

1 **Title:** Vital rates contribute differently to impacts of competition on  
2 population growth

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7

8 **Running title:** Competitive population dynamics of perennial plants

9

10 **Key words:** Competition, coexistence, complementary response, elevation gradient, integral  
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12

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14

#### 15 **Authorship**

16 J.M.A. designed the field experiment. S.L. and J.M.A. collected the data. S.L. and J.M.A.  
17 conceived the research questions. S.L. conducted the data analyses and wrote the  
18 manuscript with input from J.M.A.

19

#### 20 **Data availability statement**

21 The data underlying the results presented in the manuscript will be available on Figshare. All  
22 R scripts used for population modelling and statistical analyses will be available on GitHub.

23

24 The manuscript includes an abstract (140 words) and main text (4996 words) with  
25 introduction (870 words), material and methods (1438 words), results (1060 words) and  
26 discussion (1628 words). It has 38 references, 1 table, 3 figures and 1 supplementary  
27 document.

28

29 **Abstract**

30 Competition is among the most important factors regulating plant population and community  
31 dynamics, but it is not well understood how different vital rates respond to competition and  
32 jointly mediate competitive population dynamics and species coexistence. We used integral  
33 projection models (IPMs) to model the population growth of 112 pairwise combinations of 14  
34 competing herbaceous plant species across an elevation gradient ( $n = 324$  IPM models in  
35 total). We showed that the response of individual growth and seedling establishment  
36 contributed most strongly to competition-induced declines in population growth compared to  
37 survival, flowering probability and fecundity that frequently showed complementary  
38 responses that occurred in 92% of species pairs. Complementary responses significantly  
39 promoted population growth under competition by 22% on average and strengthened  
40 species coexistence. Our study emphasises the need to investigate demographic processes  
41 to better understand competitive population dynamics and species coexistence.

42

## 43 INTRODUCTION

44 Species' demographic responses to their abiotic and biotic environments are underlain by  
45 the responses of individual vital rates (Goldberg *et al.* 2001; Doak & Morris 2010; Radchuk  
46 *et al.* 2013). For example, responses of plant populations to competition can result from the  
47 suppression of survival (e.g., Olsen *et al.* 2016; Nomoto & Alexander 2021), individual  
48 growth (e.g., Williams & Crone 2006) or reproduction (e.g., Fréville & Silvertown 2005;  
49 Crandall & Knight 2018). Nonetheless, different vital rates might respond to competition, or  
50 other environmental perturbations, to different extents or even in different directions  
51 (Goldberg *et al.* 2001; Doak & Morris 2010). Assessing such variation is important for  
52 understanding whether particular vital rates have an especially strong bearing over  
53 competitive population dynamics, how different vital rates combine to mediate population  
54 growth under competition, and what consequences this has for species coexistence.

55

56 Vital rates of individual plants may respond to competition in different ways. First, vital rates  
57 may differ in the magnitude, but not direction, of their response to competition. For example,  
58 competition can exert stronger negative effects on individual growth than on survival (e.g.,  
59 Howard & Goldberg 2001; Liancourt *et al.* 2005). Secondly, vital rates may respond to  
60 competition in opposite directions, that is displaying complementary responses, with some  
61 vital rates suppressed but others improved by neighbours (e.g., Howard & Goldberg 2001;  
62 Doak & Morris 2010). Although such differential responses of vital rates are well established,  
63 we know less about how different vital rates quantitatively contribute to, or offset, the  
64 declines in population growth caused by competition. Quantifying these contributions can be  
65 challenging, partly because while measuring vital rate responses to competition is  
66 straightforward, combining these into estimates of population growth is more empirically and  
67 analytically demanding. Furthermore, the magnitude of a vital rate response to competition  
68 does not itself inform directly about that vital rate's contribution to competitive outcomes.  
69 This is because population growth may not be equally sensitive to changes in all vital rates  
70 (i.e., vital rate sensitivity, Caswell 2001). Demographic models provide a way to quantify the  
71 relative contributions of different vital rates to changes in population growth in response to  
72 environments, and thus can provide insights into the processes regulating population  
73 dynamics (Caswell 2001; Ellner *et al.* 2016).

74

75 Vital rate contributions to competitive population dynamics may also differ between species  
76 and across environmental gradients. Indeed, comparing studies that used demographic  
77 models to study plant competition reveals that the vital rate contributing most strongly to  
78 declines in population growth under competition can differ greatly, ranging from survival  
79 (e.g., Olsen *et al.* 2016; Nomoto & Alexander 2021), to growth (e.g., Williams & Crone

80 2006), fecundity (e.g., Fréville & Silvertown 2005), and clonal production (e.g., Crandall &  
81 Knight 2018). One explanation for such variation is that the population growth of species  
82 with different life-history strategies may be most influenced by different vital rates (Silvertown  
83 *et al.* 1993; Adler *et al.* 2014; Salguero-Gómez *et al.* 2016). In addition, it has been shown  
84 that the effects of neighbours can be highly species-specific (e.g., Gaudet & Keddy 1988;  
85 Goldberg 1996). Therefore, different competitor species may affect population growth of a  
86 focal species most strongly through different vital rates. Another explanation for observed  
87 variation in how vital rates respond to competition could be environments; that is, the  
88 impacts of competition on population growth operate through different vital rates under  
89 different environments (Maestre *et al.* 2005). However, until now we lack a comprehensive  
90 assessment of how vital rate contributions to competitive population dynamics differ across  
91 species and along environmental gradients.

92

93 Environmentally variable and complementary responses of vital rates to competition, if  
94 widespread, might play an important role in mediating competitive population dynamics and  
95 influencing species coexistence. In fact, complementary responses of vital rates to  
96 environments have been frequently documented by recent studies and shown to be able to  
97 help plant species to maintain stable populations near their range edges (i.e., demographic  
98 compensation; Doak & Morris 2010; Vilellas *et al.* 2015; Oldfather *et al.* 2021). For example,  
99 Doak & Morris (2010) showed that individual growth of two tundra plants improved towards  
100 their southern range edges, which buffered the negative impacts of deteriorating survival  
101 and recruitment on population growth, and thus helped maintain persisting populations near  
102 their range borders. Similarly, complementary responses of vital rates to competition may  
103 also buffer competitive effects on population growth and help populations to persist under  
104 competition, but to our knowledge such effects have not yet been clearly documented.

105

106 Here, we investigate how different vital rates respond to competition and jointly contribute to  
107 mediating competitive population dynamics across species and environments. To this end,  
108 we conducted a field experiment in which pairwise combinations of 14 plant species  
109 originating from high and low elevation interacted in three sites across an elevation gradient  
110 in the Swiss Alps. We modeled population growth and underlying vital rates in the absence  
111 and presence of neighbours using integral projection models. With these data, we ask: (1)  
112 Do vital rates differentially contribute to declines in population growth caused by  
113 competition? (2) To what extent do vital rate contributions differ between species and across  
114 an elevation gradient? (3) How often do vital rates show complementary responses to  
115 competition, and to what extent do these responses promote population persistence under  
116 competition?

117

## 118 **MATERIALS AND METHODS**

### 119 **Study sites and species**

120 We established a field experiment in three sites across an elevation gradient (890, 1400 and  
121 1900 m above sea level; hereafter the low, middle and high sites, respectively) in the  
122 western Swiss Alps (Canton de Vaud, 46°10'N, 6°50'E). The mean annual temperature  
123 ranged from 11.4 °C at the low site to 5.9 °C at the high site, while the soil moisture  
124 increased with elevation, as measured between 2019 and 2020 (Lyu & Alexander 2022). We  
125 selected 14 herbaceous species that frequently occur in this region, seven from low and  
126 seven from high elevation (hereafter, lowland and highland species); the species included 12  
127 perennial and two biennial species from different functional types (seven forbs, four grasses  
128 and three legumes; Table 1). Seeds were obtained from local commercial suppliers.

129

### 130 **Field experiment**

131 The field experiment was designed to estimate population growth rates ( $\lambda$ ) of focal species  
132 in the absence and presence of neighbour species (Fig. S1; see also Lyu & Alexander  
133 2022). Within each site, each of the 14 focal species grew in the absence of neighbours and  
134 interacted with eight heterospecific competitors and itself, resulting in 112 (14 focal species x  
135 8 competitors) interspecific pairs and 14 intraspecific pairs. In total, this design gave rise to  
136 3780 individuals ([112 interspecific pairs + 14 intraspecific pairs + 14 no-competition] x 9  
137 individuals x 3 sites). In spring 2017, we first established competitor monocultures for each  
138 species (as competitor species) within each site by sowing 9 g m<sup>-2</sup> viable seeds. These  
139 species established monocultures either in autumn 2017 or 2018 (see Supplementary  
140 Methods). We transplanted individuals of the 14 species (as focal species) raised in a  
141 greenhouse into the established monocultures at 14 cm apart and into no-competition plots  
142 at 25 cm apart.

143

### 144 **Data collection**

145 We collected demographic data by following all focal plants between 2017 and 2020 (Lyu &  
146 Alexander 2022). Survival or death was recorded twice a year at the beginning (May to  
147 June) and end (September) of the growing season. At the peak flowering or fruiting period of  
148 each year (August to September), we surveyed all focal plants to measure size-correlated  
149 morphological traits (the number and length of flowering stalks, ramets or leaves depending  
150 on species), to record whether they flowered or not and to measure the fruits (number and/or  
151 size depending on species). We estimated aboveground dry mass using regression models  
152 fitted using collected plant samples (Supplementary Methods). We estimated the number of  
153 seeds per flower or fruit using regression models fitted using collected fruits (Supplementary

154 Methods). The total number of seeds produced by each reproductive plant was then  
155 calculated as the estimated number of seeds per fruit multiplied by its total number of fruits.  
156 We conducted a separate germination experiment to estimate seed germination and  
157 competition-free seedling establishment of each species (Supplementary Methods). We also  
158 estimated competition-dependent establishment as the probability of survival of focal plants  
159 within their first growing season after transplanting. We estimated the offspring size  
160 distributions (mean and standard deviation) using seedlings raised in the greenhouse.

161

## 162 **Population modelling**

163 We modelled population growth used integral projection models (IPM) that incorporate all  
164 the vital rates (Ellner *et al.* 2016; Supplementary Methods). For each focal species at each  
165 site, we built IPMs describing their intrinsic population growth using plants growing in the  
166 absence of neighbours (hereafter, “intrinsic IPM”) and invasion (low-density) growth rates  
167 using plants invading the established monocultures of competitor species (hereafter  
168 “invasion IPMs”) (Fig. S1). We estimated vital rates by combining the three annual  
169 transitions together, that is, 2017-2018, 2018-2019, and 2019-2020. We compared all  
170 nested models of the full models for each vital rate of each focal species, including plant size  
171 (except for size-independent vital rates), competitor species and site and their interactions,  
172 using the Akaike information criterion corrected for small samples (AICc). We then  
173 parameterized IPMs using the best-fit models. Deterministic population growth rates ( $\lambda$ )  
174 were calculated as the dominant eigenvalue of the resulting matrices of parameterized IPM  
175 models (Caswell 2001; Ellner *et al.* 2016). More detailed information on population modelling  
176 can be found in Lyu & Alexander (2022).

177

## 178 **Estimating contributions of vital rates**

179 We manipulated the parameterized IPMs to decompose the declines in population growth  
180 rates ( $\lambda$ ) caused by competition into the contributions of different vital rates (Fig. S1),  
181 following other studies (e.g., Bruijning *et al.* 2018; Oldfather *et al.* 2021). Specifically, for  
182 each vital rate of a given invasion IPM, we generated a perturbed IPM in which all the vital  
183 rates were the same as the corresponding intrinsic IPM except for the vital rate of interest,  
184 which was extracted from the invasion IPM (i.e., vital rates estimated in the presence of  
185 neighbours). The contribution of that vital rate to the competitive response was quantified as  
186 the differences in  $\lambda$  between the perturbed and intrinsic IPMs (i.e.,  $\lambda_{\text{perturbated}} - \lambda_{\text{intrinsic}}$ ). The  
187 contributions are negative when  $\lambda_{\text{perturbated}} < \lambda_{\text{intrinsic}}$ , indicating the response of the vital rates  
188 to neighbour species had negative effects on  $\lambda$ ; the contributions are positive when  
189  $\lambda_{\text{perturbated}} > \lambda_{\text{intrinsic}}$ , indicating the response of that vital rate had positive effects on  $\lambda$ . Greater

190 absolute values indicate greater contributions, resulting from either large differences in a  
191 given vital rate with vs without competition or high sensitivity of  $\lambda$  to that vital rate, or both  
192 (Caswell 2001). Notably, since vital rates were implemented as size-dependent in the IPMs  
193 (except for seedling establishment), the positive contributions here mean that plants  
194 performed better in the presence of neighbours compared to plants of the same size growing  
195 in the absence of neighbours, although neighbours might reduce individual performance  
196 overall. Note that we excluded *Arnica montana* for this analysis because it had small sample  
197 size due to high mortality and did not flower or reproduce over the course of the experiment,  
198 leading to relatively invariant vital rates between the intrinsic and invasion IPMs (Fig. S2).

199

200 For each invasion IPM (N = 284 in total), we estimated the contributions of five vital rates  
201 that were dependent on competition, that is, survival, growth, flowering probability, fecundity,  
202 and seedling establishment, while other vital rates (germination, competition-free  
203 establishment, and recruit size distribution) were identical between the intrinsic and invasion  
204 IPM models. To facilitate comparison across species and sites, we normalized vital rate  
205 contributions by dividing the absolute values of the contributions of each vital rate by the  
206 sum of total contributions, then reassigning the sign of the effect.

207

### 208 **Assessing the effects of complementary responses on population growth**

209 We first identified vital rates that showed complementary responses in each invasion IPM  
210 (i.e., those that had positive contributions). We substituted all vital rates showing positive  
211 responses with those of the corresponding intrinsic IPM (i.e., vital rates estimated in the  
212 absence of neighbour species). We then calculated population growth rates of the  
213 substituted IPMs (i.e., complementary responses removed;  $\lambda_{\text{substituted}}$ ) and compared  $\lambda_{\text{substituted}}$   
214 with the original  $\lambda_{\text{invasion}}$  (i.e., complementary responses present) to assess the effects of  
215 complementary responses on population growth under competition. Note that we limited the  
216 analyses only to species pairs whose  $\lambda_{\text{invasion}} < \lambda_{\text{intrinsic}}$ , (i.e., indicating competition; N = 264)  
217 to exclude species pairs that experienced directly facilitative effects of neighbours (N = 20;  
218 Fig. S4).

219

### 220 **Statistical analyses**

221 First, we fitted a mixed-effects model to test the extent to which normalized contributions of  
222 vital rates to changes in  $\lambda$  (response variable) differed between vital rates, sites (low, middle  
223 or high), identity of focal and competitor species (two factors) and the elevation origins of  
224 focal and competitor species (two factors; Table S1). We included random intercepts and  
225 slopes of vital rates for focal and competitor species to account for nestedness within the

226 dataset (i.e., two random factors for the identities of focal and competitor species,  
227 respectively), and plot identity as an additional random factor. Secondly, we fitted a similar  
228 model but with a binomial error distribution to test whether the presence or absence of  
229 complementary responses depended on vital rates, site, focal and competitor species and  
230 their elevation origins (Table S1). Thirdly, to assess the effects of complementary responses  
231 on population growth rates (response variable; log-transformed), we fitted a mixed-effects  
232 model to test whether the original invasion growth rates ( $\lambda_{\text{invasion}}$  with complementary  
233 responses present) differed from  $\lambda$  estimated from the substituted IPMs ( $\lambda_{\text{substituted}}$  with  
234 complementary responses removed), and whether the differences between  $\lambda_{\text{invasion}}$  and  
235  $\lambda_{\text{substituted}}$  depended on site (fixed factor) and species (random intercepts for focal and  
236 competitor species). This analysis was limited to the IPMs that contained complementary  
237 responses (N = 239). In all cases, we used likelihood ratio tests to determine the significance  
238 of fixed and random factors. All population modelling and statistical analyses were  
239 conducted in R version 4.0.3 (R Core Team 2020).

240

## 241 **RESULTS**

### 242 **Do vital rates differentially contribute to declines in population growth caused by** 243 **competition?**

244 Competition caused low density population growth rates ( $\lambda$ ) to decline by 55% on average  
245 (Fig. S4 in the Supplementary Information). The contributions of vital rate to declines in  $\lambda$   
246 caused by competition differed significantly among the five vital rates (Fig. 1;  $F_{4, 925} =$   
247  $376.928$ ,  $P < 0.0001$ ; Table S1). On average, reduced growth of individual plants in the  
248 presence of neighbours contributed the most to declines in  $\lambda$  for 11 of the 13 focal species,  
249 with an average proportional contribution of  $-0.671$  (SE =  $\pm 0.037$ ) across species pairs and  
250 sites. Reduced seedling establishment in the presence of neighbours also contributed  
251 markedly to declines in  $\lambda$  under competition, with an average proportional contribution of  $-$   
252  $0.118$  ( $\pm 0.004$ ). The responses of reproduction and survival on average showed only minor  
253 negative effects on  $\lambda$  (proportional contribution of flowering:  $-0.036 \pm 0.011$ ; fecundity:  $-0.052$   
254  $\pm 0.045$ ; survival:  $-0.028 \pm 0.021$ ), resulting partly from the frequent positive contributions of  
255 these vital rates to changes in  $\lambda$  (Fig. 1).

256

### 257 **To what extent do vital rate contributions differ between species and across the** 258 **elevation gradient?**

259 Although most of the focal species suffered the greatest declines in  $\lambda$  from suppressed  
260 individual growth under competition, we observed substantial variation between focal  
261 species (Fig. 2a; significantly different random slopes of vital rates between focal species:

262  $F_{14, 925} = 450.75$ ,  $P < 0.0001$ ; Table S1 and S2). Compared to other species, suppressed  
263 fecundity caused  $\lambda$  of three focal species to decline markedly under competition, with  
264 proportional contributions smaller than -0.1 for *Sesleria caerulea*, *Trifolium badium*, and  
265 *Plantago alpina*. Additionally, the suppressed establishment of seedlings under competition  
266 substantially reduced the  $\lambda$  of three species, with proportional contributions smaller than -0.1  
267 for *T. badium*, *Medicago lupulina*, and *Aster alpinus*. Added to this, vital rate contributions  
268 differed significantly between focal species originating from low and high elevations (vital  
269 rate x focal species origin interaction:  $F_{4, 925} = 15.021$ ,  $P = 0.005$ ; Fig. 2a; Table S1 and S2);  
270 these showed that suppressed individual growth had greater contributions to competition-  
271 induced declines in population growth of lowland species, while suppressed survival and  
272 fecundity had greater contributions for highland species on average (Fig. 2a).

273

274 In contrast to the substantial variation between focal species, vital rate contributions to  
275 declines in  $\lambda$  were more consistent, though still significantly different, between competitor  
276 species (Fig. 2b; significantly different random slopes between competitor species:  $F_{14, 925} =$   
277  $32.44$ ,  $P = 0.003$ ; Table S1 and S2). Specifically, three competitor species reduced  $\lambda$   
278 through particularly strong effects on fecundity (proportional contributions were smaller than  
279 -0.1 when competing against *T. badium*, *M. lupulina*, and *Salvia pratensis*) and three species  
280 through particularly strong impacts on seedling establishment (proportional contributions  
281 were smaller than -0.1 when competing against *S. pratensis*, *P. alpina*, and *Anthyllis*  
282 *vulneraria* ssp. *alpestris*). In addition, we found that vital rate contributions did not differ  
283 significantly when competing against lowland vs highland species (Fig. 2b; vital rates x  
284 competitor species origins interaction:  $F_{4, 925} = 1.423$ ,  $P = 0.840$ ; Table S1 and S2).

285

286 The contributions of vital rates to the declines in  $\lambda$  differed significantly across the elevation  
287 gradient (Fig. 2c; vital rate x site interaction:  $F_{8, 925} = 29.706$ ,  $P = 0.0002$ ; Table S1).  
288 Suppressed survival due to neighbours had the most negative impacts on  $\lambda$  at the low  
289 elevation site, but this shifted to positive effects on survival at the high elevation site.  
290 Similarly, suppressed seedling establishment by competition affected  $\lambda$  most strongly at the  
291 lower two sites and only slightly at the high site. In contrast, the responses of flowering to  
292 neighbours appeared to contribute most negatively at the low and high sites but the least at  
293 the middle site. Nonetheless, the contribution of growth and fecundity responses showed no  
294 clear trend across the elevation.

295

296 **How often do vital rates show complementary responses to competition?**

297 Complementary vital rate responses to neighbours were found in 92% (243 of 264) of  
298 species pairs; that is, at least one vital rate in these invasion IPMs responded positively to  
299 competition, despite neighbours causing population growth rate to decline. Across all  
300 species pairs, 28.3% (373 of 1320) of vital rates showed complementary responses. The  
301 occurrence of complementary responses differed significantly between vital rates and focal  
302 species (Fig. 1 & 2a; significantly different random slopes of vital rates between focal  
303 species:  $F_{14, 925} = 164.71$ ,  $P < 0.0001$ ; Table S1). Enhanced size-specific flowering in the  
304 presence of neighbours was observed in 79% of species pairs, followed by survival (47%)  
305 and fecundity (46%). In contrast, individual growth or seedling establishment rarely  
306 responded positively and were only found among 5% and 6% of species pairs, respectively  
307 (Fig. 1). Note that, because these vital rates were implemented as size-dependent in the  
308 IPMs (except for seedling establishment), the positive responses of flowering, survival and  
309 fecundity observed here do not necessarily mean that plants had a greater chance to flower,  
310 survive or produce more seeds in the presence of neighbours; rather, it means that plants  
311 performed better in the presence of neighbours compared to plants of the same size growing  
312 in the absence of neighbours. For example, individuals in the presence of neighbours might  
313 produce less seeds overall but produce more seeds per unit of biomass compared to those  
314 in the absence of neighbours.

315

### 316 **To what extent do complementary responses promote population persistence under** 317 **competition?**

318 Invasion growth rates ( $\lambda_{\text{invasion}}$ ) estimated from IPMs with complementary responses present  
319 were, on average, 22.6% ( $\pm 4.5\%$ ) greater compared to models with complementary  
320 responses removed (Fig. 3;  $F_{1, 478} = 10.908$ ,  $P = 0.0009$ ). The effects of complementary  
321 responses were sufficient to lead to shifts from predictions of population declines to  
322 population persistence under competition in 5% (14 of 239) of cases (Fig. 3). Consistently,  
323 complementary responses significantly strengthened species coexistence (Fig. S8), and for  
324 7.4% (8 of 107) of species pairs, complementary responses were sufficient to shift the  
325 competitive outcome, either from competitive exclusion to coexistence ( $n = 5$  pairs) or from a  
326 priority effect to competitive exclusion ( $n = 3$  pairs; Fig. S8). The effects of complementary  
327 responses on  $\lambda$  did not differ between sites ( $F_{2, 478} = 3.106$ ,  $P = 0.212$ ) or with the identity of  
328 species (non-significant random intercepts between focal species,  $F_{2, 478} = 0.069$ ,  $P = 0.966$ ;  
329 and competitor species,  $F_{2, 478} = 0.036$ ,  $P = 0.982$ ).

330

## 331 **DISCUSSION**

### 332 **Differential contributions of vital rates to competitive effects on population growth**

333 Competitive population dynamics emerge from the responses of all vital rates to neighbour  
334 species (Goldberg *et al.* 2001; Aarssen & Keogh 2002). But since most studies so far have  
335 measured competitive effects on one or a few vital rates (Aarssen & Keogh 2002; Weigelt &  
336 Jolliffe 2003; Yang *et al.* 2022), it remains unclear which vital rates are most strongly  
337 affected by competition and thus contribute the most to the impacts of competition on  
338 population growth. A particular vital rate can have a strong influence over population growth  
339 under competition either by displaying large responses to competitors, and/or because  
340 population growth is particularly sensitive to even small changes in that vital rate. We found  
341 that individual growth was the most important vital rate mediating impacts of competition on  
342 population growth in our experiment (Howard & Goldberg 2001; Williams & Crone 2006).  
343 This was because individual growth, and especially that of smaller plants, was generally  
344 strongly suppressed by competitors (Fig. S2b), and because population growth was  
345 sensitive to these changes (Fig. S7). Seedling establishment was also greatly negatively  
346 affected by competition (Fig. S2e), giving rise to its large negative contributions to  
347 competitive effects on population growth. These results suggest that vital rates at earlier life  
348 stages, i.e., seedling establishment and growth of small plants, are especially vulnerable to  
349 competition (Fenner 2000; Fayolle *et al.* 2009). This is likely because competitive effects at  
350 early life stages are most size-asymmetric (Keddy & Shipley 1989; Weiner 1990).

351  
352 Other vital rates, specifically flowering probability and survival, on average contributed less  
353 to population responses to competition. This was because population growth tended to be  
354 less sensitive to changes in these two vital rates (Fig. S7), even though size-specific survival  
355 probability was often strongly impacted by competitors (Fig. S2a). In contrast, population  
356 growth of almost all species was highly sensitive to changes in fecundity (Fig. S7), even  
357 though size-specific fecundity was suppressed only weakly by competition (Fig. S2d). These  
358 observations are consistent with predictions of the demographic buffering hypothesis (Pfister  
359 1998; Hilde *et al.* 2020), which proposes that vital rates with a strong influence on population  
360 growth have been selected not to respond strongly to environmental perturbations (here  
361 competition). Nonetheless, both survival and fecundity made large positive or negative  
362 contributions to effects of competition on population growth; in the case of fecundity, this can  
363 be explained by the fact that small responses of fecundity to competition had large impacts  
364 on population growth. Partly this variation might be explained by variation in vital rate  
365 responses among species and across environments, and partly by compensatory responses  
366 of vital rates to competition.

367

368 **Vital rate contributions differ between species and environments**

369 Vital rate contributions to competitive impacts on population growth differed significantly  
370 among species. Part of this species-level variation could be explained by the elevation origin  
371 of species. Individual growth of lowland species had greater negative contributions than  
372 those of alpine species, implying that the individual growth of lowland species may be more  
373 suppressed by competition. This difference in individual growth response to competition  
374 between lowland and highland species may be due to their different life history strategies  
375 (Körner 2003). In particular, it is consistent with the expectation that the population growth of  
376 species with fast life history strategies, such as lowland species, are more influenced by  
377 vegetative growth than species with slow life history strategies, such as highland species,  
378 that are more influenced by survival (Adler *et al.* 2014; Salguero-Gómez *et al.* 2016).  
379 Furthermore, vital rate contributions to competitive effects on population growth also differed  
380 significantly across the elevation gradient, with survival and seedling establishment  
381 contributing less negatively, or even positively, with increasing elevation. This may be  
382 because survival and seedling establishment were less suppressed or even facilitated by  
383 neighbours at the high elevation site (Callaway 1998; also see below for other explanations  
384 for positive vital rate responses). For example, we found species whose population growth  
385 was strongly influenced by suppressed survival and establishment, such as *Aster alpinus*  
386 and *Medicago lupulina* (Fig. S5c&k), benefited greatly from the relaxation of constraints on  
387 these two vital rates and thus experienced weakened competitive effects on population  
388 growth with increasing elevation (Fig. S6). In contrast, the influence of weakened  
389 competitive effects on survival and establishment for population growth was overridden by  
390 intensified competitive effects on growth for other species, such as *Sesleria caerulea* and  
391 *Trifolium badium* (Fig. S5f&g), which led them to experience greater competitive effects on  
392 population growth at high elevation (Fig. S6). The variation in the responses of species to  
393 competition and across environments may help explain the variation in vital rate influences  
394 on competitive population dynamics observed by previous studies (e.g., Williams & Crone  
395 2006; Olsen *et al.* 2016). Interestingly, although competitor species differed greatly in their  
396 ability to exert competitive effects in this experiment (Lyu & Alexander 2022), these  
397 differences did not manifest as differences between background species in their impacts on  
398 vital rates.

399

#### 400 **Complementary vital rate responses influence competitive population dynamics**

401 Another source of variation in vital rate contributions to competitive effects on population  
402 growth are complementary responses, which were prevalent in our study, in particular for  
403 reproduction and survival. There could be at least three reasons for these complementary  
404 responses. First, if vital rates vary randomly in the absence vs presence of neighbours, both  
405 negative and positive responses would be expected by chance. However, the patterns we

406 observed were unlikely to be entirely driven by random processes, given that the occurrence  
407 of complementary responses was highly uneven between vital rates and species. Secondly,  
408 complementary responses of vital rates could arise because neighbours have independent  
409 but contrasting effects on different vital rates (Holmgren *et al.* 1997; Eckstein 2005; Olsen *et al.*  
410 *et al.* 2016). For example, neighbour species may reduce plant growth through resource  
411 competition but at the same time improve their survival and seedling establishment due to  
412 the amelioration of microclimatic conditions (Cavieres *et al.* 2005; Eckstein 2005; Liancourt  
413 *et al.* 2005). Thirdly, complementary responses may result from trade-offs (i.e., negative  
414 correlations) between vital rates (Villellas *et al.* 2015). For example, reduced individual  
415 growth under competition can potentially improve plant survival in the presence of a trade-off  
416 between growth and survival (Ejmond *et al.* 2019). In fact, our results showed some  
417 evidence for possible growth-survival trade-offs for five species whose survival probability  
418 was negatively correlated with plant size in the absence of neighbours (Fig. S2a). In  
419 addition, our results suggest that plants can shift their reproductive strategies under  
420 competition by initiating reproduction at smaller sizes (e.g., Rose *et al.* 2005), and/or  
421 producing more seeds per unit of biomass, which might come at the expense of individual  
422 growth. Therefore, both growth-survival and growth-reproduction trade-offs, which are  
423 common in plants (Stearns 1989), may have given rise to some of the complementary  
424 responses observed in our study. In line with this, a number of other recent studies have  
425 also documented complementary responses across environmental gradients (Villellas *et al.*  
426 2015; Sheth & Angert 2018; Oldfather *et al.* 2021) and in response to neighbouring species  
427 (i.e., opposite responses of vital rates to neighbours in Fréville & Silvertown 2005; Williams  
428 & Crone 2006; Olsen *et al.* 2016; Nomoto & Alexander 2021).

429

430 Although complementary responses may be prevalent under competition, ours is the first  
431 experimental demonstration to our knowledge showing that complementary vital rate  
432 responses can buffer negative effects of competition and significantly promote population  
433 growth under competition. This finding is further supported by the fact that populations with  
434 stronger complementary response (i.e., greater total proportional contribution of  
435 complementary responses to population growth) experienced weaker competitive effects  
436 (Fig. S9). The consequence of complementary responses was generally to strengthen  
437 species coexistence, by increasing the invasion growth rates of both species in a pair (Fig.  
438 S8). In a few cases, complementary responses even changed the outcomes of competition,  
439 from predictions of competitive exclusion to predictions of coexistence (Fig. S8). Together,  
440 these results suggest the potentially important role of complementary responses in  
441 stabilizing population dynamics both in response to environmental conditions, as has been  
442 shown previously (Doak & Morris 2010; Villellas *et al.* 2015), and in response to competition,

443 as shown here. Further studies are now needed to investigate how common complementary  
444 responses under competition are in different communities and through which pathways they  
445 can affect competitive outcomes (e.g., through niche differences vs. fitness differences,  
446 Chesson 2000).

447

#### 448 **Implications for quantifying species interactions**

449 Our results also have implications for empirical studies of competition, especially when it is  
450 not possible to parameterize full demographic models to predict outcomes of competition at  
451 the population level, as we have done here. The large contributions of individual growth to  
452 competitive effects that we found imply that measures made on growth alone should capture  
453 much of the effect of competition on population growth. But doing so would miss important  
454 aspects of the dynamics, such as the complementary effects described above.

455 Compensatory responses, despite net negative effects of competition, also imply that  
456 measuring some vital rates might be give a misleading picture of interaction outcomes. For  
457 example, had we only quantified competitive effects in terms of survival, we would have  
458 frequently observed facilitation, even when population growth was suppressed by  
459 competitors. Similarly, systematic variation in the relative contribution of vital rates to  
460 competitive population dynamics across environmental gradients and between species  
461 implies that focusing on a single vital rate could be misleading. This is because changed  
462 competitive effects on single vital rates across an environmental gradient may not  
463 necessarily be aligned with competitive effects on population growth, especially if that vital  
464 rate has only a minor influence on population growth. Therefore, wherever possible, impacts  
465 of competition should be studied using population models integrating multiple vital rate  
466 responses (Aarssen & Keogh 2002; Maestre *et al.* 2005; Moll & Brown 2008; Freckleton *et*  
467 *al.* 2009).

468

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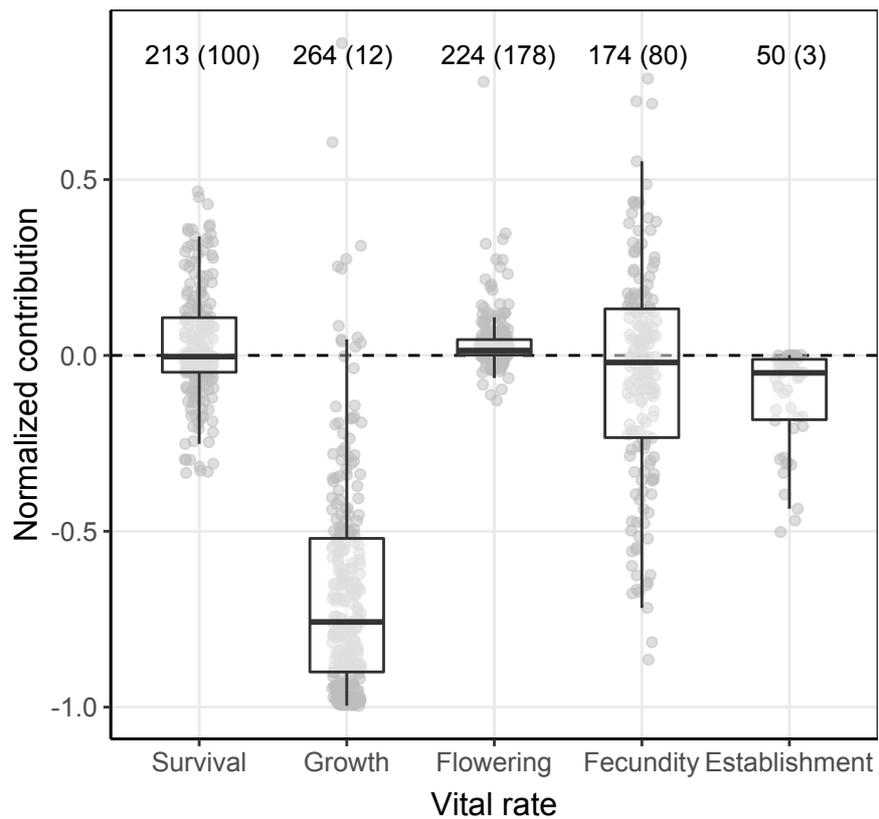
590 **Table 1.** Species included in this study. The elevation range is defined as the 10<sup>th</sup> and 90<sup>th</sup>  
 591 percentile of a species' elevation distribution in the study area.

<b>Species</b>	<b>Code</b>	<b>Family</b>	<b>Functional group</b>	<b>Elevation origin</b>	<b>Life history</b>	<b>Elevation range (m)</b>
<i>Bromus erectus</i>	Brer	Poaceae	Grass	Lowland	Perennial	598-1351
<i>Crepis biennis</i>	Crbi	Asteraceae	Forb	Lowland	Biennial	764-1299
<i>Daucus carota</i>	Daca	Apiaceae	Forb	Lowland	Biennial	683-1429
<i>Medicago lupulina</i>	Melu	Fabaceae	Legume	Lowland	Perennial	653-1408
<i>Plantago lanceolata</i>	Plla	Plantaginaceae	Forb	Lowland	Perennial	629-1657
<i>Poa trivialis</i>	Potr	Poaceae	Grass	Lowland	Perennial	527-1390
<i>Salvia pratensis</i>	Sapr	Lamiaceae	Forb	Lowland	Perennial	539-1069
<i>Anthyllis vulneraria</i> ssp. <i>alpestris</i>	Anal	Fabaceae	Legume	Highland	Perennial	1341-2217
<i>Arnica montana</i>	Armo	Asteraceae	Forb	Highland	Perennial	1622-2091
<i>Aster alpinus</i>	Asal	Asteraceae	Forb	Highland	Perennial	2002-2236
<i>Plantago alpina</i>	Plal	Plantaginaceae	Forb	Highland	Perennial	1581-2193
<i>Poa alpina</i>	Poal	Poaceae	Grass	Highland	Perennial	1674-2458
<i>Sesleria caerulea</i>	Seca	Poaceae	Grass	Highland	Perennial	1652-2371
<i>Trifolium badium</i>	Trba	Fabaceae	Legume	Highland	Perennial	1640-2253

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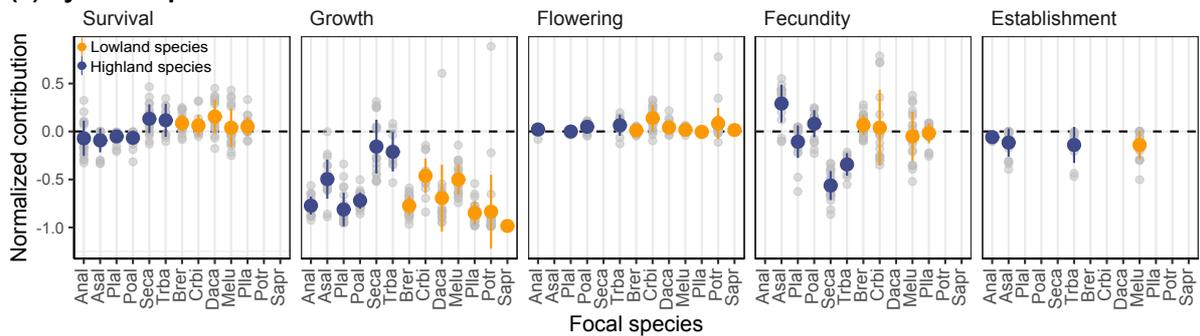
594 **Figure 1.** Normalized vital rate contributions to changes in population growth rate ( $\lambda$ ) in the  
 595 absence vs presence of neighbours. Grey points represent the vital rate contributions of  
 596 each species pair, and points are horizontally jittered for visual clarity. Boxplots represent  
 597 the median, first, and third quartiles summarized across species and sites, while the upper  
 598 and lower whiskers indicate 1.5 times of the first and third quartiles, respectively. The  
 599 number of non-zero contributions of each vital rate (i.e., cases where vital rate estimates  
 600 differed between intrinsic and invasion IPM models) is indicated at the top, with the number  
 601 of species pairs showing positive contributions shown in brackets.



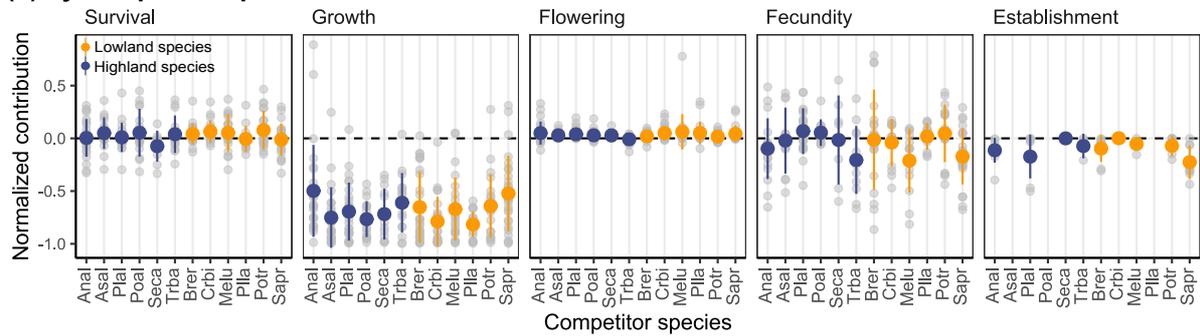
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604 **Figure 2.** Normalized vital rate contributions to changes in population growth rate ( $\lambda$ ) in the  
 605 absence vs presence of neighbours between focal species (a), background competitor  
 606 species (b), and field sites across the elevation gradient (c). Grey points represent the vital  
 607 rate contributions of a species pair, and coloured points and error bars (not always visible)  
 608 represent mean and standard deviations across species pairs for each species (a and b) or  
 609 at each site (c). In panels a and b, colours represent lowland (orange) and highland (blue)  
 610 focal or competitor species. The vital rates contributions were missing in cases where vital  
 611 rate estimates are identical between intrinsic and invasion IPM models. See Table 1 for  
 612 species codes.

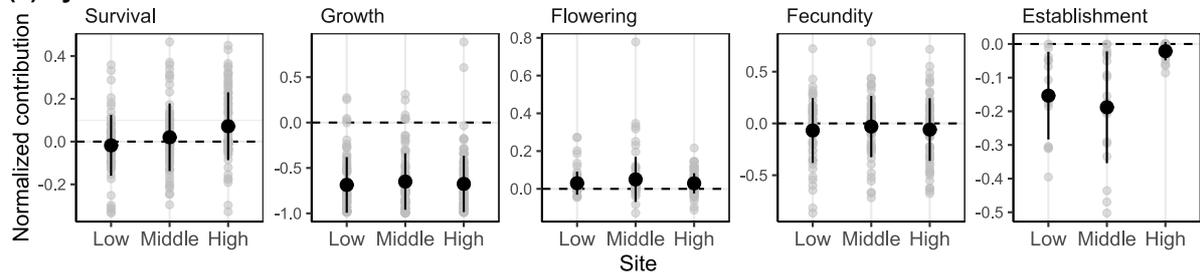
**(a) by focal species**



**(b) by competitor species**



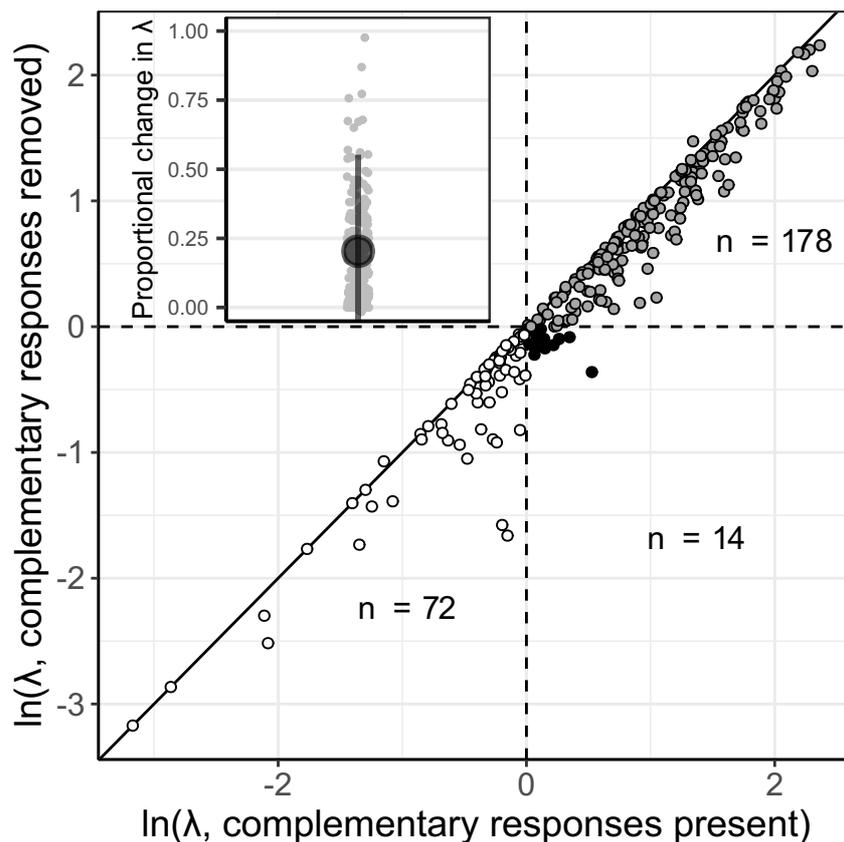
**(c) by sites**



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614

615 **Figure 3.** A comparison of population growth rates ( $\lambda$ ) estimated between original invasion  
616 IPM models ( $\lambda_{\text{invasion}}$ , with complementary responses present; x-axis) and simulated IPM  
617 models ( $\lambda_{\text{substituted}}$ , with complementary responses removed; y-axis). The solid line is a 1:1  
618 line. Each point represents an invasion IPM model (i.e., a species pair). Points in the top-  
619 right and bottom-left quadrants represent cases where species are predicted to persist under  
620 competition (i.e.,  $\ln(\lambda_{\text{invasion}}) > 0$ ; grey) or be competitively excluded (i.e.,  $\ln(\lambda_{\text{invasion}}) < 0$ ;  
621 white), respectively, both in the presence and absence of complementary responses; points  
622 in the lower-right quadrant represent cases where species are predicted to be competitively  
623 excluded in the absence of complementary responses but able to persist under competition  
624 in the presence of complementary responses (black). The number of species pairs  
625 belonging to each quadrant is also shown ( $n$ ). The inset shows the proportional change in  $\lambda$   
626 when complementary responses are present vs removed, with grey points representing  
627 species pairs and the black points indicating the average ( $\pm$  standard deviation) summarized  
628 across all species pairs.



629  
630