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1 **Accounting for stochasticity in demographic compensation along the elevational range**  
2 **of an alpine plant**

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## 31 **AUTHORSHIP**

32 MA, ITB and OEG planned the study. MA, PDV and ITB carried out field work. MA, PDV, DB and MC  
33 analysed the environmental data. MA analysed the vital rates data with help from MJF. MA constructed  
34 and analysed the population dynamics model and led the writing. All authors contributed to the writing.

## 35 **DATA ACCESSIBILITY**

36 The data and R code used in this study are openly available in GitHub at

37 [https://github.com/MarcoAndrello/Stoch\\_Demogr\\_Comp\\_Arabis](https://github.com/MarcoAndrello/Stoch_Demogr_Comp_Arabis)

38 **ABSTRACT**

39 Demographic compensation arises when vital rates change in opposite directions across populations,  
40 buffering the variation in population growth rates, and is a mechanism often invoked to explain the  
41 stability of species geographic ranges. However, studies on demographic compensation have disregarded  
42 the effects of temporal variation in vital rates and their temporal correlations, despite theoretical  
43 evidence that stochastic dynamics can affect population persistence in temporally varying environments.  
44 We carried out a seven-year-long demographic study on the perennial plant *Arabis alpina* across six  
45 populations encompassing most of its elevational range. We discovered demographic compensation in  
46 the form of negative correlations between the means of plant vital rates, but also between their  
47 temporal coefficients of variation, correlations and elasticities. Even if their contribution to demographic  
48 compensation was small, this highlights a previously overlooked, but potentially important, role of  
49 stochastic processes in stabilizing population dynamics at range margins.

## 50 INTRODUCTION

51 One of the processes shaping population performance across species ranges is demographic  
52 compensation between different vital rates, such as recruitment, survival, growth and reproduction  
53 (Doak & Morris 2010; Villellas *et al.* 2015). Demographic compensation arises when different vital rates  
54 change in opposite directions across populations in response to environmental gradients, and has been  
55 proposed as a mechanism increasing the range of environments over which a species can occur and to  
56 explain the apparent stability of species range margins despite strong temporal environmental changes  
57 (Doak & Morris 2010; Sheth & Angert 2018). So far, the paradigm of demographic compensation has  
58 considered spatial differences in vital rates averaged over years, while disregarding the role of spatial  
59 differences in temporal variation of vital rates (Villellas *et al.* 2015). However, because temporal  
60 variation in vital rates can be higher in some parts of a species geographical range (for example, at range  
61 margins; Angert 2009; Pironon *et al.* 2017), population growth rates might vary across species ranges not  
62 only because of spatial variation in mean vital rates, but also in their temporal variability.

63 Population dynamics in temporally varying environments have received much attention in ecology and  
64 conservation (Tuljapurkar 1990; Lande *et al.* 2003). Theory predicts that temporal variability should  
65 decrease population growth rates in both structured and unstructured populations (Lewontin & Cohen  
66 1969; Tuljapurkar 1990) and empirical studies support these predictions (Morris *et al.* 2008). In addition,  
67 positive temporal covariations between vital rates can potentially amplify the effects of environmental  
68 stochasticity on population dynamics, while negative temporal covariation can buffer it (Doak *et al.*  
69 2005; Jongejans *et al.* 2010; Compagnoni *et al.* 2016). For example, positive covariances between  
70 reproduction and survival rates tend to magnify the effect of variability and lead to lower population  
71 growth rates than in the case of zero or negative covariances (Jongejans *et al.* 2010). Finally, the  
72 elasticities of population growth rates, which measure the change in population growth rate caused by a

73 change in demographic parameters, determine the ultimate effects of temporal variation and vital rate  
74 correlations on the population growth rate (Caswell 2001; Tuljapurkar *et al.* 2003). The interplay of these  
75 factors is perhaps best summarized by writing the stochastic population growth rate  $\log\lambda_s$  using the  
76 small-noise approximation, as a function of the intrinsic growth rate  $\log\lambda_d$  (calculated using the temporal  
77 means of vital rates) minus a product containing temporal coefficients of variation of vital rates ( $CV_k$  and  
78  $CV_l$ ), correlations between vital rates ( $\rho_{kl}$ ) and vital rate elasticities ( $e_k$  and  $e_l$ ) (Tuljapurkar 1990):

$$79 \log\lambda_s \approx \log\lambda_d - \frac{1}{2} \sum_{k,l} CV_k CV_l \rho_{k,l} e_k e_l \quad (\text{eq. 1})$$

80 Thus, a full picture of how population dynamics change across populations requires quantifying the  
81 differences in how mean vital rates, their temporal variation, their correlations and the elasticities  
82 change between populations. Such differences between populations can ultimately determine processes  
83 of demographic compensation and can thus inform on the stability and dynamics of species ranges (Doak  
84 & Morris 2010; Villellas *et al.* 2013).

85 Elevational ranges offer a unique opportunity to study range-wide variation in vital rates and population  
86 dynamics at a tractable spatial scale. For plants, elevational ranges have been associated with large  
87 differences in life-histories (Laiolo & Obeso 2017). Species living at lower elevations have often larger  
88 sizes, higher mortality rates, shorter lifespans and higher fecundities, while species living at higher  
89 elevations have smaller sizes, lower mortality rates, longer life spans and reduced flowering rates (Nobis  
90 & Schweingruber 2013; Laiolo & Obeso 2017). These life-history patterns have been related to  
91 predictions from the r-K selection theory (Pianka 1970), the metabolic theory of ecology (Brown *et al.*  
92 2004) and the acquisitive and stress-tolerant strategies of functional ecology (Read *et al.* 2014). While  
93 many studies have uncovered elevational patterns in plant life-histories across species, studies on  
94 population dynamics are less common, and patterns of variation in plant population growth rates along  
95 elevational gradients are less clear. Indeed, the few studies focusing on dynamics of herbaceous plant

96 populations on elevational gradients report increasing (Miller *et al.* 2009; Giménez-Benavides *et al.*  
97 2011), decreasing (Kim & Donohue 2011; Pena-Gomez & Bustamante 2012) and stable (García-Camacho  
98 *et al.* 2012) patterns of population growth rates with elevation.

99 Here, we aimed at testing whether spatial patterns in temporal variation, temporal correlations and  
100 elasticities could be involved in demographic compensation beyond the spatial variation of average vital  
101 rates, thereby contributing to the stabilization of species elevational ranges. To this end, we carried out a  
102 population dynamics study on *Arabis alpina* (Brassicaceae), a broadly distributed arctic-alpine perennial  
103 herb, across most of its elevational range in the European Alps. Specifically, our goals were twofold. First,  
104 we aimed at quantifying the spatial variation of four different descriptors of stochastic population  
105 dynamics (means, coefficients of variation, correlations and elasticities of plant vital rates) across an  
106 elevational gradient. Second, we aimed at quantifying the contributions of each of the four descriptors  
107 to the stochastic population growth rate and test for demographic compensation between different  
108 descriptors.

## 109 MATERIALS AND METHODS

### 110 Model species

111 *Arabis alpina* (L., Brassicaceae) is emerging as a new model organism in plant ecology and evolutionary  
112 biology (e.g. Wang *et al.* 2009; de Villemereuil *et al.* 2018) due to its perennial life-cycle and wide  
113 elevational distribution. It occurs primarily in the subalpine and alpine belts, predominantly in open,  
114 unstable, moist sites with low vegetation cover such as glacier forelands, scree slopes, rock ledges,  
115 footpaths and small streams, often in association with calcareous soil (Lauber *et al.* 2018). Seedlings  
116 germinate and establish throughout the growing season, plants flower for a few weeks and produce  
117 fruits (siliques), and flowering stems eventually wilt and die (Wang *et al.* 2009). Seeds can persist in the  
118 soil and form a permanent seed bank (Diemer & Prock 1993; Philipp *et al.* 2018).

### 119 Data collection

120 This study was conducted in six sites spanning most of the elevational range of *A. alpina* in the European  
121 Alps using permanent plots (**Table 1, Figure S1**), which were visited once a year after flowering between  
122 2008 and 2014 to record the number of stems and siliques of each individual (See **Appendix S1.1** in  
123 **Supporting Information**). *In-situ* germination tests were not successful, so germination rates could not  
124 be estimated locally and seed bank dynamics was disregarded in the matrix population model, but we  
125 conducted a sensitivity analysis to assess the effects of uncertainty in seed germination on the results  
126 (Nguyen *et al.* 2019; **Appendix S1.5, S2.2**).

127 Microclimatic conditions, soil chemistry and species composition of the vegetation were measured in  
128 each plot to model plant vital rates in function of environmental conditions. Temperature data loggers  
129 (iButton® Hygrochron, Maxim Integrated™) provided estimates of summer daily mean temperature  
130 ( $T_{mean}$ ) and daily temperature range ( $T_{range}$ ; **Table 1**). Missing records (due to malfunctioning of the data-  
131 loggers) were imputed using data from nearby weather stations, resulting in ten resampled datasets



132 **(Appendix S1.2)**. Soil acidity (pH), total soil carbon and nitrogen content were determined following  
133 standard methods (Schinner *et al.* 1996). Abundance-dominance (Braun-Blanquet) lists of plant species  
134 were used to calculate abundance weighted means for vegetative height and specific leaf area (SLA),  
135 using values from the ANDROSACE (Thuiller *et al.* 2014) and the TRY (Kattge *et al.* 2011) databases. After  
136 performing a principal component analysis on the three soil variables and the two vegetation variables  
137 **(Appendix 2.1, Figure S3, S4)**, we retained the first two axes to predict plant vital rates: *SoilVeg<sub>1</sub>*  
138 (explaining 52% of the variance), positively related to acidic soils with high C and N content, and *SoilVeg<sub>2</sub>*  
139 (explaining 29% of the variance), summarizing variation from slow-growing short vegetation to fast-  
140 growing tall vegetation.

#### 141 **Analysis**

142 We used a five-step approach to test how four *descriptors* ( $\mu$ : means; *CV*: coefficients of variation; *e*:  
143 elasticities;  $\rho$ : temporal correlations) of seven *life-cycle components* (*S*: survival; *G*<sup>-</sup>: retrogressive growth;  
144 *G*<sup>-</sup>: stasis; *G*<sup>+</sup>: progressive growth; *F*<sub>0</sub>: reproduction; *F*<sub>1</sub>: fecundity; *F*<sub>2</sub>: recruit size) contribute to  
145 demographic compensation across the elevational range of *A. alpina*. First, we constructed matrix  
146 population models for each site and year using statistical models predicting plant vital rates from  
147 environmental variables (Step 1). Second, we used the matrix models to calculate the seven life-cycle  
148 components, stochastic population growth rate  $\log\lambda_s$  and elasticities of  $\log\lambda_s$  (Step 2). Third, we tested  
149 for significant relationships between elevation and population dynamics variables (Step 3). Fourth, we  
150 performed a stochastic life-table response experiment (SLTRE) in order to decompose the differences in  
151  $\log\lambda_s$  between sites into contributions  $C_l^k$  of each life-cycle component *l* and each descriptor *k* (Step 4).  
152 Finally, we assessed demographic compensation by testing for negative and positive correlations  
153 between the SLTRE contributions  $C_l^k$  (Step 5).

154 *Step 1. Prediction of plant vital rates*

155 The plant vital rates used to construct the matrix population models were survival (whether the plant  
156 survives to  $t + 1$  or not), size (the size of the plant at time  $t + 1$ , conditional on survival), reproduction  
157 (whether the plant bears siliques or not at time  $t$ ), reproductive output (the number of siliques of the  
158 plant at time  $t$ , conditional on reproduction) and recruit size. Plant vital rates were predicted using  
159 generalized linear mixed models (GLMMs; Zuur *et al.* 2009) as a function of plant size at time  $t$  (except  
160 for recruit size that, by definition, did not exist at time  $t$ ),  $T_{mean}$ ,  $T_{range}$ ,  $SoilVeg_1$  and  $SoilVeg_2$  treated as  
161 fixed effects; plant size at time  $t$  and  $T_{mean}$  were also included as quadratic terms. Site, year nested within  
162 site and plot nested within site were included as random effects on the intercept and the slopes when  
163 significant. The error structure of the models was Gaussian (for  $\log_{10}$ -transformed reproductive output),  
164 Bernoulli (for survival and reproduction), or negative binomial (for growth and recruit size). We  
165 accounted for uncertainty in the data using a total 2000 bootstrap samples over the ten imputed climatic  
166 datasets. For each bootstrap sample, we fitted the  $2^7=128$  models corresponding to the combinations of  
167 the predictors, sampled one of them according to its Akaike weight (Burnham & Anderson 2002),  
168 obtained site- and year-specific predictions of vital rates (by setting predictors to their mean values over  
169 the plots of each site and year) and constructed matrix models to perform all the subsequent population  
170 dynamics analyses. Means and 95% confidence intervals for the reported results were calculated from  
171 the 2000 predicted values using the percentile method. All analyses were run in R 3.6.0 with packages  
172 *lme4* 1.1-21 and *MuMIn* 1.43.6 (Bartoń 2009; Bates et al. 2015; **Appendix S1.3**).

173 *Step 2. Population dynamics analyses*

174 We defined a matrix population model (Caswell 2001) with 50 size classes of one-stem each, which  
175 covered the range of variation in plant sizes observed in the field. The projection matrix  $\mathbf{A}$  was the sum  
176 of the transition matrix  $\mathbf{P} = [p_{ij}]$  and the fecundity matrix  $\mathbf{F} = [f_{ij}]$ , which were constructed using the  
177 predicted vital rates obtained in Step 1:

178  $p_{ij} = s_j g_{ij}$

179  $f_{ij} = \varepsilon F_{0,j} F_{1,j} F_{2,i}$  (eq. 2)

180 where  $j$  is plant size in year  $t$ ;  $i$  is plant size in year  $t+1$ ;  $s_j$  (survival)  $g_{ij}$  (growth),  $F_{0,j}$  (reproduction),  $F_{1,j}$   
181 (reproductive output) and  $F_{2,i}$  (recruit size) are the predicted vital rates.  $\varepsilon = 0.02$  is a seedling  
182 establishment coefficient converting the number of fruits in one year to the number of seedling in the  
183 following year, and was set equal to the median value of the ratio of the observed number of seedlings  
184 to the number of fruits in the previous year over all plots and sites.

185 Life-cycle components for each site and year were calculated as averages of the predicted vital rates over  
186 size classes weighted by the stable stage distribution vector (Salguero-Gómez *et al.* 2016). Specifically,  $S$ ,  
187  $F_0$  and  $F_1$  were calculated as weighted averages of the  $s_j$ 's,  $F_{0,j}$ 's and  $F_{1,j}$ 's (eq. 2), respectively.  $G^-$   
188 represents transitions from larger to smaller size classes and was calculated as the weighted average of  
189 all the  $g_{ij}$ 's for which  $i < j$ . Similarly,  $G^-$  (representing individuals not changing in size) and  $G^+$  (representing  
190 transitions to larger size classes) were calculated as weighted averages of all the  $g_{ij}$ 's for which  $i = j$  and  $i$   
191  $> j$ , respectively.  $F_2$  was calculated as the mean recruit size distribution  $F_{2,i}$ .

192 For each site, we calculated the temporal means and coefficients of variation of each life-cycle  
193 component and temporal correlations between pairs of life-cycle components (Pearson's correlation)  
194 over years. The stochastic population growth rate  $\log \lambda_s$  was calculated via the simulation method by  
195 randomly sampling one of the year-specific matrix at each iteration (Caswell 2001, p. 396). We then  
196 calculated the elasticities of  $\log \lambda_s$  to changes in the mean and standard deviation of the stage-specific  
197 vital rates (Tuljapurkar *et al.* 2003). We obtained the elasticities to the mean and standard deviation of  
198 life-cycle components by summing the elasticities of the respective vital rates (Franco & Silvertown 2004;  
199 **Appendix S1.4**).

200 *Step 3. Elevational patterns*

201 We used linear regressions to test for significant relationships between elevation and population  
202 dynamics variables: mean life-cycle components, coefficients of variation of life-cycle components,  
203 temporal correlations between life-cycle components,  $\log\lambda_s$  and elasticities.

204 *Step 4. Stochastic life-table response experiment (SLTRE)*

205 We calculated the differences in  $\log\lambda_s$  ( $\Delta \log\lambda_s^{(m)}$ ) between each site  $m$  and a common reference site  
206 defined by the means of vital rates over sites. The  $\Delta \log\lambda_s^{(m)}$  were decomposed into the contributions  
207  $C_{x_i, x_j}^{k, (m)}$  of differences of each descriptor  $k$  (mean  $\mu$ ; coefficient of variation  $CV$ ; temporal correlations  $\rho$ ;  
208 elasticities  $e$ ) of stage-specific vital rates  $x_i$  (survival  $s_j$ , growth  $g_{ij}$ , reproduction  $F_{0j}$ , reproductive output  
209  $F_{1j}$  and recruit size  $F_{2i}$ ) according to the SLTRE of Davison *et al.* (2013; **Appendix S1.6**):

$$210 \Delta \log\lambda_s^{(m)} \approx \sum_i C_{x_i}^{\mu, (m)} + \sum_{i,j} C_{x_i, x_j}^{CV, (m)} + \sum_{i,j} C_{x_i, x_j}^{\rho, (m)} + \sum_{i,j} C_{x_i, x_j}^{e, (m)} \quad (\text{eq. 3})$$

211 From this decomposition, we derived the *net contributions*  $C_l^k$  of each life-cycle component  $l$  and each  
212 descriptor  $k$  by summing the  $C_{x_i, x_j}^{k, (m)}$  according to the definition of life-cycle components given above. The  
213 *total effect*  $C_l$  of each life-cycle component was calculated by summing the absolute values of its  
214 contributions over the four descriptors,  $C_l = \sum_k |C_l^k|$ . Similarly, the *total effect*  $C^k$  of each descriptor was  
215 calculated by summing the absolute values of its contributions over life-cycle components,  $C^k = \sum_l |C_l^k|$ .  
216 Finally, we used linear regressions to test for significant relationships between elevation and the net  
217 contributions  $C_l^k$ .

218 *Step 5. Demographic compensation*

219 To test for demographic compensation and its effectiveness in reducing the spatial variation in  
220 population growth rates, we extended the approach of Villellas *et al.* (2015) to all descriptors of life-cycle  
221 components. We tested for demographic compensation by testing for negative and positive Spearman

222 correlations between the net contributions  $C_l^k$ . The occurrence of a significantly higher number of  
223 significant negative correlations (or a significantly lower number of significant positive correlations) than  
224 expected by chance is indicative of demographic compensation and was tested by permuting 1000 times  
225 the  $C_l^k$  over sites. This permutation test assesses only the occurrence of demographic compensation but  
226 not its effectiveness in reducing the variance in  $\log\lambda_s$  among sites,  $\sigma_{\log\lambda_s}^2$ . We then performed additional  
227 randomization tests where we calculated  $\sigma_{\log\lambda_s}^2$  following the permutation of each net contribution  $C_l^k$   
228 at a time (thus 28 parameters). Higher values of  $\sigma_{\log\lambda_s}^2$  in the randomization indicated that the focal  
229 parameter reduced  $\sigma_{\log\lambda_s}^2$  through its negative correlations; conversely, lower values for  $\sigma_{\log\lambda_s}^2$  indicated  
230 that the focal parameter increased  $\sigma_{\log\lambda_s}^2$  through its positive correlations. Finally, we ran a  
231 randomization test where we permuted only those  $C_l^k$  that reduced  $\sigma_{\log\lambda_s}^2$ : this randomization  
232 procedure eliminates as much as possible the negative correlations while preserving the important  
233 positive correlations and indicates the overall effectiveness of demographic compensation (Villellas *et al.*  
234 2015).

## 235 RESULTS

### 236 Step 1. Prediction of plant vital rates

237 Plant size had significant effects on all vital rates (**Table 2**). Size and reproductive output were positively  
238 affected by *SoilVeg<sub>2</sub>*, which was itself positively related to vegetative height and SLA of the surrounding  
239 vegetation (**Appendix S2.1**). Survival was positively affected by mean temperature squared ( $T_{mean}^2$ ),  
240 while recruit size was negatively affected by temperature range ( $T_{range}$ ). However, the models for survival  
241 and recruit size had remarkably low explanatory power (marginal  $R^2 = 0.07$  and  $0.04$ , respectively). All  
242 vital rates showed considerable spatial and temporal variation that was unexplained by our  
243 environmental variables (conditional  $R^2$  larger than marginal  $R^2$ ).

### 244 Step 2. Population dynamics analyses

245 On average, survival probability was  $S = 0.5$  (except in GAL where  $S = 0.75$ ), progressive growth ( $G^+$ ) was  
246 larger than retrogressive growth ( $G^-$ ) and stasis ( $G^=$ ), reproduction was  $F_0 = 0.5$ , reproductive output was  
247  $F_1 = 12$  siliques and recruit size was  $F_2 = 1.5$  stems (**Figure 1 and S5**). Coefficients of variations (CV) were  
248 mostly comprised between 0.1 and 0.6 across all life-cycle components. Over all sites and pairs of life-  
249 cycle components, we observed 21 (17%) significant negative temporal correlations and 21 (17%)  
250 significant positive temporal correlations (**Figure S6**).

251 The stochastic population growth rate  $\log\lambda_s$  was negative in all sites (**Table 1**). One site (GAL) had higher  
252  $\log\lambda_s$  than the other sites. The largest elasticities of  $\log\lambda_s$  to the temporal means of life-cycle components  
253 were associated with  $S$ , while the elasticities to  $G^+$  were the second-largest (**Figure 1**). The elasticities of  
254  $\log\lambda_s$  to the standard deviation of life-cycle components were largest and negative for  $S$ , intermediate for  
255  $G^+$  and  $F_1$ , and smallest for  $G^-$ ,  $G^=$ ,  $F_0$  and  $F_2$ .

256 **Step 3. Elevational patterns**

257 Mean survival ( $S$ ), retrogressive growth ( $G^-$ ) and stasis ( $G^=$ ) increased significantly with elevation (**Figure**  
258 **1**), while mean progressive growth ( $G^+$ ), reproductive output ( $F_1$ ) and recruit size ( $F_2$ ) decreased  
259 significantly with elevation. The CV of  $S$ ,  $G^-$  and  $G^=$  decreased significantly with elevation.

260 While the elasticities to mean  $S$  did not change with elevation, the elasticities to mean  $G^+$  significantly  
261 decreased with elevation. The elasticities to the means of the other life-cycle components were much  
262 smaller and showed significant positive ( $G^-$  and  $G^=$ ) or negative ( $F_0$ ,  $F_1$  and  $F_2$ ) relationships with elevation.  
263 The elasticities to the standard deviation of life-cycle components did not change significantly with  
264 elevation, nor did the temporal correlations between life-cycle components.

265 The stochastic growth rate  $\log\lambda_s$  did not change significantly with elevation (**Figure S7**).

266 **Step 4. Stochastic life-table response experiment (SLTRE)**

267 The SLTRE showed that all four descriptors of life-cycle components (means, coefficients of variation,  
268 temporal correlations and elasticities) contributed to differences in  $\log\lambda_s$  between sites (**Figure 2**). Means  
269 had the largest total effects in all sites, but the other descriptors were not negligible and could account  
270 for up to 50% of the difference in the stochastic growth rate (**Figure 2a**): the largest effects were due to  
271 coefficients of variation, while elasticities and correlations had smaller effects. When looking at the total  
272 effects of each life-cycle component (**Figure 2b**), the largest ones were due to survival ( $S$ ) and  
273 progressive growth ( $G^+$ ), while the other life-cycle components had smaller effects.

274 The net contributions of means and coefficients of variation of  $S$  ( $C_S^\mu$  and  $C_S^{CV}$ ) increased (became more  
275 positive) with elevation, while the net contributions of mean  $G^+$  ( $C_{G^+}^\mu$ ) decreased (became more  
276 negative) with elevation (**Figure S8**).

277 **Step 5. Demographic compensation**

278 There were 18 significant positive correlations and 22 significant negative correlations between the net  
279 contributions of life-cycle components across sites. This constitutes substantial evidence for the  
280 existence of demographic compensation according to the criterion proposed by Villellas *et al.* (2015),  
281 since the number of negative correlations was much higher than expected by chance (permutation test,  
282 **Figure 3**).

283 The negative correlations involved all four descriptors of population dynamics. While the correlations  
284 linking  $G^-$ ,  $G^-$  and  $G^+$  together are trivial as they emerge from the same vital process (growth), the other  
285 correlations are ecologically meaningful (**Figure S9**). Among these, there were significant negative  
286 correlations involving mean life-cycle components ( $S$ ,  $G^+$ ,  $F_1$  and  $F_2$ ), their coefficients of variation ( $S$ ),  
287 temporal correlations ( $S$ ,  $G^-$  and  $G^-$ ) and elasticities ( $G^-$  and  $G^+$ ). Significant negative correlations linked  
288 together the same descriptor of different life-cycle component (e.g. mean  $S$  and mean  $F_1$ ), different  
289 descriptors of the same life-cycle component (e.g. mean  $G^+$  and its elasticity) and different descriptors of  
290 different life-cycle components (the CV of  $S$  and the mean of  $G^+$ ,  $F_1$  and  $F_2$ ).

291 The parameters contributing the most to demographic compensation were mean  $S$ , mean  $G^+$  and mean  
292  $F_1$ , as their permutation generally increased the variance of  $\log\lambda_s$  between sites,  $\sigma_{\log\lambda_s}^2$  (**Figure 4a-d**).

293 Conversely, the permutation of the CV of  $S$  led to smaller  $\sigma_{\log\lambda_s}^2$ , indicating that this parameter increases  
294 the variance in  $\log\lambda_s$  relative to what would be expected by chance; this was the result of the numerous  
295 positive correlations involving the CV of  $S$  (**Figure 3**). The other parameters did not change  $\sigma_{\log\lambda_s}^2$   
296 considerably. Randomizing only the parameters that reduced the variance in  $\log\lambda_s$  between sites  
297 indicated that the observed  $\sigma_{\log\lambda_s}^2$  was 59% of the median  $\sigma_{\log\lambda_s}^2$  expected under the hypothesis of  
298 minimal negative correlations, but not significantly smaller ( $p = 0.17$ ; **Figure 4e**).



299 **DISCUSSION**

300 In this work, we studied variation in population dynamics of *A. alpina* across most of its elevational range  
301 in the European Alps (2000m). Contrary to the expectation that peripheral populations have lower  
302 demographic performance than central populations (Pironon *et al.* 2017), *A. alpina* showed surprisingly  
303 little variation in population growth rates  $\log\lambda_s$  across its full elevational range. Conversely, most life-  
304 cycle components significantly varied with elevation. We showed that this pattern could be partly  
305 explained by demographic compensation, *i.e.* negative correlations between the contributions of  
306 different life-cycle components to spatial differences in  $\log\lambda_s$ . In particular, compensatory effects across  
307 the elevational range did not arise only through opposite spatial patterns in mean vital rates, but also in  
308 their temporal variation, elasticities and temporal correlations. This highlights a previously overlooked,  
309 but potentially important, role of stochastic processes in offsetting mean changes in vital rates and  
310 stabilizing population dynamics at range margins. We now discuss the origin, significance and  
311 generalities of the patterns of demographic compensation observed in this study.

312 The origin of negative correlations between the different descriptors of life-cycle components should be  
313 searched in their patterns of variation along the elevational gradient (**Figure 1**). First, mean vital rates  
314 changed in opposite directions: survival (S) increased along the elevational gradient while reproductive  
315 output ( $F_1$ ) decreased, resulting in a negative correlation between  $C_S^\mu$  and  $C_{F_1}^e$  (**Figure S9**). However,  
316 stochastic descriptors also contributed to demographic compensation along elevation. For example, the  
317 decrease in mean progressive growth ( $G^+$ ), by itself, should have resulted in lower population growth  
318 rates  $\log\lambda_s$  at higher elevations. However, the elasticity to mean  $G^+$  also decreased with elevation and  
319 counterbalanced the negative effects of lower  $G^+$ , because smaller elasticities dampen the effects of  
320 changes in life-cycle components on  $\log\lambda_s$ . The CV of survival also decreased with elevation, further  
321 offsetting the negative effects of lower  $G^+$ , since smaller CV have positive effects on  $\log\lambda_s$ . The resulting

322 negative correlations between the net contributions of these parameters to  $\log\lambda_s$  (namely, between  $C_{G^+}^\mu$   
323 and  $C_{G^+}^e$  and between  $C_{G^+}^\mu$  and  $C_S^{CV}$ ) partly explain why population growth rates did not change with  
324 elevation despite marked elevational gradients in life-cycle components. Overall, the observed patterns  
325 are in agreement with the known higher occurrences of smaller and longer lived species and individuals  
326 at higher elevations (Nobis & Schweingruber 2013; Laiolo & Obeso 2017) and higher variability of survival  
327 at lower elevations (Angert 2009).

328 Such elevational patterns could be due to opposite responses of vital rates to common environmental  
329 drivers (Knops *et al.* 2007). The main environmental driver of variation in growth and reproductive  
330 output was *SoilVeg<sub>2</sub>*, which summarizes variation in specific leaf area (SLA) and vegetative height  
331 (**Appendix S2.1**), meaning that *A. alpina* tends to grow larger and produce more fruits when the  
332 surrounding vegetation is composed of tall plants with large SLA. This relationship could indicate a  
333 response to high competitive pressure or a common effect of temperature, because SLA and vegetative  
334 height in plants tend to increase with temperature and decrease with elevation (Moles *et al.* 2014; Read  
335 *et al.* 2014; Rosbakh *et al.* 2015). In contrast, the environmental drivers of survival are not easy to  
336 identify, because the statistical model linking plant survival probability to environmental variables had  
337 very low explanatory power. These results seem corroborated by a common garden experiment using  
338 the same six populations as this study, which found that temperature was significantly associated with  
339 total fruit length (a measure of reproductive output) but not with survival (de Villemereuil *et al.* 2018).  
340 Elevational patterns in survival, growth and reproductive output could also be driven by other  
341 environmental factors not considered in our analysis, such as soil phosphorus content, diversity of root  
342 microbiota or herbivore damage, all of which affect various traits of *A. alpina* across its range (Almario *et al.*  
343 *et al.* 2017; Buckley *et al.* 2019). Negative correlations between life-cycle components could also be due to  
344 energetic trade-offs and structural constraints (Williams *et al.* 2015). In *A. alpina*, higher rates of  
345 flowering are associated with reduction of plant survival, because all stems wilt and die after setting

346 seeds, to the point that mutants for perpetual flowering show an annual life-cycle (Wang *et al.* 2009).  
347 Slower rates of stem production and/or lower rates of flowering could thus increase the longevity of the  
348 entire plant, resulting in negative correlations between growth, reproduction and survival.

349 Spatial patterns in elasticity are not very documented, but increasing elasticities to survival with  
350 elevation could result from their positive correlation with longevity (Silvertown *et al.* 1993; Franco &  
351 Silvertown 2004) and from the positive correlation between longevity and elevation (Nobis &  
352 Schweingruber 2013). In contrast, decreasing elasticities to fecundity and growth with elevation, as  
353 found in our study, could be expected given that these elasticities correlate with SLA (Adler *et al.* 2014)  
354 and SLA is known to decrease with elevation (Read *et al.* 2014). However, within-species patterns of  
355 elasticities are also influenced by the level of environmental disturbance (Oostermeijer *et al.* 1996;  
356 Silvertown *et al.* 1996), which may not show consistent variation with elevation.

357 The correlations between life-cycle components involved all descriptors of population dynamics but their  
358 effectiveness for reducing the variance in  $\log\lambda_s$  ( $\sigma_{\log\lambda_s}^2$ ) was higher in the case of mean life-cycle  
359 components. The effectiveness of a single descriptor for reducing  $\sigma_{\log\lambda_s}^2$  through demographic  
360 compensation depends on the strength and number of its negative correlations relative to its positive  
361 correlations (**Figure 3**) and its contribution to the differences in  $\log\lambda_s$  between sites,  $\Delta\log\lambda_s$  (**Figure 2**).  
362 Only parameters making large contributions change  $\sigma_{\log\lambda_s}^2$  through their correlations, decreasing it when  
363 most of their correlations are strong and negative. Mean progressive growth was the most important  
364 parameter for demographic compensation by offsetting variation in survival. Mean survival and mean  
365 reproductive output were the second most important parameters, thanks to their large contributions to  
366  $\Delta\log\lambda_s$  and the negative correlation between them. Conversely, temporal correlations and elasticities  
367 showed many significant negative correlations but they were not as important for demographic  
368 compensation because the net contributions to  $\Delta\log\lambda_s$  were small, in line with what is observed in other

369 plant species (Jongejans *et al.* 2010; Compagnoni *et al.* 2016; Davison *et al.* 2019). Finally, the CV of  
370 survival made relatively large contributions to  $\Delta\log\lambda_s$ , but showed too many positive correlations that led  
371 to an increase of  $\sigma_{\log\lambda_s}^2$  rather than a reduction.

372 Although our results are comparable to findings over multiple species in the deterministic case (Villellas  
373 *et al.* 2015), our study is the first assessing demographic compensation in a stochastic framework.

374 Assessing whether the results obtained here are representative of other species will require additional  
375 studies quantifying both the contributions of all descriptors of population dynamics to  $\Delta\log\lambda_s$  and their  
376 pairwise correlations. The first exercise has been done by Davison *et al.* (2019) on a set of 62 species,  
377 showing that more than one quarter of contributions to  $\Delta\log\lambda_s$  can be attributed to the effect of  
378 coefficients of variations, elasticities and temporal correlations. However, the importance of these  
379 descriptors of population dynamics for demographic compensation remains unknown, as it depends  
380 critically on the relative number and strength of negative vs. positive correlations in which they are  
381 involved.

382 Even with demographic compensation, the stochastic population growth rate was negative in all sites,  
383 indicating that populations are projected to decline in size and eventually go extinct locally. However, *A.*  
384 *alpina* could persist thanks to germination from its persistent seed bank and immigration from other  
385 sites (Hastings & Botsford 2006). Its frequent occurrence in unstable sites suggests that populations  
386 could show an extinction-recolonization dynamics typical of metapopulations (Ouborg & Eriksson 2004).  
387 The inclusion of a seed bank led to higher, sometimes positive population growth rates and confirmed  
388 the existence of demographic compensation (**Appendix S2.2**). The effects of immigration are more  
389 difficult to study in absence of estimates of seed dispersal rates, but the strong spatial genetic structure  
390 of the populations ( $F_{ST} = 0.6$ , de Villemereuil *et al.* 2018) suggests that dispersal rates might be low. The  
391 patterns of demographic compensation revealed here could thus be different in models integrating  
392 empirical estimates of seed dormancy and germination rates and extinction-recolonization dynamics,

393 potentially unmasking greater importance for coefficients of variation, elasticities and temporal  
394 correlations.

395 So far, demographic compensation has been discussed mainly in terms of spatial variation in mean vital  
396 rates (Doak & Morris 2010; Villellas *et al.* 2015; Sheth & Angert 2018). Our study is the first to highlight  
397 that temporal variation, elasticities and temporal correlations can be involved in demographic  
398 compensation, even if their effect was smaller than that of means. Nonetheless, temporal variation in  
399 vital rates could become more important under future expected increasing frequencies of extreme  
400 climatic events (Meehl & Tebaldi 2004; Schär *et al.* 2004), such as summer heatwaves and drought, that  
401 can cause large temporal variation in vital rates (Smith 2011; Andrello *et al.* 2012). Assessing the  
402 importance of all descriptors of population dynamics for demographic compensation could thus provide  
403 a more complete understanding of the dynamics of elevational as well as geographical species ranges in  
404 a context of global change.

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418 **LITERATURE CITED**

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568

569 Figure legends

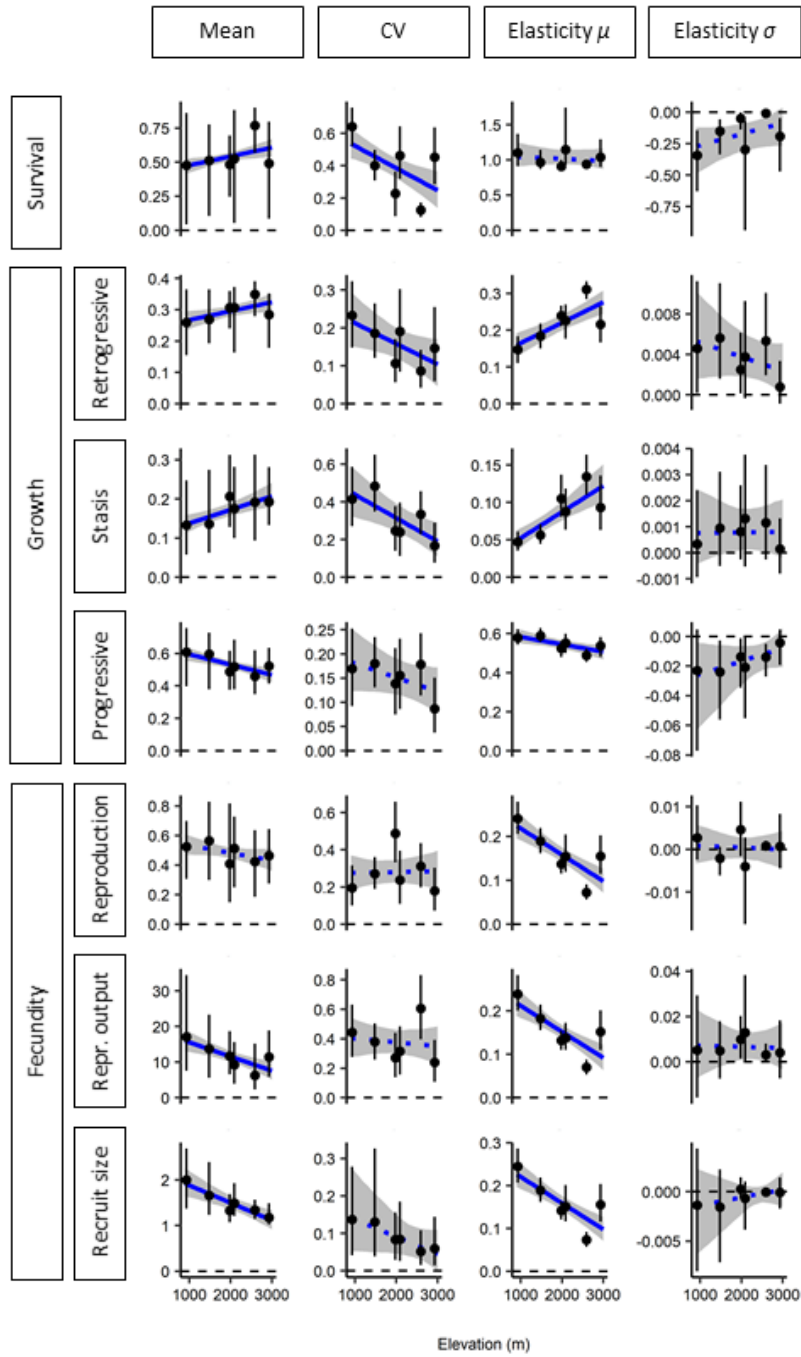
570 **Figure 1. Elevational patterns in life-cycle components and elasticities.** Elevational patterns in mean  
571 life-cycle components, coefficients of variation (CV) of life-cycle components, elasticities to means ( $\mu$ )  
572 and elasticities to standard deviation ( $\sigma$ ) of life-cycle components. Life-cycle components are survival (S),  
573 retrogressive growth ( $G^-$ ), stasis ( $G^=$ ), progressive growth ( $G^+$ ), reproduction ( $F_0$ ), reproductive output ( $F_1$ )  
574 and recruit size ( $F_2$ ). Dots are mean values and bars extend over 95% confidence intervals. The blue lines  
575 are fitted linear regressions between values and elevation, and the gray areas are 95% confidence  
576 intervals. Solid lines indicate significant regressions ( $p < 0.05$ ). Confidence intervals and significance  
577 values were calculated by randomly sampling statistical models over 200 bootstrapped demographic  
578 datasets and 10 resampled imputed climatic datasets

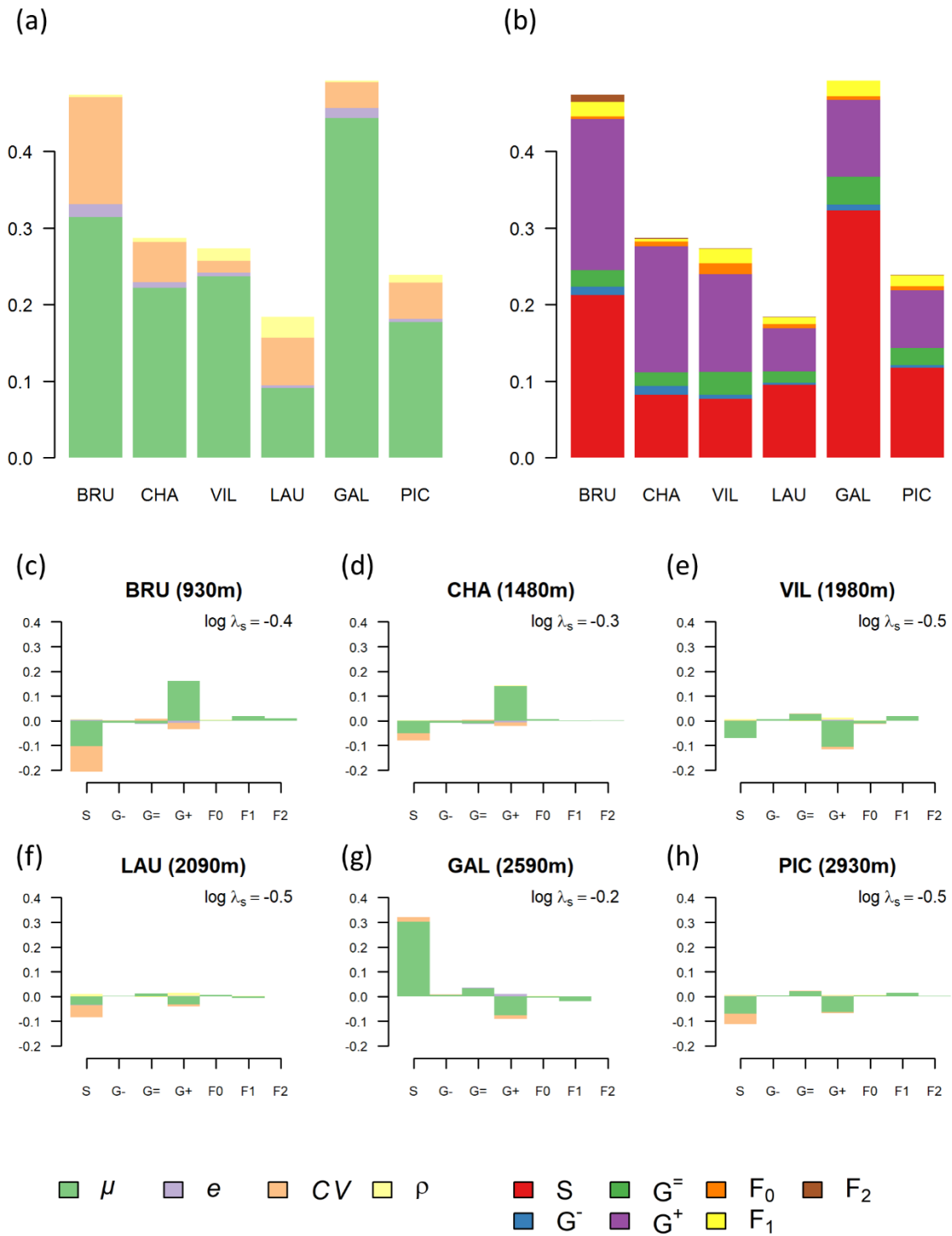
579 **Figure 2. Stochastic life-table response experiment (SLTRE).** Total effects of each descriptor (a) and life-  
580 cycle component (b) to differences in stochastic population growth rates ( $\log\lambda_s$ ) between the focal site  
581 and a reference site constructed by taking the mean of vital rates over all sites. (c) to (h), net  
582 contributions  $C_l^k$  of each descriptor  $k$  of each life-cycle component  $l$  to the difference in  $\log\lambda_s$ . Negative  
583 and positive contributions are plotted separately. Colours indicate the descriptor ( $\mu$ , means;  $e$ ,  
584 elasticities;  $CV$ , coefficients of variation;  $\rho$ , temporal correlations) or the life-cycle component (S,  
585 survival;  $G^-$ , retrogressive growth;  $G^=$ , stasis;  $G^+$ , progressive growth;  $F_0$ , reproduction;  $F_1$ , fecundity;  $F_2$ ,  
586 recruit size).

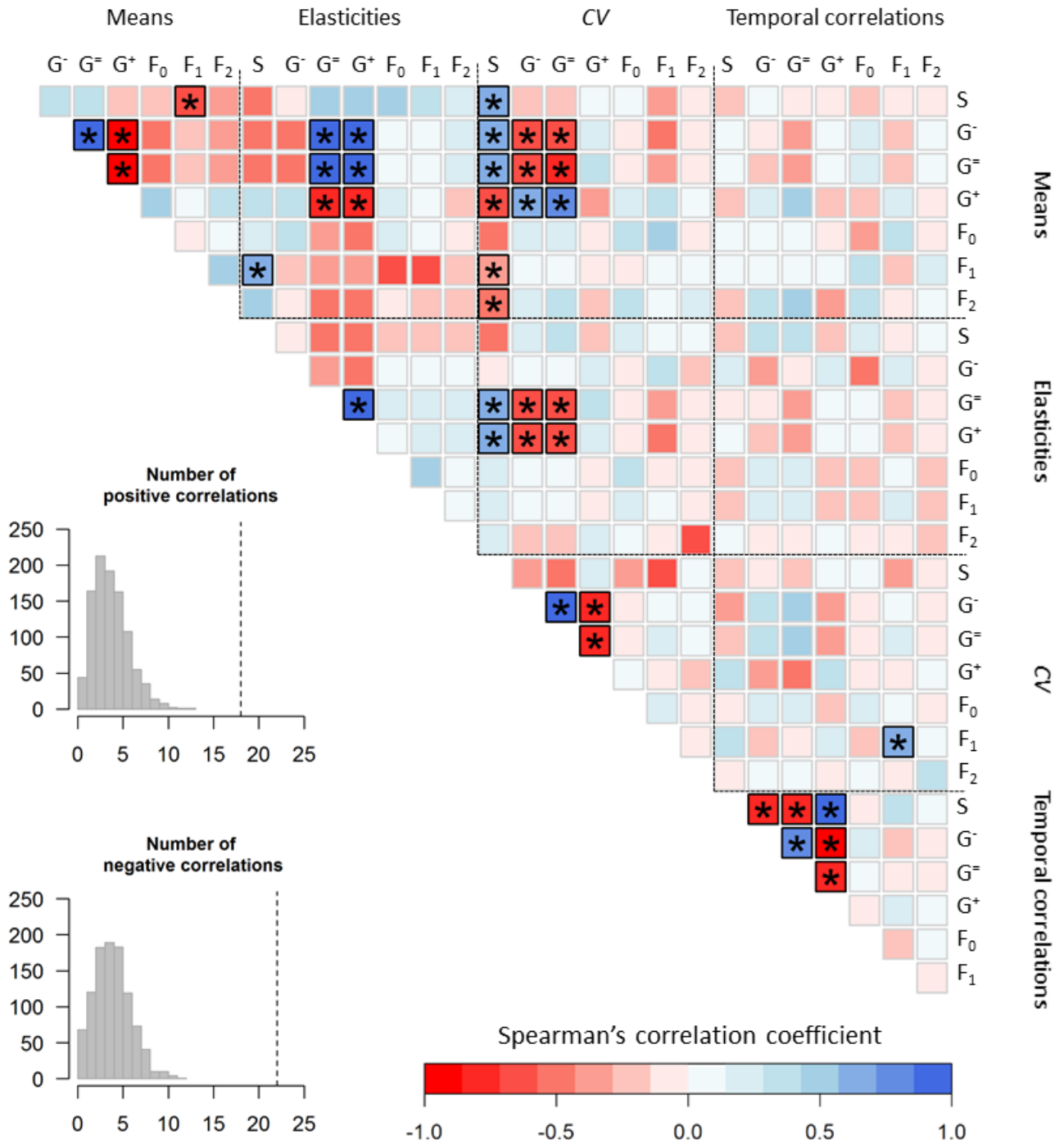
587 **Figure 3. Demographic compensation.** Correlogram of Spearman's correlation coefficients between the  
588 net contributions of different descriptors of life-cycle components to differences in stochastic population  
589 growth rates ( $\log\lambda_s$ ) between sites (SLTRE contributions). Negative correlations are in red, positive  
590 correlations are in blue. Boxes with thicker borders and an asterisk indicate significant correlations at  $p <$   
591 0.05. The insets show the number of observed significant positive and negative correlations (vertical

592 dotted lines) compared to the distribution of the number expected by chance obtained through a  
593 permutation test (histograms). See Figure 2 for definitions of descriptors and life-cycle components.

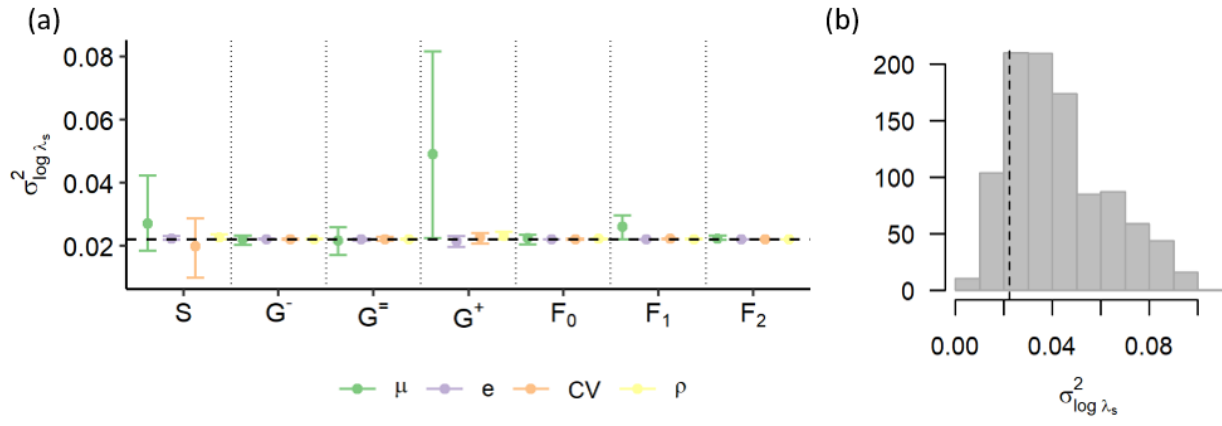
594 **Figure 4. Effectiveness of demographic compensation.** (a), variance of population growth rate  $\log\lambda_s$   
595 between sites,  $\sigma_{\log\lambda_s}^2$ , obtained by permuting each descriptor of each life-cycle component at a time.  
596 Dots are mean values and bars extend over 95% confidence intervals over 1000 permutations. Values  
597 higher than the observed  $\sigma_{\log\lambda_s}^2$  (horizontal dashed line) indicate that the corresponding parameter  
598 effectively reduces  $\sigma_{\log\lambda_s}^2$  through demographic compensation. (b), observed  $\sigma_{\log\lambda_s}^2$  (vertical dotted  
599 lines) compared to the distribution of  $\sigma_{\log\lambda_s}^2$  expected by chance obtained through permuting only the  
600 parameters effectively reducing it (histograms). See Figure 2 for definitions of descriptors and life-cycle  
601 components.







608 **FIGURE 4**



609



**Table 1. Characteristics of the study sites.**

Site	BRU	CHA	VIL	LAU	GAL	PIC
Longitude	5.61112	5.59267	5.57083	6.39034	6.40375	6.38426
Latitude	45.15065	45.07117	45.01809	45.02846	45.06049	45.06385
Elevation (m)	930	1480	1980	2090	2590	2930
Aspect	South	North	South	North	North	South
Habitat	Calcareous scree	Calcareous grassland, scree	Calcareous scree	Schists, torrent	Calcareous scree	Schistose scree
Initial $N$	46	145	104	90	110	50
Number of plots	2	3	3	3	3	4
$T_{mean}$	14.7 (12.8, 17.5)	15.7 (12.9, 18.2)	12.9 (9.3, 17.5)	10.4 (8.0, 12.1)	7.7 (5.3, 10.3)	9.1 (5.9, 12.1)
$T_{range}$	11 (6.0, 18.6)	16.9 (11.5, 21.9)	15.9 (9.7, 36.1)	6.3 (3.1, 9.6)	8.1 (5.8, 13.3)	16.3 (11.8, 23.2)
$\log\lambda_s$	-0.4 (-0.5, -0.2)	-0.3 (-0.5, -0.2)	-0.5 (-0.6, -0.4)	-0.5 (-0.8, -0.3)	-0.2 (-0.2, -0.1)	-0.5 (-0.8, -0.3)

$N$ , number of individuals. Daily mean temperature ( $T_{mean}$ ) and daily temperature range ( $T_{range}$ ) were measured with *in-situ* data-loggers. Values are means and (minimum and maximum) over plots and years for the month of July. Means and 95% confidence interval for the stochastic population growth rate ( $\log\lambda_s$ ) were calculated by randomly sampling the values calculated using matrix populations models constructed using predicted vital rates from 200 bootstrapped demographic datasets and 10 resampled imputed datasets. The  $N$  per site per year is shown in

**Figure S2.**

**Table 2. Statistical analysis of plant vital rates.**

Predictor	Survival		Growth		Reproduction		Reproductive output		Recruit size	
	mean	95% CI	mean	95% CI	mean	95% CI	mean	95% CI	mean	95% CI
Fixed effects										
Intercept	<b>0.50</b>	<b>(0.31, 0.72)</b>	<b>1.35</b>	<b>(1.24, 1.44)</b>	<b>0.75</b>	<b>(0.35, 1.26)</b>	<b>1.05</b>	<b>(0.99, 1.10)</b>	<b>-0.76</b>	<b>(-1.11, -0.50)</b>
<i>SoilVeg</i> <sub>1</sub>	-0.27	(-0.69, 0.19)	0.17	(-0.18, 0.35)	0.10	(-0.36, 0.77)	0.03	(-0.06, 0.15)	0.57	(-0.16, 1.07)
<i>SoilVeg</i> <sub>2</sub>	-0.29	(-0.77, 0.05)	<b>0.17</b>	<b>(0.03, 0.38)</b>	0.14	(-0.26, 0.69)	<b>0.10</b>	<b>(0.01, 0.18)</b>	-0.04	(-0.80, 0.49)
Plant size	<b>0.79</b>	<b>(0.47, 1.09)</b>	<b>1.26</b>	<b>(1.09, 1.43)</b>	<b>3.78</b>	<b>(3.04, 4.61)</b>	<b>0.58</b>	<b>(0.49, 0.69)</b>	-	-
(Plant size) <sup>2</sup>	<b>-0.56</b>	<b>(-0.88, -0.3)</b>	<b>-0.71</b>	<b>(-0.87, -0.57)</b>	<b>-1.37</b>	<b>(-2.21, -0.74)</b>	<b>-0.26</b>	<b>(-0.37, -0.18)</b>	-	-
<i>T</i> <sub>mean</sub>	-3.52	(-5.08, 0.22)	0.35	(-0.24, 1.75)	0.04	(-2.34, 2.53)	-0.06	(-0.58, 0.41)	0.55	(-2.47, 3.33)
( <i>T</i> <sub>mean</sub> ) <sup>2</sup>	<b>3.37</b>	<b>(0.17, 5.04)</b>	-0.51	(-1.76, 0.16)	-0.13	(-2.66, 2.24)	-0.02	(-0.42, 0.52)	0.52	(-2.67, 3.20)
<i>T</i> <sub>range</sub>	-0.40	(-0.95, 0.05)	0.01	(-0.23, 0.25)	0.33	(-0.10, 1.19)	0.11	(0.00, 0.20)	<b>-0.63</b>	<b>(-1.78, -0.07)</b>
Random effects										
Site (Intercept)	0.00	(0.00, 0.55)	0.08	(0.00, 0.55)	0.00	(0.00, 0.72)	0.12	(0.00, 0.23)	0.00	(0.00, 0.40)
Year (Intercept)	0.51	(0.22, 0.86)	0.41	(0.33, 0.50)	1.09	(0.84, 1.40)	0.15	(0.11, 0.19)	0.00	(0.00, 0.70)
Year ( <i>SoilVeg</i> <sub>2</sub> )	1.27	(0.82, 1.83)	-	-	-	-	-	-	-	-
Year (Intercept * <i>SoilVeg</i> <sub>2</sub> )	0.15	(-0.48, 0.98)	-	-	-	-	-	-	-	-
Plot (Intercept)	-	-	-	-	1.28	(0.87, 1.88)	-	-	-	-
Plot (Plant size)	-	-	-	-	1.52	(0.85, 2.56)	-	-	-	-
Plot (Intercept * Plant size)	-	-	-	-	0.95	(0.74, 1.00)	-	-	-	-
Residual	-	-	1.62	(1.39, 1.89)	-	-	0.36	(0.34, 0.38)	2.61	(0.86, 13436)
Marginal <i>R</i> <sup>2</sup>	0.07	(0.03, 0.12)	0.25	(0.2, 0.31)	0.46	(0.38, 0.56)	0.44	(0.36, 0.53)	0.04	(0.00, 0.10)
Conditional <i>R</i> <sup>2</sup>	0.41	(0.29, 0.56)	0.36	(0.3, 0.49)	0.80	(0.69, 0.88)	0.57	(0.51, 0.64)	0.05	(0.02, 0.18)

For each of the five vital rates, the table reports the standardized coefficients of fixed effect, the standard deviation of random effects (intercepts and slopes), the correlations between random intercept and slopes and marginal and conditional  $R^2$  (Nakagawa *et al.* 2017). Only the random effects that were retained after model selection on the random structure are shown. Means and 95% confidence intervals were calculated by randomly sampling statistical models over 200 bootstrapped demographic datasets and 10 resampled imputed datasets. The predictors whose confidence intervals do not overlap with zero are in **bold**.