LETTER

Novel competitors shape species' responses to climate change

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Understanding how species respond to climate change is critical for forecasting the future dynamics and distribution of pests, diseases and biological diversity[1–3]. Although ecologists have long acknowledged species' direct physiological and demographic responses to climate, more recent work suggests that these direct responses can be overwhelmed by indirect effects mediated via other interacting community members[2–7]. Theory suggests that some of the most dramatic impacts of community change will probably arise through the assembly of novel species combinations after asynchronous migrations with climate[8–10]. Empirical tests of this prediction are rare, as existing work focuses on the effects of changing interactions between competitors that co-occur today[7,11–15]. To explore how species' responses to climate warming depend on how their competitors migrate to track climate, we transplanted alpine plant species and intact plant communities along a climate gradient in the Swiss Alps. Here we show that when alpine plants were transplanted to warmer climates to simulate a migration failure, their performance was strongly reduced by novel competitors that could migrate upwards from lower elevation; these effects generally exceeded the impact of warming on competition with current competitors. In contrast, when we grew the focal plants under their current climate to simulate climate tracking, a shift in the competitive environment to novel high-elevation competitors had little to no effect. This asymmetry in the importance of changing competitor identity at the leading versus trailing range edges is best explained by the degree of functional similarity between current and novel competitors. We conclude that accounting for novel competitive interactions may be essential to predict species' responses to climate change accurately.

Climate change will alter species' competitive environments through initial shifts in the performance and relative abundance of their current competitors, and longer-term changes in the identity of their competitors caused by migration and local extinctions[2]. Empirical studies of the shorter-term changes in neighbour abundance provide evidence both for[7,11,13,15] and against[12–14] the importance of competitive interactions in mediating the impact of climate change. However, these results may underestimate the potential role of changing competition. Over longer timescales, species will experience competition from new and functionally different migrants, and if they themselves migrate to track climate change, they will probably encounter new resident competitors[2,9]. Despite the potential importance of these novel competitive interactions in determining species' persistence and future distributions with climate change[16,17], empirical evidence is scant for two reasons. First, in most systems, the combinations of species that will face one another in the future is highly uncertain. Second, the logistical challenges associated with experimentally assembling hypothetical future communities, and doing so under realistic climate scenarios, are typically prohibitive.

Elevation gradients in mountains provide a unique opportunity to test how changing competitor identity will affect species' responses to climate change. The steep climate gradient in these environments means that the novel competitors that species will face following climate warming are those already occurring only hundreds of metres away. Furthermore, perennial grasslands in these regions lend themselves to whole-community transplantation along climate gradients. We experimentally simulated the endpoints of the spectrum of competitive environments that an alpine species will experience following climate change at the leading and trailing edges of its range (Fig. 1). At its trailing range edge, a species that fails to migrate will experience warmer climate and compete with either its current community members (scenario 1 in Fig. 1), or with a novel community composed of species that have migrated upwards from lower elevation (scenario 2). By contrast, at the leading edge of its range, a species migrating to higher elevations to track its current climate will compete either with its current competitors if they also migrate (scenario 3) or with a novel higher-elevation community that has persisted in place (scenario 4).

To simulate these scenarios, we transplanted focal alpine species and intact plant communities along an elevation gradient in the Swiss Alps (Table 1), and followed their performance for 2 years. To simulate scenarios in which focal species and/or communities fail to migrate and thus experience warmer temperatures, we moved focal plants and/or communities to a lower-elevation site. To simulate scenarios in which focal species and/or communities migrate to track current climate and thus experience little change in temperature, we transplanted them back into their current elevation site. The direction of transplantation is thus meant to reflect future climate conditions, not
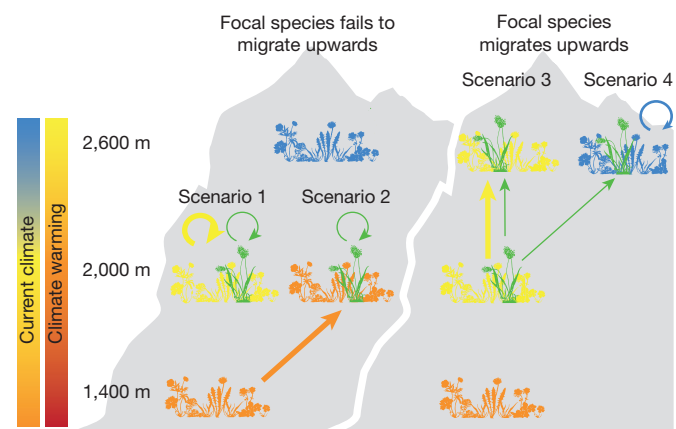

Figure 1 | Scenarios for the competition experienced by a focal alpine plant following climate warming. If the focal plant species (green) fails to migrate, it competes either with its current community (yellow) that also fails to migrate (scenario 1) or, at the other extreme, with a novel community (orange) that has migrated upwards from lower elevation (scenario 2). If the focal species migrates upwards to track climate, it competes either with its current community that has also migrated (scenario 3) or, at the other extreme, with a novel community (blue) that has persisted (scenario 4). Table 1 describes the experimental implementation of these scenarios.

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Table 1 | Experimental manipulations corresponding to the different competitive scenarios experienced by a focal plant following climate warming

Scenario	Focal species' response to warming	Origin of focal species	Competitor scenario	Origin of competitors	Elevation of transplant site
1	Focal species fails to migrate and experiences warming	2,000 m	Current competitors persist in warmer climate	2,000 m	1,400 m
2	Focal species fails to migrate and experiences warming	2,000 m	Low-elevation competitors migrate up and replace current competitors	1,400 m	1,400 m
3	Focal species migrates up to track climate	2,000 m	Current competitors migrate up to track climate and replace high-elevation competitors	2,000 m	2,000 m
4	Focal species migrates up to track climate	2,000 m	High-elevation competitors persist in warmer climate	2,600 m	2,000 m

the future location of the species (Table 1). Plants moved downhill experienced an average daily climate warming of around 3 °C (Extended Data Fig. 1 and Extended Data Table 1), which reflects the magnitude of climate change predicted for the next 50–100 years in Switzerland[18]. While abrupt climate change experiments, as imposed here, mimic future conditions[19], testing more gradual species' responses, such as adaptation, requires other approaches. We tested the influence of the four migration scenarios on the performance of four focal alpine species: *Anthyllis vulneraria* ssp. *alpestris* (alpine kidney vetch, hereafter *A. alpestris*), *Plantago atrata* (black plantain), *Pulsatilla vernalis* (spring

pasqueflower) and *Scabiosa lucida* (glossy scabious). These species differ in their dispersal potential (Extended Data Table 2), and their current ranges do not effectively extend to either the lowest- or highest-elevation field sites (see Methods and Table 1).

The response of the focal species to novel competitors depended on whether they grew at the experimental site with warmer or current climate conditions (Fig. 2; significant novel competitor × site, or novel competitor × site × species interactions in Table 2). When the focal species experienced increased temperature (transplantation to lower elevation to simulate climate warming at the trailing edge of their
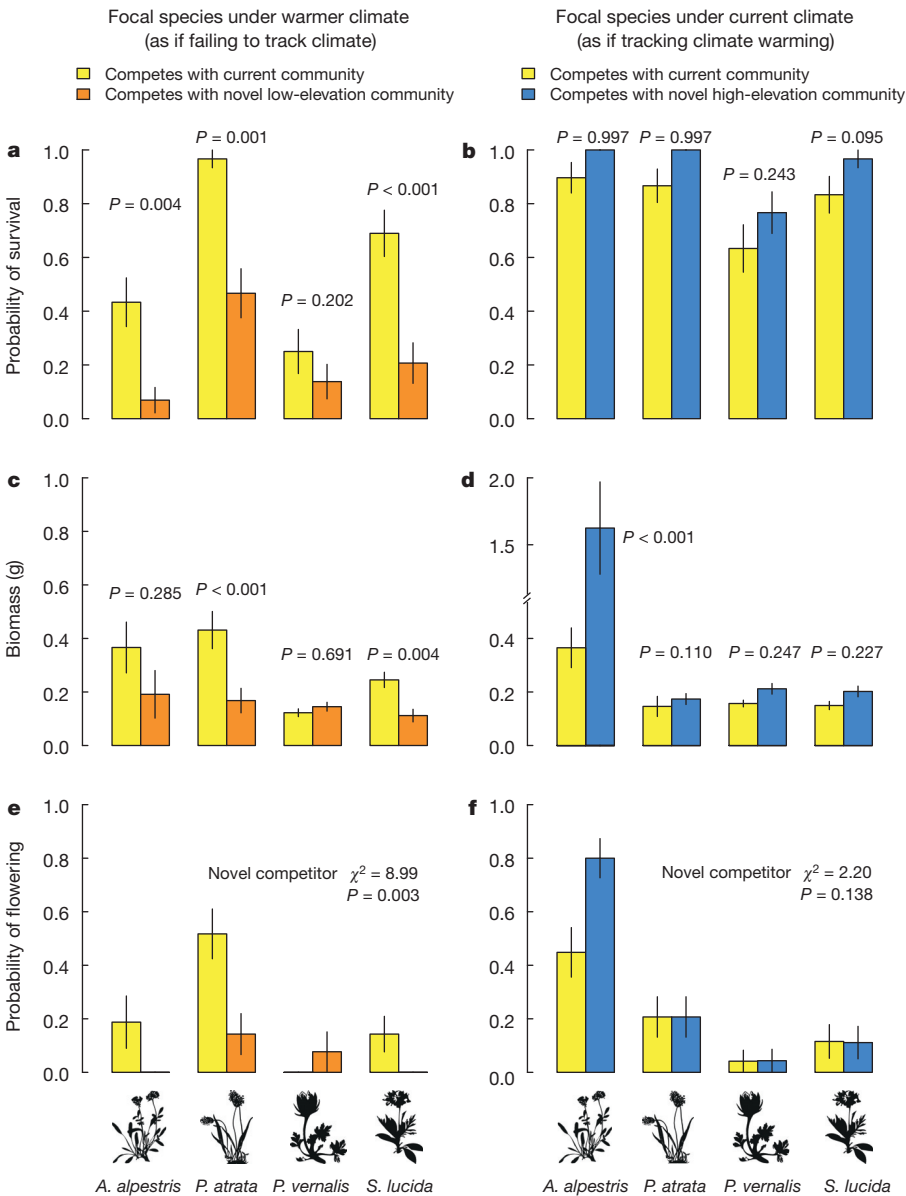

Figure 2 | Effect of novel competitors on alpine plant performance. Survival over 2 years (**a**, **b**), second year biomass (**c**, **d**) and second year flowering (**e**, **f**) of focal species exposed to different potential competition scenarios following climate warming (see Table 1). Shown are means (s.e.m.) of the raw data. When the novel competitor × site × species interaction was significant (**a**–**d**), P values for species-by-site specific contrasts were taken from the full model (see Table 2 for statistics and *n*), else from site-specific contrasts averaging over species (**e**, **f**); P values <0.005 remain significant ($\alpha = 0.05$) after Holm–Bonferroni correction for multiple comparisons.

Table 2 | Statistical analysis of focal alpine plant performance

		Survival		Biomass		Flowering	
Source	d.f.	χ^2	P	χ^2	P	χ^2	P
Novel competitor (NC)	1	2.53	0.112	0.01	0.944	0.03	0.861
Site (S)	1	32.38	<0.001	<0.01	0.991	1.08	0.298
Species (Sp)	3	67.21	<0.001	55.98	<0.001	61.87	<0.001
NC × S	1	28.55	<0.001	26.04	<0.001	5.28	0.022
NC × Sp	3	0.93	0.818	14.08	0.003	5.64	0.131
S × Sp	3	12.34	0.006	18.81	<0.001	17.41	0.001
NC × S × Sp	3	10.14	0.017	10.16	0.017	5.02	0.170
n (n blocks)		473 (20)		291 (20)		363 (20)	

Shown are likelihood ratio tests for novel competitor (current versus novel competitors), site (1,400 or 2,000 m experimental site), and species effects and their interactions on survival after 2 years, and biomass and flowering probability in the second year of the experiment. Also shown are the total number of observations (n) and experimental units (n blocks) for each model.

range), their performance 2 years after transplantation depended strongly on the origin of their competitors (Fig. 2). For three of four species, survival was reduced by 52–84% (Fig. 2a), biomass by 48–61% (Fig. 2c; n.s. for *A. alpestris*) and flowering by over 72% (Fig. 2e) when competing against a novel, low-elevation plant community (scenario 2) compared with their current alpine community (scenario 1). The biomass reduction due to these potential migrants from lower elevation was significant even in the first year of the study (Extended Data Fig. 2; novel competitor $\chi^2 = 17.66$, d.f. = 1, $P < 0.001$). We found much weaker effects of changing competitor identity when focal species were transplanted back into their current elevation to simulate migration and climate tracking. Here, whether focal species competed with a novel high-alpine community (scenario 4) or their current community (scenario 3) had no significant effect on survival (Fig. 2b) or flowering (Fig. 2f), and modest, largely non-significant effects on biomass (Fig. 2d). The one exception was the strong response of *A. alpestris* biomass to novel competitors, but this response was replicated when it grew without any competitors on the soils from the two elevations ($\chi^2 = 7.31$, d.f. = 1, $P = 0.007$; Extended Data Fig. 3), suggesting a limited role for shifting competitor identity.

Plant performance in our experiment might be affected by factors other than competitor identity that differ between the communities, including soil chemistry and biota. To evaluate soil effects on plant growth, we grew the focal species at each site without competition on soil originating from each elevation. We found that focal species tended to grow better at lower- versus higher-elevation (site $\chi^2 = 24.31$, d.f. = 1, $P < 0.001$) on a common 2,000 m soil, but their response to soil origin never matched significant biomass responses to novel competitors, suggesting that the observed changes in performance in Fig. 2 were indeed due to shifting plant competition (with the exception of *A. alpestris* as mentioned above; Extended Data Fig. 3). We also conducted a follow-up greenhouse experiment to isolate the effects of soil biota from different elevations. Soil organisms could affect plant competition if they fail to migrate synchronously with the plant communities in the future. Results suggest that soil biota from the different elevations did not affect the relative performance of alpine versus sub-alpine plant competitors (Extended Data Fig. 4 and Extended Data Table 3). Related to this, we did not find differences in the incidence of herbivory across the two community types at the low-elevation site (where competitor identity effects were strong), except for two species in the first year of the study only (and this did not relate to subsequent survival or biomass; Extended Data Table 4).

In sum, our results show that novel competitors strongly affected the performance of alpine plants under increased temperatures, as will occur at the trailing edge of their range, but had little effect on plants under current temperatures, as would occur following range expansion to higher elevation. This asymmetry in the importance of competitor identity at the leading versus trailing range edges can be explained by the greater functional similarity between the high- and middle-elevation communities, measured with field-based trait measurements on 61 species. The low- and middle-elevation communities were

2.4 times further apart along the first principal component of trait space (Fig. 3a; explaining 76% of the variation in community-weighted trait means) and their comparison produced seven times the F statistic in a permutation-based multivariate analysis of variance (MANOVA) ($F_{1,27} = 52.94$ versus 7.56, $P < 0.001$ and $P < 0.01$, respectively) than the middle- and high-elevation communities. The greater functional similarity of the two higher-elevation communities was caused by shared functional traits, particularly leaf size, leaf mass and plant height, not shared species; the communities were equally distinct in their species composition (Fig. 3b; 1,400 versus 2,000 m permutation MANOVA, $F_{1,27} = 27.74$; 2,000 versus 2,600 m $F_{1,27} = 24.63$; $P < 0.001$ for both comparisons).

Finally, first-year biomass results (before heavy mortality in the second year of the experiment) allowed us to compare the effect of warming on our focal species' interactions with current competitors with the effect of community changes that will arise from competitor migration and local extinction. We found that when the focal alpine plants grew with their current alpine community under warmer temperatures, they experienced greater competition than under current temperatures (pink versus white bars in Fig. 4), but these effects were weak and not significant for any species. This result is consistent with the mixed results from previous studies of short-term competitor dynamics under climate change[7,11–15]. By contrast, for *P. atrata* and *S. lucida*, significantly greater effects of competition arose from changing competitor identity and warmer conditions (Fig. 4). These are also two of the three species with traits predicting relatively poor dispersal (Extended Data Table 2) and thus interactions with novel low-elevation competitors may determine their eventual persistence. This result further suggests that the strongest effects of climate change on competition in this system are likely to occur after the immigration of novel competitors at species' trailing range edges.

Our study provides some of the first empirical evidence that accounting for novel competitors may be important to predicting species' responses to climate change[17,20]. Specifically, our results suggest that species' range dynamics probably depend not only on their ability to track climate, but also the migration of their competitors, and the extent to which novel and current competitors exert differing competitive effects. In our system, populations might persist at their trailing range edge in areas soon to be warmer, as long as lower-elevation migrants fail to arrive. This prediction parallels results from the few mechanistic studies of population decline following climate change, where changing biotic interactions appear more important than direct physiological effects of warmer temperature[1]. However, our results also suggest that, in some cases, changing competitor identity may be less important. We found, for example, that the shift to
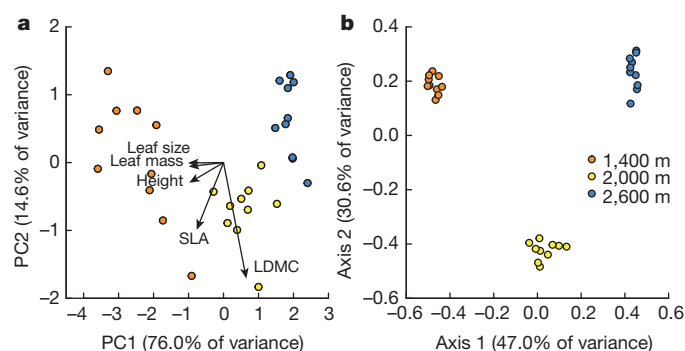

Figure 3 | Functional and floristic community composition. Ordinations of ten replicate communities from sites at 1,400 m, 2,000 m and 2,600 m elevation based on (**a**) a principal component (PC) analysis of community-weighted means of five functional traits (SLA, specific leaf area; LDMC, leaf dry matter content), and (**b**) a principal coordinates analysis of floristic composition based on Bray–Curtis dissimilarity. In **a**, arrows show the loading of individual traits on each principal component axis (loadings have been multiplied by 2 for clarity).
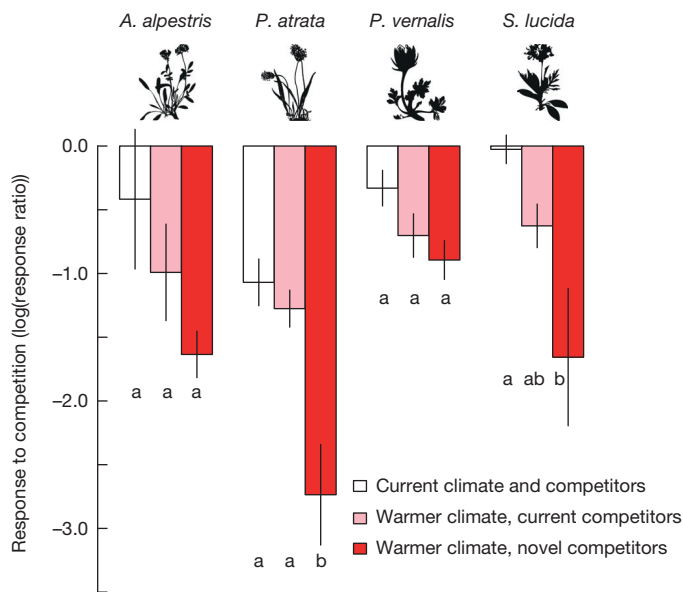
Figure 4 | The response of four alpine species to competition. Plants grew with either (1) their current competitors and climate (in a site at 2,000 m), (2) their current competitors and warmer climate (growing at 1,400 m) or (3) novel competitors from low elevation and warmer climate (growing at 1,400 m). Shown are mean log response ratios (s.e.m.) of above-ground biomass calculated from plants growing with or without competitors (n = 25, 30, 27, 29, for each species, respectively). Different letters below the bars for each species indicate significantly different contrasts (Tukey's honest significant difference test, $P < 0.05$).

novel high-alpine competitors is unlikely to influence the range expansion of focal species to higher elevation, in agreement with the rapid migration of many species upslope with recent climate warming[21,22]. Future work combining species' functional traits, detailed distribution information and ecological theory may prove particularly useful for forecasting how novel competitive interactions determine the response of biological diversity to climate change[23,24].

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Author Contributions All authors designed the study, assisted with fieldwork and wrote the paper. J.M.A. analysed the data and wrote the first draft.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to J.M.A. (jake.alexander@usys.ethz.ch).

METHODS

Field transplant experiment. We selected three perennial grassland sites (1,400, 2,000 and 2,600 m above sea level) in the Swiss Alps (Calanda mountain, Canton des Grisons), which are all dominated by compact turfs, and contain different, overlapping sets of species (Fig. 3). The sites are at maximum 3 km apart with similar southeast exposure, slope and calcareous bedrock, but span a steep climate gradient, with a temperature range of 6 °C from subalpine (1,400 m) to higher alpine (2,600 m) sites, as measured over the duration of the experiment (Extended Data Fig. 1, Extended Data Table 1). The temperature differences between the lower and middle sites, and the upper and middle sites, during the experiment were on average 2.6 °C and 3.4 °C, respectively. Precipitation changes were smaller but decreased by approximately 16% with both 600 m drops in elevation (Extended Data Table 1), also consistent with expectations for climate change[18]. The lower and middle sites are managed as summer pasture, and the upper site is grazed by native ungulates.

At the end of August 2012, 75 cm × 75 cm turfs containing intact plant communities, including roots and the organic soil layer, were excavated at each site to a depth of 20 cm. To implement the design in Table 1, the site at 1,400 m received ten transplanted communities from the 2,000 m site and ten communities transplanted from other locations at the 1,400 m site. Meanwhile the site at 2,000 m received ten transplanted communities from the 2,600 m site and ten from other locations at the 2,000 m site (Table 1). Soil was obtained from each site (after removing the vegetation) and transplanted across sites in the same design. At the two transplant destination sites, each treatment (two communities and two soils) was assigned at random to one of four plots within each of ten blocks (giving 80 plots in total). Blocks were separated by 1 m, with 0.5 m between treatments within blocks.

Focal individuals of four alpine species (*A. vulneraria* ssp. *alpestris*, *P. atrata*, *P. vernalis* and *S. lucida*) were obtained by cutting 240 plugs (about 3 cm diameter) containing a single adult plant from the 2,000 m site. These species are widespread at the 2,000 m site and are either not found or extremely rare in the communities at the 1,400 m and 2,600 m sites. Three individuals per species were planted at random, 15 cm apart in a grid within each treatment and block ($n = 30$ per species, treatment and site). The lower two transplant sites were fenced to exclude cattle, as well as marmots at the 2,000 m site (marmots are not seen at the other sites).

To minimize transplantation-related issues, we transplanted the communities and focal plants in late summer/early autumn, after the plants had already begun to senesce, so that they would first experience their new climate in their growth phase when they emerged the following spring. The communities were clipped to reduce evapo-transpirative stress during transplantation, and the transplants were watered and protected with shade cloth for 1 week after transplantation. Any focal plants that died within the first 3 weeks were replaced. We note that focal individuals and communities did not respond to transplantation in ways that would suggest they were poorly adapted to climate or other conditions at lower elevation: 2,000 m focal plants growing without competition on soils from 2,000 m were larger when transplanted downslope than when transplanted to the same elevation, and grew better on the soil from the lower elevation (1,400 m) site (Extended Data Fig. 3). The above-ground biomass of the intact transplanted communities was unaffected by transplantation downslope (Extended Data Fig. 5).

The survival, phenology and number of inflorescences of every focal individual were monitored every 2 weeks after snowmelt in 2013 and 2014 (deaths occurring in 2014 were confirmed by a final check for surviving plants in early summer 2015). We do not report flowering incidence in the first year of the study because flowering in many alpine plants is determined by conditions in the preceding year[25] (results were generally non-significant). Each focal individual's leaf number and longest leaf length were recorded at planting and in August/September 2013; leaf number and the average area of the three largest leaves were measured in September 2014. Above-ground biomass of each focal individual was estimated from linear models predicting the biomass of destructively harvested individuals from outside the experiment ($n = 27$–39), dependent on the non-destructive measures in either 2013 or 2014, including maximum number of inflorescences in 2014 for all species except *P. vernalis* ($R^2 = 0.80$–0.98). Regressions were forced through the origin, and negative biomass estimates (possible with interactions) set to 0.01 g. Individuals that died up to a month after snowmelt at each site in spring 2013 were considered to have died of transplant shock and excluded from further analysis. Community above-ground biomass was estimated towards the end of each summer using pin quadrats calibrated with destructive harvests made at each site ($n = 20$ plots at the 1,400 m site, $n = 18$ at 2,000 m, $n = 10$ at 2,600 m). The composition and cover of species in each replicate community were determined in 2013 in mid-May (1,400 m) and mid-June (2,000 m), and again in late August/ early September (all sites). Temperature and light intensity were recorded at 30-min intervals using at least one HOBO Pendant data logger (UA-002-64, onset,

www.onsetcomp.com/) at each site. At the end of each season the communities were clipped to approximate biomass removal by grazers.

Statistical analysis of field experiment. No statistical methods were used to predetermine sample size. The investigators were not blinded to allocation during experiments and outcome assessment.

The effects of novel competitors on the biomass of focal plants transplanted into competitor communities from different locations were analysed with mixed-effects models fitted by maximum likelihood. The full model contained main effects and all interactions of the 'novel competitor' treatment (novel versus current competitors), 'site' (1,400 or 2,000 m experimental sites) and 'species,' as well as initial size, as fixed effects, and plot nested in block as random effects to account for the dependency of observations. Biomass and initial size were log-transformed to meet model assumptions of normality and homogeneity of variances. The ten replicate communities per treatment and site were the biological replicates in our experiment, and this number was chosen to be in excess of previous studies that investigated effects of climate change on competition within communities (for example, refs 7, 14). Survival until the end of 2014 and the probability of flowering in 2014 were analysed in a similar way, but using generalized linear mixed models with a binomial family. We tested for over-dispersion (that is, clustering of the binary outcomes within species within plots) and found no significant contribution based on a likelihood ratio test. The statistical significance of individual terms was determined by comparing each model with the correspondingly reduced model using likelihood ratio tests. When the novel competitor × site × species interaction was significant, the significance of the novel competitor effect for each species by site combination was obtained from contrasts within the full model. Significant novel competitor × site interactions in the full model (without a significant three-way interaction) were followed by fitting site-specific models, and testing the novel competitor effect using likelihood ratio tests. When the direction of a species' significant biomass response to novel competitors paralleled its response to the bare soil from the two competitor communities, we also tested the effect of soil itself. In such cases, we used likelihood ratio tests to test the effect of soil origin on biomass for the species-site combination of interest. All models were fitted in R[26] using the lme4 package.

A different statistical model was used to compare the response of each focal species to competition from its current competitors under current versus warmer climate, or to novel competitors under warmer climate. For each species and block, log response ratios of biomass (that is, ln(biomass with competition/biomass without competition)) were calculated on the basis of the biomass of individuals competing with a particular plant community versus growing alone on soil from the same community. Differences in competitive responses between treatments were tested using Tukey's honest significant difference tests within a linear model fitted for each species. We used data from 2013 owing to the high mortality and correspondingly low replication for these tests in 2014.

To investigate the functional composition of each community, data on five functional traits (plant vegetative height, specific leaf area ($mm^2 g^{-1}$), leaf size (mm^2), leaf mass, leaf dry matter content ($mg g^{-1}$)) were collected from plants growing at the field sites in 2014 using standard methods[27] for 61 species that collectively accounted for 89.4 ± 4.8% (mean ± s.d.) of the relative cover in these communities ($n = 26$ or 10 per species for height or leaf traits, respectively). Community-weighted means of each trait were calculated by summing the trait values of species within each replicate community, weighted by their relative cover. Differences between pairs of communities (using a subset of ten replicate communities from each elevation to ensure equal sampling effort) in terms of community-weighted functional trait means were analysed with a permutation-based MANOVA (function 'adonis' in the R package 'vegan', using a Euclidean distance matrix), and visualized using a principal components analysis. The same analysis, but based on a Bray–Curtis distance matrix, was applied to community differences in floristic composition in 2013. The effect of site (1,400 m, 2,000 m, 2,600 m) was highly significant in both cases ($F_{2,27} > 26.18$, $P < 0.001$), and these analyses were followed by pairwise contrasts between the high and middle sites and between the middle and low sites as reported in the main text. Compositional differences were visualized using principal coordinates analysis on a Bray–Curtis distance matrix of log-transformed cover values (mean of the two sampling dates) for the same 61 species.

Soil biota experiment. Whether the microbial community at each elevation will migrate in unison with the plants from those elevations is not clear. We therefore conducted a follow-up greenhouse experiment to investigate potential effects of the soil biota from the lower elevation (1,400 m) and alpine (2,000 m) sites on the relative performance of lower versus higher-elevation competitors. We grew three plant species from the 1,400 m site and three 2,000 m focal species (all but *A. alpestris*) with soil inoculum from the 1,400 m and 2,000 m sites. The background soil was a mixture of soil collected at the 1,400 m site and a 2,200 m site,

which had been sieved, homogenized and sterilized. We sterilized by autoclaving at 121 °C for 20 min, and again after a 2 day incubation period. Live soil inoculum was collected from soil cores from the top *ca.* 15 cm of the soil profile at the 1,400 and 2,000 m sites in October 2014, and sieved and stored at 4 °C before use. Seedlings were germinated from field-collected seed on filter paper, and then transplanted as a single individual to a 360 ml pot containing sterilized background soil and an inoculum (9% of total soil mass) of live soil from one of the elevations. One pot from each species/soil combination was arranged at random within a block ($n = 10$ blocks) on a single bench in a glasshouse in Zurich, Switzerland (set to 20 °C, 14 h day, with supplementary lighting). Each pot received its own drip tray to minimize cross-contamination during watering. After 3 months, above-ground plant parts were harvested to determine dry mass. For each species, a linear mixed-effects model containing soil community origin as a fixed effect and block as a random effect was fitted by maximum likelihood,

and compared with a simpler model without soil community using a likelihood ratio test.

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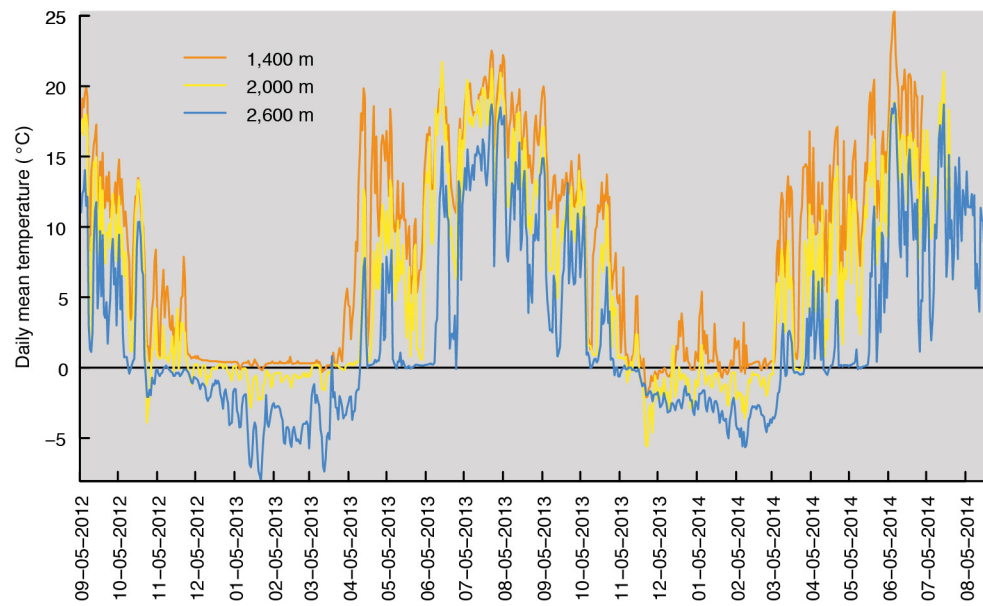
Extended Data Figure 1 | Daily mean temperature during the study at the three experimental sites.
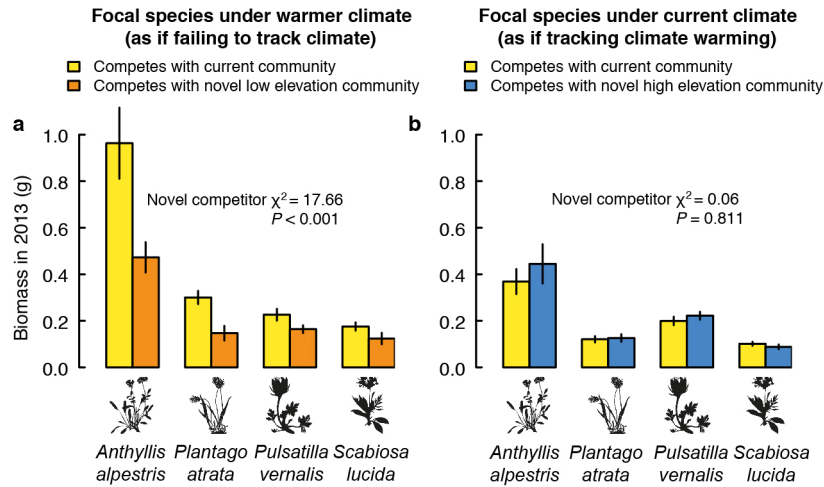
Extended Data Figure 2 | Effect of novel competitors on alpine plant biomass in 2013. Focal species were exposed to different competition scenarios, depending on whether they and/or their surrounding community would either migrate, or fail to migrate, following climate warming (see Fig. 1). Shown are means (s.e.m.) of the raw data, and likelihood ratio tests (d.f. = 1, n = 182 (**a**) and 221 (**b**), n = 10 experimental units (blocks) per site) of the novel competitor effect at each experimental site (in the main model, across all species and sites: novel competitor × site interaction χ^2 = 8.42, d.f. = 1, P = 0.004; novel competitor × site × species interaction χ^2 = 3.17, d.f. = 3, P = 0.367).
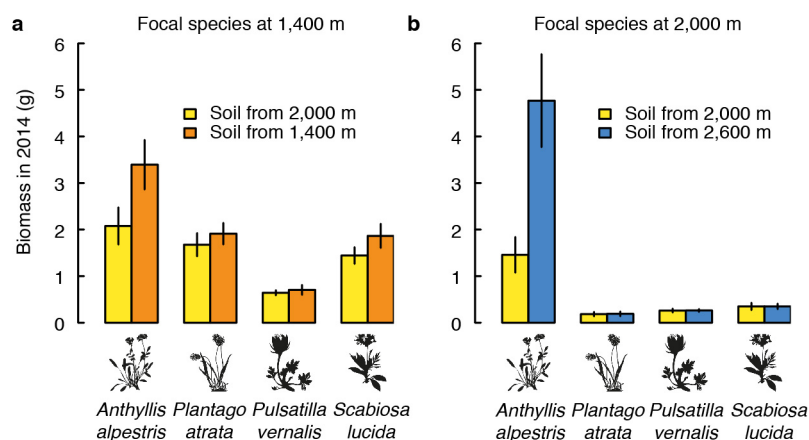
Extended Data Figure 3 | Biomass in 2014 of four alpine plant species growing on soils without competition. Plants grew under a warmer climate (**a**, at 1,400 m) or under their current climate (**b**, at 2,000 m), either on soil from that site, or on soil from a site 600 m higher up the mountain slope. Shown are means (s.e.m.) of the raw data (total $n = 314$).
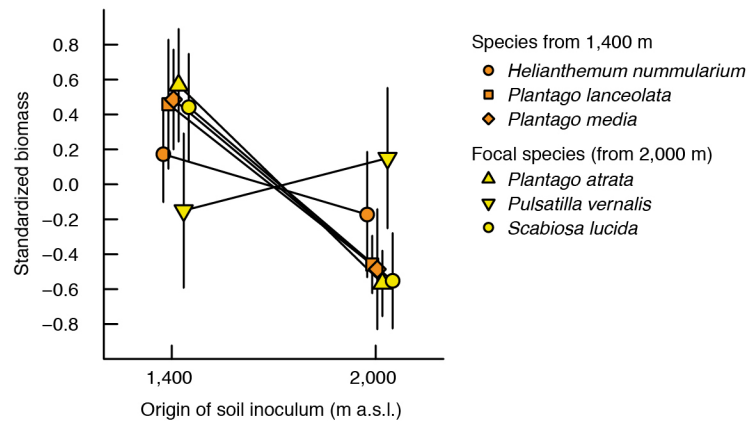
Extended Data Figure 4 | Effect of soil biota on plant biomass. Plants grew on soils inoculated with soil biota from 1,400 or 2,000 m. Plants grew better with soil biota originating from lower elevation, but this effect was shared across species from 2,000 m (in yellow, focal species from the field experiment) and 1,400 m (orange). Thus how fast the 1,400 m soil biota migrate or rise to dominance at higher elevation in the future may not strongly determine the relative performance of 1,400 and 2,000 m plants. Shown are means (s.e.m.) of standardized plant biomass. For statistics and *n* see Extended Data Table 3.
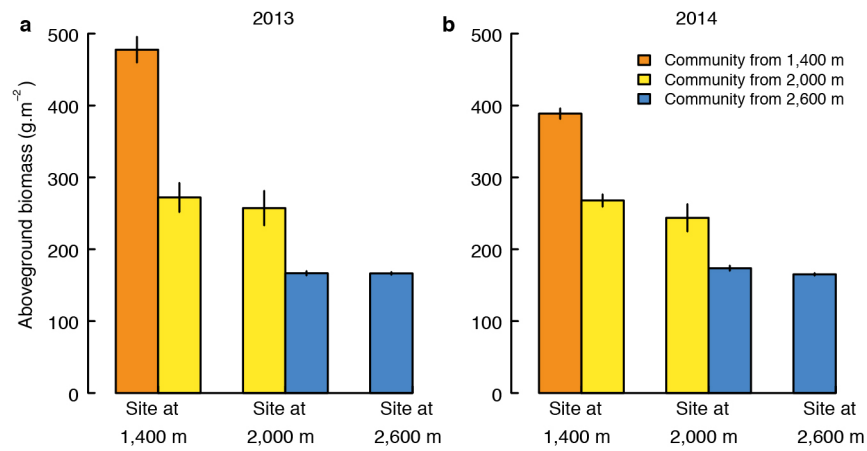
Extended Data Figure 5 | Above-ground community biomass. Standing biomass was estimated in late summer 2013 (**a**) and 2014 (**b**) in the plant communities from sites at 1,400, 2,000 and 2,600 m (mean ± s.e.m., $n = 10$ per community and site), growing in sites at either 1,400 m, 2,000 m or 2,600 m.

Extended Data Table 1 │ Environmental characteristics of the three study sites

Variable	1,400 m site	2,000 m site	2,600 m site
Latitude (°N)	46.8692	46.8879	46.8931
Longitude (°E)	9.4900	9.4895	9.4705
Aspect	SE	SE	SE
Daily mean temp. 2013 (°C)	6.8	4.2	1.2
Daily mean temp. 2014* (°C)	7.7	4.6	0.4
Two year average of daily mean temperature (°C)	7.0	4.4	1.0
Interpolated annual precipitation (mm)	1169	1355	1573

Temperatures were determined from temperature loggers placed at each site (see Extended Data Fig. 1). Precipitation data were obtained from interpolations of Swiss climate (*ca.* 1961–1990) at 50 m resolution[28].
*Until 2 July 2014.

Extended Data Table 2 | Characteristics of the focal species

Species	Family	Growth form	Seed mass (mg)	Inflorescence height (cm)	Terminal velocity of seeds (m/s)	Predicted maximum dispersal (m)
Anthyllis alpestris	Fabaceae	Erect	4.63	8.0	1.5	1.9
Plantago atrata	Plantaginaceae	Rosette	2.98	6.5	7.5	0.2
Pulsatilla vernalis	Ranunculaceae	Erect	1.73	6.0	1.0	6.9
Scabiosa lucida	Caprifoliaceae	Rosette	1.14	13.0	2.1	0.6

Terminal velocity was taken from the Dispersal and Diaspore database[29]. Maximum dispersal was predicted from species' family, terminal velocity and dispersal mode (only *P. vernalis* seeds are specialized for wind dispersal), following statistical model 1 of ref. 30 implemented in R with the function 'dispeRsal' where growth form = herb for all species.

Extended Data Table 3 | Statistical analysis of the effects of soil biota on plant biomass

Species	Seed origin	n	χ^2	P
Helianthemum nummularium	1,400 m	20	0.88	0.349
Plantago lanceolata	1,400 m	16	8.13	0.004
Plantago media	1,400 m	20	8.27	0.004
Plantago atrata	2,000 m	20	6.72	0.010
Pulsatilla vernalis	2,000 m	12	0.37	0.544
Scabiosa lucida	2,000 m	18	5.38	0.020

All models contained block as a random effect; d.f. = 1 for χ^2 tests of the effects of soil biota (from 1,400 or 2,000 m above sea level) on above-ground biomass.

Extended Data Table 4 | Analysis of herbivory on four alpine plant species

Year	Species	Site	χ^2	P	n	n block	r with survival	r with biomass
2013	Anthyllis alpestris	1,400 m	4.93	0.026	31	9	-0.16	0.08
		2,000 m	0.03	0.854	59	10	-0.01	**-0.27**
	Plantago atrata	1,400 m	1.16	0.282	56	10	-0.08	**-0.29**
		2,000 m	0.06	0.808	59	10	-0.21	0.17
	Pulsatilla vernalis	1,400 m	3.03	0.082	46	10	0.13	-0.12
		2,000 m	NA*	NA	NA	NA	NA	NA
	Scabiosa lucida	1,400 m	4.55	0.033	49	10	-0.25	-0.08
		2,000 m	0.25	0.614	56	10	0.02	0.00
2014	Anthyllis alpestris	1,400 m	0.77	0.380	14	7	-0.17	0.29
		2,000 m	4.66	0.031	49	10	-0.07	0.24
	Plantago atrata	1,400 m	1.77	0.183	40	10	-0.08	0.02
		2,000 m	0.53	0.467	52	10	0.04	0.00
	Pulsatilla vernalis	1,400 m	0.05	0.824	16	8	-0.20	0.27
		2,000 m	1.86	0.173	42	10	-0.12	**-0.38**
	Scabiosa lucida	1,400 m	NA*	NA	NA	NA	NA	NA
		2,000 m	0.52	0.470	48	10	NA	0.20

The effect of competitor community identity on the incidence of herbivory on focal species was assessed with mixed-effects models fitted separately for each species and site, including plot nested in block as random effects and log(initial size) as a fixed effect. Shown are likelihood ratio tests (d.f. = 1), and the total number of observations (n) and experimental units (n block) for each model. Also shown are correlations of the incidence of herbivory with biomass and survival after 2 years ($P < 0.05$ indicated in bold). No tests are significant after Holm–Bonferroni correction.
*Model could not be fitted because herbivory was constant.