

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

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#### **Authorship**

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

#### **Data availability statement**

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

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

## **Abstract**

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

## INTRODUCTION

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

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

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

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

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

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

## **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) 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, while the soil moisture increased with elevation, as measured between 2019 and 2020 (Lyu & Alexander 2022). We selected 14 herbaceous species that frequently occur in this region, seven from low and seven from high elevation (hereafter, lowland and highland species); the species included 12 perennial and two biennial species from different functional types (seven forbs, four grasses and three legumes; Table 1). Seeds were obtained from local commercial suppliers.

### **Field experiment**

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

### **Data collection**

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

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

## Population modelling

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

## Estimating contributions of vital rates

We manipulated the parameterized IPMs to decompose the declines in population growth rates ( $\lambda$ ) caused by competition into the contributions of different vital rates (Fig. S1), following other studies (e.g., Bruijning *et al.* 2018; Oldfather *et al.* 2021). Specifically, for each vital rate of a given invasion 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 invasion IPM (i.e., vital rates estimated in the presence of neighbours). The contribution of that vital rate to the competitive response was quantified as the differences in  $\lambda$  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 rates to neighbour species had negative effects on  $\lambda$ ; the contributions are positive when  $\lambda_{\text{perturbed}} > \lambda_{\text{intrinsic}}$ , indicating the response of that vital rate had positive effects on  $\lambda$ . Greater

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

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

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

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

### **Statistical analyses**

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

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

## RESULTS

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

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

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

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



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

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

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

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

Complementary vital rate responses to neighbours were found in 92% (243 of 264) of species pairs; that is, at least one vital rate in these invasion IPMs responded positively to competition, despite neighbours causing population growth rate to decline. Across all species pairs, 28.3% (373 of 1320) of vital rates showed complementary responses. The occurrence of complementary responses differed significantly between vital rates and focal species (Fig. 1 & 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 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 and were only found among 5% and 6% of species pairs, respectively (Fig. 1). Note that, because these vital rates were implemented as size-dependent in the IPMs (except for seedling establishment), the positive responses of flowering, survival and fecundity observed here do not necessarily mean that plants had a greater chance to flower, survive or produce more seeds in the presence of neighbours; rather, it means that plants performed better in the presence of neighbours compared to plants of the same size growing in the absence of neighbours. For example, individuals in the presence of neighbours might produce less seeds overall but produce more seeds per unit of biomass compared to those in the absence of neighbours.

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

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

## **DISCUSSION**

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

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

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

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

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

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

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

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

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

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

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

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

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

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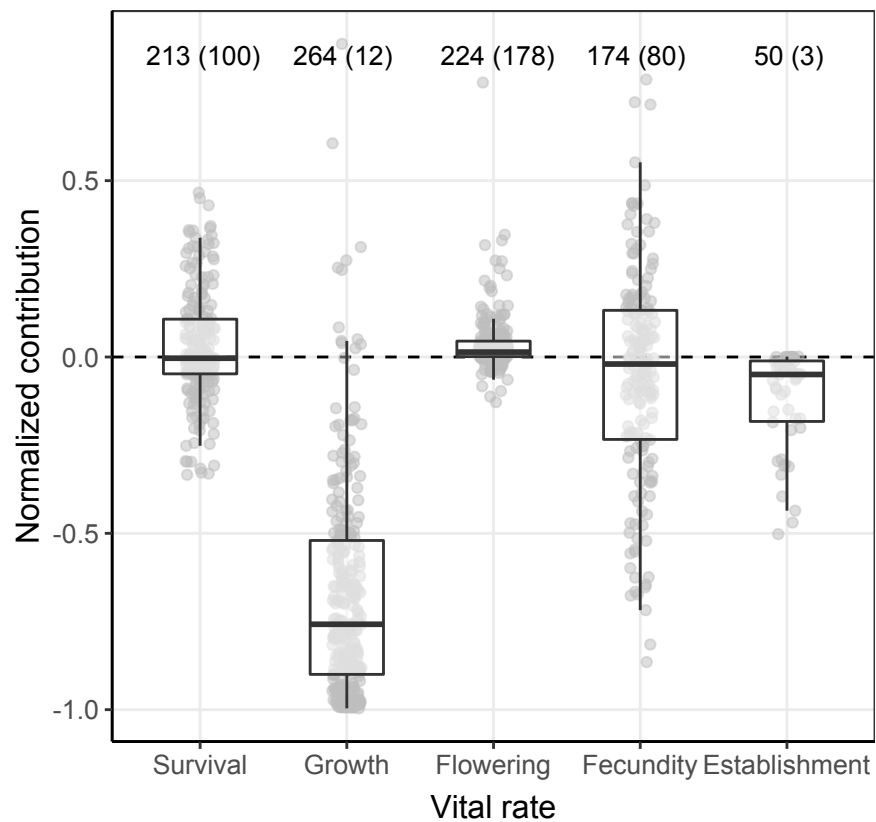
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**Table 1.** Species included in this study. The elevation range is defined as the 10<sup>th</sup> and 90<sup>th</sup> percentile of a species' elevation distribution in the study area.

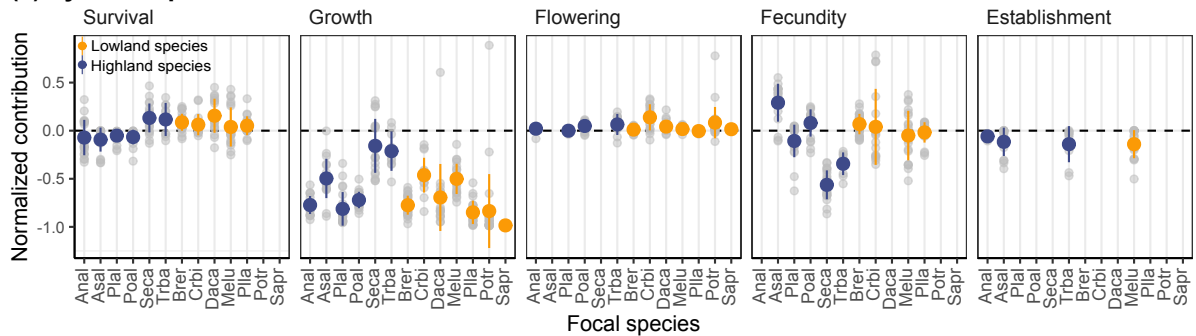
Species	Code	Family	Functional group	Elevation origin	Life history	Elevation range (m)
<i>Bromus erectus</i>	Brer	Poaceae	Grass	Lowland	Perennial	598-1351
<i>Crepis biennis</i>	Crbi	Asteraceae	Forb	Lowland	Biennial	764-1299
<i>Daucus carota</i>	Daca	Apiaceae	Forb	Lowland	Biennial	683-1429
<i>Medicago 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 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

**Figure 1.** Normalized vital rate contributions to changes in population growth rate ( $\lambda$ ) in the absence vs presence of neighbours. Grey points represent the vital rate contributions of each species pair, and points are horizontally jittered for visual clarity. Boxplots represent the median, first, and third quartiles summarized across species and sites, while the upper and lower whiskers indicate 1.5 times of 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 invasion IPM models) is indicated at the top, with the number of species pairs showing positive contributions shown in brackets.

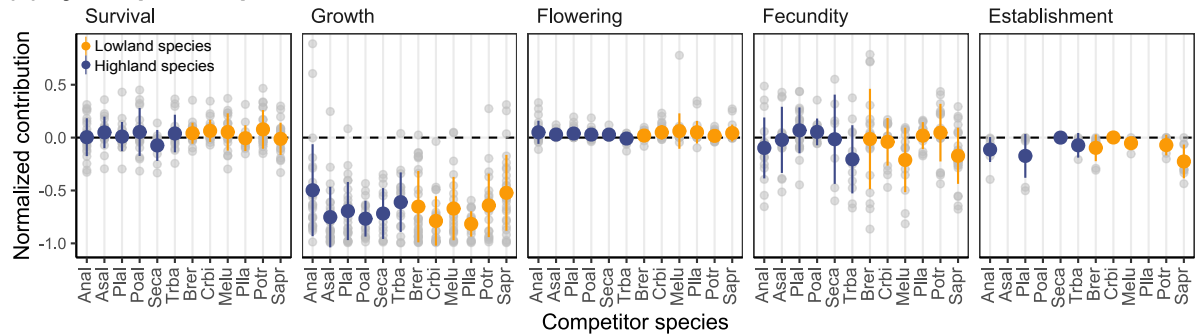


**Figure 2.** Normalized vital rate contributions to changes in population growth rate ( $\lambda$ ) in the absence vs presence of neighbours between focal species (a), background competitor species (b), and field sites across the elevation gradient (c). Grey points represent the vital rate contributions 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 and b) or at each site (c). In panels a and b, colours represent lowland (orange) and highland (blue) focal or competitor species. The vital rates contributions were missing in cases where vital rate estimates are identical between intrinsic and invasion IPM models. See Table 1 for species codes.

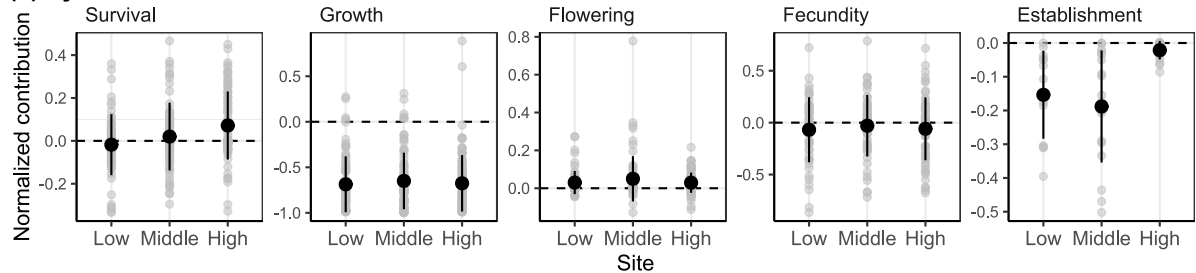
**(a) by focal species**



**(b) by competitor species**



**(c) by sites**



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

