

TROPIC ECOLOGY

Novel trophic interactions under climate change promote alpine plant coexistence

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Herbivory and plant defenses exhibit a coupled decline along elevation gradients. However, the current ecological equilibrium could be disrupted under climate change, with a faster upward range shift of animals than plants. Here, we experimentally simulated this upward herbivore range shift by translocating low-elevation herbivore insects to alpine grasslands. We report that the introduction of novel herbivores and increased herbivory disrupted the vertical functional organization of the plant canopy. By feeding preferentially on alpine plants with functional traits matching their low-elevation host plants, herbivores reduced the biomass of dominant alpine plant species and favored encroachment of herbivore-resistant small-stature plant species, inflating species richness. Supplementing a direct effect of temperature, novel biotic interactions represent a neglected but major driver of ecosystem modifications under climate change.

Herbivores regulate plant biomass (1), community structure (2), and ecosystem processes (3). Along climatic gradients, shifts in the prevalence of herbivores are associated with variations in plant functional traits such as physical and chemical defenses, underlining the strong top-down effect of herbivores on ecosystem functioning (3, 4). At higher elevations, plants generally experience lower levels of herbivory (5–8; fig. S1) and are less defended, principally through relaxed chemical defenses (5, 7, 9, 10; but see 6). Climate change is expected to modify the current organization of trophic interactions between plants and herbivores along climatic gradients (11). Climate-driven elevational range shifts of insects have been shown to be much faster than those of plants (12), which tend to lag behind (13, 14). Therefore, a faster climate-driven range shift of insect herbivores into alpine ecosystems may generate opportunities for them to feed on poorly defended plants and could modify the current structure and functioning of alpine plant communities (15, 16). Climate change experiments have primarily focused on direct effects of abiotic factors, mainly temperature, on plant communities (17, 18) or on altered interactions between trophic groups within closed systems (19, 20). So far, few investigations have included novel trophic interaction networks be-

tween resident and range-shifting species (but see 21, 22). Including direct and indirect ecological responses to climate change will provide a comprehensive view of the effects of climate change on biodiversity (23).

Colonization of alpine plant communities by lowland insect herbivores represents an indirect effect of climate change on ecosystems. Increased growing season length and a reduced number of freezing events under climate warming are expected to facilitate the settlement of insect herbivores at higher elevations by favoring their growth, development, and reproduction (24). We studied the effect of increased orthopteran herbivory on plant communities because orthoptera are among the most abundant grazers of alpine grasslands in the European Alps (25). Using niche-based models (26), we predicted an average elevation shift of orthopteran species in the Swiss Alps of 490 m by the year 2080 ($\Delta T = +3.56^\circ\text{C}$; mean \pm SD = 489.7 ± 312.9 m; table S1). On the basis of our projections, this shift will result in a twofold increase in herbivore richness (Fig. 1, B and C) and more than a threefold increase in herbivore abundance above the tree-line [i.e., 1800 m above sea level (a.s.l.); Fig. 1D]. As a result, current high-elevation herbivore densities (i.e., 1 to 7 orthoptera/m² at ~2000 m a.s.l.) could reach the levels currently found 500 to 800 m lower (i.e., 8 to 17 orthoptera/m²; fig. S2) within the next decades.

We experimentally simulated the predicted herbivore range shifts in three alpine grassland communities (27). To do so, we translocated an orthopteran community from a lower elevation (i.e., 1400 m a.s.l.; table S2) into cages at three locations above the treeline in the Swiss Alps (1800, 2070, and 2270 m a.s.l.; Fig. 1, A and B, and fig. S3). We measured changes in the biomass, structure, and composition of alpine plant communities using point-intercept vegetation observations over four growing seasons. We tracked the response of alpine plant commu-

nities to enhanced herbivore pressure using a set of leaf traits, including physical and structural properties [specific leaf area (SLA), leaf dry matter content (LDMC), toughness, and silica and chlorophyll content] and chemical properties [leaf carbon to nitrogen ratio (C:N) and expression of flavonoids, terpenoids, alkaloids, phenolics, and tannins extracted from plant metabolomics profiles]. We also distinguished indirect changes resulting from novel biotic interactions from a direct effect of warming by modifying in situ abiotic conditions using open-top chambers (OTCs) (figs. S3, S4, and S5). Herbivore incursion and warming treatment plots were compared with cage control plots (without translocated herbivores) and ambient (no cage) control plots, respectively. It was previously shown that alpine plants are generally more palatable than low-elevation plants because of the relaxation of plant defenses at high elevation (5, 6, 9). We therefore expected herbivores colonizing alpine communities to be released from the bottom-up constraints in their lower-elevation origin and to feed on a broad range of plant lineages, in turn generating a community-wide decline in plant biomass.

The multilayered canopy functional structure of alpine grasslands was modified by the introduction of novel herbivores. The point-intercept vegetation observations provided a three-dimensional view of the (re)organization of the canopy. Before herbivore translocation, the community-weighted mean (CWM) of LDMC, leaf toughness, leaf silica content, and leaf C:N was highest at the top of the canopy (linear mixed-effects model: positive slopes, $P < 0.001$), whereas SLA, flavonoid, terpenoid, alkaloid, phenolic, tannin, and chlorophyll contents were highest in the understory of the vegetation, where light is the most limiting (negative slopes, $P < 0.043$; Fig. 2A and table S3). Novel herbivores decreased the vegetation biomass (linear mixed-effects model: slope = -139.5 , $P < 0.001$; Fig. 1E) and changed the functional dominance of the entire plant communities (SLA: slope = 0.93; LDMC: slope = -12.29 ; leaf toughness: slope = -2.01 ; silica content: slope = -0.08 ; chlorophyll content: slope = 5.13×10^{-3} ; C:N: slope = -0.68 ; terpenoids: slope = 1.39×10^{-3} ; phenolics: slope = 2.39×10^{-3} ; tannins: slope = 2.14×10^{-3} ; $P < 0.05$ for all traits except alkaloids and flavonoids) compared with the cage control plots. Specifically, the novel herbivore community decreased the biomass of the upper canopy (10 to 50 cm height: mean = -56.6 contact points) more than they affected the understory of the vegetation (0 to 10 cm height: mean = -8.9 contact points; interaction herbivore treatment \times vegetation height: $P < 0.001$), which altered the functional dominance of the CWM of traits along the vertical structure of the vegetation (interaction herbivore treatment \times vegetation height: $P < 0.05$ for all traits except C:N, phenolics, and

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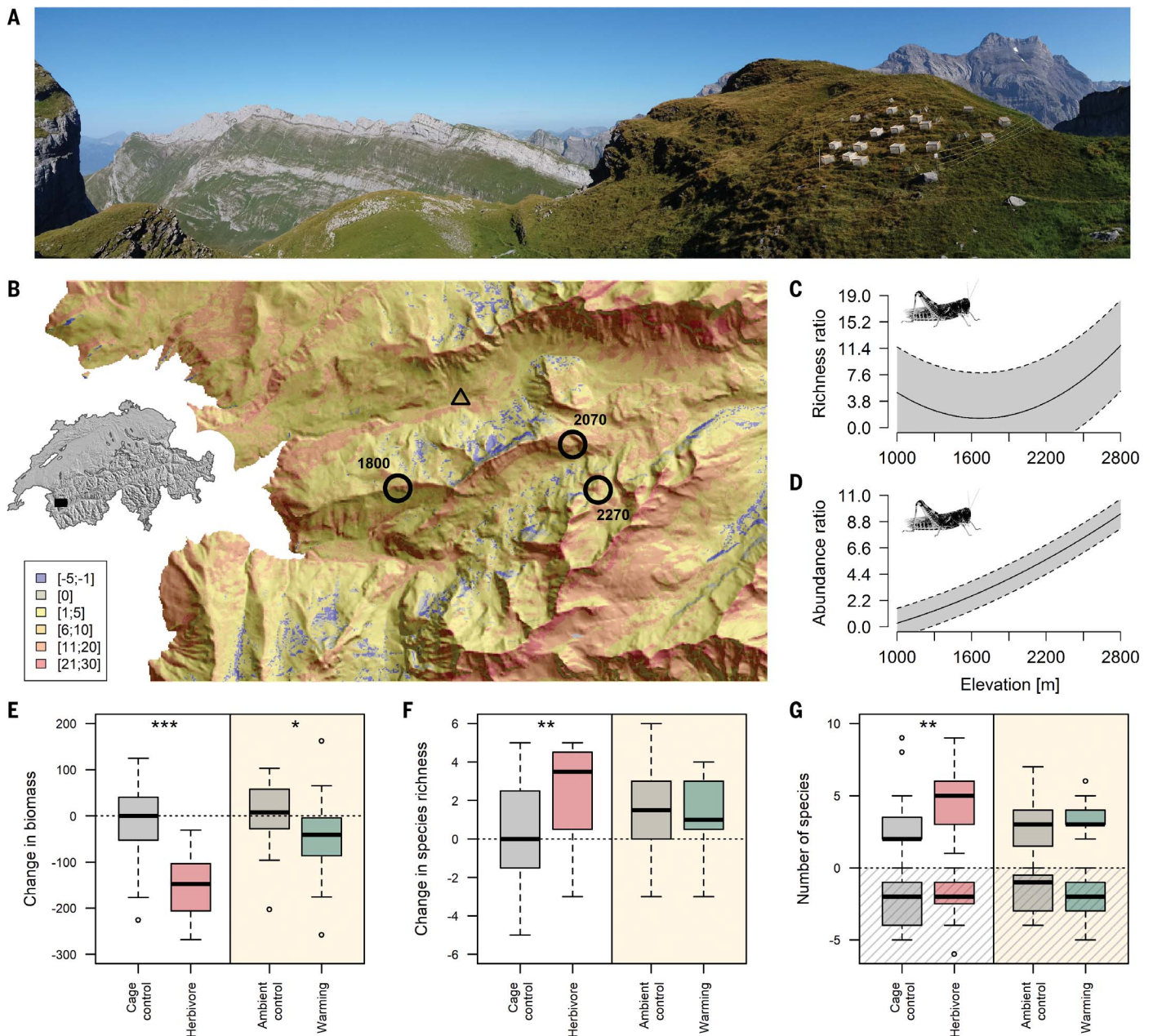


Fig. 1. Forecasted changes in herbivore and plant communities under climate change in the study area. (A) The herbivore incursion and warming experiment was performed in three species-rich alpine grasslands above the treeline in Switzerland. Photo credit: P. Descombes, ETH Zürich, Switzerland. (B) The three experimental sites were located in the western Swiss Alps (black polygon on the Swiss map) at 1800, 2070, and 2270 m a.s.l. (black circles). The black triangle corresponds to the orthopteran collection site (1400 m a.s.l.). The colors on the map represent the changes in orthopteran species richness (blue indicates a decrease in the number of species, gray indicates that the number is stable, and yellow to red indicates an increase) between today

terpenoids; Fig. 2B and table S4). The reorganization of the vertical structure of the canopy may change interactions among plant species and shift plant species colonization-extinction dynamics (28), responses previously reported in tropical forest systems (29).

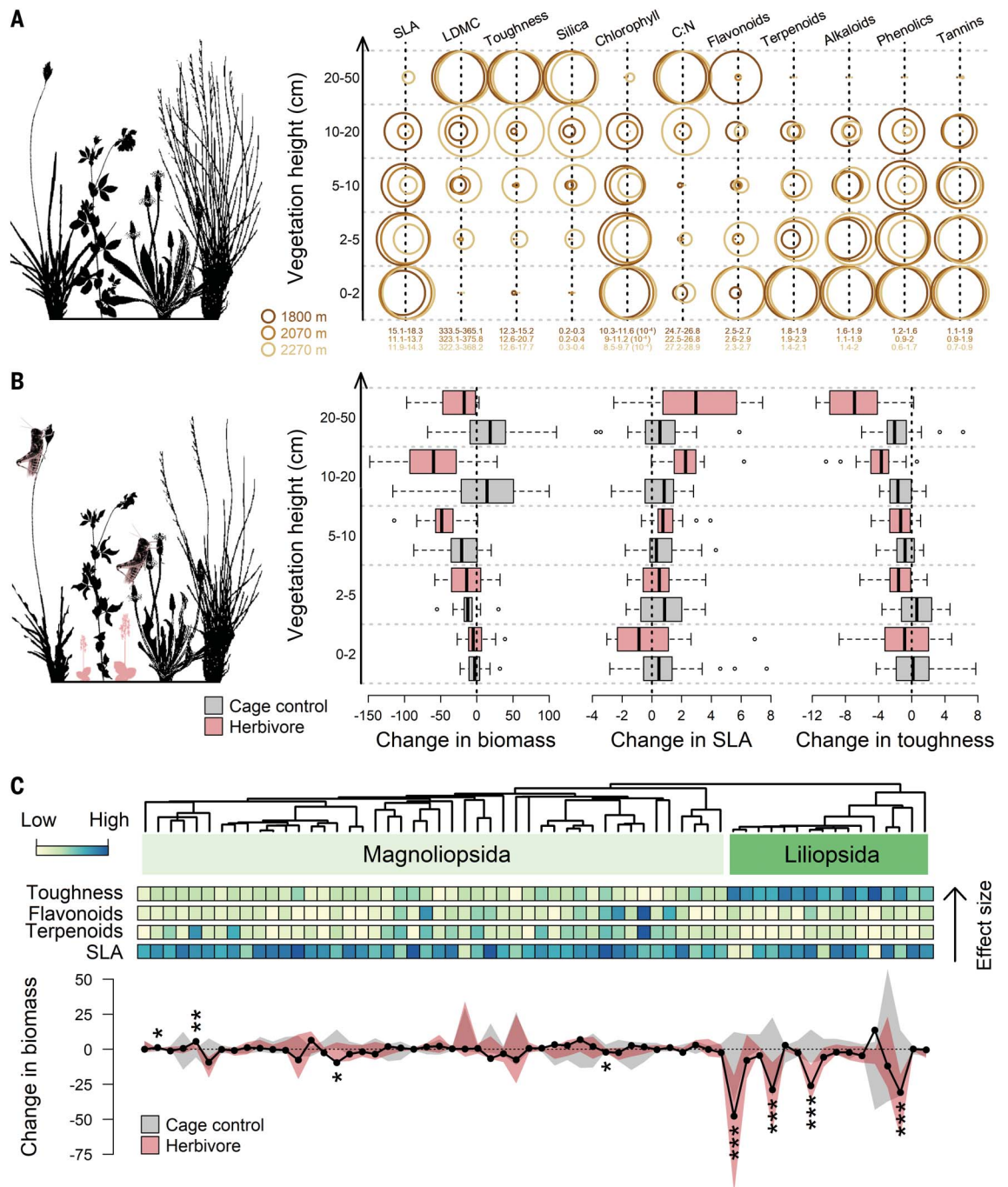
Novel herbivores induced an increase in plant species richness of 8.6 percentage points on average (linear mixed-effects model: slope = 2.25, $P = 0.004$; initial species richness: mean = 26.5; Fig. 1F) compared with the cage control plots. The increase in species richness in the

and 2080 under a business-as-usual scenario (Representative Concentration Pathway 8.5; mean global temperature increase of 3.7°C), as simulated in niche-based models. (C and D) Relative increase (ratio >1) or decrease (ratio <1) in orthopteran herbivore richness (C) and abundance (D) from current to future climate conditions in the study region. The curves were fitted with a linear regression with polynomial terms, and the gray area represents the 95% prediction interval. (E to G) Change in estimated plant biomass (E), plant species richness (F), and the number of plant species lost (hatched background) and gained (solid background) (G) in experimental plots under herbivore incursion and warming treatments ($n = 24$). Linear mixed-effects models: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

herbivore treatment was driven by higher species gains (linear mixed-effects model: slope = 1.71, $P = 0.007$), rather than lower species losses (slope = -0.54, $P = 0.16$; Fig. 1G), compared with control plots. Across all elevations, novel herbivores increased the gains of small-stature

Fig. 2. Changes in vegetation structure under herbivore incursion.

(A) Structure of the functional dominance (CWM) of plant leaf traits along the vegetation height before any treatments were initiated. The size of the circle represents the CWM value of the trait averaged for each vegetation height and normalized by experimental site (shown as different-colored circles). (B) Changes from 2014 to 2017 in estimated plant biomass, SLA (mm^2/mg), and leaf toughness ($\text{GN}/\text{m}^2/\text{m}$) along the vegetation height under herbivore incursion treatment and in cage controls ($n = 24$). (C) Changes in estimated plant biomass under herbivore incursion and in cage controls (polygon area: mean \pm SD) associated with plant traits. Trait values were averaged across the three field sites, log + 1 transformed and normalized. The color scale represents the magnitude of the trait value. Traits are ranked according to their effect size and their association with biomass changes under the herbivore treatment (table S15 and fig. S6). The black line represents the net effect of the treatment on the plant biomass. Only species with at least four plot replicates are presented in this figure. Significant differences between the treatment and control are highlighted with asterisks (Student's t test): * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.



plant species with high tannin expression and low SLA (table S5), such as *Viola calcarata* L. (+18.7 percentage points compared with control plots), *Agrostis alpina* Scop. (+25), *Myosotis alpestris* F. W. Schmidt (+31.3), and *Gentiana nivalis* L. (+37.5). Therefore, increased light availability and reduced competition through biomass removal favored higher species richness by promoting the establishment of species growing near the ground (2, 19, 20). Furthermore, herbivore incursion favored the establishment of plants

with higher concentration of tannins, a family of compounds that deter many invertebrate and vertebrate herbivores (30). Species gains were based on species from the local species pool rather than from lower elevation, a process that is likely to occur over a much longer time frame than the four growing seasons of this experiment, whereas the abundance of the plant species on the sites did not influence plant species recruitment in the herbivore treatment (table S6). By contrast, the OTCs, which reproduced a milder temperature in-

crease scenario (+1.1°C on average, but +3.8°C on average during the day; figs. S4 and S5), did not significantly affect plant community composition (linear mixed-effects model: all metrics $P > 0.1$; Fig. 1, F and G) and had a limited effect on plant community functional structure (tables S6 to S8) and plant biomass (linear mixed-effects model: slope = -48.04, $P = 0.02$; Fig. 1E, fig. S6, and tables S7 and S9). Our results indicate that in addition to direct effects of abiotic factors (31), novel trophic interactions and increased herbivore pressure

represent key drivers of change in natural alpine ecosystems under climate change (23). Given their potential role in reshaping plant community assemblages, modeling novel trophic interactions between range-shifting organisms across ecosystems can offer the possibility to better predict changes in ecosystem structure and function under climate change.

Conserved trophic preferences induced predictable demographic and functional changes in alpine plant communities. On the basis of feeding preferences quantified using DNA meta-barcoding techniques applied to feces, we determined that the structures of the plant-orthoptera interaction network were generally phylogenetically and functionally conserved and predictable after translocation to alpine grasslands (Fig. 3, fig. S7, tables S10 and S11, and supplementary text). We found that Caelifera and Ensifera orthopteran species showed distinct feeding preferences for Liliopsida and Magnoliopsida species, respectively, and these preferences were maintained after translocation to alpine grasslands (Spearman correlations: $r > 0.8$; Fig. 3 and fig. S7). The orthopteran feeding preferences were associated with plant functional traits [MCMCgmm; Caelifera: toughness 95% confidence interval (CI) = 0.77 to 1.90; SLA 95% CI = 0.15 to 1.27; C:N 95% CI = -1.42 to -0.02; Ensifera: C:N 95% CI = -1.52 to -0.20; tables S12 and S13] and were predictable (MCMCgmm predictions; Spearman correlations: Caelifera, $r = 0.40$, $P < 0.001$; Ensifera, $r = 0.21$, $P < 0.001$; table S14). Caelifera species, which dominate orthopteran communities in Alpine grasslands (5) (table S2) and are endowed with high mandibular capacities (32), feed preferentially on tough plant species. As a result, plants with a high leaf toughness (MCMCgmm: 95% CI = -7.90 to -3.14), low SLA (95% CI = 0.34 to 4.48), low flavonoids (95% CI = -5.24 to -0.72), and low terpenoids (95% CI = 0.22 to 4.50), predominantly dominant Liliopsida species (Spearman correlation: $r = 0.64$, $P < 0.001$), showed a decrease in biomass with higher herbivore pressure (Fig. 2C, fig. S6, and table S15). In particular, the observed decrease in estimated plant biomass was marked for *Festuca rubra* aggr. (-47.7 contact points), *Carex sempervirens* Vill. (-30.8), *Sesleria caerulea* (L.) Ard. (-28.9), and *Agrostis capillaris* L. (-26.0; Fig. 2C and fig. S6). Despite trait variability within plant species along the site elevation gradient (fig. S8), the effect of the herbivore treatment on a given plant species was steady (fig. S9). Therefore, whereas plant species might adjust to climate change or new herbivores through intraspecific trait plasticity or adaptation, these evolutionary processes may not change the overall response of the system. The colonizing herbivores from low elevation showed different feeding preferences ($84 \pm 11\%$ eaten dry leaf mass on tougher Liliopsida) compared with the less abundant high-elevation

herbivores occurring on the recipient sites ($71 \pm 22\%$ eaten dry leaf mass on Magnoliopsida), demonstrating the significance of novel interactions under herbivore range shifts (table S16 and fig. S10). Orthopteran herbivores maintained their innate trophic preferences by selectively feeding on alpine plant species phylogenetically and functionally similar to species they prefer in the lowlands. In turn, novel interactions introduced a new functional role in the alpine ecosystem and induced differing plant demographic responses (23).

Our findings indicate that novel trophic interactions between lowland colonizing herbivores and alpine plants mediated a distinct top-down effect on the structure of the alpine plant communities compared with current plant-herbivore interactions. A systematic increase in

herbivory under climate change is expected to reshape the vegetation structure of alpine grasslands by generally decreasing the biomass of dominant plants and favoring coexistence (2). The higher herbivore pressure from the translocated lowland herbivores reduced the frequency of dominant plant species with tougher leaves and a distinct chemistry matching the trophic preferences of the herbivores in their habitat of origin. Consequently, increased herbivory fostered the coexistence of subordinate species by enhancing light availability at the ground level and induced a net increase in species richness, especially of plant species with higher tannin concentrations in their leaves and low stature (19, 20). The reduction in plant biomass mediated by novel insect herbivores could facilitate colonization by lowland plants

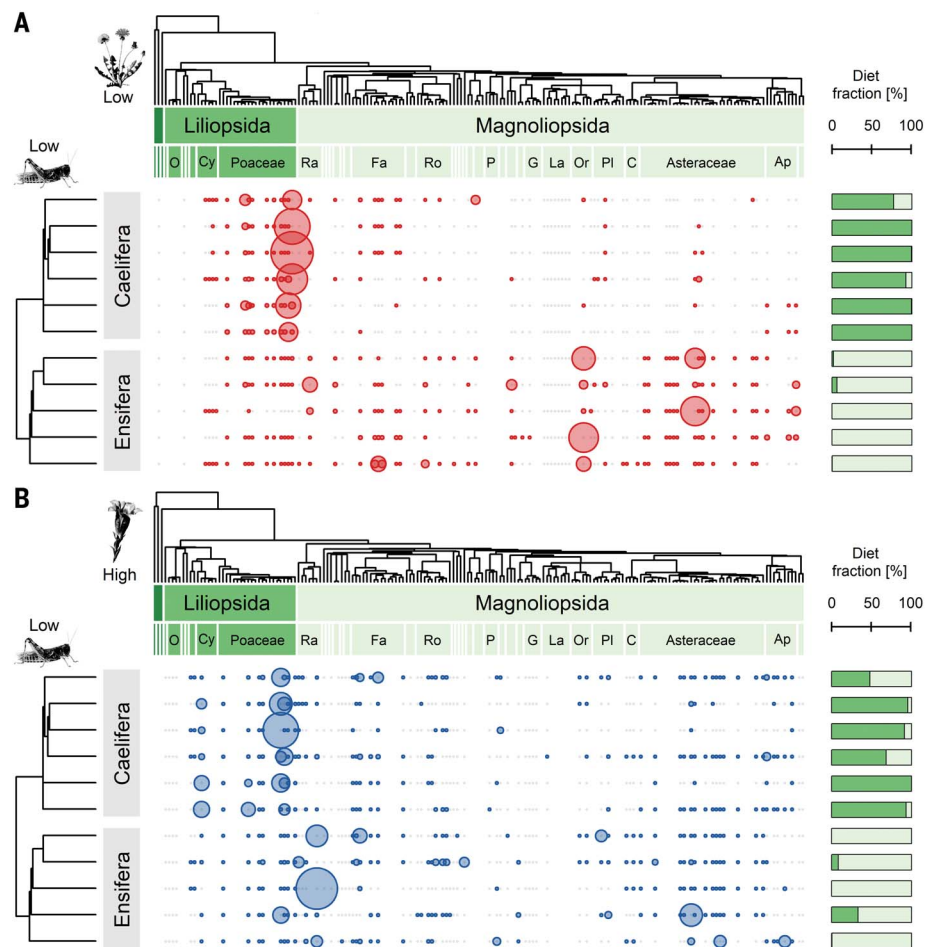


Fig. 3. Diet shifts of lowland orthopteran Ensifera and Caelifera herbivores when feeding on lowland and alpine plant species. Shown are feeding patterns of orthopteran species from the lower-elevation collection site on lowland plants occurring at the collection site (A) and alpine plant species occurring at the mid-elevation experimental site (B). The size of the circles is proportional to the number of reads detected in the feces with DNA meta-barcoding, which is a semiquantitative approximation of the plant biomass ingested by the herbivore (interaction intensity). Values were normalized for each orthopteran species. Gray dots correspond to plant species occurring on the site that were not consumed by the herbivores. The diet fraction represents the proportion of Liliopsida and Magnoliopsida plants in each orthopteran diet. See fig. S7 for the reconstructed trophic network of the two other experimental sites. O, Orchidaceae; Cy, Cyperaceae; Ra, Ranunculaceae; Fa, Fabaceae; Ro, Rosaceae; P, Primulaceae; G, Gentianaceae; La, Lamiaceae; Or, Orobanchaceae; Pl, Plantaginaceae; C, Campanulaceae; Ap, Apiaceae.

through enhanced establishment rates in a less competitive environment (21). The density of orthopteran herbivores used in this study is at the higher end of observed herbivore densities at lower elevations in the study area and thus corresponds to a rather severe scenario (fig. S2). Nevertheless, our results suggest that colonization by novel herbivores in alpine ecosystems can be expected to result in a rapid reorganization of plant community structure that will supplement the direct effects of climate change (23).

Meta-barcoding analyses showed that orthopteran species can associate with novel host plant species as long as they are functionally and phylogenetically similar to their lowland resources, allowing these herbivores to track climate change without biotic constraints. Other components of the community, such as predators or pathogens (33, 34), could also shift their range and further affect future ecosystem functioning under climate change. However, abiotic and biotic effects are unlikely to be additive, and climate change could result in ecosystem modifications from interacting abiotic and biotic changes (35). Predicting ecosystem responses to these combined direct and indirect effects mediated by climate change requires estimating the future suitable area of novel interactions, dispersal rates, the functional impact on ecosystems (36), and possible evolutionary responses of interacting species (37). When interactions are functionally conserved, including biotic interactions in forecasts should boost the predictability of the fate of ecosystems as climate warming continues.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Figs. S1 to S10
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