

1 **Demographic compensation among populations: what is it, how does it arise, and what**
2 **are its implications?**

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32

33 **Abstract**

34

35 Most species are exposed to significant environmental gradients across their ranges, but
36 vital rates (survival, growth, reproduction, and recruitment) need not respond in the same
37 direction to those gradients. Opposing vital rate trends across environments, a phenomenon
38 that has been loosely called “demographic compensation”, may allow species to occupy
39 larger geographical ranges and alter their responses to climate change. Yet the term has
40 never been precisely defined, nor has its existence or strength been assessed for multiple
41 species. Here we provide a rigorous definition, and use it to develop a strong test for
42 demographic compensation. By applying the test to data from 26 published, multi-
43 population demographic studies of plants, we show that demographic compensation
44 commonly occurs. We also investigate the mechanisms by which this phenomenon arises by
45 assessing which demographic processes and life stages are most often involved.
46 Additionally, we quantify the effect of demographic compensation on variation in
47 population growth rates across environmental gradients, a potentially important
48 determinant of the size of a species’ geographical range. Finally, we discuss the implications
49 of demographic compensation for the responses of single populations and species’ ranges
50 to temporal environmental variation and to ongoing environmental trends, e.g. due to
51 climate change.

52

53

54 **Introduction**

55 Environmental conditions typically vary across the geographical ranges of species. In
56 turn, these environmental gradients often cause average vital rates (survival, growth,
57 reproduction, and recruitment) to differ among local populations. The range limit is reached
58 where the combined contributions of the vital rates to the population growth rate at low
59 density are just sufficient to maintain a steady population (Birch 1953). On one side of the
60 limit, populations can increase from low numbers, and on the other side they cannot (for
61 elaborations to this basic scenario, see Pulliam 2000 and Holt 2009).

62 However, average vital rates may respond in more than one way to environmental
63 changes along a geographical gradient. A typical simplifying assumption in analyses of range
64 limits is that all vital rates will decline across the gradient (Fig. 1A) until a point is reached at
65 which the low-density population growth rate equals 1 (i.e., at the range limit L1 in Fig. 1C;
66 but see Maurer & Brown 1989). Indeed, many theoretical and empirical studies begin with
67 the expectation that any measure of demographic performance will either decline or remain
68 constant as a range boundary is approached (e.g., Jump & Woodward 2003; Stokes *et al.*
69 2004; Holt *et al.* 2005). However, vital rates need not respond in lockstep to shifting
70 environmental conditions along a geographical gradient. If they did, we would expect all
71 measures of individual and population performance to decline monotonically from the
72 range center to the periphery, a pattern that is not generally observed (Channell & Lomolino
73 2000; Sagarin & Gaines 2002; Sexton *et al.* 2009). Instead, vital rates may often change in
74 opposite directions along spatial or environmental gradients (some deteriorating and others
75 improving; Fig. 1B), a phenomenon that has been termed “demographic compensation”
76 (Doak & Morris 2010). Vital rates that improve towards range margins will cause the
77 population growth rate to decline less steeply, even more so if those vital rates have a large

78 influence on the population growth rate (i.e., have high sensitivities; Caswell 2001). The
79 result could be a larger geographical range size, or a greater occupancy of sites within the
80 range, than would be the case in the absence of demographic compensation (Fig. 1C,D).
81 Currently, there is a growing interest in large-scale information about species' demographic
82 performance (e.g. Schurr et al. 2012; Merow et al. 2014; Ehrlén & Morris 2015), and
83 understanding how vital rates covary along geographical and environmental gradients
84 becomes necessary for correctly predicting shifts in species' ranges in the present situation
85 of global change.

86 To clarify the phenomenon we are considering here, we note that the term
87 “demographic compensation” has been used in the ecological and evolutionary literature to
88 refer to multiple, disparate processes. For example, in the wildlife management literature,
89 focused largely on vertebrates, the term has been used to refer to density-dependent
90 improvements in some vital rates of a population in response to harvesting (e.g., Sterling *et al.*
91 *1983*; Weaver *et al.* 1996; Boyce *et al.* 1999; Perón 2013), natural fluctuations in
92 mortality (Gittleman 1993), or disease-driven population declines (Lachish *et al.* 2009). In
93 this context, the term has sometimes been extended to cover behavioral changes that
94 reduce human impacts on animal populations (McGowan *et al.* 2011). “Demographic
95 compensation” has also been used to refer to demographic changes within one population
96 following extreme climatic events that compensate for the negative impacts of those
97 events, possibly through density-dependent processes (Lloret *et al.* 2012). Finally, the term
98 has been applied to compensatory changes in parasite density in response to host
99 resistance in host-parasite coevolution models (Nuismer & Kirkpatrick 2003). Given this
100 diverse past usage, authors should indicate clearly which definition of “demographic

101 compensation” they are using. Here, we mean changes in opposite directions in mean vital
102 rates across populations.

103 Recent studies that have measured all vital rates across continental-scale gradients
104 have found negative correlations between pairs of vital rates among populations for three
105 plant species (Doak & Morris 2010; Vilellas *et al.* 2013b). There are also numerous other
106 examples in the literature of negative vital rate correlations across time (Ferson & Burgman
107 1995; Van Tienderen 1995; Doak *et al.* 2005; Bell *et al.* 2013), across space (Elder & Doak
108 2006; Barbeta *et al.* 2011; García-Camacho *et al.* 2012; Martone & Micheli 2012) or both
109 (Jongejans and de Kroon 2005), or between individuals within populations (e.g., Bigler and
110 Veblen 2009). Moreover, classical life-history theory is built upon the analysis of negative
111 correlations or tradeoffs between traits or fitness components (Stearns 1989, 1992; Roff
112 1992). However, to our knowledge, no previous studies have attempted to find general
113 patterns across multiple species in vital rate correlations among populations. While
114 empirical evidence certainly supports the existence of compensatory changes in vital rates,
115 three key questions about this phenomenon remain unanswered.

116 First, how should we test for the presence of demographic compensation in a set of
117 demographic data? Precise criteria for its detection were not defined by Doak and Morris
118 (2010) or others using the term in this context. Here, we propose a randomization
119 procedure as a strong test for the presence of demographic compensation, and we apply it
120 to 26 published, multi-population demographic studies on plants.

121 The second question is: how does demographic compensation arise? Do certain types
122 of demographic processes (survival, growth, reproduction, recruitment and shrinkage rates)
123 or life history stages (e.g., early vs. late in life) tend to be involved in demographic
124 compensation more often than others? Does the importance of different processes or life

125 stages for demographic compensation depend on the longevity of the species? Does it
126 depend on the potential influence of vital rates on population growth rates (sensitivity)?
127 Finally, does compensation tend to involve pairs of vital rates of the same (e.g., early- and
128 late-life survival) or different (e.g., survival and growth) types of demographic process, and
129 does it tend to involve pairs of rates affecting the same (e.g., early-life survival and growth)
130 or different (e.g., early-life survival and late-life growth) life stages? Patterns among species
131 in the way demographic compensation arises may indicate that certain kinds of life history
132 adjustments to environmental gradients are easier to attain than others. For example, it
133 may be easier for different types of vital rates than to similar ones to respond in opposite
134 ways to the same environmental gradient. Comparisons of the patterns of demographic
135 compensation among species have never been made before, but we begin to do so here.

136 The third question is: how effective is demographic compensation at reducing spatial
137 variation in population growth rates? The variance in growth rate among populations is an
138 inverse proxy for the potential range size of species, and thus informs us about the benefits
139 of demographic compensation. Specifically, in the absence of demographic compensation
140 across the sites a species inhabits, the variance in population growth rates would be high
141 because there would be populations with intrinsic growth rate well above one, but also
142 locations where the growth rate falls below one (and where the species cannot persist for
143 long on its own). In contrast, in the case of complete compensation, the spatial variance in
144 population growth rate would be zero despite trends in individual vital rates. Low spatial
145 variation in population growth, all else being equal, should translate into a larger
146 geographical range, since more populations would present growth rates above one and thus
147 persist in their locations (Fig. 1C,D). Doak and Morris (2010) have similarly argued that
148 compensatory changes among vital rates contributed to the absence of a trend in the

149 population growth rate across the continental ranges of two tundra plant species, despite
150 significant trends in the underlying vital rates. However, neither they nor any other authors
151 of whom we are aware directly quantified the magnitude of the effect of demographic
152 compensation on population growth across geographical ranges. Here, we propose a
153 method to gauge the stabilizing effect of demographic compensation on the population
154 growth rate across space, and we apply it to published multi-population datasets.

155 After addressing these three questions, we compare our approach to alternative ways
156 of analyzing correlations among traits present in the literature, and we consider broader
157 implications of demographic compensation for responses of populations and geographical
158 distributions to ongoing changes in environmental conditions, for example due to global
159 climate change. Finally, we highlight some future directions for research into demographic
160 compensation and its effects.

161

162 **How should we test for demographic compensation?**

163 A good test for demographic compensation should not simply ask if any of the vital
164 rates are negatively correlated across populations, but must also account for additional
165 complications. First, even if each vital rate varies randomly among populations, we would
166 expect to see some negative correlations arising by chance. Thus a more stringent criterion
167 for demographic compensation would ask: are there *more* negative correlations among the
168 vital rates as a group than we might expect to see if each vital rate varied at random? While
169 demographic compensation involving only a few negative correlations might arise by
170 chance, an excess of negative correlations relative to random expectations would strongly
171 suggest that demographic compensation is intimately linked to life history trade-offs and
172 reflects the action of natural selection. Second, we must recognize that spatial variation in

173 population growth rates can be reduced not only by negative correlations in vital rates, but
174 also by an absence of positive correlations. Thus a strong criterion for demographic
175 compensation might be the presence of more negative correlations or fewer positive
176 correlations than would be expected if all vital rates varied at random among populations.

177 To handle these multiple needs, we propose using a randomization procedure as a
178 strong test for demographic compensation. Specifically, the estimated values of each vital
179 rate from multiple populations of a species are first randomly reassigned among
180 populations, and the correlations between all pairs of vital rates are computed. The
181 numbers of statistically significant ($P < 0.05$) negative and positive correlations are recorded,
182 as judged by one-sided Spearman tests. This procedure is repeated 10,000 times, and the
183 numbers of negative and positive correlations observed in the real demographic data are
184 compared to the percentiles of the randomization distributions. If the observed vital rate
185 correlation matrix includes more negative correlations than the 95th percentile of the
186 distribution of counts of negative correlations, or fewer positive correlations than the 5th
187 percentile of the distribution of counts of positive correlations, we would conclude that the
188 observed correlation matrix shows substantial evidence of demographic compensation.

189 To put the basic procedure just described into practice, we modified it in one
190 important way, by computing the correlations not between the vital rates directly, but
191 between the “contributions” of each vital rate to variation in population growth rates, as
192 computed from a Life Table Response Experiment (LTRE) analysis (Caswell 2001; García-
193 Camacho *et al.* 2012; see Appendix S1 in Supporting Information). Using LTRE contributions
194 yields the same absolute value of the correlation coefficient between two vital rates, but
195 has two advantages over tests based directly on vital rates. First, contributions account for
196 the fact that while most vital rates, e.g. survival, increase the population growth rate

197 (positive sensitivity), some others, e.g. shrinkage to a smaller size, decrease it (negative
198 sensitivity). Thus, our method ensures that compensatory changes between a vital rate with
199 positive sensitivity and a rate with negative sensitivity would show a negative correlation
200 between their vital rate contributions, even though the vital rates themselves would be
201 positively correlated. Second, LTRE contributions allow tests for compensation not only
202 between individual vital rates but also between groups of rates classified by demographic
203 process or life stage (e.g., all survival rates vs. all growth rates), since the contributions of
204 individual rates are additive (see Appendix S1, Table S1).

205 We applied this randomization test to 26 multi-population demographic studies of
206 plants (Table 1). Specifically, from the studies reviewed by Crone et al. (2011), we selected
207 all studies that included six or more populations, and we augmented these studies with
208 additional recently published papers that met the same criterion. The studies included plant
209 species of different life forms and habitats, and with populations arrayed at a range of
210 spatial scales, from local to continental. We calculated the vital rates for each population in
211 each study directly from the average projection matrices presented in the original
212 publications (which typically did not present the actual vital rates). We focus on the vital
213 rates that are estimated with the largest sample size, and are thus more accurately
214 calculated, by defining the vital rates as in Morris et al. (2008). Details of the estimation and
215 selection of vital rates and the computation of their LTRE contributions are given in
216 Appendix S1.

217 Twenty four out of 26 studies showed more - not fewer - positive correlations than
218 would be expected if vital rates varied independently, suggesting that there is an overall
219 tendency for vital rates to respond similarly to environmental gradients (see Appendix S1).
220 On the other hand, nine studies showed a higher proportion of significant negative

221 correlations among contributions of vital rates than would be expected by chance either
222 when looking at single or grouped vital rates, and two more showed a marginally
223 significantly higher proportion of negative correlations ($0.05 < p < 0.1$; see Table S2). It is
224 thus against a background of frequent positive vital rate correlations that demographic
225 compensation operates through more-than-expected negative correlations. Given these
226 patterns, below we only analyze demographic compensation operating through negative
227 correlations. Demographic compensation was found with the same frequency at the level
228 of single vital rates and when vital rates were grouped by demographic process or life stage
229 (Table S2), which shows that similar vital rates can also act together to contribute to this
230 phenomenon.

231 The general prevalence of demographic compensation across taxa is difficult to
232 evaluate, considering the exploratory nature of our study and our limited sample of
233 demographic studies. But in a frequentist sense, we would expect to encounter by chance
234 only one or two studies out of 26 (5%) with apparent demographic compensation if vital
235 rate correlations were in fact random. The finding of excess negative correlations in 9
236 studies (or 11 including marginally significant ones) indicates this phenomenon is unlikely to
237 represent fortuitous variation. In addition, our ability to detect demographic compensation
238 seems to be impeded by methodological aspects of the studies that affect data quality and
239 statistical power. For example, four of the studies we analyzed were experimental (i.e., the
240 environmental gradient was created at the beginning of the study by the researchers), and
241 none of them showed demographic compensation. The imposed gradient in these studies
242 may not have mimicked the relevant one against which compensatory vital rate patterns
243 have evolved in natural populations, or the experiments may not have allowed enough time
244 for demographic compensation to appear. Besides, for the 22 studies utilizing natural rather

245 than experimental gradients, we found that species showing demographic compensation
246 had been monitored for longer than those not showing it (mean: 3.4 vs. 2.2 years; Mann-
247 Whitney test, $W = 21$, $P = 0.009$; see also Appendix S1), and included on average more
248 populations (mean: 11.4 vs. 7.8 populations; Mann-Whitney test, $W = 32$, $P = 0.074$). Longer
249 studies should have better estimated the mean vital rates for each population, while
250 imprecision of those estimates for shorter-term studies may have obscured additional
251 demographic compensation that we did not detect. Similarly, a higher number of
252 populations would allow smaller but statistically significant negative correlations to be
253 detected. Thus it seems likely that the true frequency of demographic compensation is
254 higher than what we found.

255 There was no relationship between the longevity of the species (short- vs. long-lived)
256 and the occurrence of demographic compensation ($\chi^2 = 0.521$, $df = 1$, $P = 0.471$). Indeed,
257 compensation was found in annuals, short- and long-lived perennial herbs, and trees, and
258 studies without compensation included a similar variety of life forms (cf. Tables 1 and S2).
259 We also found no difference between studies with vs. without a clearly defined
260 environmental gradient ($\chi^2 = 1.09$, $df = 1$, $P = 0.297$), indicating that the underlying gradient
261 may be unapparent to researchers. Interestingly, all four taxa (*Plantago coronopus*,
262 *Polygonum viviparum*, *Silene acaulis*, and *Clarkia xantiana* ssp. *xantiana*; Table 1) that were
263 monitored across transects that spanned their geographical ranges showed strong evidence
264 of compensation. The ability of compensation to span whole distribution areas implies that
265 it may play a role in increasing range size, even for species such as *Clarkia xantiana* ssp.
266 *xantiana* that has a relatively small range, but one that spans a steep environmental
267 gradient (in this case, in precipitation; Eckhart et al. 2011). Considering the limited number

268 of studies in our review, the patterns we have pointed out here are only suggestive, but
269 worthy of future study.

270

271 **How does demographic compensation arise?**

272 Having found evidence for demographic compensation in a substantial fraction of
273 published studies, in this section we analyze the mechanisms whereby demographic
274 compensation most frequently arises, looking for patterns across species. First, we examine
275 the relative roles of different types of demographic processes (i.e., survival, growth,
276 shrinkage, fecundity, and recruitment) and life stages in demographic compensation. Then,
277 we explore how the sensitivity, variance among populations, and LTRE contributions of vital
278 rates influence their role in demographic compensation.

279

280 *Role of demographic processes and life stages*

281 To assess whether some types of demographic processes participated in negative
282 correlations among vital rates more often than others, we first tallied the numbers of vital
283 rate correlations including each demographic process that were significantly negative or
284 not. We then used a generalized linear mixed model (GLMM, with binomial errors) to assess
285 whether the frequency of significant negative correlations differed among these processes
286 (our model included a random effect of study to account for the fact that the overall
287 fraction of vital rate correlations that were negative - regardless of the vital rates involved -
288 differed among studies; see details in Appendix S1). Because the likelihood that a particular
289 process is involved in negative correlations might depend on the longevity of the species,
290 we also included in the GLMM a categorical variable for longevity (short- vs. long-lived; see
291 Table 1) and an interaction between longevity and type of demographic process.

292 The frequency of negative correlations differed among demographic processes, and
293 the pattern of variation differed between species depending on their longevity (see Fig. 2A,
294 Table S3). In short-lived species, survival was more commonly involved in negative
295 correlations than were growth or shrinkage, whereas in long-lived species survival was the
296 process least frequently involved in negative correlations. However, fecundity and
297 recruitment were the processes contributing the most to compensation both in short- and
298 long-lived species.

299 Next we asked whether different life stages were more or less likely across species to
300 participate in negative correlations. To make studies more comparable (they differed in the
301 number of stages originally reported in the projection matrices), we combined the stages
302 occurring in the first, middle, and last thirds of the life cycle (we refer to the combined
303 stages as “early”, “middle”, and “late”, respectively; see details in Appendix S1). We then
304 repeated the preceding analysis, using stage in place of demographic process. As for
305 processes, short- and long-lived species differed regarding the relative importance of
306 different life stages in their contribution to demographic compensation (see Fig. 2B, Table
307 S3). Late stages are most commonly involved in negative correlations in short-lived plants,
308 while both early and late stages are commonly involved in long-lived plants, plants in the
309 middle life stage contributing little to demographic compensation in both long- and short-
310 lived species.

311 Finally, we evaluated whether demographic compensation tended to involve
312 negative correlations between vital rates that represent the same vs. different types of
313 demographic processes or life stages, again using the GLMM approach. A significantly
314 greater fraction of vital rate pairs were negatively correlated when those rates represented
315 different demographic processes or affected different life stages (see Fig. 2, Table S3).

316 Although sample size is small, this result suggests that it may be easier to achieve opposing
317 responses to environmental gradients the more different the processes or stages are, or put
318 another way, that it may be difficult for the same type of demographic process or life stage
319 to avoid responding in the same way to an environmental gradient.

320

321 *Sensitivity, variance and LTRE contributions*

322 Fully understanding the roles of different demographic processes or life stages in
323 demographic compensation will require us to grapple with complex relationships between
324 the sensitivity, among-population variance, and LTRE contribution of different vital rates. All
325 else being equal, vital rates can play a more effective role in demographic compensation if
326 they make a larger contribution to the differences in population growth rate among
327 populations. Otherwise, they would be irrelevant to the among-population variance in
328 population growth, whether or not they are compensated by other rates (although we could
329 also find that multiple rates with low contributions jointly compensate for one or a few
330 rates with high contributions). A higher contribution requires high sensitivity of the
331 population growth rate to that vital rate, high among-population variance in the vital rate,
332 or both (Caswell 2001). However, we might also expect to find that vital rates with high
333 sensitivities experience selection to reduce among-population variance in their means, the
334 spatial equivalent of the pattern of reduced temporal variance in high-sensitivity rates
335 pointed out by Pfister (1998). Although consequences of extreme variation in vital rates
336 might be more detrimental at the temporal scale (permanent extinction) than across
337 species' ranges (lack of extinction of a whole species if one population disappears), the
338 evolutionary constraints that sensitivity might pose on moderate amounts of both types of
339 variation can be similar. Indeed, we find across all studies that the demographic process

340 with the highest average sensitivity across rates (recruitment) has the lowest average
341 variance among populations, while the demographic process with the second lowest
342 average sensitivity (fecundity) has the highest average variance among populations (Fig. 3).
343 In reality, for most of the species we analyzed, the relationship between among-population
344 variance and sensitivity of individual vital rates follows a triangular pattern in which high-
345 variance/high-sensitivity rates are uncommon (results not shown). These considerations
346 suggest the conceptual model shown in Fig. 4, in which vital rates with high sensitivity could
347 be either more or less likely to play a role in demographic compensation, depending on
348 which path from sensitivity to compensation is stronger.

349 To further explore the role in demographic compensation of vital rates' LTRE
350 contributions, sensitivity and variance, we classified vital rates according to whether their
351 LTRE contributions (in absolute value) were above or below the median contribution for
352 each species (for studies that show strong evidence for demographic compensation at the
353 level of single vital rates; see Table S2). We also classified vital rates into four groups based
354 on whether each rate's sensitivity (in absolute value) and variance were above or below the
355 median value of all rates for that species. Then we tested for differences in the percentage
356 of significant negative correlations among these categories, using GLMMs (see Appendix
357 S1). Rates that made high LTRE contributions were indeed more often negatively correlated
358 with other rates than were rates with low contributions (see Fig. 5, Table S4), and this
359 difference was consistent across all species (see Table S5). This confirms our prediction that
360 rates with higher LTRE contributions play more of a role in demographic compensation.
361 Moreover, rates that had both above-average sensitivity and above-average variance (which
362 would certainly be in the "high contribution" group) showed the highest frequency of
363 negative correlations (see Fig. 5, Table S4). Thus even though the negative correlation

364 between sensitivity and variance (Fig. 3) means these rates are uncommon, they do occur
365 (see also Wisdom *et al.* 2000), and seem to be disproportionately important in demographic
366 compensation. On the contrary, rates with both low sensitivity and low variance were least
367 likely to be negatively correlated with other rates (see Fig. 5, Table S5). The previous finding
368 that fecundity and recruitment rates were most frequently involved in demographic
369 compensation (Fig. 2) was likely related to their high variance and sensitivity, respectively
370 (Fig. 3). However, detailed analyses of stage-specific vital rates (rather than rates grouped
371 according to general demographic processes or stages) in short- and long-lived species will
372 be needed to understand the preliminary patterns shown here and their ecological
373 implications. Sensitivity, variance, and LTRE contributions all seem to shape the roles that
374 particular vital rates play in demographic compensation, but in complex ways that warrant
375 further examination using a greater number of studies.

376

377 **How effective is demographic compensation at reducing spatial variation in population**
378 **growth rates?**

379 As we noted in the Introduction, we can assess the effectiveness of demographic
380 compensation by quantifying the degree to which it reduces variation in population growth
381 rates across space. To do so, we used an approach similar in spirit to the randomization
382 procedure we used to test for strong demographic compensation. Our goal in these
383 randomizations was to eliminate as much as possible the observed negative correlations
384 among vital rates while minimizing changes to the positive vital rate correlations (which
385 showed no role in demographic compensation). First, we determined, for each vital rate
386 involved in significant negative correlations, whether the sum of the LTRE contributions of
387 all of the vital rates with which that rate was negatively correlated was greater than the

388 equivalent sum of contributions for its positively correlated rates. We randomized only
389 those focal vital rates that met this criterion. The correlations between pairs of vital rates
390 that both failed to meet the “sum of contributions” criterion were therefore unchanged.
391 This randomization procedure eliminates as much as possible the negative correlations
392 while preserving the important positive correlations, and results in a valid correlation
393 matrix. For each randomized set of vital rates (10,000 replications), we then constructed a
394 projection matrix, estimated the population growth rate for each population, and computed
395 the among-population variance in the population growth rate. Finally, we obtained the null
396 distribution for variance in population growth rates. This analysis was applied to each
397 species showing strong demographic compensation at the level of single vital rates.
398 Alternative approaches based on direct manipulations of the vital rate correlation matrices,
399 e.g. converting all negative values to zero, would not be valid due to mathematical
400 constraints on correlation matrices (see Appendix S1).

401 On average, the variance of population growth rates estimated from the observed
402 projection matrices, reflecting actual populations, is 48% of the median variance in the
403 random permutations, indicating that demographic compensation approximately halves the
404 variance in population growth (see Table S2). Such reduction in variance was significant in
405 four out of seven studies, and marginally significant in two other studies. However, this may
406 be an underestimate of the importance of demographic compensation: although in the
407 randomizations we deleted virtually all the negative correlations, the constraints of our
408 procedure also removed on average 20% of the positive correlations (the least we could
409 achieve), which also influenced variance in population growth rates. We found indeed that
410 the ratio of observed to randomization variance decreased with a higher proportion of the
411 original positive correlations retained in the randomizations (see Fig. S2). For species for

412 which we kept 90% or more of the original positive correlations in the randomizations, the
413 observed variance of the population growth rate was on average about a quarter of the
414 median variance in the randomizations. Additionally, we found no differences in the mean
415 population growth rates between observed and randomized data, indicating that our results
416 were due to changes in the correlations per se (results not shown). In summary, the levels of
417 demographic compensation we observe in the published studies suggest that it can
418 substantially reduce spatial variation in population growth, and thus may considerably
419 increase the size of a species' geographical range relative to the case in which all vital rates
420 respond similarly to environmental gradients.

421

422 **Alternative ways of analyzing trait correlations**

423 The search for patterns in the correlations between vital rates to better understand
424 if and how demographic compensation arises is reminiscent of the search for patterns in the
425 correlations between traits of individual organisms, often used to better understand
426 morphological integration (e.g., Cheverud *et al.* 1989) or to identify suites of traits that have
427 been selected as a whole (e.g., Pérez-Barrales *et al.* 2014). In this section, we compare the
428 methodological approaches we have used to examine demographic compensation with
429 approaches used in trait-based studies to examine trait correlations. Our primary goal is to
430 discuss why several of these trait-based approaches are not appropriate for testing
431 demographic compensation. Readers not interested in this comparison can skip to the
432 following section.

433 In the trait literature, one approach has been to use Mantel tests to assess the fit of
434 the observed correlations to a theoretical matrix representing a hypothesis of how the traits
435 should be related (Cheverud *et al.* 1989). For example, one might hypothesize that traits

436 describing a particular body region or involved in a similar function should be positively
437 correlated while traits of different regions or functions should be uncorrelated, and this
438 hypothesis could be represented by a theoretical matrix of 0's and 1's (or -1's if there is
439 reason to expect traits to be negatively correlated). But the approach we take to analyze
440 demographic compensation is different for several reasons. We do not necessarily expect
441 that *all* rates describing a particular demographic process (for example) will be negatively
442 correlated with other rates. Instead, we have asked whether negative correlations are more
443 frequent for certain processes or stages than others (or when processes or stages are the
444 same or different). Another limitation of the Mantel test approach is that there is a ceiling
445 to the number of negative values that can occur in a correlation matrix, so we could not
446 have a reasonable hypothesis that *all* correlations involving different types of rates would
447 be negative.

448 Another approach that has been applied in the trait literature is to conduct a non-
449 parametric bootstrap from the original data to place confidence limits on the mean
450 correlation between pairs of traits involved in the same vs. different functions, such as
451 insect attraction vs. pollen transfer (Conner & Stirling 1995; Pérez-Barrales *et al.* 2014). This
452 approach could be applied in studying demographic compensation. For example, we could
453 repeatedly sample populations with replacement from the set of populations in a study,
454 compute the vital rate correlations across populations, calculate the mean correlation for all
455 vital rate pairs involving, say, survival, and use the confidence limits for the mean
456 correlation to ask if survival has a lower average correlation with other rates. However, as
457 most vital rate pairs are positively correlated or uncorrelated, calculating the average
458 correlation for a type of vital rate (instead of its frequency of negative correlations, as we

459 compute in the present study) might mask the presence of uncommon negative
460 correlations, even though they are important for demographic compensation.

461 An underutilized approach that holds promise for visualizing correlation patterns in
462 both traits and vital rates is to use exploratory methods such as “corrgrams”, which are
463 simply colour-coded correlation matrices that reveal groups of variables that show similar
464 correlation patterns with other variables (Friendly 2002). While one can use principal
465 components analysis to optimally define groups of variables based on their correlation
466 patterns (for details, see Friendly 2002), perhaps more useful for exploring patterns of
467 demographic compensation are corrgrams in which vital rates are grouped by either life
468 stage or by type of demographic process. Such corrgrams for one of the studied species,
469 *Silene acaulis* (Fig. 6), reveal that vital rates for a given life stage show a mixture of positive
470 and negative correlations with vital rates for other stages (Fig. 6A), in contrast with the
471 general trend across species shown in Fig. 2B. But when vital rates are grouped into
472 different types of demographic process (Fig. 6B), the corrgram reveals frequent negative
473 correlations between vital rates representing different types of process (e.g., survival and
474 fecundity, or survival and growth), in accordance with Fig. 2A. Thus corrgrams are an easy
475 way to see that for *Silene acaulis*, demographic compensation arises through opposing
476 responses of different types of demographic process rather than different life stages.

477

478 **Broader implications, caveats, and future directions**

479 In this study, we have searched for patterns in mean vital rates across populations
480 that indicate the potential for demographic compensation across space. However,
481 environmental conditions and vital rates vary in both space and time. Opposing patterns of
482 variation in vital rates across time within a single population have the potential to increase

483 the long-run stochastic population growth rate (Tuljapurkar 1990). These different types of
484 demographic compensation, which might be called spatial vs. temporal compensation,
485 respectively, may be produced by the same underlying mechanism. If the effects of
486 particular biotic or abiotic factors (e.g., temperature) on vital rates are consistent in all
487 populations, the same relationship between vital rates and temperature (Fig. 7A) may
488 produce both spatial compensation among populations (Fig. 7B) and temporal
489 compensation within populations (Fig. 7C). For example, Doak and Morris (2010) found that
490 vital rates responded similarly to among-year temperature variation in populations
491 throughout the continent-wide ranges of two tundra plants (although they also observed
492 site-specific components of the vital rates). This same vital rate/temperature relationship
493 across a species' range may also produce compensatory responses in the means of different
494 vital rates to trends in average environmental conditions, such as climate warming (Fig. 7D),
495 which in turn may buffer local populations against those environmental trends (although as
496 emphasized by Doak and Morris (2010), such buffering may not last indefinitely).

497 However, a given vital rate may not follow the same relationship with an
498 environmental driver in all populations, in particular if there is adaptation to local conditions
499 across a species range. If the responses of one or more vital rates to the same
500 environmental driver differ among populations, then we may observe spatial compensation,
501 temporal compensation, both, or neither (Fig. 8). We might also find for some taxa that vital
502 rates covary positively along the most favorable stretches of environmental gradients
503 (perhaps due to fewer resource limitations) and demographic compensation is thus more
504 restricted to environmental – and geographical - extremes. To fully understand which types
505 of demographic compensation are operating and in which populations, we must measure
506 the relationships between vital rates and environmental drivers in multiple populations

507 spanning the conditions experienced across the species' range. Although doing so would
508 require longer and larger scale demographic studies, as well as measurements of potential
509 drivers, it would yield better insight into the nature and mechanisms of demographic
510 compensation than simply analyzing patterns in the correlations of mean vital rates among
511 populations. Once the relationships between vital rates and environmental drivers are
512 established, we could compute mean values of vital rates across species' ranges given local
513 environmental conditions, and test for the presence of demographic compensation with
514 randomization procedures as we did here. However, our ability to do so at present is
515 severely limited by the fact that very few studies have quantified the relationships between
516 demographic processes and environmental conditions at large geographical scales or across
517 multiple populations (but see Doak & Morris 2010; Eckhart *et al.* 2011; Villellas *et al.* 2013a).
518 More such studies are clearly needed.

519 Knowing how vital rates respond to environmental drivers would also be valuable for
520 predicting shifts in species' geographical ranges induced by climate change. The dominant
521 methodology now used to forecast range shifts is species distribution models (SDMs; also
522 known as niche or climate envelope models), which correlate known presences (and
523 sometimes absences) of a species with environmental factors (Elith & Leathwick 2009). An
524 alternative would be to use multi-site demographic models with vital rates tied to specific
525 environmental drivers to identify locations where populations can increase (Merow *et al.*
526 2014) or where equilibrium abundance is above zero (Ehrlén & Morris 2015). SDMs and
527 demographic models don't always make the same assessments of the environmental
528 suitability where present-day populations are found (Eckhart *et al.* 2011, Gerst *et al.* 2011,
529 Pironon *et al.* 2015), so their predictions about future range shifts may not be consonant. In
530 particular, while demographic models can account explicitly for demographic compensation,

531 it would seem a significant challenge for SDMs to correctly predict the consequences of
532 ongoing compensation in the face of climatic trends of the sort shown in Fig. 7D, as more
533 extreme climates not experienced by current populations would be inferred by SDMs to be
534 outside the “climate envelope”, even though compensation could allow populations to
535 persist under those extremes. But it remains to be seen whether more mechanistic,
536 demographic models will do a better job of predicting future range shifts than purely
537 correlational, but simpler, SDMs.

538 An issue that has not been addressed in this study is the role played by phenotypic
539 plasticity and local adaptation in the variation in mean vital rates among populations. The
540 relative roles played by phenotypic plasticity vs. local adaptation in shaping the
541 performance of a species across its range are still vigorously debated (Sultan 2004; Sexton *et*
542 *al.* 2009; Valladares *et al.* 2014). Both of these processes, alone or in combination, could be
543 responsible for improvements in some vital rates that compensate for deterioration of
544 others near range limits (Fig. 9). Only by performing field reciprocal transplants or
545 laboratory experiments under controlled environmental conditions will we be able to
546 partition the roles played by phenotypic plasticity and local adaptation in demographic
547 compensation.

548 Demographic compensation and life-history tradeoffs are related, but not necessarily
549 identical, phenomena. The strongest indicator of a life-history tradeoff is a negative genetic
550 correlation between two fitness components in a set of genotypes or families, typically from
551 the same population, such as when genotypes with higher early-life reproduction show
552 lower subsequent survival, growth, or reproduction (Reznick 1992; Roff 1992). However,
553 negative correlations between fitness components (also known as vital rates) across
554 populations - or even species - have also been interpreted as the result of natural selection

555 acting on life histories in the face of negative genetic correlations (Stearns 1992). Thus fixed
556 genetic differences between populations could both underlie negative correlations between
557 mean vital rates (i.e., demographic compensation) and reflect the consequences of life-
558 history tradeoffs. In this context, an interesting question is whether vital rates of different
559 genotypes within populations show negative correlations that are similar to those between
560 mean vital rates across populations. But demographic compensation could also arise if all
561 populations contain a single, but plastic, genotype, provided that plasticity in different vital
562 rates leads to opposing changes in mean vital rates across populations. Clearly, the
563 relationship between demographic compensation and life-history tradeoffs deserves more
564 attention in the future.

565 An important caveat of our analysis is that the demographic studies we analyzed did
566 not manipulate intraspecific density, or use statistical methods to distinguish the impact of
567 density from the impact of environmental factors on the patterns of vital rate variation
568 among populations. In fact, given that demographers have a practical tendency to conduct
569 their studies where the focal species is fairly abundant, the populations we analyzed were
570 likely to have been at or even above the local carrying capacity (Buckley *et al.* 2010),
571 although a few studies claimed that density effects in the monitored populations were
572 negligible (Werner & Caswell 1977; Ehrlén 1995; Valverde & Silvertown 1998; Kaye *et al.*
573 2001). As Birch (1953) and others have argued, the population growth rate at low density
574 (i.e., the finite rate of increase) is perhaps the most cogent indicator of the potential
575 geographical range of a species. Thus to assess the role that demographic compensation
576 plays in increasing a species' range, we would want to know how it operates at low density,
577 but what we know best is likely to be how it operates near carrying capacity. However, the
578 effect of environmental factors and intraspecific density on the vital rates need not be

579 additive, and disentangling whether vital rates show similar patterns of demographic
580 compensation at low and high density remains an important unsolved challenge.

581 Our analysis only involved demographic studies of plants. Fewer multi-population
582 demographic studies have been conducted for animal species than for plants (but see, e.g.,
583 Martone & Micheli 2012), making it more difficult to assess the frequency of demographic
584 compensation for animals. Future comparative analysis, as more studies spanning the
585 ranges of animals become available, would advance our knowledge of whether
586 demographic compensation is a general feature of living organisms. The growing availability
587 of data sets such as COMPADRE and COMADRE (Salguero-Gómez *et al.* 2015) may make
588 such analyses increasingly feasible, although these databases would be even more useful if
589 they reported vital rates directly, so that they did not have to be extracted from the matrix
590 elements as we did here.

591 The fact that we found strong evidence for demographic compensation when we
592 analyzed demographic studies that measured all vital rates suggests that we may fail to
593 understand the demographic causes of geographical range limits if we consider only one or
594 a few processes in the life cycle. This is especially true in light of evidence presented here
595 that demographic compensation commonly takes place between rates of different
596 processes or stages. The demography of multiple populations should be quantified as
597 comprehensively as possible in order to understand the mechanisms responsible for the
598 sizes of species' geographical ranges. On the other hand, if additional studies strengthen
599 generalities about which processes are usually involved in demographic compensation, this
600 information may help us to save time or money in monitoring by targeting efforts on
601 processes that most frequently present opposing patterns of variation across gradients. One

602 well-studied example is the tradeoff between survival and growth rates of conifers that
603 appears at multiple scales and for multiple species (Bigler & Veblen 2009).

604 Demographic compensation, through negative correlations between vital rates,
605 seems to be a relatively common phenomenon across populations of plant species,
606 although our ability to detect it depends on the spatial and temporal scope of a study. We
607 have started to untangle some mechanisms whereby demographic compensation takes
608 place, such as the involvement of vital rates of differing demographic processes or life
609 stages. In addition, the high sensitivity and variance found in the vital rates involved in
610 negative correlations strongly suggest that demographic compensation has not arisen as a
611 random phenomenon, but as an advantageous process with potential evolutionary
612 implications in terms of species performance and geographical distribution. Of course, the
613 detection of demographic compensation in multi-population demographic studies does not
614 discount the possibility that some species may persist in a variable world by means of small
615 ranges with little environmental variation, or by narrowly tracking particular environmental
616 conditions over broader areas (i.e., extreme habitat specialists). Finally, we found in our
617 study that, on average, negative correlations between vital rates reduce by half the variance
618 among population growth rates, a reduction likely underestimated due to constraints of the
619 analysis. Demographic compensation thus might be crucial for understanding the current
620 distribution of species and accurately predicting range shifts in the face of ongoing
621 environmental changes. At present, a scarcity of studies with large temporal and spatial
622 scales limits our ability to further analyze this phenomenon. However, a growing
623 accumulation of demographic data - particularly for underlying vital rates - for species with a
624 variety of life histories and environments, coupled with information on the biotic and abiotic

625 drivers of those vital rates, can only improve our ability to understand demographic
626 compensation and its consequences in the future.

627

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908 **Tables**

909 **Table 1** Characteristics of the studies used to assess demographic compensation. In Life-form, species were assigned to one of two categories:
 910 S (short-lived) for annual and short-lived perennial plants, and L (long-lived) for other longer-lived life forms (we used the life-forms provided
 911 by authors in the studies). We also provide information on habitat and location of the study (US = United States, UK = United Kingdom, CR =
 912 Czech Republic), on the environmental/geographical factor (unknown or unclear for some studies), and on the number of populations (“N
 913 pops”), years (“N Yrs”), vital rates (“N rates”) and life stages (“N stages”). In number of rates, the parenthesis shows the rates finally used after
 914 discarding less important/reliable ones (See *Calculation of vital rates* in Appendix S1).

915

Study	Species	Life-form	Habitat - Location	Environmental factor	N Pops	N Yrs	N rates	N stages
1 - Bruna (2003)	<i>Heliconia acuminata</i>	L (long-lived perennial herb)	Amazonian forest; Brazil	Forest fragmentation	13	2	31 (25)	6
2 - Davelos & Jarosz (2004)	<i>Castanea dentata</i>	L (deciduous tree)	Eastern deciduous forest; Michigan, US	Pathogen	6	4	30 (26)	8

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918 **Table 1 (cont).**

Study	Species	Life-form	Habitat - Location	Environmental factor	N Pops	N Yrs	N rates	N stages
3 - Davison et al. (2010)	<i>Anthyllis vulneraria</i>	S (short-lived perennial herb)	Calcareous grassland; Belgium	Unknown	9	3	14 (14)	4
4 - Doak & Morris (2010)	<i>Silene acaulis</i>	L (long-lived perennial cushion)	Boreoalpine habitats; US, Canada	Range position, climate	17	5	71 (53)	12+
5 - Doak & Morris (2010)	<i>Polygonum viviparum</i>	L (long-lived perennial herb)	Boreoalpine habitats; US, Canada	Range position, climate	16	5	189 (43)	13
6 - Eckhart et al. (2011)	<i>Clarkia xantiana</i>	S (winter annual herb)	Sandy soil slopes; California, US	Range position	20	4	13 (13)	3+
7 - Ehrlén (1995)	<i>Lathyrus vernus</i>	L (long-lived perennial herb)	Mixed forests; SE Sweden	Unclear	6	3	31 (31)	7+
8 - Endels et al. (2007)	<i>Primula vulgaris</i>	L (long-lived perennial herb)	Ditch banks, rivulets; N Belgium	Disturbance	10	3	30 (26)	6

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921 **Table 1 (cont).**

Study	Species	Life-form	Habitat - Location	Environmental factor	N Pops	N Yrs	N rates	N stages
9 - Ghimire et al. (2008)	<i>Nardostachys grandiflora</i>	L (long-lived perennial herb)	Rocky outcrop, meadows; Himalaya	Harvesting	6	3	27 (24)	6
10 - Hunt (2001)	<i>Atriplex vesicaria</i>	L (long-lived perennial shrub)	Paddocks; S Australia	Distance to water	9	1	16 (15)	4
11 - Hyatt & Araki (2006)	<i>Polygonum perfoliatum</i>	S (annual vine)	Roadsides, fields; Pennsylvania, US	Unknown	6*	2	11 (11)	7+
12 - Jacquemyn & Bris (2008)	<i>Primula elatior</i>	L (long-lived perennial herb)	Temperate forests; Belgium	Forest age	7	3	15 (15)	5
13 - Jiménez-Sierra et al. (2007)	<i>Echinocactus platyacanthus</i>	L (cactus)	Semiarid valley; Mexico	Unknown	6	2	19 (19)	7+
14 - Jongejans et al. (2010)	<i>Carlina vulgaris</i>	S (short-lived perennial herb)	Grasslands; Sweden, Germany, CR	Unknown	8	2	16 (15)	4

924 **Table 1 (cont).**

Study	Species	Life-form	Habitat - Location	Environmental factor	N Pops	N Yrs	N rates	N stages
15 - Jongejans et al. (2010)	<i>Tragopogon pratensis</i>	S (short-lived perennial herb)	Grasslands; Holland, CR	Unknown	6	2	16 (15)	4
16 - Jongejans et al. (2010)	<i>Hypochaeris radicata</i>	S (short-lived perennial herb)	Grasslands; Holland, Germany, CR	Unknown	6	2	44 (41)	6
17 - Kaye et al. (2001)	<i>Lomatium bradshawii</i>	L (long-lived perennial herb)	Prairies; Oregon, US	Fire	6	5	32 (25)	6
18 - Kaye & Pyke (2003)	<i>Haplopappus radiatus</i>	S (short-lived perennial herb)	Arid rangelands; Oregon, US	Grazing exclosure	10	8	13 (13)	4
19 - Knight et al. (2009)	<i>Trillium grandiflorum</i>	L (long-lived perennial herb)	Deciduous forests; Pennsylvania, US	Herbivory	12	3	13 (13)	6
20 - Lofgren et al. (2000)	<i>Carlina vulgaris</i>	S (short-lived perennial herb)	Semi-natural pastures; Sweden	Unknown	8	2	6 (6)	3

927 **Table 1 (cont).**

Study	Species	Life-form	Habitat - Location	Environmental factor	N Pops	N Yrs	N rates	N stages
21 - McCauley & Ungar (2002)	<i>Froelichia floridana</i>	S (annual herb)	Sandy soils; Ohio, US	Unclear	6*	2	11 (11)	5+
22 - Münzbergová (2007)	<i>Aster amellus</i>	L (long-lived perennial herb)	Open xerothermic habitats; CR.	Ploidy, habitat productivity	9	3	8 (8)	3
23 - Piñero et al 1984	<i>Astrocaryum mexicanum</i>	L (palm tree)	Tropical rain forests; Mexico	Density	6	1	36 (36)	14+
24 - Valverde & Silvertown (1998)	<i>Primula vulgaris</i>	L (long-lived perennial herb)	Decidious temperate forests; UK	Canopy openness	8	2	20 (19)	5
25 - Vilellas et al. (2013)	<i>Plantago coronopus</i>	S (short-lived perennial herb)	Coastal habitats; coasts in Atlantic Europe	Range position, climate	11	3	17 (17)	4
26 - Werner & Caswell (1977)	<i>Dipsacus sylvestris</i>	S (short-lived perennial herb)	Late-succession fields; Michigan, US	Unknown	8	4	20 (20)	7+

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930 **Table 1 (cont).**

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932 * Manipulated (McCauley & Ungar 2002) or invasive (Hyatt & Araki 2006) populations were discarded for this study.

933 † Studies including seed bank stages.

934 **Figure legends**

935

936 **Fig. 1.** Consequences of demographic compensation for geographical range size
937 (represented by red arrows). (A) In the absence of demographic compensation both vital
938 rates (lines of different colour) decline along the geographical gradient (e.g., latitude or
939 elevation) until the range limit at L_1 is reached (C), beyond which populations cannot
940 increase from low density. (B) With demographic compensation, vital rates change in
941 opposite directions (line thickness is proportional to the influence of each vital rate on the
942 population growth rate, i.e., to that rate's sensitivity). Improvements in one vital rate cause
943 the population growth rate to decline less steeply (D), resulting in range limit L_2 and a larger
944 range size than would be true in the absence of demographic compensation.

945

946 **Fig. 2.** Percentage of correlations between vital rate contributions that are significantly
947 negative, and thus involved in demographic compensation. Vital rates are classified by (A)
948 type of demographic process or (B) life stage. Left panels: short-lived species; middle panels:
949 long-lived species; right panels: results for all species comparing grouped pairs of the same
950 vs. different process (A) or stage (B). Groups sharing lower case letters above the bars do
951 not differ significantly within each category, according to post-hoc analyses (see Appendix
952 S1). Abbreviations of 1) Demographic processes: Fec=fecundity; Rec=recruitment;
953 Sur=survival; Gro=growth; Shr=shrinkage; 2) Life stages: Early, Middle and Late; and 3) Vital
954 rate similarity: Diff=different type of process or stage; Same=same type of process or stage.

955

956 **Fig. 3.** Sensitivity and variance of vital rates grouped by process. The magnitudes of the
957 sensitivities and variances differed greatly among vital rates and species, so we computed

958 the median (rather than the mean) across vital rates for each process and then the median
959 of those across species. Note the logarithmic y axis. Processes are recruitment, survival,
960 growth, shrinkage, and fecundity.

961

962 **Fig. 4.** Proposed relationships between sensitivity, variance, and LTRE contributions of vital
963 rates, and demographic compensation across multiple populations. Vital rates with high
964 influence on population growth rates (i.e., high sensitivity) and with high variance among
965 populations are expected to show a high contribution to the differences in population
966 growth rates, which in turn is expected to promote the participation of these rates in
967 demographic compensation. However, sensitivity might also have an opposite indirect effect
968 through its indirect negative correlation with variance (dashed arrow).

969

970 **Fig. 5.** Percentage of correlations between vital rate contributions that are significantly
971 negative, and thus involved in demographic compensation, depending on LTRE
972 contributions (C), variance among populations (V) and sensitivity (S). Vital rates were
973 grouped in two ways, depending on whether their C, V and S values were above or below
974 the median across all rates for a species: low vs. high contribution (left panel), and the four
975 possible combinations of high vs. low sensitivity and high vs. low variance (right panel).
976 Groups sharing a letter above the bars do not differ significantly within each category,
977 according to post-hoc analyses (see Appendix S1).

978

979 **Fig. 6.** Spatial correlations between mean annual vital rates for populations of the tundra
980 plant *Silene acaulis* across North America (Doak and Morris 2010). The corrgrams (sensu
981 Friendly 2002) shown are simply colour-coded correlation matrices; darker red indicates

982 increasingly negative correlations, and darker blue indicates increasingly positive
983 correlations. Each row and column represents a different vital rate, and as the correlation
984 matrix is symmetrical about the diagonal, only the upper right portion of the matrix is
985 shown. (A) Vital rates grouped by life stage (S = seeds and seedlings; numbers indicate
986 successively larger size classes for plants older than seedlings). (B) Vital rates grouped by
987 demographic process (R = rates governing recruitment of seedlings; rates are ordered by
988 size class within type of process). More pattern is revealed in B than in A.

989

990 **Fig. 7.** Three types of compensation may all be driven by (A) the same opposing trends in
991 different vital rates (red vs. blue) in response to environmental drivers (such as
992 temperature) in all populations: (B) spatial compensation across populations; (C) temporal
993 compensation within one population; and (D) compensation against environmental trends,
994 e.g., climate warming, within one population.

995

996 **Fig. 8.** If the responses of vital rates to environmental drivers (e.g., temperature) are not the
997 same in two populations (in contrast with Fig. 7), we may not observe all types of
998 demographic compensation simultaneously. All combinations of presence/absence of
999 spatial and temporal compensation between two vital rates (red vs. blue) for two
1000 populations are shown here (A-D). Spatial compensation involves changes in opposite
1001 directions in the temporal mean vital rates between populations (note that with spatial
1002 compensation, the mean of the red rate is higher in the northern than in the southern
1003 population, but the opposite is true of the blue rate), while temporal compensation involves
1004 changes among years in opposite directions in the two rates within single populations.
1005 Vertical dashed lines show mean temperatures and two-headed arrows show the range of

1006 temperatures experienced by each population. For simplicity, we have assumed that both
1007 rates change linearly with temperature.

1008

1009 **Fig. 9.** Two mechanisms that may produce an improvement in a vital rate (here,
1010 individual growth) in peripheral populations. Doak and Morris (2010) found that the growth
1011 rates of small individuals of two tundra plant species were higher in populations near the
1012 southern range limits, which compensated for deterioration in other vital rates. Higher
1013 plant growth could reflect (A) phenotypic plasticity (PP); (B) local adaptation (LA); or (C) a
1014 combination of the two processes. G_s , G_n and T_s , T_n correspond to individual growth rates
1015 and temperature in southern and northern populations, respectively. G_n^* is the growth rate
1016 plants from the northern population would show if grown at the mean temperature for the
1017 southern population. Populations share genotypes in A), but not in B) and C), where each
1018 colour represents a different (locally adapted) set of genotypes. Demographic compensation
1019 would require a second vital rate to follow opposite patterns to those shown here.

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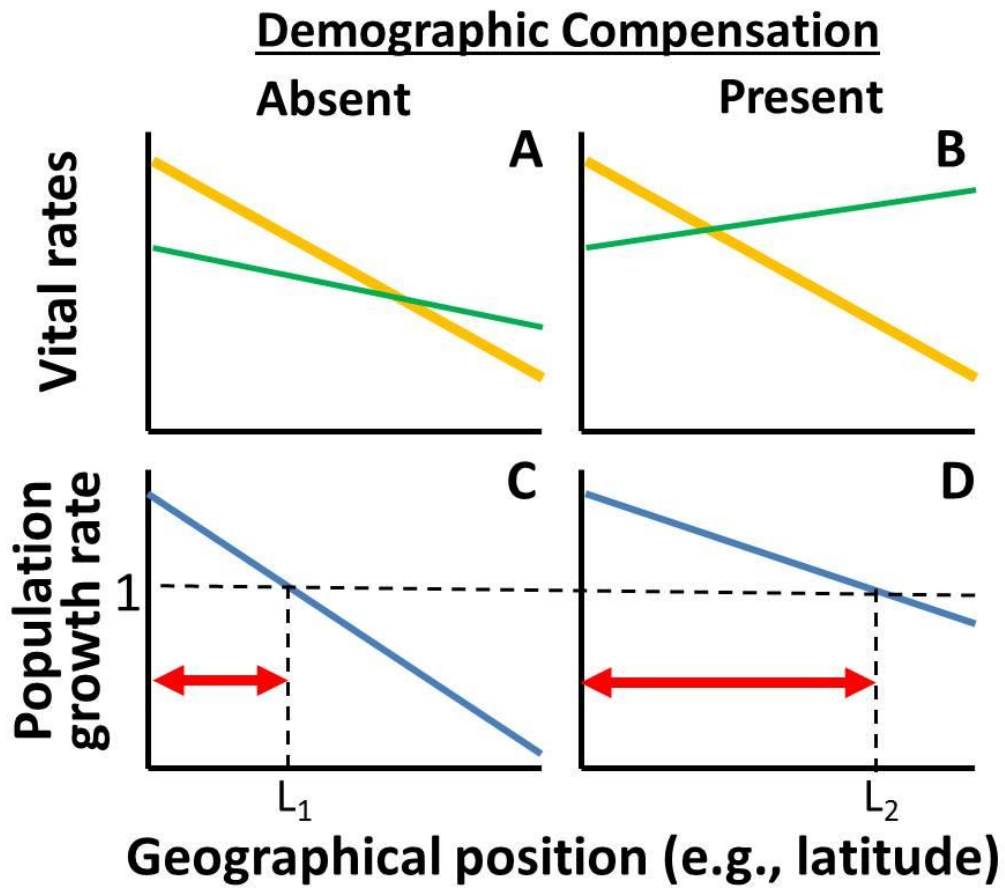
1030 **Figures**

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1032 **Fig. 1**

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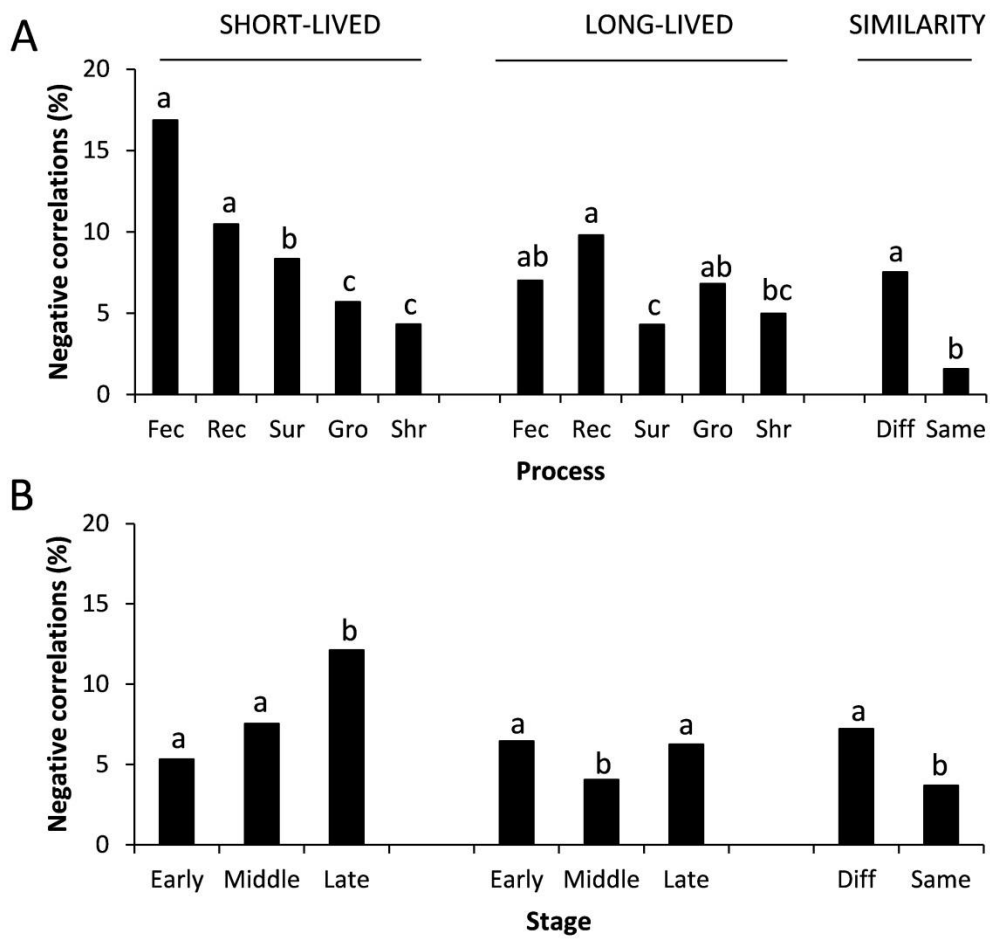
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1042 **Fig. 2**

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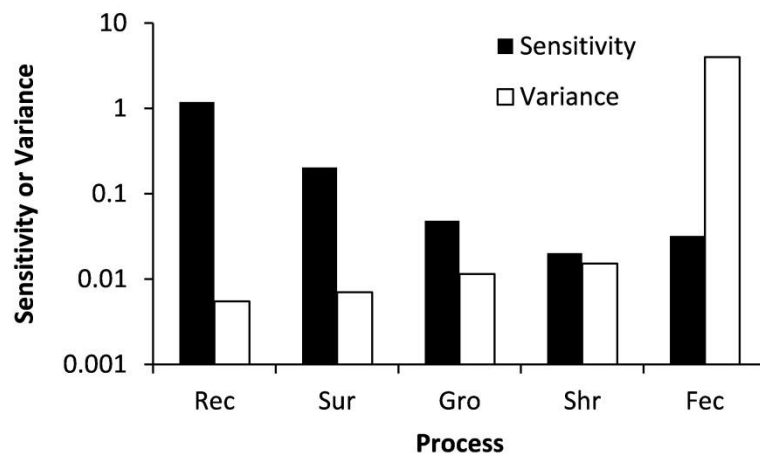
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1054 **Fig. 3**

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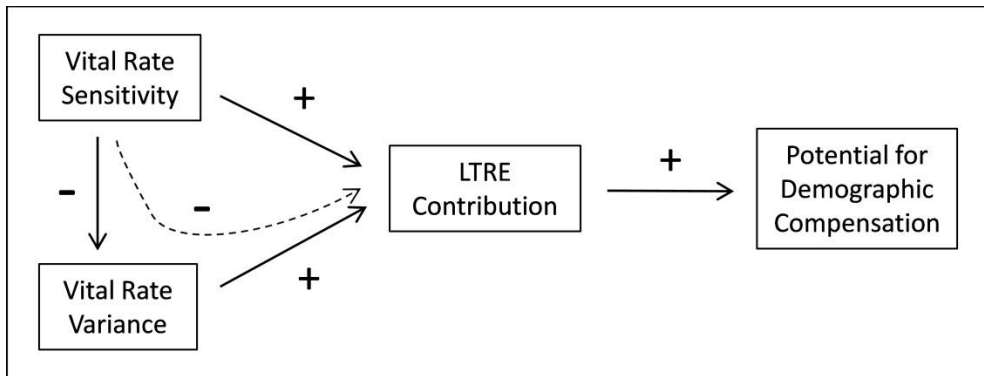
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1072 Fig. 4

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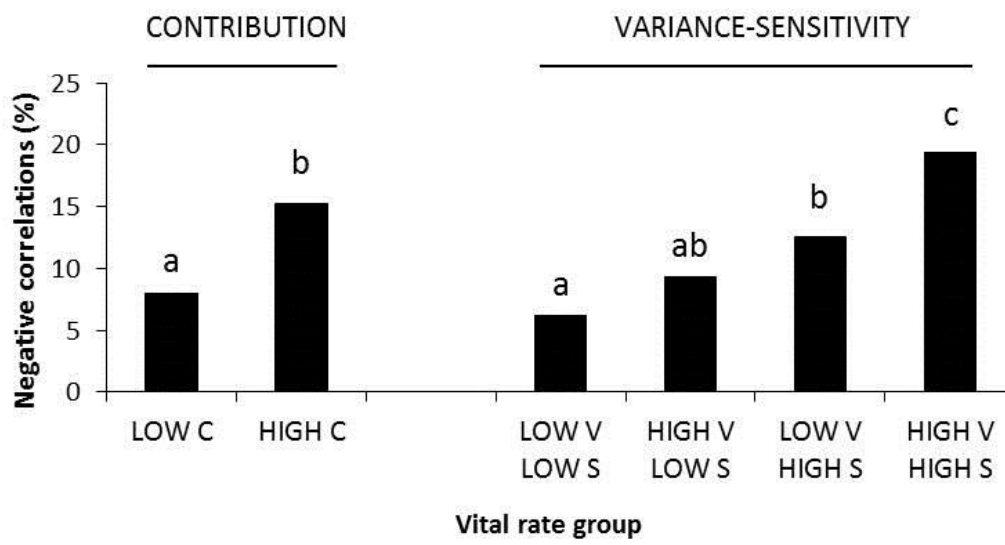
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1080 Fig. 5

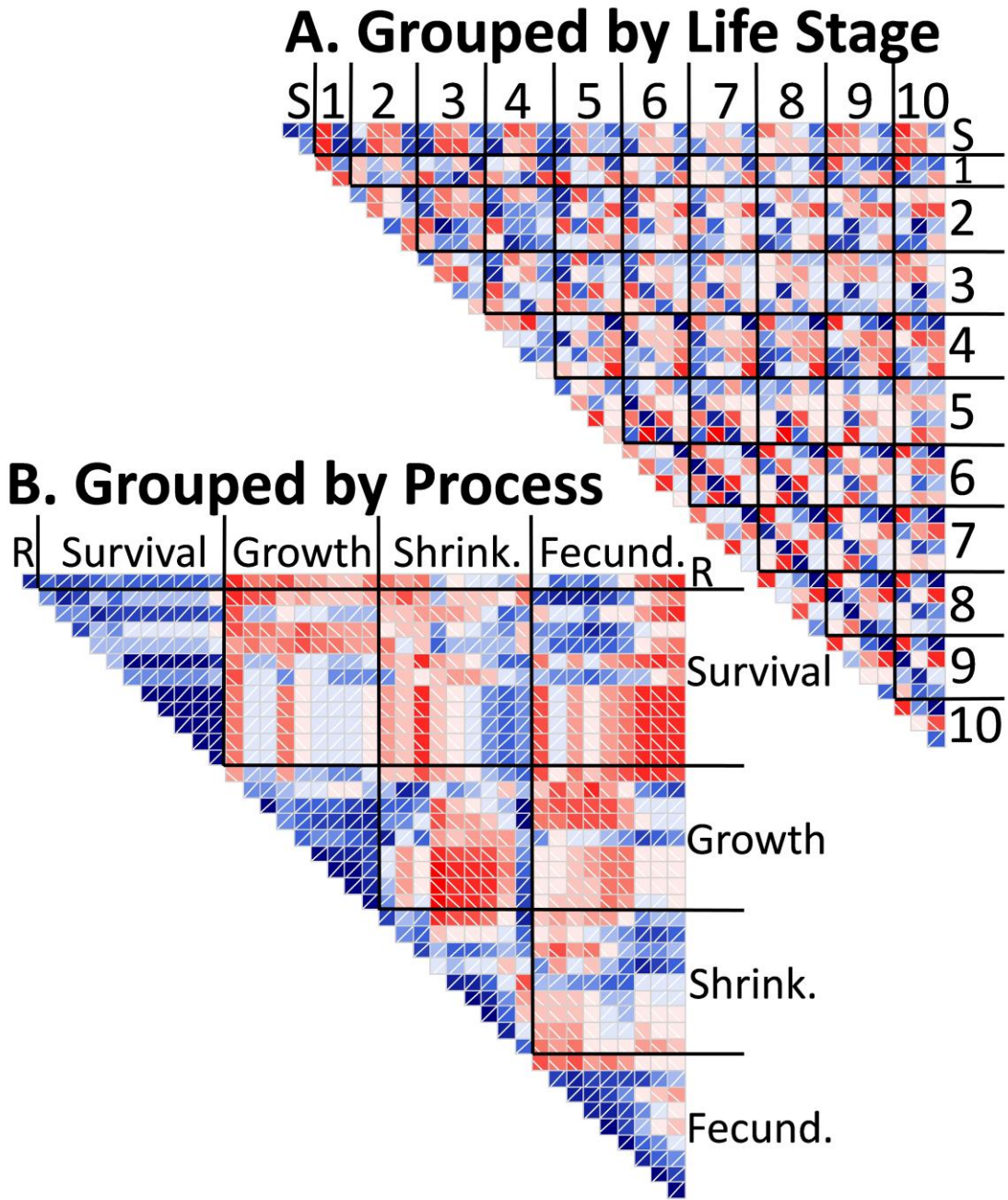
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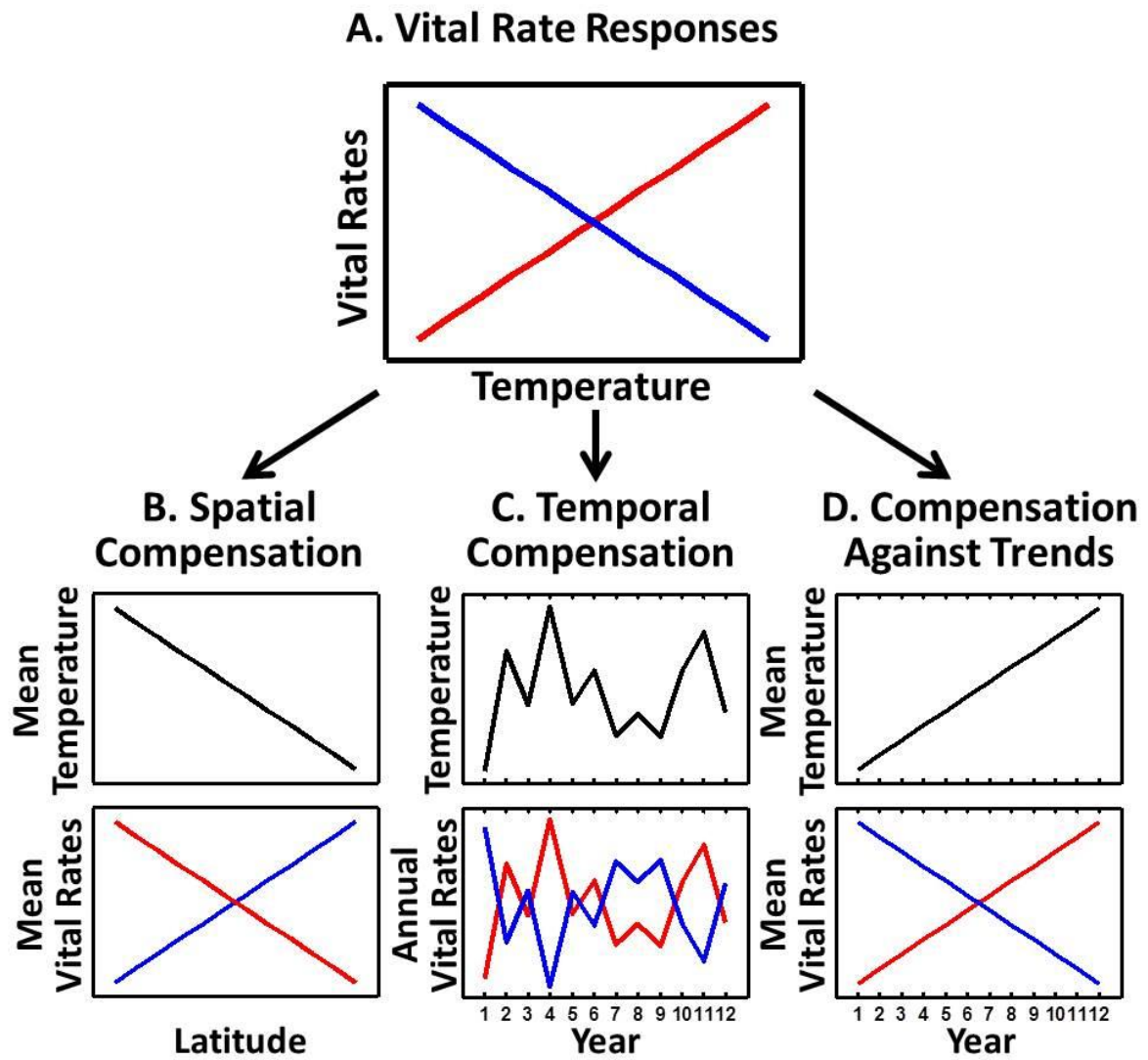


1088 Fig. 7

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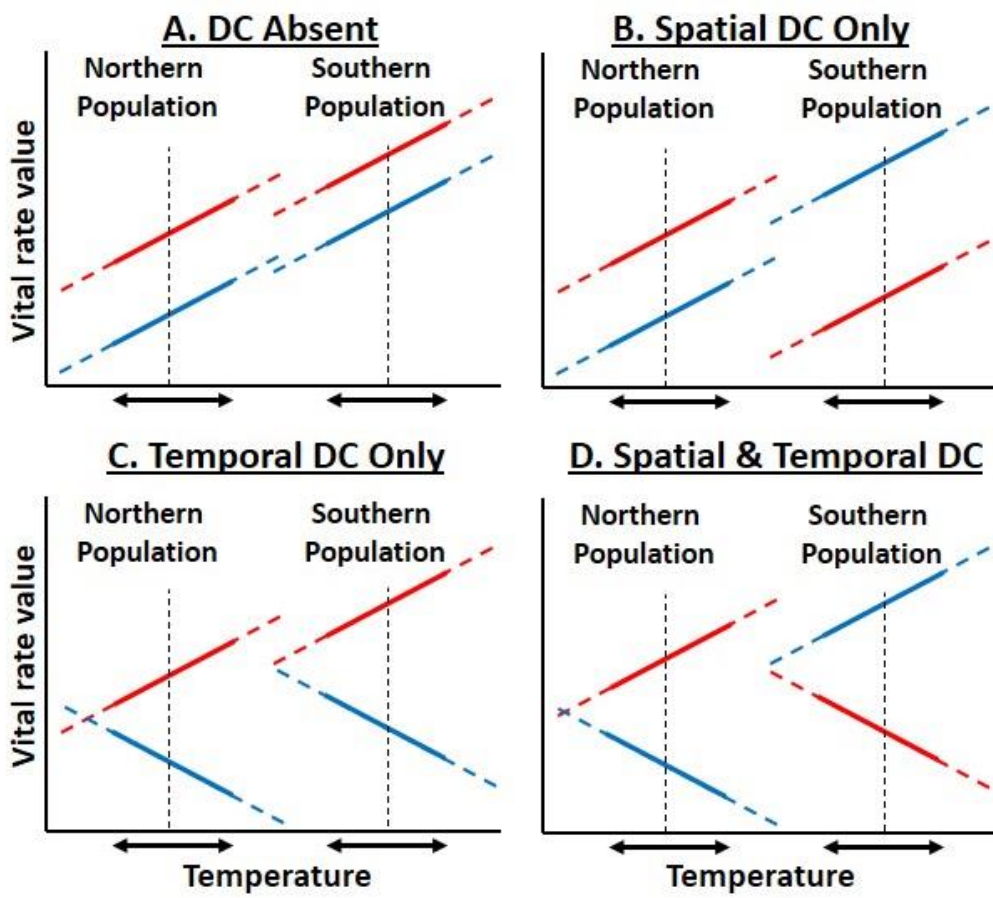


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1094 Fig. 8

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1098 Fig. 9

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