

LETTER

Compensatory responses of vital rates attenuate impacts of competition on population growth and promote coexistence

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Funding information

H2020 European Research Council, Grant/
Award Number: 678841; ETH Zürich;
European Union; Horizon 2020

Editor: Montserrat Vila

Abstract

Competition is among the most important factors regulating plant population and community dynamics, but we know little about how different vital rates respond to competition and jointly determine population growth and species coexistence. We conducted a field experiment and parameterised integral projection models to model the population growth of 14 herbaceous plant species in the absence and presence of neighbours across an elevation gradient (284 interspecific pairs). We found that suppressed individual growth and seedling establishment contributed the most to competition-induced declines in population growth, although vital rate contributions varied greatly between species and with elevation. In contrast, size-specific survival and flowering probability and seed production were frequently enhanced under competition. These compensatory vital rate responses were nearly ubiquitous (occurred in 92% of species pairs) and significantly reduced niche overlap and stabilised coexistence. Our study highlights the importance of demographic processes for regulating population and community dynamics, which has often been neglected by classic coexistence theories.

KEYWORDS

coexistence theory, compensatory responses, competition, elevation gradient, integral projection model (IPM), life history strategy, niche overlap, perennial plants, population growth, relative fitness differences, vital rates

INTRODUCTION

The ability of a population to grow or persist in a given environment depends on the combined responses of all vital rates across the species' life cycle, including survival, growth and reproduction (Arnold, 1983; Radchuk et al., 2013; Yang et al., 2018). These responses may be aligned, for example if environmental conditions favour both individual growth and survival, with both promoting population growth (Fay et al., 2022). Alternatively, responses can be opposing, such that negative effects of the environment on one vital rate are compensated by positive responses of another; for example, such compensatory responses have been shown to buffer population declines at species' range margins (Cayuela et al., 2022; Doak & Morris, 2010; Oldfather et al., 2021; Villellas et al., 2015). Similarly,

population growth in response to species interactions, such as competition, is the net result of the responses of all vital rates to neighbour species (Aarssen & Keogh, 2002; Freckleton et al., 2009; Goldberg et al., 2001). However, so far, most empirical studies of species interactions have taken an individual-based approach, that is, measuring the responses of a single or a few vital rates of individual plants to neighbours (Aarssen & Keogh, 2002; Weigelt & Jolliffe, 2003; Yang et al., 2022b). Therefore, until now we only poorly understand how the response to competitors of different vital rates combine to determine population growth and hence coexistence, and whether compensatory responses of different vital rates may buffer impacts of competitors on population dynamics.

While measuring vital rate responses to competition is straightforward, translating them into impacts of

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competition on population growth is more challenging. This is because population growth is not equally sensitive to changes in different vital rates, as revealed by vital rate sensitivities (or elasticity) from demographic models (Adler et al., 2014; Franco & Silvertown, 2004). Consequently, a vital rate, like survival, may be strongly depressed by competition but only have a small impact on population growth when its elasticity is small, or vice versa. Demographic models, such as integral projection models (IPMs), allow us to quantify the relative contributions of different vital rates to population growth (Caswell, 2001; Easterling et al., 2000; Ellner et al., 2016), but are empirically and analytically demanding and, so far, have only rarely been used to study plant competition (e.g. Chu & Adler, 2015; Nomoto & Alexander, 2021; Olsen et al., 2016; Williams & Crone, 2006).

Vital rate contributions to competitive impacts on population growth may vary greatly between species and across environmental gradients. First, competitive effects on individual vital rates have been shown to be highly species specific (e.g. Gaudet & Keddy, 1988; Goldberg, 1996) and contingent on the environmental conditions under which plants are grown (Callaway et al., 2002; He et al., 2013; Maestre et al., 2005; Yang et al. 2022b). Second, the influence of vital rates on population growth can also vary systematically between species and across environments. For instance, the population growth of species with a 'fast' life history strategy (e.g. species with shorter generation times) relies more on plant growth and reproduction compared with 'slow' species, whose population growth relies more on survival (Adler et al., 2014; Franco & Silvertown, 2004). Recent studies have also revealed shifts in species' life history strategy along environmental gradients, such as species displaying faster life histories when growing in warmer environments (Sheth & Angert, 2018; Williams et al., 2015). Therefore, we might expect growth and reproduction to contribute more to effects of competition on the population growth of 'fast' species, such as those originating from lower elevations, or for species growing in warmer environments, such as at low elevation. In contrast, survival may make a greater contribution to effects of competition on population growth of 'slow' species, such as those originating from high elevations, or when growing under cooler environments.

As well as revealing how different vital rates contribute to a species' response to competition, adopting a demographic approach makes it possible to examine the possible consequences of variable vital rate responses to species coexistence. Just as compensatory vital rate responses promote the persistence of populations in unfavourable environments (Cayuela et al., 2022; Doak & Morris, 2010; Oldfather et al., 2021; Villellas et al., 2015; Yang et al. 2022a), so too may they help attenuate effects of competitors on population growth and so favour coexistence. For example, Goldberg et al. (2001) found that the presence of neighbours reduced growth and

recruitment but improved plant survival; these sorts of responses may have important consequences for coexistence. As predicted by coexistence theory, competitive outcomes between species depend on the relative magnitudes of niche differences (i.e. 1—niche overlap), that facilitate their coexistence, and relative fitness differences (i.e. competitive ability differences), that drive one species to competitively exclude the other (Chesson, 2000b). Accordingly, compensatory vital rate responses to competitors may promote coexistence by decreasing the sensitivity of species to interspecific competition and thereby reducing niche overlap between them (Carroll et al., 2011); alternatively, if compensatory responses benefit competing species unequally, they may amplify or dampen the advantage of the superior competitor and thus hinder or promote coexistence, respectively (Chesson, 2000b; Godoy & Levine, 2014). Despite the potentially important consequences for species coexistence, compensatory responses under competition have, to our knowledge, not been studied.

Here, we investigated how the responses of individual vital rates to competition determine population growth and the outcomes of competition. Specifically, we asked: (1) How do different vital rates contribute to declines in population growth under competition? (2) To what extent do vital rate contributions differ between species and across an elevation gradient? (3) How do compensatory vital rate responses affect species coexistence? To answer these questions, we conducted a field experiment and parameterised integral projection models (IPMs) to model the population growth of 14 plant species (seven highland and seven lowland species) in the absence and presence of neighbours across an elevation gradient in the Swiss Alps. We hypothesised that vital rates would differ in their contributions to population growth under competition, but that this variation would be related to differences in life history (lowland vs. highland plants) and differences in the environment (elevation gradient) in which the plants grew, as outlined above. We further hypothesised that compensatory response would have opposing effects on coexistence, with the net effect depending on the relative magnitudes of their impacts on niche overlap versus relative fitness differences between species.

MATERIALS AND METHODS

Study sites and species

We established a field experiment in three sites across an elevation gradient (890, 1400 and 1900 m above sea level; hereafter the low, middle and high sites, respectively; Figure S1) in the western Swiss Alps (Canton de Vaud, 46°10' N, 6°50' E). The mean annual temperature ranged from 11.4°C at the low site to 5.9°C at the high site. We selected 14 herbaceous species that frequently occur in this

region, seven from low and seven from high elevation (hereafter, lowland and highland species; Table 1). Seeds were obtained from regional commercial suppliers.

Field experiment design

The field experiment was designed to estimate population growth rates in the absence and presence of neighbour species and to evaluate pairwise competitive outcomes. At each site, each of the 14 focal species interacted with eight heterospecific competitors, resulting in 112 (14 focal species \times 8 competitors) of the possible 182 interspecific pairs. Pairs were chosen to evenly represent the functional trait differences among all pairwise combinations (Lyu & Alexander, 2022) and to be reciprocal (i.e. 56 reciprocal pairs). We also included the 14 intraspecific pairs and grew species in the absence of neighbours. In total, this design yielded 3780 focal individuals (9 individuals \times [112 interspecific pairs + 14 intraspecific pairs + 14 no-competition] \times 3 sites). We first sowed seeds at relatively high density (9 gm⁻² viable seeds) to establish background monocultures (i.e. competitor species) and transplanted focal individuals (i.e. focal species) raised in a greenhouse into established monocultures and non-competition plots (Supplementary Methods).

Demographic data collection

See Supplementary Methods for full details of demographic data collection. In brief, we collected demographic data on survival, growth, flowering, and fecundity by observing all focal plants from 2017 to 2020. We estimated germination and competition-free seedling establishment of each species in a separate experiment.

We estimated competition-dependent establishment as the survival probability of focal plants in their first growing season after transplant. We estimated the off-spring size distributions (mean and standard deviation) using seedlings raised in the greenhouse.

Population modelling

We used integral projection models (IPMs) to model population growth and estimate population growth rates (Easterling et al., 2000; Ellner et al., 2016). IPMs consist of a series of functions describing individual vital rates that were either size dependent (survival probability, growth, flowering probability and fecundity) or size independent (seed germination and seedling establishment). We modelled the probability of survival and flowering using generalised linear models with a binomial distribution and logit link function. We modelled growth and fecundity using linear models. We combined the three annual transitions (2017–2018, 2018–2019 and 2019–2020) to estimate vital rate parameters. To evaluate the effects of plant size (except for size-independent vital rates), competitor identity and elevation on vital rate parameters, we compared all nested models of the global models including these factors and their interactions using the Akaike information criterion corrected for small samples (AICc; Supplementary Methods). We then parameterised IPMs using the most parsimonious vital rate models. Deterministic population growth rates, λ , were calculated as the dominant eigenvalue of discretised IPMs assuming populations have reached stable size distributions (Caswell, 2001; Ellner et al., 2016). We constructed ‘intrinsic IPMs’ to estimate intrinsic growth rates, $\lambda_{\text{intrinsic}}$, using plants growing in the absence of neighbours, and ‘competition IPMs’ using plants

TABLE 1 Species included in this study. The elevation range is defined as the 10th and 90th percentile of a species' elevation distribution based on a dataset of 550 vegetation plots from the study area (Randin et al., 2009). *Anthyllis alpestris* is *Anthyllis vulneraria* ssp. *alpestris*

Species	Code	Family	Functional group	Elevation origin	Life history	Elevation range (m)
<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 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

growing within the competitor monocultures to estimate low-density growth rates, $\lambda_{\text{low-density}}$. Here, $\lambda_{\text{low-density}}$ is the growth rate of a focal species in the presence of inter- but not intraspecific competitors. A species is predicted to persist with its competitor if $\lambda_{\text{low-density}} > 1$. For further details on population modelling see Supplementary Methods and Lyu and Alexander (2022).

Vital rate contributions

We conducted retrospective perturbation analyses to quantify the contributions of vital rates to the declines in population growth rates caused by competition, $\Delta\lambda$ (Griffith, 2017; Jacquemyn et al., 2010; Oldfather et al., 2021). Specifically, for each vital rate of a given competition IPM, we generated a perturbed IPM in which all the vital rates were the same as the corresponding intrinsic IPM except for the vital rate of interest, which was extracted from the competition IPM (Figure S1). The contribution of that vital rate to $\Delta\lambda$ was quantified as the difference in λ between the perturbed and intrinsic IPMs (i.e. $\lambda_{\text{perturbed}} - \lambda_{\text{intrinsic}}$). The contributions are negative when $\lambda_{\text{perturbed}} < \lambda_{\text{intrinsic}}$, indicating the response of the vital rate to neighbour species had a negative effect on λ ; the contributions are positive when $\lambda_{\text{perturbed}} > \lambda_{\text{intrinsic}}$, indicating the response of that vital rate had a positive effect on λ (i.e. a compensatory response when λ is suppressed by neighbours). Greater absolute values indicate greater contributions, resulting from either large differences in a given vital rate with versus without competition, or a high sensitivity of λ to that vital rate (Caswell, 2001).

We estimated the contributions of five competition-dependent vital rates (survival, growth, flowering probability, fecundity and seedling establishment) to the declines in λ caused by competition, $\Delta\lambda$. To facilitate comparisons across species and elevations, we normalised vital rate contributions by dividing the absolute values of the contributions of each vital rate by the sum of absolute total contributions, then reassigning the sign of the effect. Notably, positive contributions here mean that size-specific vital rates (except for seedling establishment) were enhanced when neighbours were present (i.e. displaying compensatory responses), even though neighbours may reduce plant performance overall by suppressing individual size. For example, individuals growing in the presence of neighbours might produce more seeds per unit of biomass compared to those in the absence of neighbours but still produce fewer seeds overall due to their reduced sizes. We excluded *Arnica montana* from this analysis due to small sample size caused by high mortality and its failure to reproduce during the experiment (Figure S2). In addition, we only included populations whose $\lambda_{\text{low-density}} < \lambda_{\text{intrinsic}}$ (i.e. indicating competition; $n = 264$ out of 284; Figure S4) in this analysis and other analyses described below to disentangle

the direct facilitative effects of neighbours on population growth from compensatory responses of vital rates.

Species coexistence

For each species pair, we quantified niche overlap (NO), relative fitness differences (RFD) and predicted outcomes of competition using estimates of $\lambda_{\text{intrinsic}}$ and $\lambda_{\text{low-density}}$ following Carroll et al. (2011; Supplementary Methods), assuming that background monocultures are at equilibrium density (see Figure S5 for a test of this assumption). In modern coexistence theory, coexistence depends on the relative magnitudes of niche overlap and relative fitness differences (Chesson, 2000b). Niche overlap inhibits species coexistence by increasing the intensity of interspecific competition (Chesson, 2000b; Godoy & Levine, 2014), while large relative fitness differences, that is large differences in species' competitive abilities, drive competitive exclusion. Coexistence theory predicts that in addition to competitive exclusion of an inferior competitor by a superior one, there are two other possible outcomes of competition. Stable coexistence is possible when the niche overlap between a pair of species is small enough to overcome the negative effects of asymmetries in competitive ability, that is, $\text{NO} < 1$ and $\text{RFD} < 1/\text{NO}$. Priority effects, where the species initially established within a community excludes the other, occur when species have high niche overlap and small relative fitness differences, that is, $\text{NO} > 1$ and $\text{RFD} < 1/\text{NO}$ (Grainger et al., 2019).

Effects of compensatory responses on population growth and coexistence

To evaluate the effects of compensatory responses on λ and species coexistence, we first identified all the vital rates displaying compensatory responses (i.e. those had positive contributions to $\Delta\lambda$) within the competition IPMs and then substituted them with corresponding vital rates estimated in the absence of neighbours (from intrinsic IPMs), which we termed 'substituted IPMs'. Note that if more than one vital rate displayed compensatory responses in a competition IPM, we substituted them all at once to evaluate their combined effects on λ . With substituted IPMs, we calculated population growth rates ($\lambda_{\text{substituted}}$), niche overlap and fitness differences and predicted the outcome of competition as described above.

Statistical analyses

First, we fitted a mixed effect model (Equation 5 in Supplementary Methods) to test the extent to which vital rate contributions to $\Delta\lambda$ (response variable) differed between vital rates, elevation (low, middle and high sites) and the origin of focal species (lowland and highland) and all

interactions (all fixed factors), and the identity of focal and background species (both fitted with random intercepts and slopes for vital rates) and plot identity (random intercepts only). Second, we fitted a similar model (Equation 6 in Supplementary Methods) but with a binomial error distribution to test whether the presence versus absence of compensatory responses (response variable) depended on these factors. Third, to test whether the original $\lambda_{\text{low-density}}$ when compensatory responses were present differed significantly from $\lambda_{\text{substituted}}$ when compensatory responses were removed, we fitted a mixed-effects model (Equation 7 in Supplementary Methods) with log-transformed population growth rates (response variable) depending on elevation (categorical as above; fixed factor) and focal and competitor species (random factors). Lastly, we used t -tests to ask whether the changes in niche overlap and relative fitness differences in the absence versus presence of compensatory responses were significantly different from zero. All population modelling and statistical analyses were conducted in R version 4.0.3 (R Core Team, 2020).

RESULTS

How do different vital rates contribute to declines in population growth under competition?

Competition caused population growth rates, λ , to decline by 55% on average (Figure S4). The contributions of vital rates to declines in λ caused by competition ($\Delta\lambda$) differed significantly among the five vital rates (Figure 1; $F_{4,925}=376$, $p<0.0001$; Table S1). On average, reduced growth of individual plants in the presence of neighbours contributed most to $\Delta\lambda$ (for 11 of the 13 focal species), with an average proportional contribution of -0.67 (SE = ± 0.03) across species pairs and sites. Competitive suppression of plant growth was especially strong on small plants, as shown by the fact that the difference in predicted size at time $t+1$ in the absence versus presence of neighbours was much greater for smaller individuals with lower aboveground biomass than those of larger individuals (e.g. *Anthyllis alpestris* and *Bromus erectus* in Figure S2b). Reduced seedling establishment also contributed markedly to $\Delta\lambda$, with an average proportional contribution of -0.11 (± 0.004). Reproduction and survival on average showed only minor negative contributions to $\Delta\lambda$ (proportional contribution of flowering: -0.03 ± 0.01 ; fecundity: -0.05 ± 0.04 ; survival: -0.02 ± 0.02), resulting partly from their frequent positive contributions, that is compensatory responses (Figure 1).

To what extent do vital rate contributions differ between species and with elevation?

Despite the overarching contributions of individual growth, we observed substantial variation between focal species in the contribution of vital rates to declining λ under

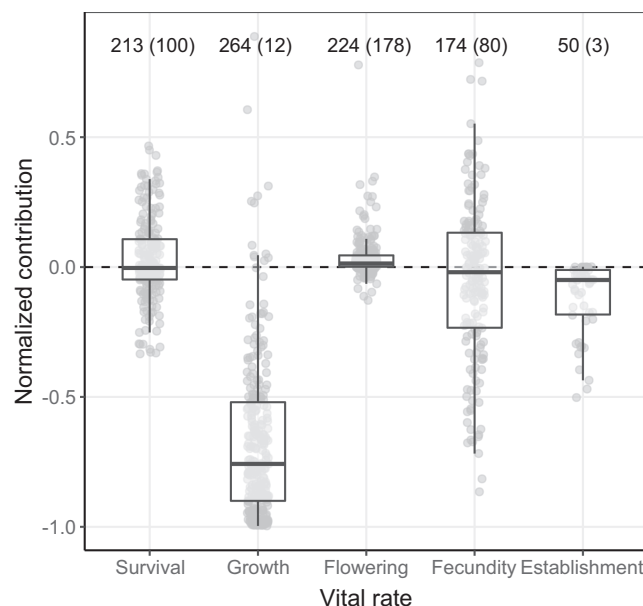


FIGURE 1 Normalised vital rate contributions to changes in population growth rate ($\Delta\lambda$) in the absence versus presence of neighbours. Grey points represent the vital rate contributions of each species pair, horizontally jittered for visual clarity. Boxplots represent the median, first and third quartiles summarised across species and sites, while the upper and lower whiskers indicate 1.5 times the first and third quartiles, respectively. The number of non-zero contributions of each vital rate (i.e. cases where vital rate estimates differed between intrinsic and competition IPM models) is indicated at the top, with the number of species pairs showing positive contributions (i.e. compensatory responses) shown in brackets.

competition (Figure 2a; significantly different random slopes of vital rates between focal species: $F_{14,925}=450.7$, $p<0.0001$; Tables S1, S2). Compared to other species, suppressed fecundity caused λ of three focal species to decline markedly under competition, with proportional contributions below -0.1 for *Sesleria caerulea*, *Trifolium badium* and *Plantago alpina*. Additionally, suppressed seedling establishment substantially reduced λ (proportional contributions below -0.1) in *T. badium*, *Medicago lupulina* and *Aster alpinus*. On average, vital rate contributions differed significantly between focal species originating from low and high elevations (vital rate \times focal species origin interaction: $F_{4,925}=15$, $p=0.005$; Figure 2a; Tables S1, S2), with suppressed plant growth and survival on average making greater contributions to $\Delta\lambda$ of lowland and highland species, respectively (Figure 2a; Table S2).

The contributions of vital rates to $\Delta\lambda$ differed significantly across the elevation gradient (Figure 2b; vital rate \times site interaction: $F_{8,925}=29.706$, $p=0.0002$; Tables S1, S2). Suppressed survival under competition had the most negative impacts on λ at the low elevation site, but this shifted to positive effects of neighbours on survival at the high elevation site. Similarly, suppressed seedling establishment affected λ most strongly at the lower two sites and only slightly at the high site. However, the contributions of growth, flowering

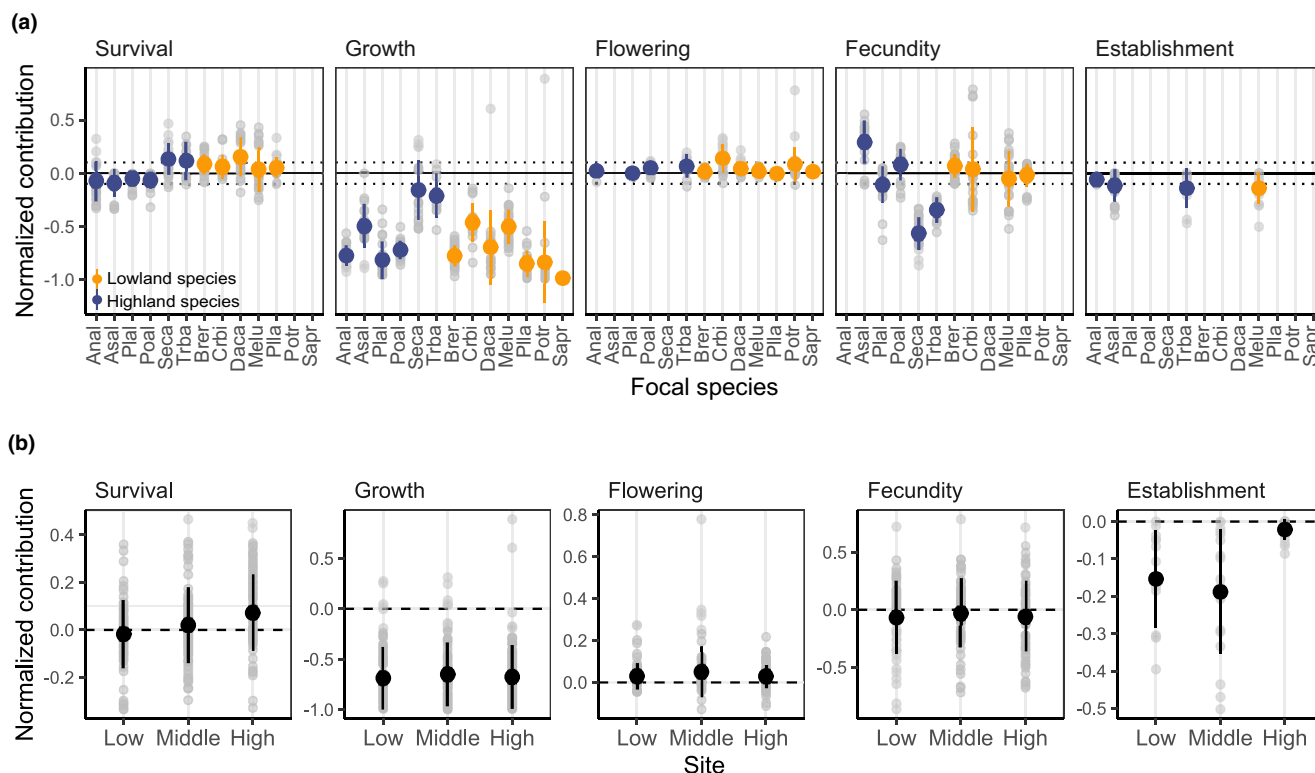


FIGURE 2 Normalised vital rate contributions to changes in population growth rate ($\Delta\lambda$) in the absence versus presence of neighbours between focal species (a) and field sites across the elevation gradient (b). Grey points represent the vital rate contributions of a species pair, and coloured points and error bars (not always visible) represent mean and standard deviations across species pairs for each species (a) or at each site (b). In panel a, colours represent lowland (orange) and highland (blue) focal species, and the dotted lines represent vital rate contributions of 0.1 and -0.1, respectively. Vital rate contributions are missing in cases where vital rate estimates were identical between intrinsic and competition IPM models. See Table 1 for species codes.

probability and fecundity to $\Delta\lambda$ showed no clear trend across the elevation gradient.

How common are compensatory responses under competition?

Compensatory vital rate responses to neighbours were found in 92% (243 of 264) of species pairs, with 134, 88 and 21 competition IPMs including one, two and three vital rates enhanced under competition, respectively, despite the net negative effects of neighbours on λ . The occurrence of compensatory responses differed significantly between vital rates and focal species (Figures 1 and 2a; significantly different random slopes of vital rates between focal species: $F_{14, 925} = 164.71$, $p < 0.0001$; Table S1). Enhanced size-specific flowering probability in the presence of neighbours was observed in 79% of species pairs, followed by survival (47%) and fecundity (46%). In contrast, individual growth or seedling establishment rarely responded positively (5% and 6% of species pairs respectively; Figure 1).

How do compensatory responses affect species coexistence?

Estimated low-density growth rates, $\lambda_{\text{low-density}}$, with compensatory responses present were, on average, 22.6%

($\pm 4.5\%$) greater compared with those when compensatory responses were removed (Figure S8; $F_{1,478} = 10.908$, $p = 0.0009$). Compensatory responses affected species coexistence in opposite ways (Figure 3). On average across species, compensatory responses decreased niche overlap by 39.2% (paired t test; $t_{92} = 9.4$; $p < 0.0001$) while slightly increasing relative fitness differences by 12.2% (paired t test; $t_{92} = 2.9$; $p = 0.003$). Because of their greater effects on niche overlap, however, the net effects of compensatory responses were to strengthen species coexistence (Figure 3). For 7.4% (8 of 107) of species pairs, compensatory responses were sufficient to shift the competitive outcome, either from competitive exclusion to coexistence (five pairs) or from a priority effect to competitive exclusion (three pairs; Figure 3). For 9.3% (10 of 107) of pairs, compensatory responses changed the identity of the dominant competitor (arrows crossing x-axis where $\log(\text{RFD}) = 0$ in Figure 3).

DISCUSSION

Greater impacts of vital rates acting at earlier life stages

Vital rates across species' life cycles can respond to neighbours in different ways and jointly determine population growth under competition and species

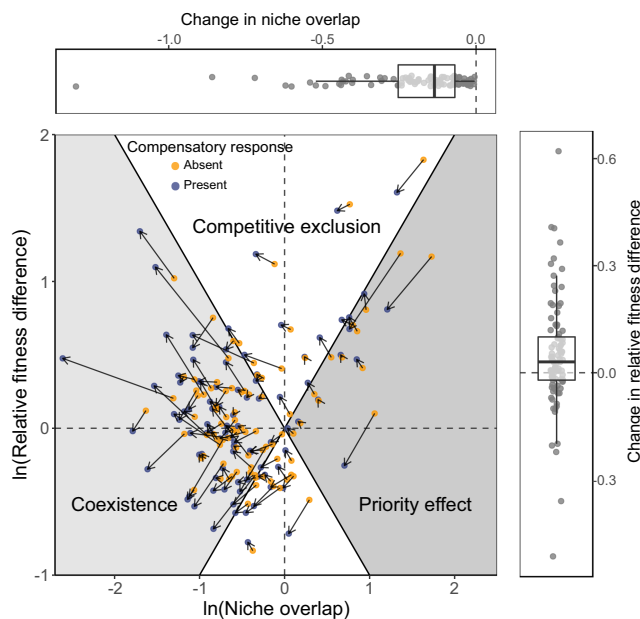


FIGURE 3 Outcomes of competition in the absence versus presence of compensatory responses. Each arrow represents a specific species pair, indicating the shift in predicted competitive outcomes from when compensatory responses are absent (orange; arrow tails) to when compensatory responses are present (blue; arrow points). Species pairs within the shaded area when $NO < 0$ are predicted to coexist stably, while those within the shaded area when $NO > 0$ are predicted to show priority effects; otherwise, competitive exclusion occurs (unshaded area). The sign of $\ln(RFD)$ depends on the identity of the dominant competitor; for example, for a pair of species A and B, A or B is predicted to be the dominant competitor when $\ln(RFD) > 0$ or $\ln(RFD) < 0$, respectively. The surrounding boxplots show the changes in niche overlap and relative fitness differences (both on logarithmic scales).

coexistence. However, since demographic approaches to studying competition in plants have been scarce (Hart et al., 2018), especially for perennials, we know little about the relative importance of different vital rates in influencing population growth under competition and the consequences of variable vital rate responses for species coexistence. In our experiment, vital rates acting at relatively early life stages drove impacts of competition. First, we found that declines in individual growth under competition, especially growth of smaller plants, had the largest impact on population growth across all species. Second, the suppression of establishment of juvenile plants was commonly observed across species. These responses likely reflect intense resource competition within our experimental plots. While we cannot unravel the mechanisms of competition with our data, it is probable that plants competed strongly for light because we observed that competitive effects on plant growth were usually size-asymmetric (Keddy & Shipley, 1989; Weiner, 1990; DeMalach et al., 2017; Xiao et al., 2021; also see Figure S2b). In contrast, vital rates at later life stages, specifically reproduction and survival of more mature plants, on average contributed less negatively to population responses to competition. In the cases of

flowering probability and fecundity, this is partly because population growth tended to be less sensitive to changes in these two vital rates (Figure S6), and partly because they were only weakly suppressed by competitors (Figure S2c,d). In addition, the fact that reproduction and survival frequently displayed compensatory responses also partly led to their small contributions to the impacts of competition on population growth. These results suggest that early costs of competition in terms of growth may be compensated by vital rate responses at later life stages, the implications of which we discuss below.

Vital rate contributions differ between lowland and alpine species and with elevation

The variation we observed in the contributions of vital rates to impacts of competition on population growth could be at least partly explained by the origin of species and the environment in which they grew. Species with slow life histories are expected to be longer-lived and characterised by high elasticity of population growth rate to survival, while species with fast life histories are shorter-lived and characterised by high elasticities to growth and reproduction (Franco & Silvertown, 2004; Adler et al., 2014; also see Figure S6). This is consistent with our observation that reductions in survival caused by competitors contributed strongly to total effects of competition in four of six alpine species, while growth had greater contributions to the population growth of lowland species. Alpine species are expected to have 'slower' life history strategies to cope with shorter growing seasons and more environmentally challenging conditions at higher elevation, while a 'faster' life history is more typical of plants from low elevation environments (Körner, 2021; Sheth & Angert, 2018). Indeed, generation times predicted from our population models tended to be longer for highland than lowland species (Figure S7). Nonetheless, there was relatively large heterogeneity within these groups that was not explained by elevation origin.

The contributions of vital rates also varied with the elevation of the experimental sites, although elevational variation was rather lower than variation between species origins. This may be partly because species' life history strategies did not differ greatly between the study sites, as indicated by the relatively similar vital rate elasticities (Figure S6) and predicted generation times (Figure S7) across the elevation gradient. However, seedling establishment and survival played a stronger role at lower elevation, perhaps because of more intense competition for light at early life stages under warmer environments where productivity is high (DeMalach et al., 2017; Malhi et al., 2017). The contribution of survival even became positive at high elevation, consistent with observations that facilitation by neighbours can attenuate

environmental conditions and thereby promote survival in alpine environments (Callaway et al., 2002; Olsen et al., 2016). Nonetheless, in our experiment we also see how positive and negative effects of neighbours on vital rates act in tandem (Cheney & Côté, 2005; Michalet et al., 2014; Stephan et al., 2021), with net interactions being overwhelmingly competitive, even at the high elevation site. The systematic variation in the magnitudes and directions of vital rate responses to neighbours between species and across environments that we observed suggests that measurements based on single vital rates might give a misleading picture of the role of species' interactions in regulating community dynamics across environmental gradients (Aarssen & Keogh, 2002; Freckleton et al., 2009; Maestre et al., 2005; Moll & Brown, 2008).

Compensatory vital rate responses occur frequently under competition

Compensatory responses of vital rates, like the positive effects of neighbours on survival just mentioned, were almost ubiquitous in our experiment, and are in line with several other recent studies documenting compensatory responses across environmental gradients (Oldfather et al., 2021; Sheth & Angert, 2018; Villellas et al., 2015) and in response to neighbouring species (i.e. contrasting responses of vital rates to neighbours in Fréville & Silvertown, 2005; Williams & Crone, 2006; Olsen et al., 2016; Nomoto & Alexander, 2021). One possible reason for compensatory responses is that neighbours can simultaneously suppress one vital rate while improving another (Eckstein, 2005; Holmgren et al., 1997; Olsen et al., 2016). This may help explain some of the positive responses observed in survival, as we discussed above. Another possible reason for compensatory response is trade-offs between vital rates (Villellas et al., 2015). For example, reduced individual growth under competition can potentially improve plant survival in the presence of a trade-off between growth and survival (Ejzmond et al., 2019). Our results showed some evidence for possible growth–survival trade-offs for five species whose survival probability was negatively correlated with plant size in the absence of neighbours (Figure S2a). Moreover, our results suggest that plants can shift their reproductive strategies under competition by initiating reproduction at smaller sizes and/or producing more seeds per unit of biomass, which might come at the expense of individual growth (Jacquemyn et al., 2010; Kentie et al., 2020; Rose et al., 2005; Williams et al., 2015). Notably, the compensatory responses of size-specific vital rates observed here mean that plants performed better in the presence of neighbours compared to plants of the same size growing in the absence of neighbours. Therefore, competition can still reduce overall population performance by decreasing the average size and therefore the

performance of individuals. Since growth–survival and growth–reproduction trade-offs are thought to be common in plants (Stearns, 1989), we therefore hypothesise that vital rate trade-offs, rather than facilitative interactions, are more likely to explain the frequent compensatory responses observed in this experiment.

Opposing effects of compensatory responses on coexistence

Although compensatory responses may be prevalent under competition, ours is the first experimental demonstration to our knowledge showing that compensatory responses can facilitate species coexistence. This occurred mainly by compensatory responses reducing niche overlap. Compensatory responses may reduce niche overlap by promoting population growth under competition and thereby weakening interspecific competition. This result adds to a growing body of studies suggesting that demographic processes within species with complex life histories can generate niche differentiation and stabilise coexistence (de Roos, 2021; Miller & Rudolf, 2011). However, these processes have often been neglected by classic coexistence theories focusing exclusively on between-species differences, such as resource partitioning (Chesson, 2000b; Tilman, 1982) or species-specific natural enemies (Connell, 1971; Janzen, 1970), and empirical studies focusing on species with simpler life histories, such as annual plants (Kraft et al., 2015; Levine & HilleRisLambers, 2009; Van Dyke et al., 2022). Interestingly, our results also suggest that compensatory responses could potentially increase the likelihood of competitive exclusion by amplifying inequalities in species' competitive abilities. This would occur when compensatory responses disproportionately favour the superior competitor, as indicated by our results showing that superior competitors often displayed stronger compensatory responses (Figure S9). However, the effects of increased inequalities in competitive ability were overridden by the effects of reduced niche overlap in this experiment, leading compensatory responses in general to strengthen coexistence.

Overall, our results support the important role of compensatory responses in mediating population dynamics, both in response to environmental conditions, as has been shown previously (Cayuela et al., 2022; Doak & Morris, 2010; Oldfather et al., 2021; Villellas et al., 2015), and in response to competition, as shown here. Nonetheless, our experiment was conducted under relatively homogeneous conditions and over a short timeframe, which may cause our estimates of vital rate impacts on population growth to differ from those estimated under more natural conditions. First, we may have overestimated the importance of plant growth for regulating population growth because the experiment may miss other important processes underlying species interactions

(e.g. environmental heterogeneity and fluctuations; Chesson, 2000a; Usinowicz et al., 2012). Second, while our pairwise experiments allowed us to isolate effects of vital rates on competitive population dynamics, it remains unclear how consistent these effects would be in more complex multispecies communities. Third, the prevalence of projections of stable coexistence, even when compensatory responses were absent, may be because some of the monocultures did not reach their equilibrium density (Lyu & Alexander, 2022; also see Figure S5) and partly explain why compensatory responses qualitatively changed the outcomes of competition only for a few species pairs. Therefore, future studies conducted within natural communities are needed to better understand how the responses of individual vital rates to neighbours determine population growth and the impacts of compensatory responses on community dynamics. Together, this study highlights how bridging demography and community ecology can lead to novel insights into the demographic processes and life history trade-offs that regulate population and community dynamics.

AUTHOR CONTRIBUTIONS

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

ACKNOWLEDGEMENTS

We thank members of the Plant Ecology group at ETH Zürich for their help with field work, in particular Loïc Liberati and Tim Murray. We thank the Commune de Bex and Jean-Louis Putallaz for the access to the field sites. We also thank the reviewers for their comments and suggestions that helped to improve the manuscript greatly. S.L. also thanks the Chinese Scholarship Council for financial support (No.201706100184). J.M.A. received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 678841.

FUNDING INFORMATION

H2020 European Research Council, Grant/Award Number: 678841; ETH Zürich; European Union; Horizon 2020

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.14167>.

DATA AVAILABILITY STATEMENT

The data and R scripts used for population modelling and statistical analyses in this study are available on GitHub: https://github.com/ShengmanLyu/Compensatory_Responses_and_species_coexistence and also archived in Figshare: <https://doi.org/10.6084/m9.figshare.21821577.v1>

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variable and weakly dependent on climate at the global scale.
Ecology Letters, 25, 1580–1593.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Lyu, S. & Alexander, J.M. (2023) Compensatory responses of vital rates attenuate impacts of competition on population growth and promote coexistence. *Ecology Letters*, 00, 1–11. Available from: <https://doi.org/10.1111/ele.14167>