

## SUPPLEMENTARY INFORMATION

### Vital rates contribute differently to impacts of competition on population growth

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## SUPPLEMENTARY METHODS

### Field experiment

In spring 2017, we established 18 plots (1 x 1.6 m and 0.2 m deep) within each site and filled them with homogenized soil originating from a low elevation site within the study area. We sowed each species in each plot with 9 g m<sup>-2</sup> viable seeds and allowed them to grow for a whole growing season to establish monocultures. Most species established monocultures and received focal plants in autumn 2017, except for those that were resown and received focal plants either in spring 2018 (*Poa trivialis* and *Poa alpina* in the low site and *Bromus erectus* in the middle site) or autumn 2018 (*Aster alpinus*, *Poa trivialis* and *Poa alpina* in the middle site and *Sesleria caerulea* in the low and high sites). Seedlings were raised on standard compost soil for six weeks in a greenhouse and acclimated in a common garden for one week before transplanting to the field. About 5% of transplants died within two weeks of transplanting and were subsequently replaced. We also replaced died focal plants (ca. 10%) in the spring and autumn of 2018 and 2019.

### Data collection

To estimate plant size, we collected individuals of various sizes of each species within the background monocultures (N = 67-169 individuals per species) and measured morphological traits in the same way as we measured focal plants. These samples were then oven-dried at 70 °C and weighted for dry mass. We fitted linear regression models between dry mass (response variable) and morphological traits for each species to estimate the dry mass of focal plants. To estimate the number of seeds produced, we collected intact fruits of different sizes of each species at the early fruiting stage on background plants (N = 22-145 fruits per species). We measured the sizes of these fruits, air-dried them, and counted the seeds of each fruit. We fitted regression models between the number of seeds per fruit (response variable) and the sizes to estimate the number of seeds of focal plants.

### Germination experiments

In autumn 2018, we established a 1 x 1 m plot filled with sterilized soil within each site. We glued seeds to toothpicks (N = 20 toothpicks per species and site) using water soluble PVA glue and inserted these into the plot at 5 cm spacing, resulting in ca. 240-1660 seeds per species and site depending on the seed size. In spring 2019, we counted the germinated seedlings to estimate germination. We then followed these seedlings to monitor their establishment. To assess competition-free establishment (in the absence of interactions), we thinned the seedlings to one single seedling per stick and a maximum of ten sticks per species within each plot. We left only one seedling per toothpick and a maximum of 10 toothpicks per species per site. We recorded the survival or mortality of these seedlings at the end of growing season to estimate intrinsic seedling establishment in the absence of competition. We followed the same protocol to estimate seed germination rates and intrinsic seedling establishment of *Daucus carota* between 2019 and 2020.

### Integral projection models

Integral projection models (IPM) consist of a series of vital rates functions, representing the pathways by which individuals contribute to population growth. The contributions of an individual to population growth depends on its state,  $z$ . We used plant size as the continuous state variable (dry aboveground biomass; on natural logarithm scale), ranging from a lower bound,  $L$ , to upper bound  $U$  (i.e., the smallest and biggest individuals within the population). An individual can contribute to population growth by surviving to the next census,  $s(z)$ , and growing from size  $z$  at census  $t$  to  $z'$  at census  $t + 1$ ,  $G(z', z)$ . It can also contribute by flowering,  $f(z)$ , and producing seeds,  $b(z)$ . These seeds germinate with a probability of  $p_g$ , and seedlings establish with a probability of  $p_r$  and contribute to the population as new recruits,  $C1(z')$ . Seedling establishment in our IPMs has two components,  $p_r$  and  $p_{r,c}$ , corresponding to competition-free and competition-dependent establishment (see Data collection in the main text for more information). IPMs describe the transition of the size distribution the population at time  $t$ ,  $n(z, t)$ , to  $t + 1$ ,  $n(z', t + 1)$ , by summing the contributions of all individuals within the population, as denoted by the integral:

$$n(z', t + 1) = \int_L^U [s(z)G(z', z) + f(z)b(z)p_gp_r p_{r,c}C1(z')]n(z, t)dz \quad (1)$$

Similar to other studies (e.g., Williams & Crone 2006), we assumed that seed germination, seedling establishment and the size of recruits were independent of maternal plant size. We modelled the probability of survival and flowering using generalized linear models with a binomial distribution. We modelled growth and fecundity using linear models. We described the size-constant variation in growth and offspring size distributions using Gaussian probability density functions. See Lyu & Alexander (2022) for more detailed information on model structure and parameters.

#### **Life-table response experiments**

In addition to quantifying vital rate contributions using the approach described in the main text, vital rate contributions to declines in  $\lambda$  can also be quantified using life-table response experiments (LTREs, Caswell 1989; Ellner *et al.* 2016). For a given pair of species, we obtained the mid-kernel by averaging the intrinsic and invasion IPM models and calculated the sensitivity of  $\lambda$  to vital rate parameters by adding 0.01 to each parameter of this mid-kernel (i.e., the first-order partial derivatives). We obtained the contributions of each vital rate parameter by multiplying the parameter sensitivity by the parameter difference between the intrinsic and invasion IPM models. The contributions of vital rates were obtained by summing the parameter contributions within each vital rate (e.g., growth intercept and slope) assuming no non-additive interactions between vital rate parameters. We normalized the vital rate contributions while maintaining the signs unchanged, as we did for vital rate replacement analyses (see Materials and Methods in the main text). Vital rate contributions based on the conventional life-table response experiments were very similar to those based on vital rate replacement analysis ( $R^2 = 0.725$  based on a linear regression model pooling all vital rates together; Fig.S3). However, we presented the contributions based on the vital rate replacement in the main text because it aligned with our analyses on complementary responses of vital rates (see Materials and Methods in the main text).

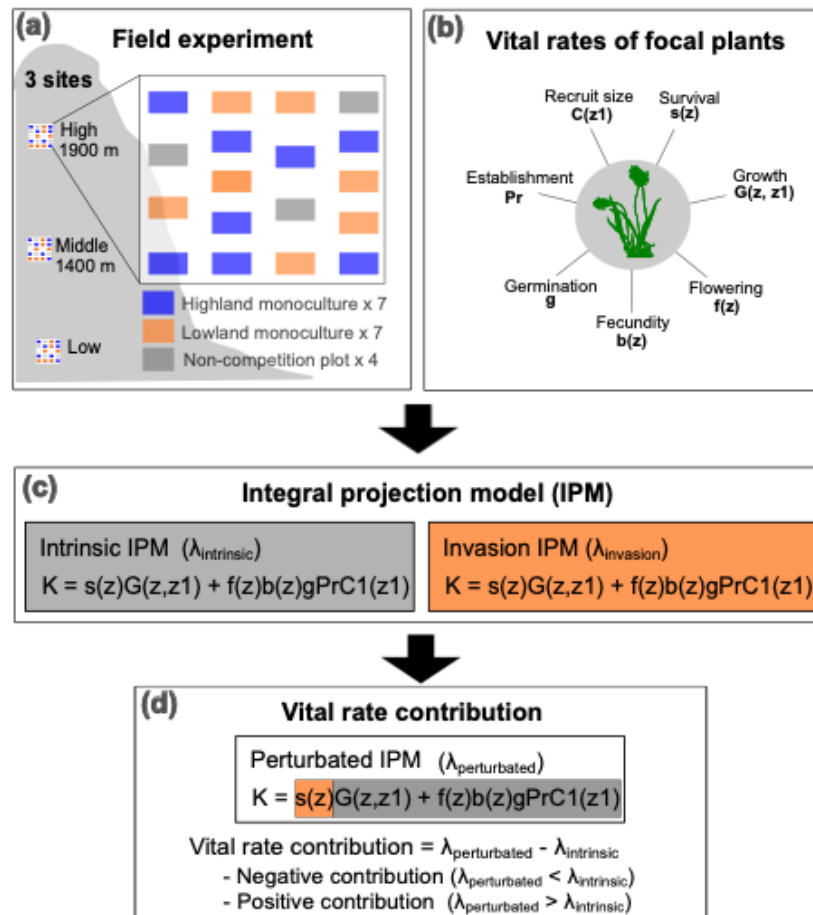
**Table S1.** Analysis of vital rate contributions to declines in population growth rate ( $\lambda$ ) in the absence vs presence of neighbours and the occurrence of complementary responses. The results were derived from mixed-effect models (see section “Statistical analyses”). Factors were vital rates (survival, growth, flowering probability, fecundity, and seedling establishment), site (low, middle, and high elevation), elevation origin of focal and competitor species (lowland or highland), identity of focal and competitor species (two random factors), and all two-way interactions. The total number of non-zero vital rate contributions (i.e., the vital rates were different between intrinsic and invasion IPM models) is also shown ( $n$ ). Significance of factors were determined using likelihood ratio tests. Significant factors are in bold ( $P < 0.05$ ).

	Vital rate contributions			Presence of complementary responses		
Factors	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
Site	<b>2</b>	<b>7.738</b>	<b>0.021</b>	2	1.231	0.540
Vital rate	<b>4</b>	<b>376.928</b>	<b>&lt; 2.2e-16</b>	<b>4</b>	<b>33.996</b>	<b>7.468e-07</b>
Focal origin	<b>1</b>	<b>17.013</b>	<b>3.713e-05</b>	<b>1</b>	<b>6.696</b>	<b>0.009</b>
Competitor origin	1	0.169	0.681	1	0.209	0.647
Site x vital rate	<b>8</b>	<b>29.706</b>	<b>0.0002</b>	8	9.582	0.296
Site x focal origin	<b>2</b>	<b>6.894</b>	<b>0.032</b>	2	2.352	0.308
Site x competitor origin	2	4.829	0.089	2	0.594	0.743
Vital rate x focal origin	<b>4</b>	<b>15.021</b>	<b>0.005</b>	4	9.312	0.054
Vital rate x competitor origin	4	1.423	0.840	1	0.814	0.936
Focal origin x competitor origin	1	1.767	0.184	<b>1</b>	<b>4.107</b>	<b>0.043</b>
Vital rate x Focal species (random effects)	<b>14</b>	<b>450.75</b>	<b>&lt; 2.2e-16</b>	<b>14</b>	<b>164.71</b>	<b>&lt; 2.2e-16</b>
Vital rate x Competitor species (random effects)	<b>14</b>	<b>32.44</b>	<b>0.003</b>	14	22.605	0.067
<i>n</i>	925			925		

**Table S2.** Analysis of vital rate contributions to declines in population growth rate ( $\lambda$ ) in the absence vs presence of neighbours for each vital rate separately. Factors were site (low, middle, and high elevation), elevation origin of focal and competitor species (lowland or highland), identity of focal and competitor species (two random factors), and two-way interactions. The number of non-zero contributions for each vital rates (i.e., the vital rates were different between intrinsic and invasion IPM models) is also shown ( $n$ ). The results were derived from mixed-effects models fitted separately for each vital rate. Significance of factors were determined using likelihood ratio tests. Significant factors are in bold ( $P < 0.05$ ).

		Survival		Growth		Flowering		Fecundity		Establishment	
Factors	d.f.	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Site	2	<b>15.103</b>	<b>0.0005</b>	1.562	0.458	4.626	0.098	2.451	0.294	<b>20.001</b>	<b>4.53e-5</b>
Focal origin	1	3.703	0.054	2.151	0.142	0.112	0.738	0.736	0.392	0	0.996
Competitor origin	1	0.073	0.786	0.031	0.861	0.430	0.512	0.290	0.590	0.156	0.693
Site x focal origin	2	2.695	0.259	<b>9.611</b>	<b>0.008</b>	4.076	0.130	0.341	0.843	4.324	0.115
Site x competitor origin	2	1.165	0.439	5.172	0.075	0.757	0.685	0.960	0.619	0.178	0.915
Focal species (random effects)	12	<b>25.60</b>	<b>4.2e-7</b>	<b>148.72</b>	<b>&lt; 2e-16</b>	<b>28.9</b>	<b>7.6e-9</b>	<b>115.98</b>	<b>&lt; 2.2e-16</b>	0.945	0.331
Competitor species (random effects)	12	0.489	0.484	0.110	0.740	0.230	0.633	<b>5.742</b>	<b>0.016</b>	1.601	0.206
<i>n</i>		213		264		224		174		50	

**Figure S1.** Field experiment and population modelling. (a) We let seven lowland and seven highland species to interact in three sites across an elevation gradient. Within each site, focal plants were transplanted into non-competition (i.e., bare soil; grey) and competition plots, that is established monocultures of lowland (orange) or highland (blue) species. (b) Data on vital rates of focal plants were collected, which were then used to parameterize integral projection models (IPM) and estimate population growth rate ( $\lambda$ ). (c) “Intrinsic IPMs” were fitted using plants growing in the absence of neighbour species ( $\lambda_{\text{intrinsic}}$ , grey), while “invasion IPMs” were fitted using plants invading the established monocultures of competitor species ( $\lambda_{\text{invasion}}$ , orange). (d) The contribution of a given vital rate, such as survival as shown in this example, to the impact of competition on population growth was estimated by comparing  $\lambda_{\text{intrinsic}}$  with  $\lambda$  estimated from perturbed IPMs ( $\lambda_{\text{perturbated}}$ ), in which all vital rates were same as the intrinsic IPM except the vital rate of interest (e.g., survival) that was extracted from the invasion IPM.

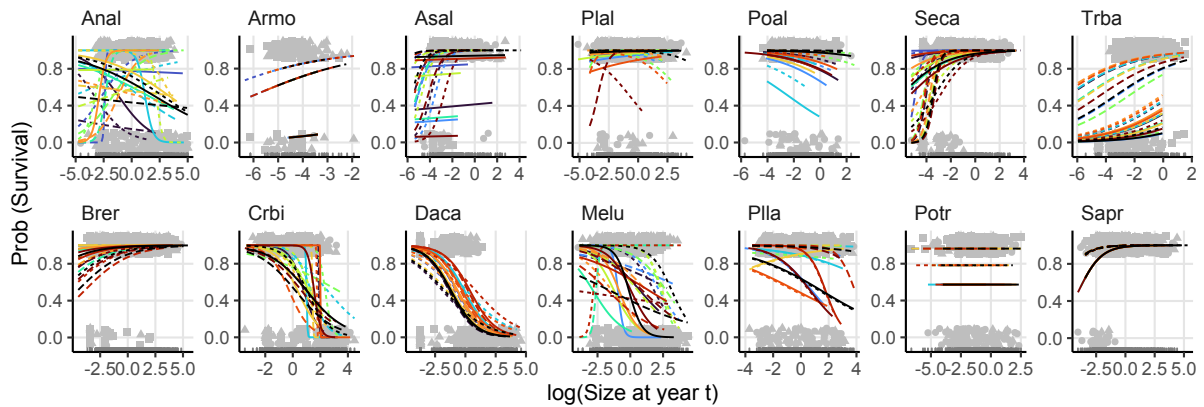


**Figure S2.** Competition-dependent vital rates of each focal species interacting with different competitors and in different sites. Vital rates are either size-dependent (a, survival; b, growth; c, flowering; d, fecundity) or size-independent (e, seedling establishment under competition). For each vital rate, highland focal species are in the upper row and lowland species in the lower row. Grey points in the background are observed values, colored lines or dots represent fitted vital rates implemented in the IPM models. Colours represent different competitor species (black for no-competition), line types represent sites (low, solid; middle, dotted; high, dashed). Overlapping lines and points indicate that the vital rates were implemented as site or competitor-independent in the IPM models based on model selection (see section “Population modelling” in the main text). The size range of the fitted lines represents the size bounds implemented in the IPMs ( $L$  and  $U$ ). Rugs at the bottom indicate the distributions of data points. Points were jittered for visual clarity for the probability of survival, flowering, and establishment. See Table 1 for species codes. This figure was reproduced from the Supplementary Figure 1 in Lyu & Alexander (2022).

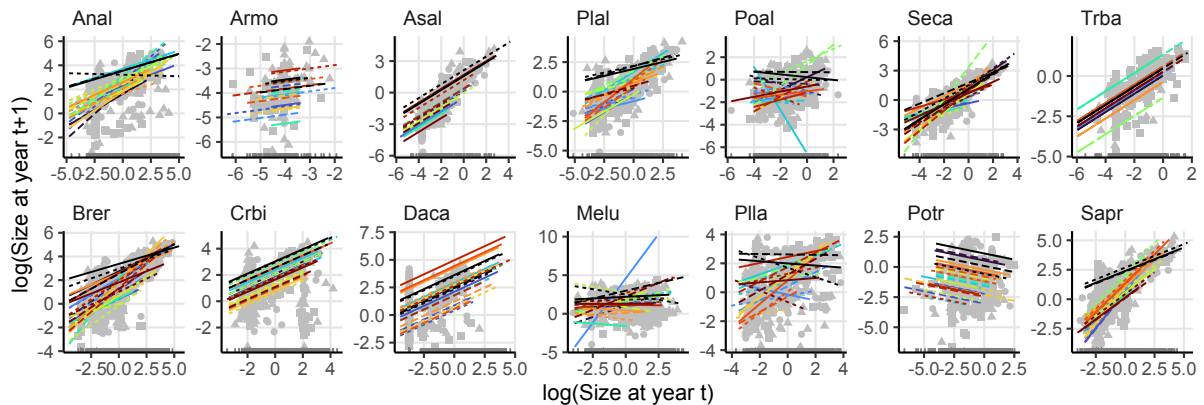
(a)

Legend

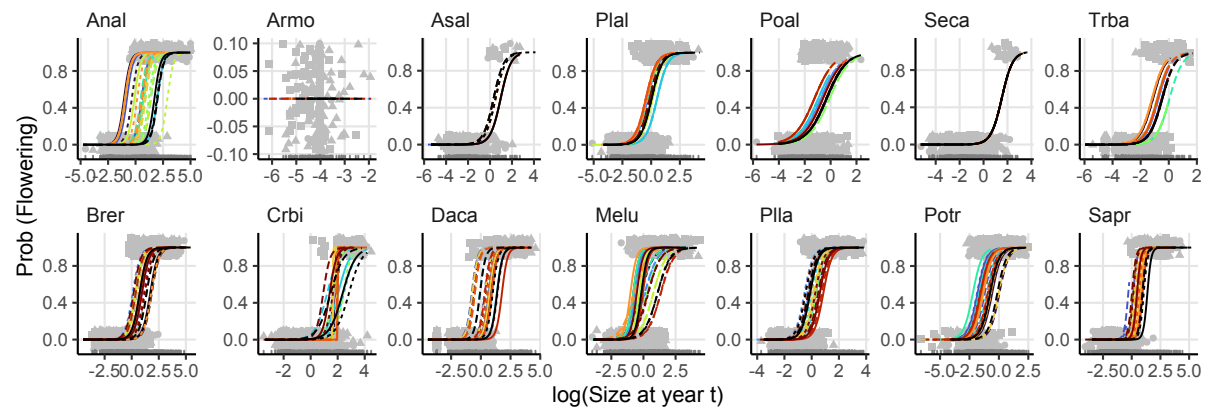
Highland competitor species — Anal — Asal — Plal — Poal — Seca — Trba —  
Lowland competitor species — Brer — Crbi — Melu — Plla — Potr — Sapr —  
Non-competition — Site — low — middle — high



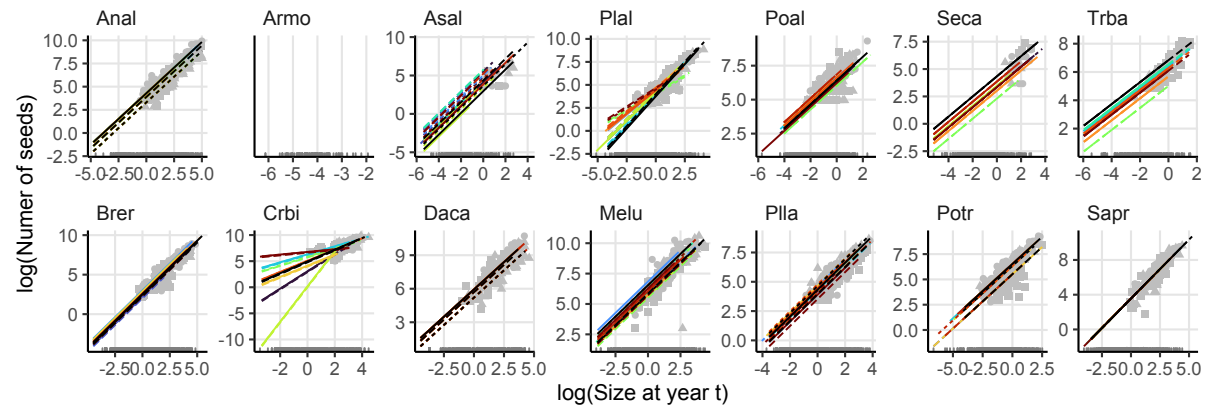
(b)



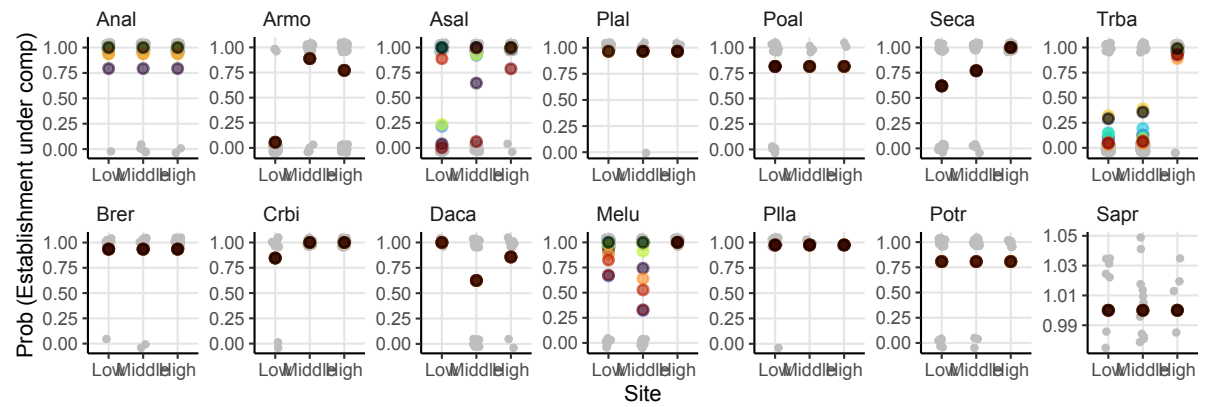
(c)



(d)

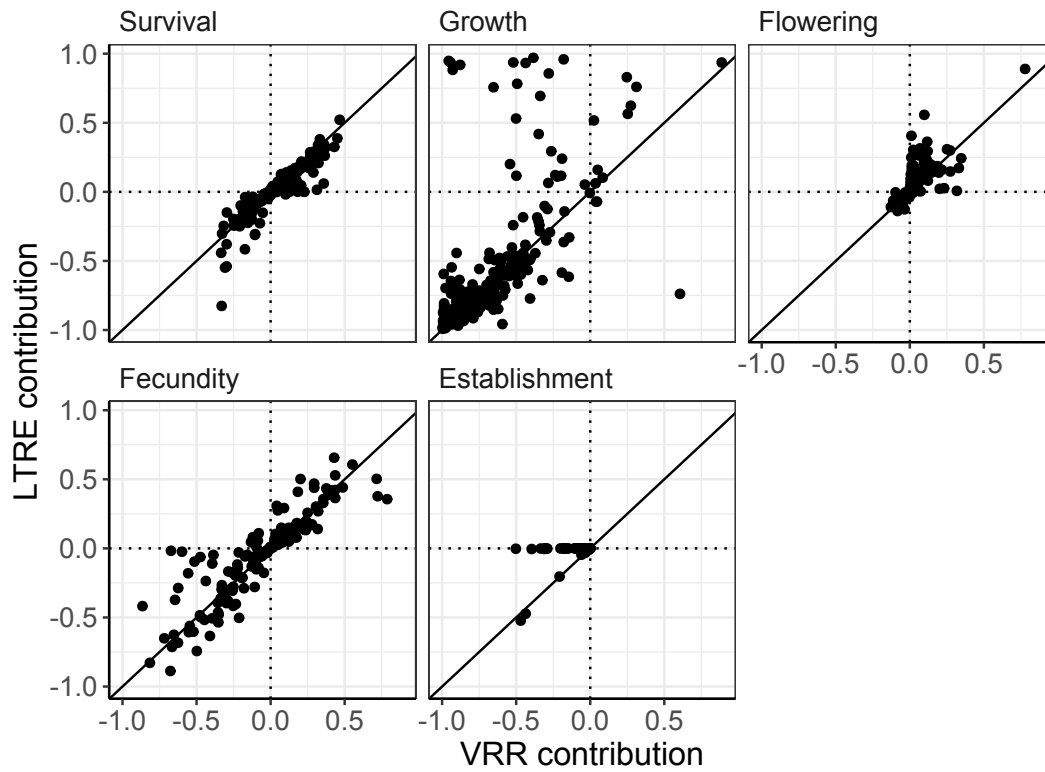


(e)

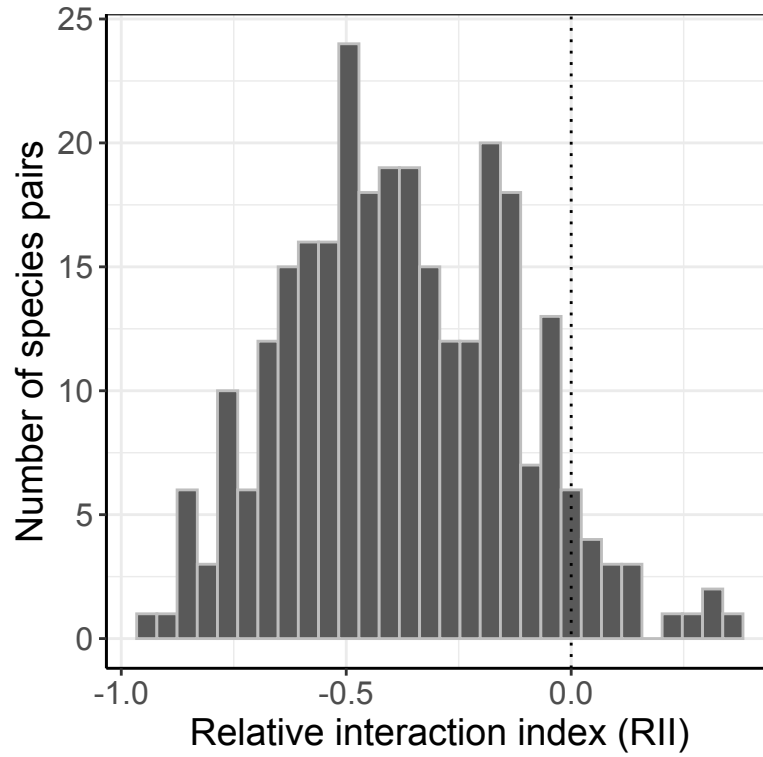




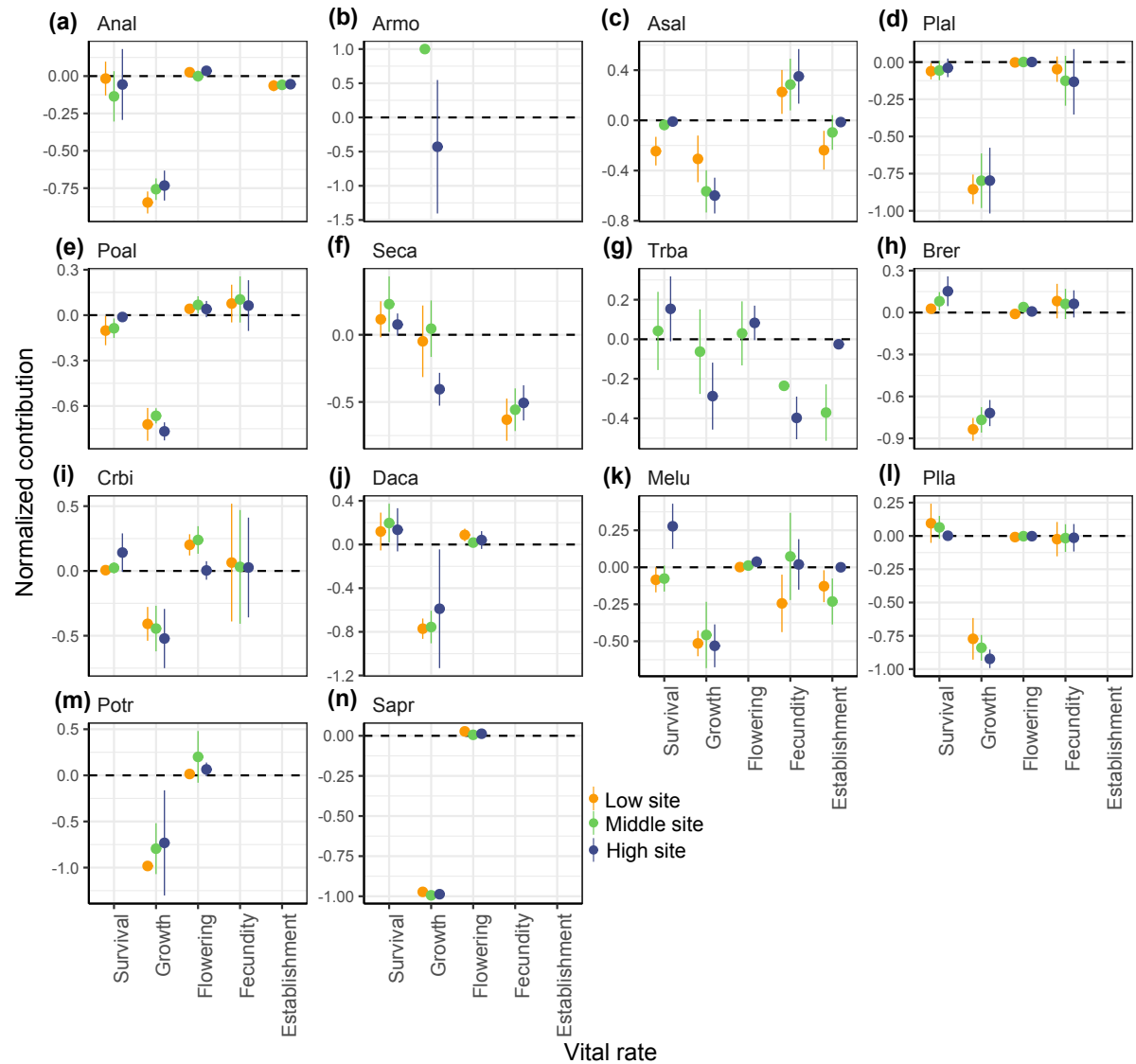
**Figure S3.** A comparison of two methods to assess vital rate contributions to declines in population growth rate ( $\lambda$ ) in the absence vs presence of neighbours. Relative contributions of each vital rate to changes in  $\lambda$  based on vital rate replacements (x-axis, VRR contribution; presented in the main text) vs life-table response experiments (y-axis, LTRE contribution). The solid line in each panel is the 1:1 line.



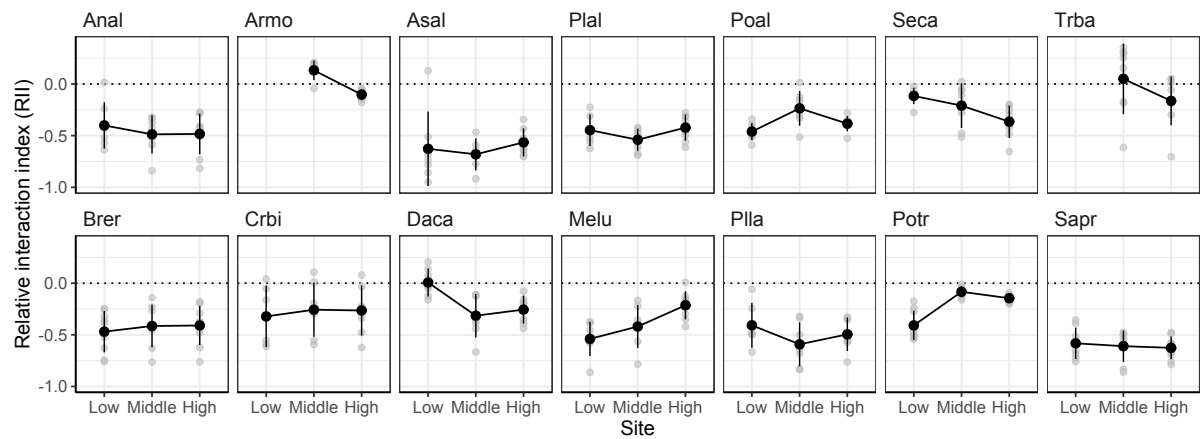
**Figure S4.** The effects of neighbour species on population growth. The intensity of species interactions was calculated as the relative interaction index, RII (Weigelt & Jolliffe 2003):  $(\lambda_{\text{invasion}} - \lambda_{\text{intrinsic}}) / (\lambda_{\text{invasion}} + \lambda_{\text{intrinsic}})$ . Negative RII values indicate competitive interactions (264 of 284 species pairs). The more negative the values, the more intense the competition experienced by the focal species.



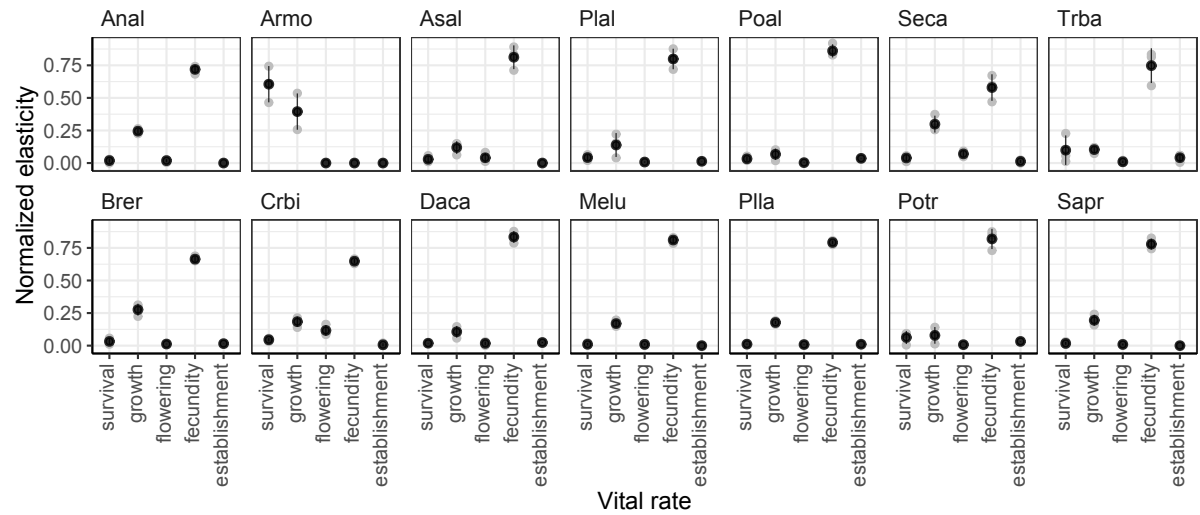
**Figure S5.** Normalized vital rate contributions to declines in population growth rate ( $\lambda$ ) in the absence vs presence of neighbours of each focal species across the three sites (low, orange; green, middle; high, blue). Panels a-f are highland focal species and panels g-n are lowland species. Points and error bars (not always visible) represent averages and standard deviations summarized across species pairs at each site (low site, orange; middle site, green; high site, blue). See Table 1 for species codes.



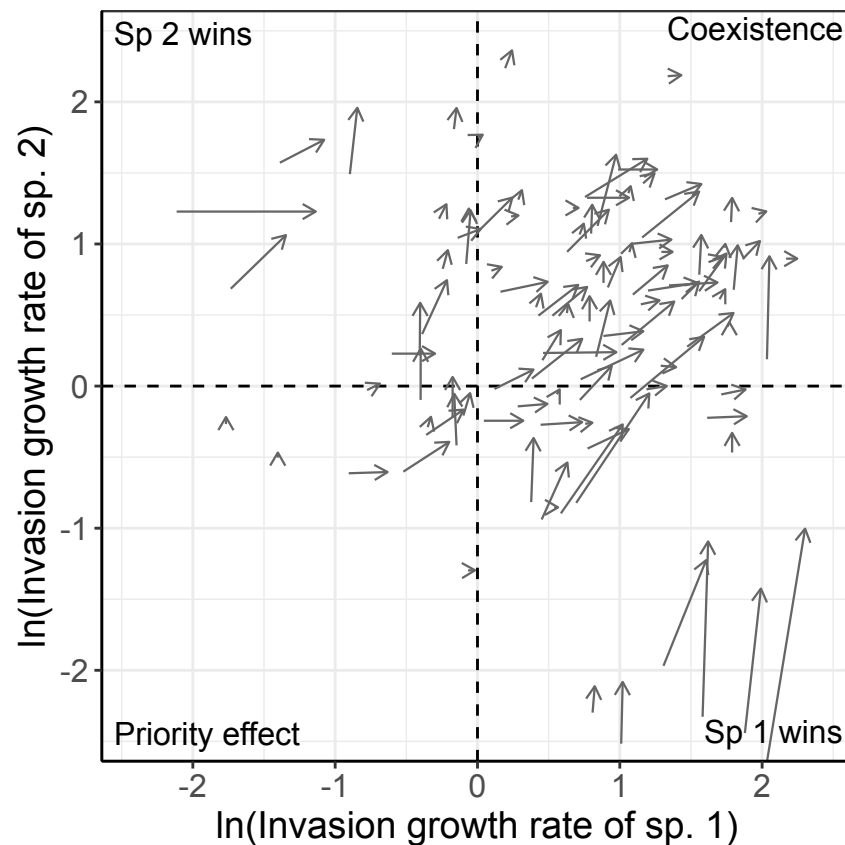
**Figure S6.** Interaction intensity experienced by highland (first row) and lowland (second row) focal species across the elevation gradient. Interaction intensity was quantified using the relative interaction index (RII, Weigelt & Jolliffe 2003). Each grey point represents a RII value of a species pair, while black points are averages ( $\pm$  standard deviations) across species pairs at each site. Overall, the effects of neighbours on population growth across the elevation gradient varied greatly among focal species (significantly different random intercepts and slopes of sites between focal species based on a mixed-effects model:  $F_{5, 297} = 27.539$ ,  $P = 4.477\text{e-}5$ ). See Table 1 for species codes.



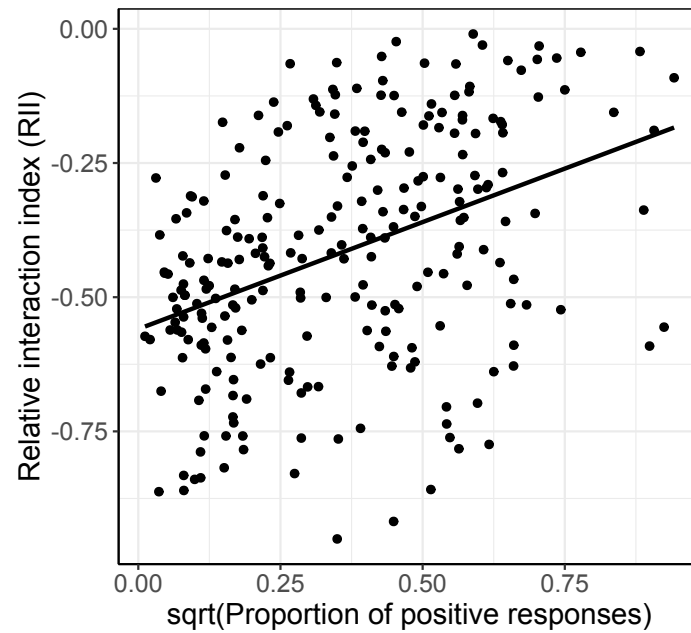
**Figure S7.** Elasticity (i.e., scaled sensitivity) of intrinsic (i.e., without competition) population growth rates ( $\lambda_{\text{intrinsic}}$ ) to the five vital rates of each focal species. The elasticity was calculated based on the intrinsic IPM at each site. Grey points (not always visible) are elasticity at each site, and black points are averages ( $\pm$  standard deviation) summarized across the three sites. See Table 1 for species codes.



**Figure S8.** Shift in outcomes of competition in the absence vs presence of complementary responses. Each arrow represents a species pair, indicating the shift in predicted competitive outcomes from models in which complementary responses are absent (arrow tail) to models with complementary responses present (arrow point). The competitive outcomes can be evaluated based on the population growth rates when the focal species is rare, while its competitor is at equilibrium density (i.e., invasion growth rates,  $\lambda_{\text{invasion}}$ ; Chesson 2000). A pair of species is predicted to coexist stably if both species can maintain positive invasion growth rates (i.e.,  $\ln(\lambda_{\text{invasion}}) > 0$ ; top-right quadrant); if only one species can maintain positive invasion growth rate then its competitor is predicted to be excluded (top-left and bottom-right quadrants for species 2 and species 1 winning, respectively); otherwise, priority effects occur if neither species can maintain positive invasion growth rates (i.e.,  $\ln(\lambda_{\text{invasion}}) < 0$ ; bottom-left quadrant).



**Figure S9.** Species with greater strength of complementary responses (i.e., total proportional contribution of complementary responses; square-root transformed) experienced weaker competition, (i.e., RII values were less negative). Competition intensity was quantified using relative interaction index (RII, Weigelt & Jolliffe 2003). Each point represents an invasion IPM model (i.e., a species pair), while the line represented fitted line based on a linear model with RII as a response variable and the strength of complementary responses as an explanatory variable ( $F_{1,243} = 53.904$ ,  $P = 2.106\text{e-}13$ ).



### Supplementary References

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