ 's were calculated as  $C_{sd} = (x^P - x^R) \times S_{sd}$ , where the  
 281  $x$ 's are now vital rate standard deviations and  $S_{sd}$  is the stochastic sensitivity to changes  
 282 in vital rate's standard deviation. We calculated  $S_m$  and  $S_{sd}$  using the perturbation  
 283 method of Tuljapurkar et al. (2003) modified for vital rates (cf. Morris et al. 2006).

284 To facilitate interpretation we grouped the vital rate contributions into  
 285 contributions of five life cycle components: fecundity ( $C_m^{Fe}$  and  $C_{sd}^{Fe}$ , which contain the  
 286 sum of  $C_m$  and  $C_{sd}$ , respectively, of vital rates  $f$  and  $p$ ), growth ( $C_m^{Gr}$  and  $C_{sd}^{Gr}$ , for rates  $g$   
 287 and  $k$ ), shrinkage ( $C_m^{Sh}$  and  $C_{sd}^{Sh}$ , for rates  $r$  and  $h$ ), survival ( $C_m^{Su}$  and  $C_{sd}^{Su}$ , for rate  $s$ ) and  
 288 recruitment ( $C_m^{Re}$  and  $C_{sd}^{Re}$ , for rate  $z$ ). Then, we calculated across populations the  
 289 percentage contribution of means (%  $C_m$ ) and standard deviations (%  $C_{sd}$ ) for each life  
 290 cycle component, relative to the sum of absolute values of all contributions (Appendix  
 291 C).

#### 292 Relationship between population dynamics and environmental factors

293 To test whether populations showing demographic differences also differed in  
 294 environmental conditions, we grouped them within central and peripheral areas  
 295 according to the pattern of vital rate contributions (see Results). Groups C1 (T, CA and  
 296 F) and C2 (C and TB) contained central populations, and groups P1 (DH, DS, ST and  
 297 EA) and P2 (SG and ES) contained peripheral populations. The environmental variables  
 298 analyzed were: mean annual temperature (hereafter "temperature"), mean annual  
 299 precipitation (hereafter "mean precipitation"), CV in monthly precipitation (hereafter

300 “precipitation variability”), soil organic matter content and resource area. CV in annual  
 301 precipitation was discarded due to its similarity to CV in monthly precipitation and its  
 302 lower correlation with demographic differences. To evaluate how the environmental  
 303 variables explained demographic differences among groups, we performed a Linear  
 304 Discriminant Analysis (*lda* procedure, package *MASS* in R). We tested the significance  
 305 of differences among groups regarding environmental variables with a Wilks’ lambda  
 306 test (*manova* procedure, package *stats* in R).

307

## 308 **Results**

### 309 Stochastic growth rates

310 Populations showed large differences in stochastic growth rate within regions,  
 311 ranging from 0.53 (population F) to 1.01 (C) in the central area and from 0.57 (DS) to  
 312 1.11 (ST) in the peripheral area (Fig. 2). For all populations, 95% confidence intervals  
 313 of growth rates were narrower than  $\pm 0.01$ . Nine of the 11 populations showed  
 314 stochastic growth rate values below one. We found no significant differences in  
 315 stochastic growth rates between central and peripheral populations (Mann-Whitney test;  
 316  $W = 15, P = 1$ ).

### 317 SLTRE analyses

#### 318 *Stochastic sensitivities*

319 For the three reference populations (GR, CR and PR), the vital rates’  $S_m$  were on  
 320 average *ca.* 10 times higher in absolute value than their corresponding  $S_{sd}$  values  
 321 (Appendix D, Fig. D1), indicating that the stochastic growth rate of these populations is  
 322 far more sensitive to the average than to temporal variability in performance.  $S_m$  was  
 323 positive for all rates except for the shrinkage rates  $r_2$ ,  $r_3$  and  $h_3$ . Most  $S_{sd}$  were instead  
 324 negative, showing that demographic fluctuations had an overall detrimental effect on

325 population growth, although some vital rates, such as  $p_y$  and  $p_3$ , showed positive  $S_{sd}$ .  
 326 Recruitment was the vital rate with by far the highest  $S_m$  and  $S_{sd}$  in absolute value in the  
 327 three reference populations, followed by yearling vital rates ( $s_y$ ,  $p_y$  and  $g_y$ ). Differences  
 328 in vital rates' means and standard deviations between study populations and their  
 329 corresponding reference population are shown in Appendix D, Table D1.

330 *Contributions of single vital rates*

331 In all SLTRE analyses (both between and within central and peripheral regions),  
 332  $C_m$  of vital rates was much larger than  $C_{sd}$  in absolute value (Appendix D, Figs. D2 and  
 333 D3), which indicates that temporal variability of vital rates played a much smaller role  
 334 than mean values in explaining spatial variability in stochastic population growth rates.  
 335 Recruitment was always the rate with the highest  $C_m$  (Appendix D, Fig. D2). In  
 336 addition, yearlings showed higher  $C_m$  than other stages in survival ( $s$ ) and growth rates  
 337 ( $g$ ,  $k$ ), whereas in fecundity rates ( $f$ ,  $p$ ) the highest  $C_m$  corresponded either to stage 3 or  
 338 to yearlings. There was less consistency among the three SLTREs regarding  $C_{sd}$  of vital  
 339 rates, although recruitment and yearling survival tended to show the highest values in  
 340 all three analyses (Appendix D, Fig. D3).

341 *Contributions of life cycle components*

342 In the SLTRE<sup>b</sup>, fecundity and recruitment showed by far the largest percentage  
 343 contribution of mean values, and shrinkage the lowest (Fig. 3a). In CR,  $\%C_m^{Fe}$  was  
 344 positive and  $\%C_m^{Re}$  was negative, and the net contribution of mean values was slightly  
 345 positive, whereas in PR the opposite pattern was found. The net contribution of standard  
 346 deviation values was positive in CR and negative in PR, recruitment making the largest  
 347 contribution (Fig. 3d). The percentage contributions of the variabilities of the other life  
 348 cycle components were smaller due to low sensitivities in the case of growth (Appendix

349 D, Fig. D1), and to opposition between positive and negative contributions in survival  
 350 and fecundity (results not shown).

351 In the SLTRE<sup>w</sup> analyses, recruitment had in general the largest percentage  
 352 contributions of mean values (Fig. 3b, c). Two differentiated groups of populations  
 353 emerged both in the central and peripheral areas: in three central populations (T, CA  
 354 and F; group C1) and four peripheral populations (DH, DS, ST and EA; group P1),  
 355  $\%C_m^{Gr}$  and  $\%C_m^{Sh}$  were generally positive, and  $\%C_m^{Re}$  and  $\%C_m^{Su}$  were negative; the  
 356 remaining two central (C and TB; group C2) and two peripheral populations (SG and  
 357 ES; group P2) generally showed the opposite pattern (with a few exceptions with  
 358 respect to growth or survival). Equivalent patterns of differentiation among populations  
 359 in life cycle components were thus found within both regions. Survival, fecundity and  
 360 recruitment showed the largest percentage contributions of variability (Fig. 3e, f).

361 Population dynamics and environmental factors

362 In the Linear Discriminant Analysis, temperature loaded most strongly on the first  
 363 axis, which explained 92 % of the differences in environmental conditions among the  
 364 four groups identified in Figure 3, followed by soil organic matter, precipitation  
 365 variability and resource area (Fig. 4, Appendix E). The second axis explained 7 % of the  
 366 spatial variation, and was mainly determined by mean precipitation and to a lesser  
 367 extent by precipitation variability. Central populations (groups C1 and C2)  
 368 differentiated from peripheral populations (groups P1 and P2) along the first axis,  
 369 showing higher temperatures and lower soil organic matter. Groups of populations that  
 370 were defined within regions on the basis of demographic performance were instead  
 371 separated along the second axis: populations from groups C1 and P1 showed lower  
 372 mean precipitation and higher precipitation variability than populations from groups C2



373 and P2. Differences among groups regarding the environmental variables under study  
 374 were significant (Wilks' lambda = 0.10,  $F_5 = 9.38$ ,  $P = 0.014$ ).

375

376 **Discussion**

377 In our study across the European latitudinal range of the widespread *Plantago*  
 378 *coronopus*, we found large intraspecific variation in stochastic demography both at  
 379 continental and regional scales. Despite that variation, we can formulate some general  
 380 patterns. Some vital rates showed lower mean values and greater variability in  
 381 peripheral than in central populations, but led to no significant differences in stochastic  
 382 growth rates between regions. Although different life cycle components accounted for  
 383 differences in population dynamics depending on spatial scale, recruitment was the vital  
 384 rate with the highest contribution both between and within central and peripheral  
 385 regions. Our results also showed that demographic variation among populations seemed  
 386 to be related with differences in temperature at the continental scale, whereas it was  
 387 correlated with variation in precipitation regime within both central and peripheral  
 388 areas.

389 **Variation in population dynamics across spatial scales**

390 We found no significant differences in stochastic growth rates between central and  
 391 peripheral populations, which contrasts with classical predictions of a generalized  
 392 reduction in population performance in the range periphery (Lawton 1993, Lesica and  
 393 Allendorf 1995). Other recent studies have failed to find decreased growth rates towards  
 394 range margins, using both deterministic (Stokes et al. 2004, Kluth and Bruelheide 2005,  
 395 Eckstein et al. 2009) and stochastic approaches (Angert 2009, Doak and Morris 2010,  
 396 García et al. 2010). Indeed, although multiple studies have shown reduced values in  
 397 some demographic parameters at range edges, such as density or some vital rates (e.g.

398 Carey et al. 1995, García et al. 2000, Tremblay et al. 2002), few have reported a worse  
 399 overall performance in terms of population growth rates (Nantel and Gagnon 1999,  
 400 Angert 2009, Eckhart et al. 2011).

401 Irrespective of their position, most populations in our study showed stochastic  
 402 growth rates lower than one, which deserves some attention. Deviation from  
 403 equilibrium in population growth is indeed typical of short-lived plants (García et al  
 404 2008). Populations of *P. coronopus* can be relatively transient in space (J. Vilellas and  
 405 M. B. García, *personal observation*), such that plant patches that established and grew  
 406 in a certain year may decline following a perturbation, or invasion of more competitive  
 407 taxa in the following years. However, the species may compensate for such declines by  
 408 spreading to nearby sites within the same locations. Thus, although permanent plots are  
 409 often set up in places where plants are relatively dense, the situation can change over  
 410 years for short-lived species, given the large fluctuations in local populations they  
 411 commonly experience (Glazier 1986). Buckley et al. (2010) also referred to the potential  
 412 problems of choosing “good sites” within populations at the beginning of demographic  
 413 studies.

414 Numerous studies to date have analyzed temporal variability in vital rates across  
 415 ranges, with contrasting results. A previous study with *P. coronopus* showed higher  
 416 temporal variability in peripheral than in central populations in some life cycle  
 417 components, such as recruitment, and lower fluctuations in others, such as fecundity,  
 418 but differences were not statistically significant (Vilellas et al. 2012). Studies with  
 419 other plant taxa showed higher temporal variability in vital rates in peripheral  
 420 populations (Nantel and Gagnon 1999, Vucetich and Waite 2003, Gerst et al. 2011), in  
 421 central populations (Kluth and Bruelheide 2005), or failed to find any clear pattern  
 422 (Angert 2009). However, to our knowledge, this is the first study that quantifies the real

423 effect on population growth rates of such differences across ranges, discounting as well  
 424 for sampling variation to reduce the implicit overestimation of temporal variability. In  
 425 *P. coronopus*, the overall effect of temporal variability was slightly negative for the  
 426 population growth of peripheral populations, and originated almost exclusively from  
 427 differences in recruitment variability. The contribution of variation in other life cycle  
 428 components was negligible due to low sensitivity values or opposition between positive  
 429 and negative contributions.

430 In all the SLTREs performed, vital rate means showed in general higher  
 431 sensitivities and greater contributions to differences in population growth rates than did  
 432 temporal variability, as expected (Davison et al. 2010, Jacquemyn et al. 2012).  
 433 However, the net contribution of the mean values of all vital rates together was lower  
 434 than that of the standard deviations in three populations in the within-region SLTREs  
 435 (central TB, and peripheral DS and SG; Fig. 3). In these populations, positive and  
 436 negative contributions of mean vital rates cancelled each other, whereas contributions of  
 437 standard deviations did not. This result highlights the importance of considering  
 438 stochasticity, and not only mean performance, when assessing demographic differences  
 439 among populations (Gillespie 1977, Tuljapurkar et al. 2003, Davison et al. 2010).

440 Previous studies in *P. coronopus* had already suggested a key role of recruitment  
 441 (Waite 1984, Braza and García 2011). Our analyses of sensitivities and contributions  
 442 showed that, irrespective of the spatial scale of comparison, recruitment was indeed the  
 443 most relevant vital rate for stochastic population growth. The importance of the early  
 444 stages in the life cycle of *P. coronopus* was further confirmed by the high sensitivities  
 445 and contributions of vital rates (*e.g.* survival) of newly recruited yearlings. Similar  
 446 results were found in the short-lived congener *P. lanceolata* (van Groenendael and Slim  
 447 1988) and in other short-lived perennials (Pico et al. 2003, García et al. 2008, Davison

448 et al. 2010), whereas population dynamics in the longer-lived congener *P. media* were  
 449 more influenced by survival of the oldest stages (Eriksson and Eriksson 2000).

450 Despite a consistently high relevance of recruitment for the population dynamics  
 451 of *P. coronopus*, we found that the set of life cycle components contributed in distinct  
 452 ways to differences in population growth rates depending on the spatial scale of  
 453 analysis. At continental scale, the present work confirmed previous findings (Villellas et  
 454 al. 2012) that fecundity (higher in central populations) and recruitment (higher in  
 455 peripheral locations) underlie demographic differences between the core and the  
 456 northern edge of the species' range. Within central and peripheral regions, in contrast,  
 457 there was a more balanced contribution of different life cycle components: recruitment  
 458 showed the highest contribution, but growth, survival and fecundity were also relevant.  
 459 Similarly, Jongejans et al. (2010) found in three perennial plants that, although a single  
 460 vital rate was the most important for differences in deterministic population growth  
 461 rates both between and within regions, the role of the remaining vital rates varied across  
 462 scales. Changes in the relative importance of vital rates can also be found among nearby  
 463 populations (Morris and Doak 2005), which indicates that the importance of life cycle  
 464 components may vary within plant taxa even at small spatial scales.

465 The role of environmental conditions in life cycle variation

466 Differences in population dynamics across the range of *P. coronopus* are better  
 467 understood when accounting for variation in environmental conditions. In the central-  
 468 peripheral comparison, demographic differences seem to be correlated with  
 469 temperature, and secondarily with other factors such as soil conditions or precipitation,  
 470 although direct causal relationships are difficult to establish. Within central and  
 471 peripheral areas, in contrast, demographic differences were clearly associated with  
 472 precipitation regime: in both regions, populations with positive contributions of

473 recruitment and survival, and negative contributions of growth and shrinkage (groups  
 474 C2 and P2) showed higher and more constant precipitation, whereas populations with  
 475 the opposite demographic pattern (groups C1 and P1) showed lower and more variable  
 476 rainfall. These differences among populations seem to be reflected in additional  
 477 demographic and morphological parameters analyzed elsewhere, as populations from  
 478 wetter locations present higher densities and lower plant sizes than populations from  
 479 drier sites (Villellas et al. 2012). Higher densities in wetter locations are likely the result  
 480 of high recruitment. In turn, a negative effect of higher intraspecific competition on  
 481 plant growth would result in lower plant sizes. Individual plant growth is indeed lower  
 482 on average (and shrinkage higher) in these wetter sites.

483       The effects of environmental conditions on demography across distribution ranges  
 484 seem to vary among taxa, and results from other studies differ from those presented here  
 485 for *P. coronopus*. Among populations of the widespread *Stipa capillata*, for example,  
 486 differences in plant performance are driven by climate in core areas and by soil  
 487 conditions in the northwestern periphery (Wagner et al. 2011). In *Silene regia*, regional  
 488 differences in population growth rates seem to respond in part to differences in the  
 489 frequency of summer droughts, although variation in fire regime has an overall higher  
 490 effect across the species' range (Menges and Dolan 1998). In the context of global  
 491 change, studies such as these that relate demography and environmental conditions at  
 492 different spatial scales may become powerful tools to assess current and future  
 493 population performance throughout species' distributions (Jongejans et al. 2010).

494       To conclude, the large variation found in the life cycle of *P. coronopus* did not  
 495 lead to diminished performance of any group of populations across the species' range as  
 496 measured by stochastic growth rates. Instead, compensatory changes in vital rates  
 497 among populations allow life cycle adjustments to regional and local environmental

498 conditions. Similar shifts in the role of vital rates have been also documented among  
 499 populations of other plant species along environmental or geographical gradients  
 500 (Elder and Doak 2006, Doak and Morris 2010). This flexibility in the life cycle  
 501 appears to be common in widespread plants, and would explain the success of these taxa  
 502 across large and environmentally heterogeneous ranges. Further research would be  
 503 needed to determine whether the demographic differences we have observed across the  
 504 range reflect phenotypic plasticity vs. local adaptation in response to spatially varying  
 505 selection on life history traits.

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523 **References**

- 524 Altwegg, R., M. Schaub, and A. Roulin. 2007. Age-specific fitness components and  
 525 their temporal variation in the barn owl. *American Naturalist* 169:47-61.
- 526 Angert, A. L. 2009. The niche, limits to species' distributions, and spatiotemporal  
 527 variation in demography across the elevation ranges of two monkeyflowers.  
 528 *Proceedings of the National Academy of Sciences of the United States of*  
 529 *America* 106:19693-19698.
- 530 Braza, R., J. Arroyo, and M. B. García. 2010. Natural variation of fecundity  
 531 components in a widespread plant with dimorphic seeds. *Acta Oecologica-*  
 532 *International Journal of Ecology* 36:471-476.
- 533 Braza, R., and M. B. García. 2011. Spreading recruitment over time to cope with  
 534 environmental variability. *Plant Ecology* 212:283-292.
- 535 Brown, J. H. 1984. On the relationship between abundance and distribution of species.  
 536 *American Naturalist* 124:255-279.
- 537 Buckley, Y. M., S. Ramula, S. P. Blomberg, J. H. Burns, E. E. Crone, J. Ehrlén, T. M.  
 538 Knight, J.-B. Pichancourt, H. Quested, and G. M. Wardle. 2010. Causes and  
 539 consequences of variation in plant population growth rate: a synthesis of matrix  
 540 population models in a phylogenetic context. *Ecology Letters* 13:1182-1197.
- 541 Carey, P. D., A. R. Watkinson, and F. F. O. Gerard. 1995. The determinants of the  
 542 distribution and abundance of the winter annual grass *Vulpia ciliata* ssp.  
 543 *ambigua*. *Journal of Ecology* 83:177-187.
- 544 Caswell, H. 2001. *Matrix Population Models. Construction, Analysis and Interpretation.*  
 545 2nd edition. Sinauer, Sunderland, MA, USA.
- 546 Caswell, H. 2010. Life table response experiment analysis of the stochastic growth rate.  
 547 *Journal of Ecology* 98:324-333.

- 548 Chater, A. O., and D. Cartier. 1976. *Plantago* L. Pages 38-44 in T. G. Tutin, V. H.  
 549 Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters, and D.  
 550 A. Webb, editors. *Flora Europaea*. Cambridge University Press, Cambridge.
- 551 Davison, R., H. Jacquemyn, D. Adriaens, O. Honnay, H. de Kroon, and S. Tuljapurkar.  
 552 2010. Demographic effects of extreme weather events on a short-lived  
 553 calcareous grassland species: stochastic life table response experiments. *Journal*  
 554 *of Ecology* 98:255-267.
- 555 Doak, D. F., and W. F. Morris. 2010. Demographic compensation and tipping points in  
 556 climate-induced range shifts. *Nature* 467:959-962.
- 557 Eckhart, V. M., M. A. Geber, W. F. Morris, E. S. Fabio, P. Tiffin, and D. A. Moeller.  
 558 2011. The geography of demography: long-term demographic studies and  
 559 species distribution models reveal a species border limited by adaptation.  
 560 *American Naturalist* 178:S26-S43.
- 561 Eckstein, R. L., J. Danihelka, and A. Otte. 2009. Variation in life-cycle between three  
 562 rare and endangered floodplain violets in two regions: implications for  
 563 population viability and conservation. *Biologia* 64:69-80.
- 564 Elderd, B. D., and D. F. Doak. 2006. Comparing the direct and community-mediated  
 565 effects of disturbance on plant population dynamics: flooding, herbivory and  
 566 *Mimulus guttatus*. *Journal of Ecology* 94:656-669.
- 567 Eriksson, A., and O. Eriksson. 2000. Population dynamics of the perennial *Plantago*  
 568 *media* in semi-natural grasslands. *Journal of Vegetation Science* 11:245-252.
- 569 Franco, M., and J. Silvertown. 2004. Comparative demography of plants based upon  
 570 elasticities of vital rates. *Ecology* 85:531-538.



- 571 García, D., R. Zamora, J. M. Gómez, P. Jordano, and J. A. Hodar. 2000. Geographical  
 572 variation in seed production, predation and abortion in *Juniperus communis*  
 573 throughout its range in Europe. *Journal of Ecology* 88:436-446.
- 574 García, M. B., D. Goni, and D. Guzmán. 2010. Living at the edge: local versus  
 575 positional factors in the long-term population dynamics of an endangered orchid.  
 576 *Conservation Biology* 24:1219-1229.
- 577 García, M. B., F. X. Pico, and J. Ehrlén. 2008. Life span correlates with population  
 578 dynamics in perennial herbaceous plants. *American Journal of Botany* 95:258-  
 579 262.
- 580 Gaston, K. J. 2009. Geographic range limits: achieving synthesis. *Proceedings of the*  
 581 *Royal Society B-Biological Sciences* 276:1395-1406.
- 582 Gerst, K. L., A. L. Angert, and D. L. Venable. 2011. The effect of geographic range  
 583 position on demographic variability in annual plants. *Journal of Ecology* 99:591-  
 584 599.
- 585 Gillespie, J. H. 1977. Natural selection for variances in offspring numbers: a new  
 586 evolutionary principle. *American Naturalist* 111:1010-1014.
- 587 Glazier, D. S. 1986. Temporal variability of abundance and the distribution of species.  
 588 *Oikos* 47:309-314.
- 589 Gould, W. R., and J. D. Nichols. 1998. Estimation of temporal variability of survival in  
 590 animal populations. *Ecology* 79:2531-2538.
- 591 Heanes, D. L. 1984. Determination of total organic-C in soils by an improved chromic  
 592 acid digestion and spectrophotometric procedure. *Communications in Soil*  
 593 *Science and Plant Analysis* 15:1191-1213.
- 594 Holt, R. D. and T. H. Keitt. 2000. Alternative causes for range limits: a metapopulation  
 595 perspective. *Ecology Letters* 3:41-47.

- 596 Holt, R. D., and T. H. Keitt. 2005. Species' borders: a unifying theme in ecology. *Oikos*  
 597 108:3-6.
- 598 Horvitz, C. C., and D. W. Schemske. 1995. Spatiotemporal variation in demographic  
 599 transitions of a tropical understory herb: projection matrix analysis. *Ecological*  
 600 *Monographs* 65:155-192.
- 601 Hultén, E., and M. Fries. 1986. Atlas of North European vascular plants. North of the  
 602 Tropic of Cancer. Maps 1-996. Koeltz Scientific Books, Königstein.
- 603 Jacquemyn, H., R. Brys, R. Davison, S. Tuljapurkar, and E. Jongejans. 2012. Stochastic  
 604 LTRE analysis of the effects of herbivory on the population dynamics of a  
 605 perennial grassland herb. *Oikos* 121:211-218.
- 606 Jongejans, E., and H. de Kroon. 2005. Space versus time variation in the population  
 607 dynamics of three co-occurring perennial herbs. *Journal of Ecology* 93:681-692.
- 608 Jongejans, E., L. D. Jorritsma-Wienk, U. Becker, P. Dostál, M. Mildén, and H. de  
 609 Kroon. 2010. Region versus site variation in the population dynamics of three  
 610 short-lived perennials. *Journal of Ecology* 98:279-289.
- 611 Keith, D. A., H. R. Akcakaya, W. Thuiller, G. F. Midgley, R. G. Pearson, S. J. Phillips,  
 612 H. M. Regan, M. B. Araujo, and T. G. Rebelo. 2008. Predicting extinction risks  
 613 under climate change: coupling stochastic population models with dynamic  
 614 bioclimatic habitat models. *Biology Letters* 4:560-563.
- 615 Kluth, C., and H. Bruehlheide. 2005. Effects of range position, inter-annual variation and  
 616 density on demographic transition rates of *Hornungia petraea* populations.  
 617 *Oecologia* 145:382-393.
- 618 Lavergne, S., N. Mouquet, W. Thuiller, and O. Ronce. 2010. Biodiversity and Climate  
 619 Change: Integrating Evolutionary and Ecological Responses of Species and

- 620 Communities. Annual Review of Ecology, Evolution, and Systematics, Vol 41  
 621 41:321-350.
- 622 Lawton, J. H. 1993. Range, population abundance and conservation. Trends in Ecology  
 623 & Evolution 8:409-413.
- 624 Lennon, J. J., W. E. Kunin, S. Corne, S. Carver, and W. W. S. Van Hees. 2002. Are  
 625 Alaskan trees found in locally more favourable sites in marginal areas? Global  
 626 Ecology and Biogeography 11:103-114.
- 627 Lewontin, R. C., and D. Cohen. 1969. On population growth in a randomly varying  
 628 environment. Proceedings of the National Academy of Sciences of the United  
 629 States of America 62:1056-1060.
- 630 Menges, E. S., and R. W. Dolan. 1998. Demographic viability of populations of *Silene*  
 631 *regia* in midwestern prairies: relationships with fire management, genetic  
 632 variation, geographic location, population size and isolation. Journal of Ecology  
 633 86:63-78.
- 634 Morris, W. F., C. A. Pfister, S. Tuljapurkar, C. V. Haridas, C. L. Boggs, M. S. Boyce,  
 635 E. M. Bruna, D. R. Church, T. Coulson, D. F. Doak, S. Forsyth, J. M. Gaillard,  
 636 C. C. Horvitz, S. Kalisz, B. E. Kendall, T. M. Knight, C. T. Lee, and E. S.  
 637 Menges. 2008. Longevity can buffer plant and animal populations against  
 638 changing climatic variability. Ecology 89:19-25.
- 639 Morris, W. F., J. Altmann, D. K. Brockman, M. Cords, L. M. Fedigan, A. E. Pusey, T.  
 640 S. Stoinski, A. M. Bronikowski, S. C. Alberts, and K. B. Strier. 2011. Low  
 641 demographic variability in wild primate populations: fitness impacts of  
 642 variation, covariation, and serial correlation in vital rates. American Naturalist  
 643 177:E14-E28.

- 644 Morris, W. F., and D. F. Doak. 2005. How general are the determinants of the stochastic  
 645 population growth rate across nearby sites? *Ecological Monographs* 75:119-137.
- 646 Morris, W. F., S. Tuljapurkar, C. V. Haridas, E. S. Menges, C. C. Horvitz, and C. A.  
 647 Pfister. 2006. Sensitivity of the population growth rate to demographic  
 648 variability within and between phases of the disturbance cycle. *Ecology Letters*  
 649 9:1331-1341.
- 650 Nantel, P., and D. Gagnon. 1999. Variability in the dynamics of northern peripheral  
 651 versus southern populations of two clonal plant species, *Helianthus divaricatus*  
 652 and *Rhus aromatica*. *Journal of Ecology* 87:748-760.
- 653 Pico, F. X., P. F. Quintana-Ascencio, E. S. Menges, and F. Lopez-Barrera. 2003.  
 654 Recruitment rates exhibit high elasticity and high temporal variation in  
 655 populations of a short-lived perennial herb. *Oikos* 103:69-74.
- 656 R Development Core Team. 2011. *R: A language and environment for statistical*  
 657 *computing*. R Foundation for Statistical Computing, Vienna, Austria.
- 658 Sagarin, R. D., and S. D. Gaines. 2002. The 'abundant centre' distribution: to what  
 659 extent is it a biogeographical rule? *Ecology Letters* 5:137-147.
- 660 Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology  
 661 of species range limits. *Annual Review of Ecology, Evolution, and Systematics*  
 662 40:415-436.
- 663 Stokes, K. E., J. M. Bullock, and A. R. Watkinson. 2004. Population dynamics across a  
 664 parapatric range boundary: *Ulex gallii* and *Ulex minor*. *Journal of Ecology*  
 665 92:142-155.
- 666 Tremblay, M. F., Y. Bergeron, D. Lalonde, and Y. Mauffette. 2002. The potential  
 667 effects of sexual reproduction and seedling recruitment on the maintenance of

- 668 red maple (*Acer rubrum* L.) populations at the northern limit of the species  
 669 range. *Journal of Biogeography* 29:365-373.
- 670 Tuljapurkar, S., C. C. Horvitz, and J. B. Pascarella. 2003. The many growth rates and  
 671 elasticities of populations in random environments. *American Naturalist*  
 672 162:489-502.
- 673 van Groenendael, J. M., and P. Slim. 1988. The contrasting dynamics of two  
 674 populations of *Plantago lanceolata* classified by age and size. *Journal of*  
 675 *Ecology* 76:585-599.
- 676 Villellas, J., J. Ehrlén, J. M. Olesen, R. Braza, and M. B. García. 2012. Plant  
 677 performance in central and northern peripheral populations of the widespread  
 678 *Plantago coronopus*. *Ecography*, doi: 10.1111/j.1600-0587.2012.07425.x.
- 679 Villellas, J., and M. B. García. 2012. The role of the tolerance-fecundity trade-off in  
 680 maintaining intraspecific seed trait variation in a widespread dimorphic herb.  
 681 *Plant Biology*, doi: 10.1111/j.1438-8677.2012.00684.x
- 682 Vucetich, J. A., and T. A. Waite. 2003. Spatial patterns of demography and genetic  
 683 processes across the species' range: Null hypotheses for landscape conservation  
 684 genetics. *Conservation Genetics* 4:639-645.
- 685 Wagner, V., H. von Wehrden, K. Wesche, A. Fedulin, T. Sidorova, and I. Hensen.  
 686 2011. Similar performance in central and range-edge populations of a Eurasian  
 687 steppe grass under different climate and soil pH regimes. *Ecography* 34:498-  
 688 506.
- 689 Waite, S. 1984. Changes in the demography of *Plantago coronopus* at two coastal sites.  
 690 *Journal of Ecology* 72:809-826.

691 Waite, S., and M. J. Hutchings. 1979. Comparative-study of establishment of *Plantago*  
692 *coronopus* L from seeds sown randomly and in clumps. *New Phytologist*  
693 82:575-583.

694 Waite, S., and M. J. Hutchings. 1982. Plastic energy allocation patterns in *Plantago*  
695 *coronopus*. *Oikos* 38:333-342.

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704 **Supplemental material**

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706 **Appendix A** Map showing the location of populations sampled in the study.

707 **Appendix B** Vital rate mean values for each population and transition.

708 **Appendix C** Description of calculation of percentage contribution of mean and

709 standard deviation values of life cycle components.

710 **Appendix D** Components of SLTRE: stochastic sensitivities, differences in vital

711 rates between study and reference populations and contributions of single vital rates.

712 **Appendix E** Environmental variables in sampled populations and canonical

713 correlations of environmental variables from the Linear Discriminant Analysis.

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715

716 **Figure legends**

717

718 **Figure 1** Projection matrix (a) and life cycle (b) of *Plantago coronopus*, with  
 719 transitions between stages of one year (t) and the next (t +1). Individuals were classified  
 720 into four classes: yearlings (y) and three size classes (1, 2 and 3). Vital rates, with  
 721 subindices according to classes, correspond to: survival (s); probability of growing to  
 722 any larger size class conditional on surviving (g); probability of growing two size  
 723 classes conditional on surviving and growing (k); probability of shrinking to any smaller  
 724 size class conditional on surviving and not growing (r); probability of shrinking two  
 725 size classes conditional on surviving and shrinking (h); probability of reproducing (p);  
 726 seed production conditional on reproducing (f); and recruitment, *i.e.* the proportion of  
 727 seeds giving rise to yearlings the following year (z). All life cycle transitions were  
 728 recorded in this study, but only the calculation of those starting from class 2 is detailed  
 729 in b), for clarity.

730

731 **Figure 2** Stochastic growth rates in central (black circles) and peripheral (white  
 732 circles) populations of *Plantago coronopus*. Confidence intervals are too small to be  
 733 shown (see Results). Dotted line corresponds to stochastic growth rate of one.

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735 **Figure 3** Percentage contributions of differences in mean values (%  $C_m$ ) and  
 736 standard deviation values (%  $C_{sd}$ ) of vital rates of *Plantago coronopus*, grouped into life  
 737 cycle components: survival, growth, recruitment, fecundity and shrinkage. Results from  
 738 the SLTRE between central and peripheral regions (a, d), and from the SLTRE within  
 739 central (b, e) and within peripheral (c, f) regions. Percentage contributions may be  
 740 positive or negative, but the sum of absolute values of %  $C_m$  and %  $C_{sd}$  of all life cycle

741 components must be 100 for each population. In b) and c), the dashed line separates  
 742 groups of populations (C1, C2, P1 and P2) with different patterns in contributions. Note  
 743 the difference in scale in Y-axis between top and bottom graphics. See Methods for  
 744 population acronyms.

745

746 **Figure 4** Canonical correlations of environmental variables from the Linear  
 747 Discriminant Analysis in *Plantago coronopus*, indicating their contribution to the first  
 748 and second discriminant function (arrows). Variables are mean annual temperature (tm),  
 749 mean annual precipitation (pm), coefficient of variation in monthly precipitation  
 750 (pmcv), soil organic matter content (som) and resource area as an inverse proxy for  
 751 intraspecific competition (area). The position of populations (see Methods for  
 752 population acronyms) according to their corresponding group centroids is also shown.  
 753 Note the separation among groups of populations (C1, C2, P1 and P2) between regions  
 754 (left-right) and within regions (top-bottom).

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**Figures**

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**Figure 1**

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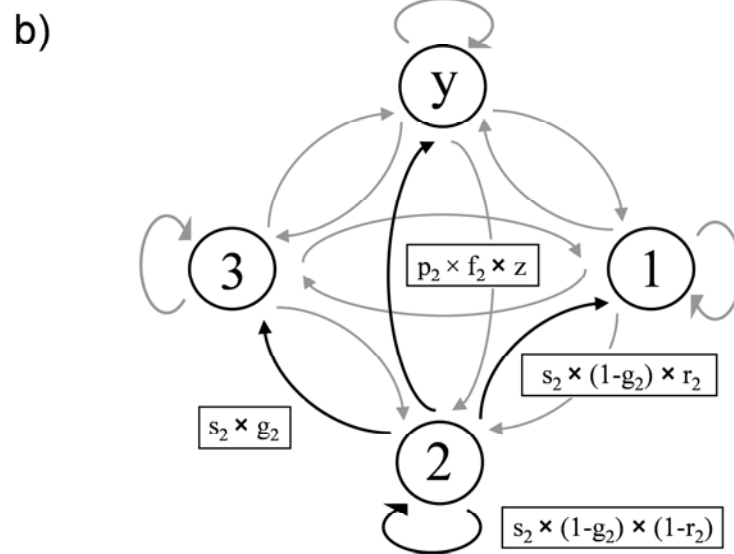
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a)

	$\mathbf{y}_t$	$\mathbf{1}_t$	$\mathbf{2}_t$	$\mathbf{3}_t$
$\mathbf{y}_{t+1}$	$p_y \times f_y \times z$	$p_1 \times f_1 \times z$	$p_2 \times f_2 \times z$	$p_3 \times f_3 \times z$
$\mathbf{1}_{t+1}$	$s_y \times (1-g_y)$	$s_1 \times (1-g_1)$	$s_2 \times (1-g_2) \times r_2$	$s_3 \times r_3 \times h_3$
$\mathbf{2}_{t+1}$	$s_y \times g_y \times (1-k_y)$	$s_1 \times g_1 \times (1-k_1)$	$s_2 \times (1-g_2) \times (1-r_2)$	$s_3 \times r_3 \times (1-h_3)$
$\mathbf{3}_{t+1}$	$s_y \times g_y \times k_y$	$s_1 \times g_1 \times k_1$	$s_2 \times g_2$	$s_3 \times (1-r_3)$



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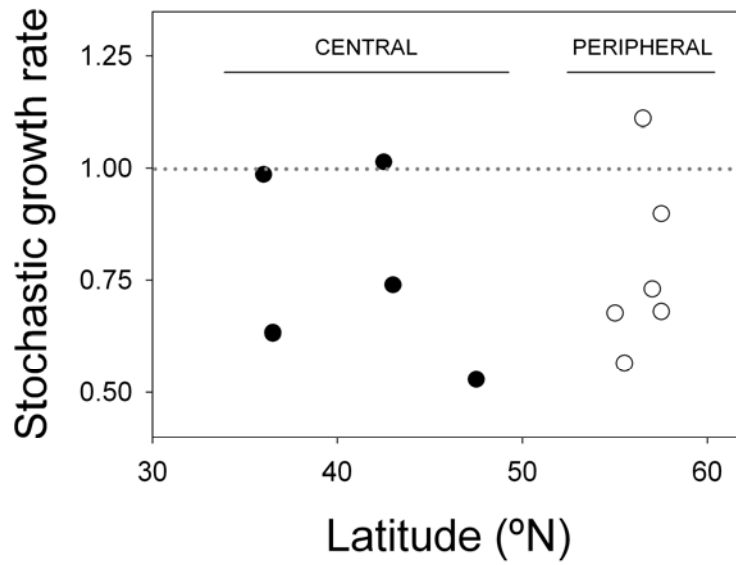
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**Figure 2**

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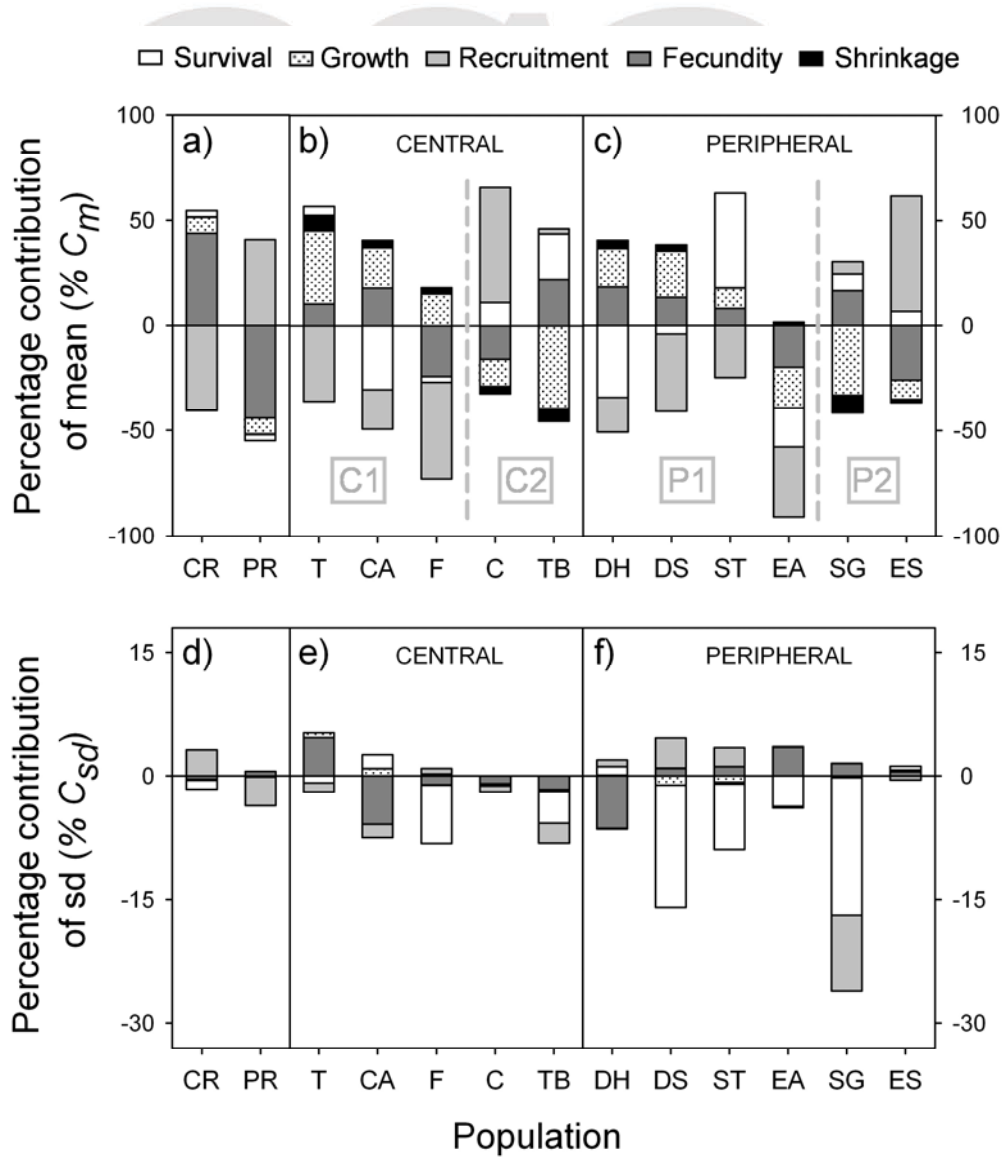
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Figure 3

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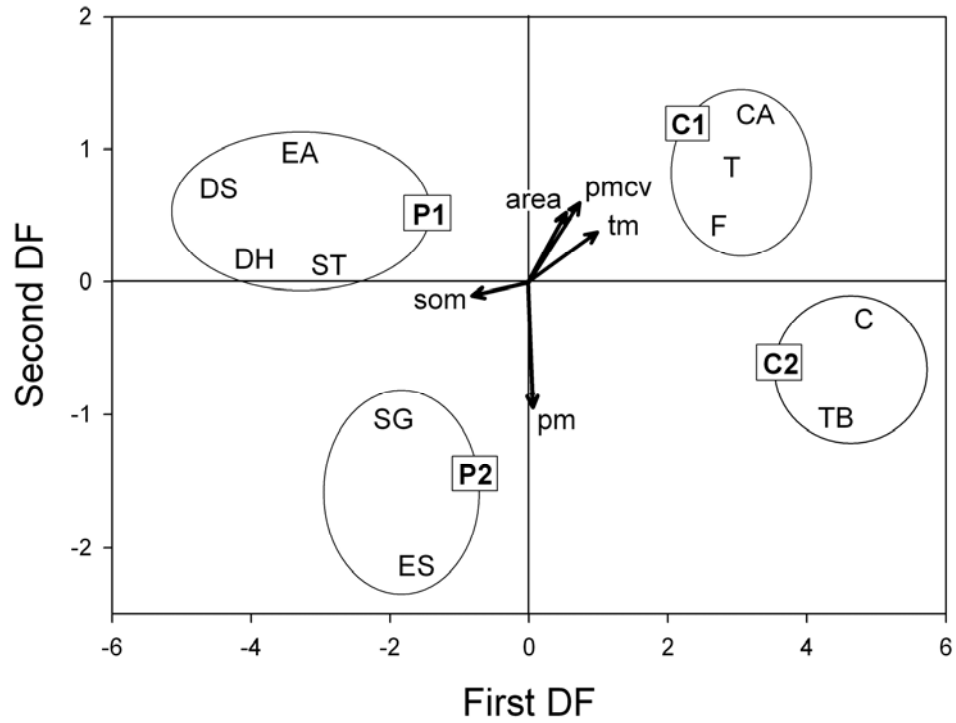
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Figure 4

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