

Degeneration of foundation species induced by climate change could induce alpine biodiversity collapse

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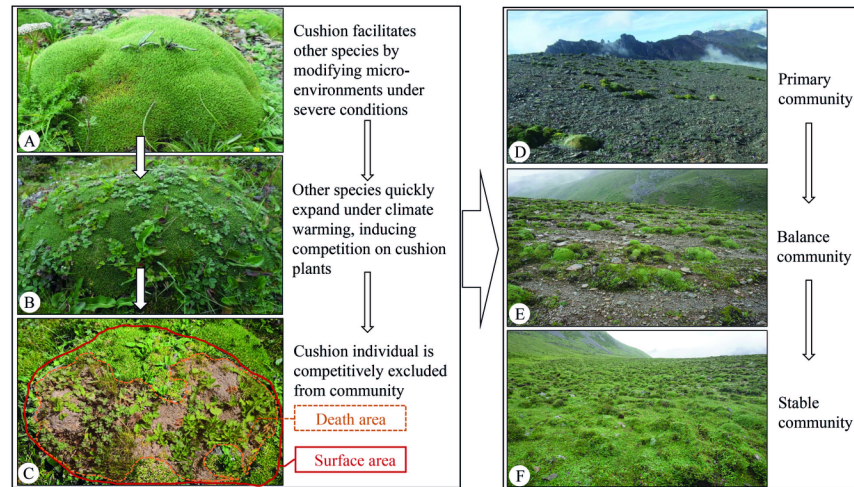
Abstract

Foundational cushion plants sustain a prominent proportion of alpine biodiversity, but they are quite sensitive to climate warming hence their population dynamics have important implications for biodiversity. The potential biodiversity changes with the population dynamics of cushion plants in alpine ecosystems remain, however, unclear. Using eight communities along a climatic and community successional gradient, we assessed ecological drivers of population dynamics and associated plant diversity changes in alpine communities dominated by the foundational cushion plant *Arenaria polytrichoides*. The population degeneration of *Arenaria* is attributed to ecological constraints, including temperature, water and light availability, extreme climate events, and interspecific competition, at a series of life history stages. Once *Arenaria* populations completely degenerate, previously cushion-dominated communities shift to climax communities that are overwhelmingly dominated by sedges. Future degeneration of foundational cushion populations induced by climate warming will therefore induce a biodiversity collapse in alpine ecosystems.

INTRODUCTION

The changes of biodiversity with ongoing climate warming have continuously raised public concerns and fascinated scientists and policy makers from all over the world (Grabherr et al., 1994; Lenoir et al., 2008; Chen et al., 2011; Elmendorf et al., 2012; Gottfried et al., 2012; Pecl et al., 2017; Steinbauer et al., 2018). Alpine ecosystems play irreplaceable roles in human well-being (Martin-Lopez et al., 2019) but are quite sensitive to climate change (Grabherr et al., 1994; Lenoir et al., 2008; Gottfried et al., 2012; Steinbauer et al., 2018). Amongst the high diversity of plant life forms displayed in alpine biomes (Körner, 2003), the cold-adapted cushion-forming growth has evolved independently more than 115 times in angiosperm evolutionary history (Boucher et al., 2016) and act as foundation species (Schöb et al., 2012; Kikvidze et al., 2015). Foundation species are those that can modulate ecosystem processes that can greatly affect local conditions experienced by other species and, consequently, re-organize community structure and sustain diversity to a considerable extent (Ellison et al., 2005; Thomsen et al., 2018; Lamy et al., 2020). Therefore, any changes in foundation species populations have consequences for local/regional biodiversity (Ellison et al., 2005), especially in sensitive and/or fragile ecosystems, like alpine and arctic ecosystems. As foundation species, alpine cushion plants can re-organize community structures (Badano et al., 2006), increase and sustain alpine plant diversity (Cavieres & Badano, 2009; Cavieres et al., 2014; Chen et al., 2015a, b), inhibit the loss of phylogenetic diversity (Butterfield et al., 2013) and construct and maintain species interaction networks (Losapio & Schöb, 2017; Losapio et al., 2019), thereby maintaining ecosystem functions and services (Badano et al., 2006; Chen et al., 2015a; Kikvidze et al., 2015). Accordingly, cushion-dominated communities provide

ideal model systems to assess potential biodiversity changes with the dynamics of foundation species which are induced by climate warming (Box 1).



Great efforts by ecologists have been made to predict plant community dynamics with ongoing climate change (Grabherr et al., 1994; Lenoir et al., 2008; Gottfried et al., 2012; Pecl et al., 2017; Steinbauer et al., 2018; Briscoe et al., 2019; Oldfather et al., 2021). However, up to date, there is not a single model to perfectly forecast biodiversity changes, especially those associated with foundation species. Generally, plant population demographic rates are determined by diverse ecological factors at different life history stages, including the recruitment of new individuals (*e.g.*, reproduction, seed germination and seedling survival) and the mortality of old individuals. For example, the seed germination and seedling establishment rates, which can dictate the potential magnitude of future populations and scale of associated recruitment dynamics (Gimenez-Benavides et al., 2008), are strongly influenced by diverse abiotic and biotic factors (Butterfield, 2009; Klanderud, 2010; Klanderud et al., 2017; Chen et al., 2020a). Additionally, those factors may also cause, or contribute to, the mortality of individuals at any life stage, together with competitive exclusion (Hardin, 1960). Taking alpine cushion plants as examples, once established, they grow very slowly but may persist for centuries (Molau, 1997). During these long periods of life history, cushion plants accrue increasing facilitative effects on beneficiary species through modifications of the micro-environments. However, as numbers of beneficiary species/individuals grow, they may exert constraints on plants' long-term survival, growth and reproductive output (Schöb et al., 2014a, b).

Continually upslope shifting of lowland species has induced various challenges in alpine ecosystems (Lenoir et al., 2008; Chen et al., 2011; Gottfried et al., 2012). However, how that affect the foundational cushion plants and how the biodiversity sustained by cushion plants will change remain largely unclear. Here, we delve into the complex drivers of these biodiversity changes by combining laboratory experiments with demographic data along two "space-for-time" (Pickett, 1989) gradients in the Himalaya-Hengduan Mountains, SW China. One gradient is along a spatial elevation gradient where the air and soil temperatures gradually decrease with increasing elevation (Wang, 2006; Chen et al. 2019), thus serving as a surrogate for temporal climate warming. Another gradient is along a microsite gradient from cushion-dominated to cushion-free microsites and from high to low vegetation cover, thus serving as a surrogate for different community successional stages. Under these circumstances, we can explicitly assess the community dynamics of foundational cushion plants under anticipated climate warming and the associated biodiversity changes. Specifically, we selected eight populations of the cushion plant *Arenaria polytrichoides* distributed along an elevational gradient to, firstly, reveal the current and historical individual distributions within communities using a landscape ecological conception and approach (Pickett & Cadenasso, 1995); after this, we determined the current population age structure, density and productivity. We predict that cushion populations that experience climate warming

(lower elevation) will become gradually fragmented (degenerated) because *i*) they are particularly cold-adapted (Körner, 2003; Aubert et al., 2014; Boucher et al., 2016), thus sensitive to climate warming (Cranston et al., 2015), *ii*) cushion plants' reproductive output are constrained by increasing beneficiary species (Schöb et al., 2014a) thus reducing population recruitment probability and *iii*) seedling establishment is difficult due to their low competitiveness (Chen et al., 2020a). Secondly, we elucidated the successional processes of cushion-dominated communities and the associated plant diversity changes. We predict that plant diversity will significantly decrease when cushion plants completely degenerate, because those species exclusively sustained by cushion plant may lose safe microsites and hence go secondly extinct (Losapio & Schöb, 2017). Finally, we determined the ecological factors that drive cushion population dynamics in consecutive life history stages, including flower and fruit production, seed germination and seedling establishment both in simulated and field climates, and the mortality of aged individuals. We predict that both climate change and the associated changes in interspecific interactions simultaneously regulate the cushion population dynamics hence plant diversity.

MATERIAL AND METHODS

Study systems

This study was conducted in the Himalaya-Hengduan Mountains (HHM) in SW China, where is one of the richest and most complex floras in the temperate zone of the Northern Hemisphere (Sun et al., 2017). See Text S1 for the details. Field experiments were conducted in northwestern Yunnan province (Figure S1), which is in the core area of alpine plant diversity of the HHM (Zhang et al., 2021). We selected eight communities dominated by the typical cushion plant *Arenaria polytrichoides* Edgew. (Caryophyllaceae) as our study systems. As foundation species, *A. polytrichoides* plays key roles in the alpine ecosystem functions in this region (Text S2). Specifically, we selected four populations along an altitudinal gradient in Pujin pasture of the Baima Snow Mountains (Figure S1) to elucidate the cushion plant's population dynamics, the associated plant diversity changes and the underlying mechanisms. In addition, another four populations in different mountain ranges were also selected to assess and compare current population dynamics at larger scale and predict potential biodiversity changes in alpine ecosystems more broadly (Figure S1). See Text S3 for the details.

Population dynamics

We selected the four populations in Pujin pasture (Figure S1) to identify the current and historical distribution patterns of individual cushions in their communities, by taking a landscape conception and approach (Pickett & Cadenasso, 1995). See Text S4 for the details.

To characterize the current population structures, we determined the age structure and density of each population. Since it is impossible to determine the real age of this slowly-growing cushion species, we used the size of individuals as a proxy for age (Molau, 1997; Benedict, 1989; Chen et al., 2020a). See Text S5 for the details.

To characterize population productivity, each population's flower production was assessed in early July 2021, when *A. polytrichoides* plants were blooming. The flowering ratio (*i.e.*, flowering area/total cushion surface area) of each individual was assessed and recorded. The same process was applied to determine fruit production in late September when fruits had matured. The fruits are very small (*ca.* 3-4 mm) and each contains nearly three seeds on average (2.87 ± 0.14 , mean \pm s.e.), so rather than laboriously collecting and dissecting fruits we simply used fruit production as a proxy of population production in this study. We initially followed a previously published protocol (Zhang et al., 2020) to assess the flowering/fruitlet ratio of 50 randomly chosen individuals in each population, then by experience visually assessed the reproductive production of the remaining individuals due to time constraints. See Text S6 for the details.

Population succession and associated plant diversity change

In efforts to elucidate the succession processes of cushion-dominated communities, we randomly selected 90 living and 109 trace individual cushions of the PJ1 population, 98 and 94, respectively, of the PJ2

population, as well as 154 and 149, respectively, of the PJ3 population. As the vegetation cover and number of individual cushion traces decrease and the population density increases with increases in elevation, we considered PJ1 as a ‘climax (relatively stable) community’, PJ2 as a ‘balanced community’ and PJ3 as a ‘primary community’. We counted and recorded all beneficiary species associated with each selected individual, and their abundance (number of individuals). The PJ4 population was ignored in this analysis because beneficiary cover in individual cushions of this population was too low, *i.e.*, few beneficiaries occupied the cushion surfaces, and no cushion trace was detected. Thus, we could not assess the potential replacement of the species in the PJ4 population.

Ecological constraints on cushion population dynamics

To assess effects of temperature, light and water availability on seed germination and subsequent seedling survival, we carried out experiments in three artificial climate chambers with temperatures of 0/5, 10/15 and 20/25 °C in 12 h night (dark)/12 h day (light) cycles. Seeds were collected from the populations in Pujin pasture in late September in 2020 and were mixed since they had no differences in term of seed quality (Chen et al., 2020a). See Text S7 for the details.

Since extreme climate events frequently occur in the study region (Wang, 2006; Ning et al., 2012), a further aim was to elucidate their effects on establishment of the cushion species’ seedlings. For this, we set two kinds of extreme climate events. They were short-term events which were considered to simulate the frequent extreme climate events in the plant growing season, and long-term events which was designed to test and compare the over-wintering capacity of seedlings that had, and had not, experienced climate events during the growing season. Text S8 for the details.

Since allelopathy is one of the important biotic mechanisms that affect seed germination and seedling performance and hence community dynamics (Fenner & Thompson, 2005; Zhang et al., 2015; Pilsbacher et al., 2021). To detect whether allelopathy exists and (if yes) how it affects cushion seed germination and seedling performance, we collected potentially allelopathic materials from PJ1 and PJ3 sites and tested the effects of them on seed germination and seedling survival. See Text S9 for the details.

Additionally, we also assessed seeds’ and seedlings’ performance in the real natural conditions by subjecting them to burial and transplantation treatments in the Pujin populations. See Text S10 for the details.

To assess potential effects of beneficiary plants on the process of cushion population degeneration, we first selected the PJ2 population to test effects of beneficiary plants on the nutrient contents of *A. polytrichoides* cushions in mid-August 2020. Then, we assessed the physiological status of *A. polytrichoides* cushions along an elevational/climate gradient and associated series of community successional stages. Specifically, we determined the specific leaf area (SLA, the ratio of fresh leaf area to leaf dry mass in m² kg⁻¹) and leaf dry matter content (LDMC, the ratio of leaf dry mass to fully rehydrated fresh mass in g kg⁻¹) in three populations in Pujin pasture. See Text S11 for the details.

Finally, a further aim was to elucidate effects of beneficiary plants on cushions’ reproductive outputs. See Text S12 for the details.

Data analyses

We applied a landscape ecological conception (Pickett & Cadenasso, 1995) to analyze the spatial distributions of current and historical individual cushions within communities. For this, we used Fragstats4.2 software (McGarigal & Ene, 2013) to calculate the following six landscape metrics for cushion patches (McGarigal & Ene, 2013; Lustig et al., 2017; Wang et al., 2014): the total area of cushion patches (CA), the edge density (ED), the mean cushion patch area (Area_{Mn}), the percent of core area of landscape (CPLAND), the total patch number (NP), and sixth the percentage of like adjacencies (PLADJ). See Text S13 for the details.

To illustrate the abundance of beneficiary species and successional processes in different successional stages (represented by the PJ1 to PJ3 communities) of cushion-dominated communities, we generated stacked graphs at species level for each community.

Since population ID includes information on the study site, including elevation and potential relevant micro-climates, we applied one-way ANOVA to assess the differences in population density and productivity between populations, with population density and productivity as dependent variables and population ID as an independent variable. Tukey HSD tests were applied to assess the significance of differences between populations.

Linear mixed-effects models were applied to assess the following effects. 1) The effects of simulated climate events on seed germination and subsequent seedling survival, with temperature, light availability, water availability and their potential interactions as fixed effects and pot replicate as a random effect. 2) The germination and viability of seeds buried in the natural field, with elevation, checking time and their interaction as fixed effects and tea bag replicate as a random effect. 3) The survival of seedlings transplanted in the natural field, with elevation, micro-habitat and their interaction as fixed effects and plot replicate as a random factor. 4) The effects of simulated extreme climate events on seedling survival, with climate treatment, seedling age and their interaction as fixed effects and pot replicate as a random effect. 5) The effects of beneficiary species on nutrient contents (and stable isotope ratios) of cushion leaves, with beneficiary cover ratio, leaf source (beneficiary-covered or beneficiary-free) and their interaction as fixed effects and sample replicate as a random effect. 6) The effects of beneficiary species on the physiological traits (SLA and LDMC) of individual cushions, with elevation, beneficiary cover ratio, dominating beneficiary species (*Kobresia pygmaea* or *Saussurea leontodontoides*) and their interactions as fixed effects and sample replicate as a random effect. 7) The effects of allelopathical materials on the seed germination and seedling survival, with allelopathical source (aboveground or belowground), extracting mode (aqueous or ethanol), elevation, concentration and their interactions as fixed effects and sample replicate as a random effect. Nutrient content and physiological trait values were square root-transformed to meet assumptions of parametric statistics, while seed germination, viability and seedling survival data were standardized between 0 and 1 by the formula $(X - X_{min}) / (X_{max} - X_{min})$, where X is the relevant value of seed germination or seedling survival. The significance of each contrast (Rosenthal & Rosnow, 2010) was assessed using type-I analysis of variance with Satterthwaite's method for all linear mixed-effects models.

To assess effects of beneficiary species on the performance (including flowering, fruiting, surface death ratio and physiological status) of *A. polytichoides* cushions, we calculated Pearson correlation coefficients.

R v.4.1.1 (R. C. Team, 2021) was used for all the above analyses, the lme4 packages was used for the linear mixed-effects modeling (Bates et al., 2015), the ggplot2 package (Wickham, 2016) was used to plot all reported figures and the layout was designed with Adobe Illustrator 2021.

RESULTS

Population dynamics

Confirming the first prediction, the landscape metrics indicate that the cushion individual distributions in low-elevation communities (*i.e.*, experiencing warmer conditions) are more fragmented than that in high-elevation communities (*i.e.*, experiencing colder conditions; Figure 2). Specifically, we found that four key metrics are *ca.* 40–90% lower in warmer communities than in colder communities (Table S1). Two are the total cushion patch area (CA) and the mean cushion patch area (Area_Mn), the other two are the percentage of core area of the landscape containing cushions (CPLAND) and percentage of like adjacencies of patch types (PLADJ). However, the number of cushion patches (NP) and edge density (ED) in warmer communities are *ca.* 30% - 1000% higher than these parameters in colder communities (Table S1). Additionally, a large proportion of the area of the warmest (*i.e.*, lowest elevation) community was previously occupied by individual cushions (now traces of dead cushions), but this proportion decreases with decreases in temperature (*i.e.*, elevation) and no cushion traces were detected in the coldest (*i.e.*, highest elevation) community (Figure 1). All above results suggest that a large number of individual cushions will be excluded due to ongoing climate warming (Figure 1), resulting in more rapid population turnover.

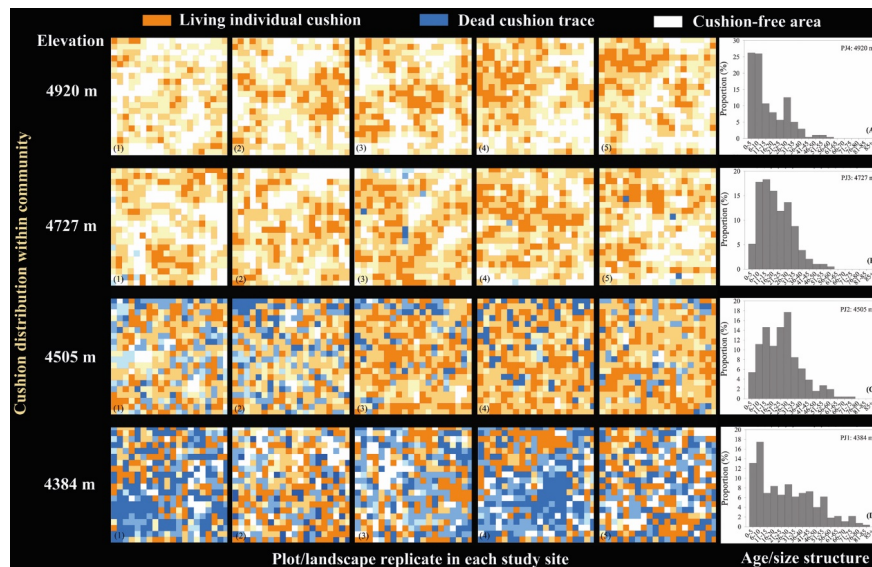


FIGURE 1. Distribution patterns of individual cushions (left; in five replicate 20×20 m plot in each community, shown in separate columns) and age/size structure of populations of the *A. polytrichoides* cushion plant (right; individuals are presented in different size categories of diameter in centimeter) in the four communities with increasing elevation (in other words, along with different community successional stages possibly driven by climate warming) in Pujin pasture. Communities are presented along with increasing elevation as PJ1 (4384 m; ‘climax community’), PJ2 (4505 m; ‘balance community’), PJ3 (4727 m; ‘primary community’) and PJ4 (4920 m; ‘initial community’). Orange, blue and white squares represent living individual cushions, dead cushion traces, and cushion-free areas, respectively. The darkness of the orange and blue colors is positively related to the size of the cushion patches/individuals and cushion traces, respectively.

Generally, colder populations are dominated by young and juvenile individuals (diameter < 25 cm), while warmer populations are dominated by adult (diameter 25 - 45 cm) and old individuals (diameter > 45 cm) (Figure 1A-D; Figure S2). Population density varied among study sites ($DF = 7$, $F = 33.39$, $P < 0.001$), and increases with elevation hence with decreasing temperature in Pujin pasture; but the recorded densities of CM populations did not differ (Figure 2A).

Population productivity varied among study sites ($DF = 7$, $F = 17.76$, $P < 0.001$), and was highest for populations in Pujin pasture (Figure 2B). In Pujin pasture, the warmest population (PJ1) had significantly higher productivity than the other three colder populations, which did not significantly differ in this respect (Figure 2B). No significant differences in productivity between CM and PY populations was detected either, but the YL population had extremely low population productivity compared with all other populations (Figure 2B).

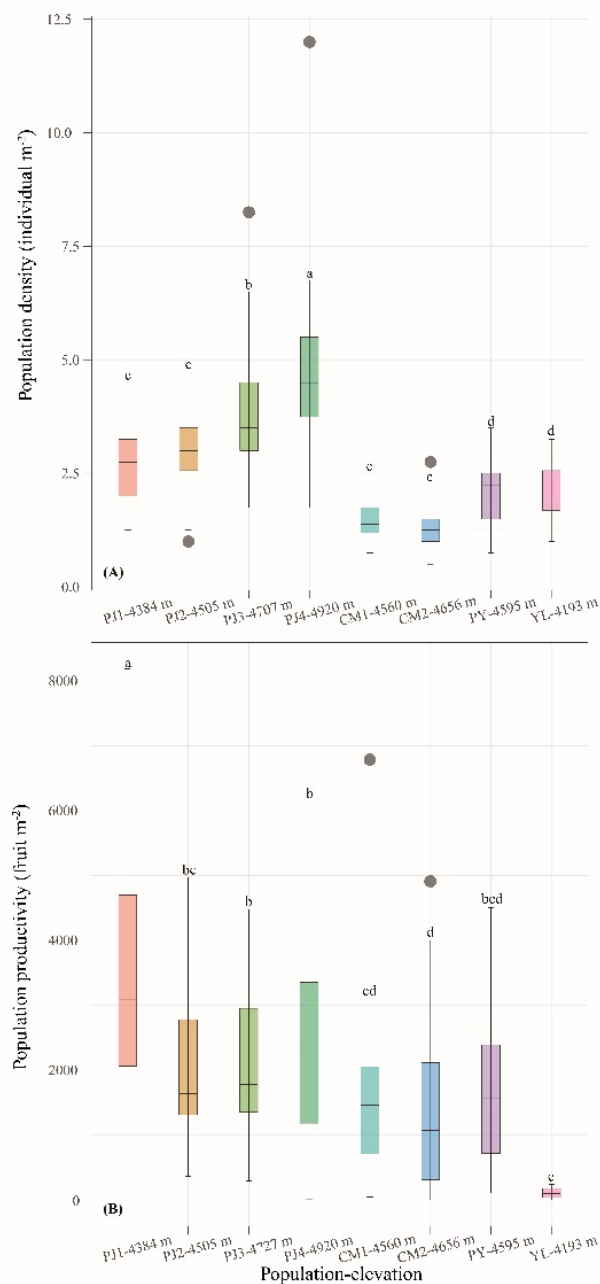


FIGURE 2. Population density (A) and productivity (B) of *A. polytrichoides* cushions at indicated study sites.Populations are presented along with increasing elevation as PJ1 (4384 m), PJ2 (4505 m), PJ3 (4727 m) and PJ4 (4920 m) in the Pujing pasture, and CM1 (4560 m) and CM2 (4656 m) in the Core mine mountain range, respectively, both on the Baima snow mountains; only one population was selected at the Puyong pass on the Daxueshan snow mountains (PY, 4595 m) and Yulong snow mountain ridge (YL, 4193 m), respectively. $n = 25$ (2×2 m quadrat) for PJ1, PJ3, PJ4, CM2 and PY populations, $n = 24$ for CM2 and YL population, and $n = 22$ for PJ2 populations, respectively. Different letters indicate significant differences at the $\alpha < 0.05$ level (one-way ANOVA with Tukey HSD tests).

Beneficiary plants sequentially intrude into cushion surfaces, culminating in the exclusion of individual cushion plants (Box 1). Specifically, in the early successional stage (represented by ‘primary community’; *e.g.* , PJ3), *Kobresia vidua* is the most abundant beneficiary species, followed by *Saussurea leontodontoides*, *Sibbaldia purpurea* and *Polygonum macrophyllum* and various others. However, when individual cushions have been completely excluded (leaving only dead traces of cushions), only the abundance of *Kobresia vidua* is higher and the abundances of all other species is lower (Figure 3). Subsequently, at an intermediate successional stage (represented by ‘balanced communities’; *e.g.* , PJ2), there is a different set of abundant beneficiary species, with *S. leontodontoides*, *K. pygmaea* , and *Cyananthus macrocalyx* occupying most of the living cushion surfaces. At this stage, when individual cushions have been excluded, only *S. leontodontoides* is more abundant, while the abundance of the other beneficiary species remains very similar (Figure 3). Finally, when the succession reaches the ‘climax community’ stage (relatively stable community; *e.g.* , PJ1), most of the vegetation area (including living cushion surfaces and surrounding habitats) is occupied by *K. pygmaea* followed by *Hedysarum tanguticum* and *Potentilla saundersiana* (Figure 3). The abundance of other species, such as *P. saundersiana* and *P. macrophyllum* , is only slightly lower following the exclusion of individual cushions. In summary, from primary to climax stages, the sequence of intruding beneficiary plants and the interactions between them and cushions both change. *Kobresia vidua* , *S. leontodontoides*, *P. macrophyllum* and *S. purpurea* may intrude first, followed by *K. pygmaea*, *C. macrocalyx* , *P. saundersiana* and then others. Finally, *K. pygmaea* will overwhelmingly dominate the communities once cushion plants completely disappear (Box 1; Figure 3).

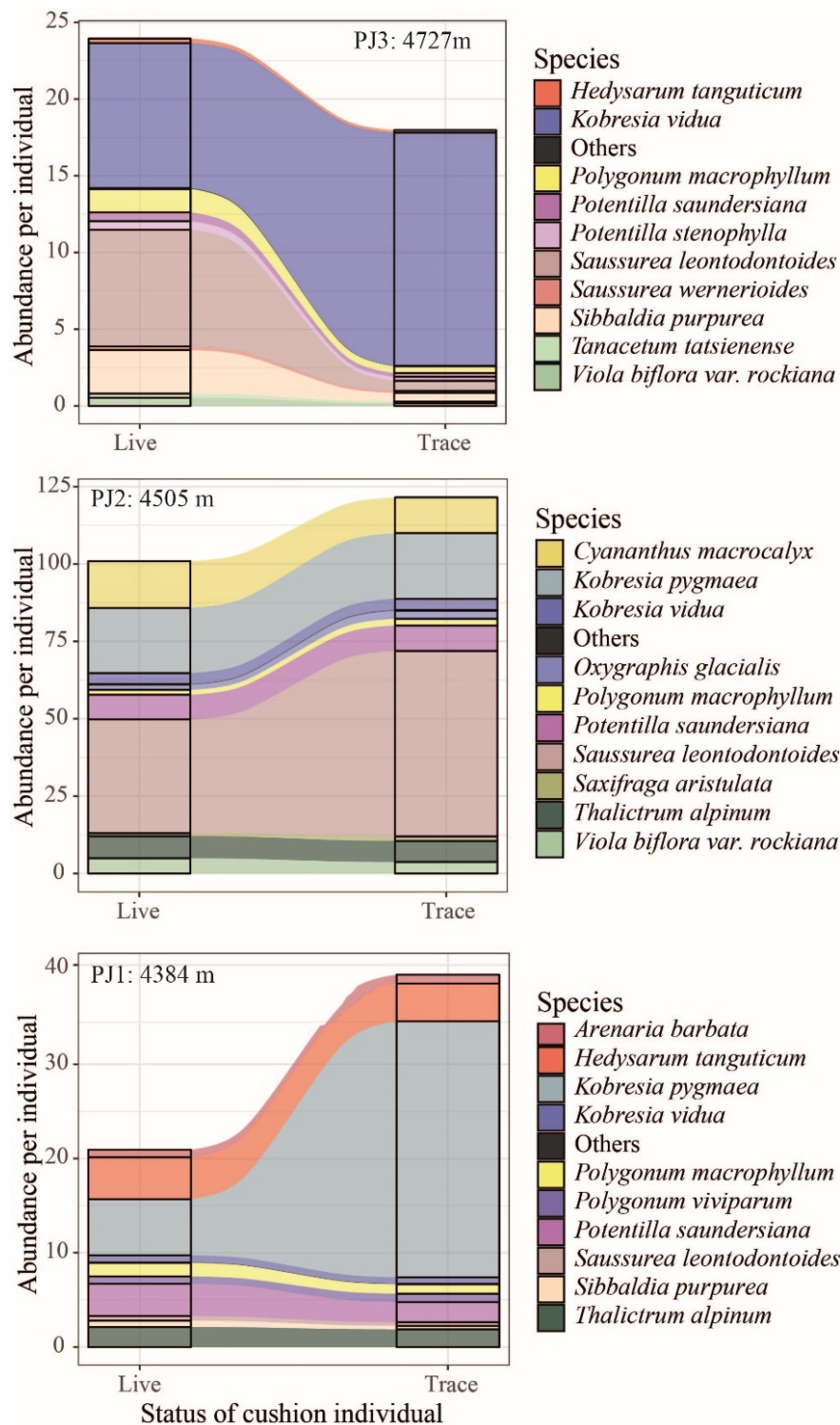


Figure 3. Successional processes and diversity changes of cushion-dominated communities. Relative abundance of the top 10 beneficiary species associated with living individual cushions and dead cushion traces in communities from cold (high, PJ3) to warm (low, PJ1) climates, representing primary to

climax successional stages, respectively. See Figure 1 for the abbreviation of each population.

Ecological constraints on population dynamics

Results indicated that seed germination rate of *Arenaria polytrichoides* was lower at both low (0/5) and high (20/25) temperatures than at intermediate (10/15) temperatures, while high light availability (more than 50% of full light, with full light defined as 7000 lx) promoted it (Figure S3 and S4B, C). Thus, the intermediate temperature was the most ‘conductive’ for seed germination. However, seedlings persisted longer at lower temperatures, and the higher water and light availability treatments also promoted their survival (Figure S4).

Simulated short-term extreme climate events significantly reduced the survival rate of seedlings younger than 60 days old, but had weaker effects on seedlings grown for 90 days under ‘conductive’ conditions (Figure 4A; Table S3). The latter also had high tolerance of a long-term extreme climate treatment simulated as long winter (Figure 4B). In contrast, seedlings that had been exposed to the short-term extreme climate treatment were highly vulnerable to the long-term treatment, although their degree of vulnerability depended on their age when exposed to the short-term treatment (Figure 4B). Generally, older seedlings had higher tolerance of the long-term extreme climate treatment, and thus higher overwintering capacity.

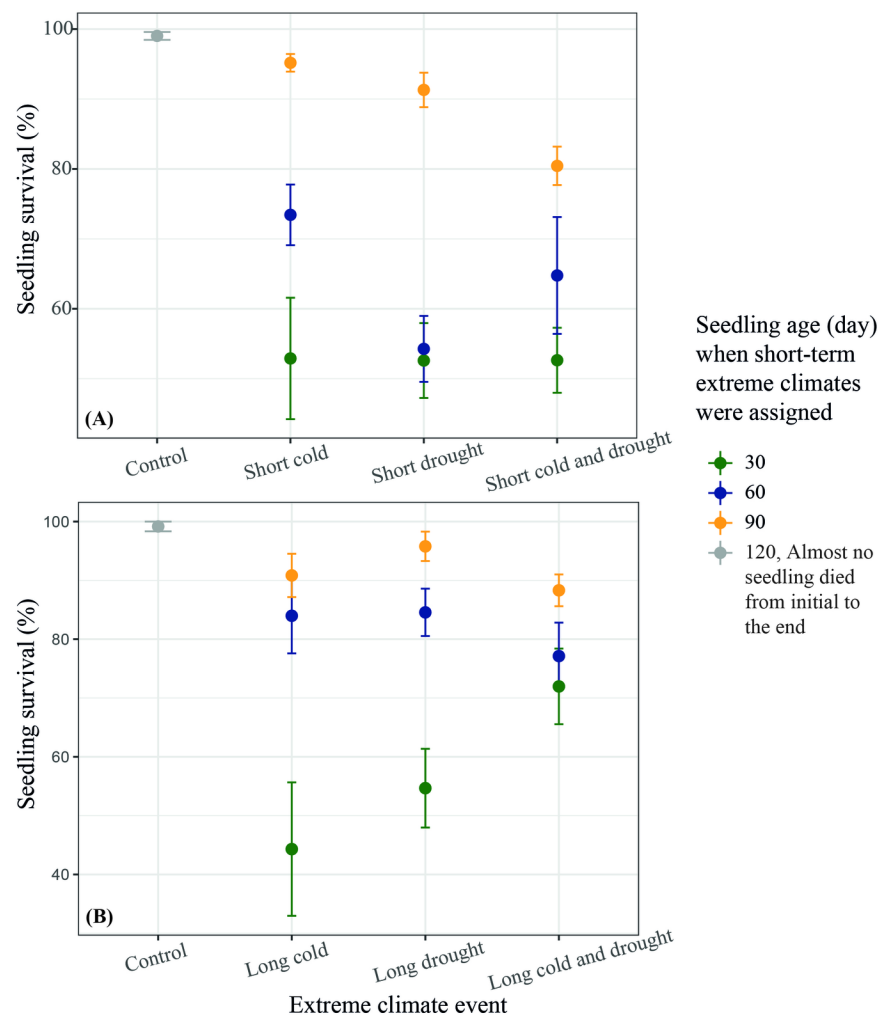


FIGURE 4. Effects of simulated extreme climate events on seedling survival. (A) Survival rates

of seedlings assigned to indicated short-term extreme climate events starting at indicated ages; (B) survival rates of seedlings that survived short-term extreme climate events subjected to indicated long-term extreme climate events after growth for 120 days in ‘conductive’ conditions. $n = 6$ (replicate pots with 30 initially sown seeds), data are mean and standard error (s.e.). See Table S3 for the complete statistical details (Linear mixed-effects models). Very few seedlings in the control (‘conductive’) group died from the start to the end of the experiment, so only their final survival rate is shown.

Germination rates of seeds buried in the field (2 cm deep) were relatively high (more than 60%) in the following May and July. Seeds buried at lower elevation (warmer condition) generally showed higher frequencies of germination than those buried at higher elevation (colder condition; Table S4; Figure S5). No viable seeds remained in July, because if they did not germinate, seeds rotted in the soil. Most seeds and seedlings had rotted in September, and only a small proportion of the seedlings survived to the end of September if they did not break out of the soil (Figure S5).

All transplanted seedlings were still living a week after transplantation, suggesting that the establishment of seedlings in the field was not inhibited by transplantation. However, two months later few seedlings survived possibly due to constraints from surrounding environments (Table S5). More specifically, in late September survival rates of seedlings transplanted within vegetation and in bare ground micro-habitats were similar at high elevation, but at low elevation the seedlings transplanted into bare ground had higher survival rates than those transplanted into vegetation. Surprisingly, no seedlings survived until mid-November in any of the micro-habitats used in the experiment.

Finally, surrounding vegetation also imposed certain allelopathic constraints on seed germination and seedling growth (Table S6; Figure S6).

Beneficiary plants generally reduced the cushions’ nutrient contents and two stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), although not all effects were significant (Table S7, Figure S7). Beneficiary plants also reduced the specific leaf area (SLA) and leaf dry matter content (LDMC) of individual cushions in all study populations, and these effects were independent of the dominating beneficiary species (Table S8; Figure S8A, C). However, when beneficiary plants’ cover increased, both SLA and LDMC significantly increased (Figure S8B, D).

Beneficiary plant cover and cushion flower production were not correlated in the CM1 population, weakly negatively correlated ($P = 0.118$) in the PJ4 population and strongly negatively correlated in the other populations (Figure 5A-H). These findings clearly indicate that beneficiary species can significantly reduce the cushion plant’s flower production. A significant negative correlation between beneficiary cover and fruit production was also detected in the PY population (Figure 5), but this relationship was neutral in the PJ3, CM1, CM2 and YL populations, and weakly negative in the others (PJ1, PJ2 and PJ4). Thus, beneficiary plants seem to generally have slightly negative effects on the cushion plant’s fruit production.

Moreover, beneficiary plant cover also positively correlated with the mortality of individual cushions in all study populations (Figure 5I-K), indicating that increases in this variable can promote the mortality of cushion plants and accelerate their exclusion.

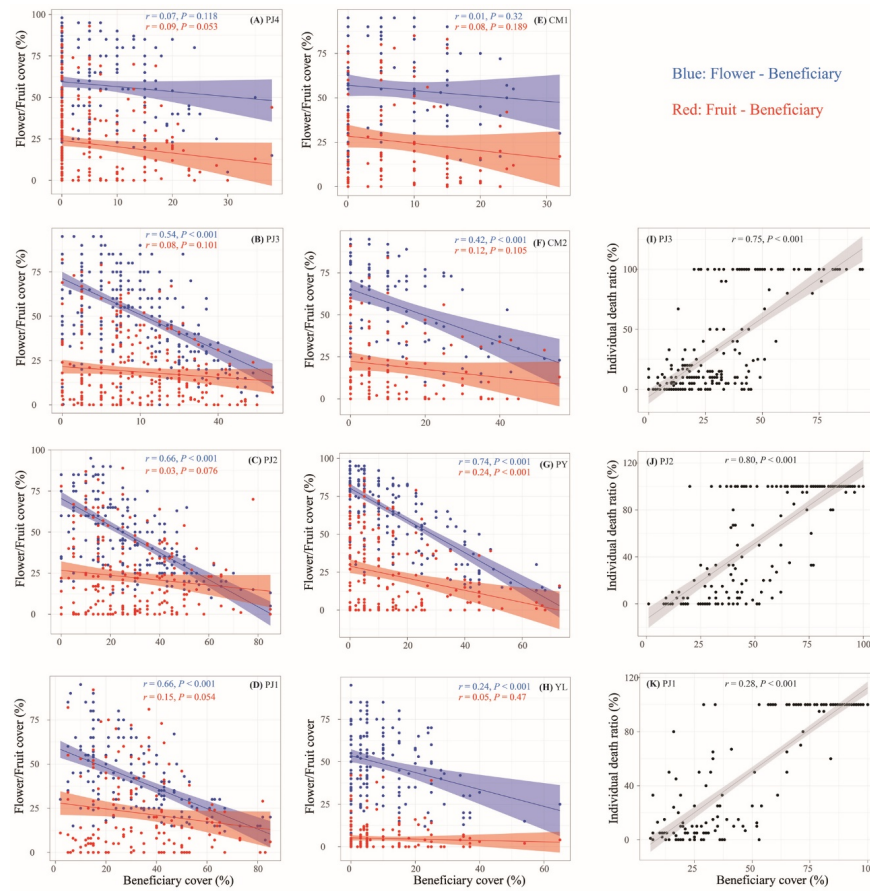


FIGURE 5. Pearson correlations between beneficiary cover in the study populations and (A-H) cushion reproduction (flower and fruit), and (I-K) death ratio of individual cushions. $n = 169, 221, 304, 300, 119, 113, 214$ and 199 for PJ1, PJ2, PJ3, PJ4, CM1, CM2, PY and YL populations, respectively.

DISCUSSION

Foundation species, by virtue of its special structural or functional attributes, can create an entire ecological community or ecosystem, sustain ecosystem functions and biodiversity; thus, the loss of foundation species can induce broad consequences for associated biota and ecosystem functions (Ellison et al., 2005; Schöb et al., 2012; Thomsen et al., 2018). Thus, explicitly elucidating how foundation species respond to climate warming and how the associated biodiversity changes are crucial for robustly predicting changes in ecosystems, and thus their long-term sustainable management.

As foundation species, cushion plants sustain a prominent proportion of alpine biodiversity (Cavieres & Badano, 2009; Butterfield et al., 2013; Chen et al., 2015a; Kikvidze et al., 2015). Thus, together with climate change, their population dynamics may imply future biodiversity changes in alpine ecosystems. We found that large numbers of cushion individuals that once existed in low-elevation communities had been excluded, making warmer populations now more fragmented than colder populations (Figure 1). This was supported by the facts that the warmer populations show lower population density but more old individuals than those colder populations (Figure 1A-D; Figure 2A; Figure S2) which indicate a lower demographic rate in warmer conditions. After exclusion from communities, the previously cushion-dominated communities gradually turned to climax communities that are overwhelmingly dominated by sedge species (Figure 3; Box 1). All these results suggest that populations of the cushion *A. polytrichoides* that are experiencing

climate warming are simultaneously experiencing degeneration, while populations under cold conditions are maintaining recruitment and keep expanding (Chen et al., 2020a).

Newly established cushion populations in high-elevation habitats, especially those newly uncovered by glacial retreat (Baker & Moseley, 2007), could facilitate the establishment of other species, thereby increasing local plant diversity (Cavieres & Badano, 2009). In contrast, population degeneration after climate warming could potentially induce a thorough change in community structures and (possibly reduced) biodiversity (Figure 3). In our study sites, the mean annual temperature in the past decades has increased at a rate of $0.06\text{ }^{\circ}\text{C yr}^{-1}$, resulting in *ca.* 70 m in elevation upward shift of the treeline (Baker & Moseley, 2007), which could induce negative influences on high-elevation vegetation (Grabherr et al., 1994). Moreover, upward shifts of lowland species will inevitably induce increases in the diversity, cover and productivity of alpine plant communities (Chen et al., 2011; Gottfried et al., 2012; Steinbauer et al., 2018) which could impose strong competition on cushion plants. Consequently, high-elevation populations of the *A. polytrichoides* cushion plant would face the same challenges that low-elevation populations face now. Thus, in the long-term, low-elevation populations could become locally extinct and there could be serious risks of degeneration of the high-elevation populations. If cushion plants disappear, secondary extinctions are likely to occur, especially of species exclusively sustained by cushion plants (Losapio & Schöb, 2017). Furthermore, species interaction networks that are now mainly sustained by cushion plants (Losapio & Schöb, 2017; Losapio et al., 2019) would inevitably collapse.

Plants' dynamics are influenced by ecological factors at different life history stages (Gimenez-Benavides et al., 2008; Oldfather et al., 2021). We found that all study populations except the Yulong population produced sufficient seeds in a single growing season (Figure 2B), suggesting that the species is not subject to seed limitation (Turnbull et al., 2000). Thus, the seed germination and seedling establishment rates in the following growing season could strongly affect recruitment rates. We found that, generally, low temperature and light availability can delay seed germination and reduce final germination percentages, indicating that the frequently low temperatures in the early growing season and cover by snow (Wang, 2006) or surrounding vegetation/litter, may delay and/or reduce soil seed germination in the field. In addition, very few seedlings survived for 17 weeks (Figure S4) which equals to the length of the growing season in their natural alpine ecosystems. These results imply large difficulties for *A. polytrichoides* seedlings to establish successfully *in situ*.

Even worse, *A. polytrichoides* seeds cannot persist in the soil for more than a year (Table S4; Figure S5), indicating that the species has a transient soil seed bank. Thus, if seeds cannot germinate or seedlings cannot survive through the first winter, population recruitment will be extremely constrained. Moreover, extreme climate events (*e.g.*, drought and coldness) frequently occur in our study region (Wang, 2006). We found that short periods of extreme water stress and low temperature can significantly reduce seedling survival (Figure 4A), but prior growth in mild conditions for sufficient time (90 to 120 days) significantly increases their ability to survive long-term extreme climate events (simulating a long winter; Figure 4; Table S3). Thus, timely germination early in the growing season and the occurrence of extreme climate events during the growing season may be key determinants of recruitment rates. These findings are consistent with expectations that a sufficiently long growing season without damaging events could be essential for seedlings to accumulate resources (*e.g.*, carbohydrates and various nutrients), allocate them appropriately, and maintain a healthy physiological status, thereby establishing high over-wintering capacity (Luscher et al., 2001). The finding that all transplanted seedlings died by the end of the growing season (Table S5) corroborates this conclusion, because the growing season was too short (*ca.* 60 days) for them to develop over-wintering capacity.

Furthermore, our transplantation experiment implied that inter-specific competition can hinder seedlings' establishment. This could be because that other competitive species can delay seed germination and accelerate the death of *A. polytrichoides* seedlings (Chen et al., 2020a). In addition, surrounding vegetation may also impose certain allelopathic constraints on seed germination and seedling growth (Table S6; Figure S6).

Competitive stress imposed by beneficiary plants plays key role in the decay of previously established individual cushions. Firstly, beneficiary plants generally reduced the cushions' nutrient contents and two stable

isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) ratios that provide information on plants' water-use efficiency and carbon, water and nitrogen balances (Table S7; Figure S7) (Dawson et al., 2002). Secondly, beneficiary plants significantly constrain physiological traits (SLA and LDMC) of cushion individuals (Table S8; Figure S7A, C), which implies short leaf longevity and low resource use efficiency (Wright et al., 2004). SLA is also positively correlated with temperature, light availability (Poorter et al., 2009) and soil nitrogen availability (Ordonez et al., 2009). High cover of beneficiary plants can clearly reduce light availability on cushions' surfaces, thereby reducing SLA (Figure S8A). Thirdly, beneficiary species could generally reduce the LDMC of individual cushions (Figure S7C), indicating that they may inhibit cushion individuals partially through competition for water and associated stress (Cornelissen et al., 2003). However, SLA increases but LDMC decreases with increases in beneficiary cover (Figure S7B, D). Nevertheless, the combined effects of high SLA and low LDMC induced by increases in beneficiary species probably accelerate the competitive exclusion process of individual cushions (Figure 5I-K) and hence degeneration of cushion populations.

Furthermore, possibly due to the trophic and physiological constraints, beneficiary species significantly reduced flower production of cushion individuals (Figure 5A-H), and had context-dependent, but generally no or slightly negative, effects on their fruit production (Figure 5A-H). This may be partly because the vegetative growth of the beneficiary plants hindered pollinators' visitations of the flowers, and consequently reduced pollination efficiency and fruit set. In addition, increases in beneficiaries' cover may induce changes in cushions' resource allocation patterns, through competition-driven increases in allocations to growth and/or defenses (Schöb et al., 2014b). These results demonstrate that beneficiary species may constrain reproductive functions of cushion plants, and hence future population recruitment.

In conclusion, taking communities organized by typical foundational cushion species as a model system, we here explicitly revealed that when foundation species degenerate due to climate warming, the associated species composition and diversity both change with a possible biodiversity collapse. Additionally, such changing processes are influenced by the changes in series ecological factors which are induced by climate warming. As a result, we strongly suggest that to assess the processes of the dynamics of foundation species and the associated biodiversity changes is critic and effective for future biodiversity conservation concerns.

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