

RESEARCH PAPER

Degeneration of foundation cushion species induced by ecological constraints can cause massive changes in alpine plant communities

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Foundational cushion plants can re-organize community structures and sustain a prominent proportion of alpine biodiversity, but they are sensitive to climate change. The loss of cushion species can have broad consequences for associated biota. The potential plant community changes with the population dynamics of cushion plants remain, however, unclear. Using eight plant communities along a climatic and community successional gradient, we assessed cushion population dynamics, the underlying ecological constraints and hence associated plant community changes in alpine communities dominated by the foundational cushion plant *Arenaria polytrichoides*. The population dynamics of *Arenaria* are attributed to ecological constraints at a series of life history stages. Reproductive functions are constrained by increasing associated beneficiary plants; subsequent seedling establishment is constrained by temperature, water and light availability, extreme climate events, and interspecific competition; strong competitive exclusion may accelerate mortality and degeneration of cushion populations. Along with cushion dynamics, species composition, abundance and community structure gradually change. Once cushion plants completely degenerate, previously cushion-dominated communities shift to relatively stable communities that are overwhelmingly dominated by sedges. Climate warming may accelerate the degeneration process of *A. polytrichoides*. Degeneration of this foundational cushion plant will possibly induce massive changes in alpine plant communities and hence ecosystem functions in alpine ecosystems. The assessment of the population dynamics of foundation species is critical for an effective conservation of alpine biodiversity.

alpine ecosystem | biodiversity change | climate change | plant community dynamics | foundation species | global warming | population dynamics

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 (Chen et al., 2011; Elmendorf et al., 2012; Gottfried et al., 2012; Grabherr et al., 1994; Lenoir et al., 2008; 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 (Gottfried et al., 2012; Grabherr et al., 1994; Lenoir et al., 2008; 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 acts as foundation species (Kikvidze et al., 2015; Schöb et al., 2012). Foundation species are species 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; Lamy et al., 2020; Thomsen et al., 2018). Therefore, any changes in populations of foundation species could have consequences for community structure, species composition and hence local/regional biodiversity (Badano and Cavieres, 2006; Badano et al., 2006; Ellison et al., 2005; Kikvidze et al., 2015). As foundation species, alpine cushion plants can re-organize community structures (Badano et al., 2006), increase and sustain alpine plant diversity (Cavieres and Badano, 2009; Cavieres et al., 2014; Chen et al., 2015a; Chen et al., 2015b), inhibit the loss of phylogenetic diversity (Butterfield et al., 2013) and construct and maintain species interaction networks (Losapio and 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 changes in community dynamics based on population dynamics of foundation species.

Great efforts by ecologists have been made to predict plant

community dynamics, including dynamics of functional traits, with ongoing climate change (Briscoe et al., 2019; Gottfried et al., 2012; Grabherr et al., 1994; Lenoir et al., 2008; Oldfather et al., 2021; Pecl et al., 2017; Steinbauer et al., 2018; Zhang et al., 2023). However, up to date, there is not a single model to perfectly forecast alpine plant community and biodiversity changes, especially those associated with foundation species. Generally, plant population dynamics are determined by diverse ecological factors at different life history stages, including plants' reproduction, the recruitment of new individuals (e.g., 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 (Giménez-Benavides et al., 2008), are strongly influenced by diverse abiotic and biotic factors (Butterfield, 2009; Chen et al., 2020; Klanderud, 2010; Klanderud et al., 2017). 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 (Kikvidze et al., 2015; Schöb et al., 2014a; Yang et al., 2017). 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; Schöb et al., 2014b).

The Qinghai-Tibetan Plateau (QTP) in southwestern China is a diversity center of alpine cushion plants, which hosts more than 130 cushion plant species (Zhang et al., 2022). Cushion plants play important roles in organizing community structures and sustaining alpine biodiversity, including plants and arthropods, on this plateau (Chen et al., 2015a; Chen et al., 2015b; Chen et al., 2019; Chen et al., 2021; Jiang et al., 2018; Liu et al., 2016; Yang et al., 2010), thus the long-term persistence of cushion plants is crucial for the maintenance of biodiversity and ecosystem functions on the entire QTP. However, upward migration of lowland species induced by climate warming has consistently been confirmed in this region (He et al., 2019; Liang et al., 2018; Zhao et al., 2011). Actually, continued upslope shifting of lowland species has induced various challenges in alpine ecosystems around the globe (Chen et al., 2011; Gottfried et al., 2012; Lenoir et al., 2008). Some studies noted that the expansion of lowland species has already induced certain shrinkage or degradation of cushion-dominant communities (Huang and Wang, 1991; Zhao et al., 2011). Our previous field observation empirically suggested that the dynamics of plant communities dominated by cushions might basically be driven by the population dynamics of the cushion plants (Figure S1 in Supporting Information). However, how the increasing vegetation coverage, which is possibly induced by upward shifts of lowland vegetation, affects the cushion dynamics and hence dynamics of cushion-dominated communities, and what factors drive such processes remain largely unclear.

Here, we delve into the complex drivers of alpine cushion-dominant community dynamics by adopting 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 (Chen et al., 2019; Wang, 2006), 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 dynamics of foundational cushion-dominant plant communities under anticipated climate changes. Specifically, we selected eight communities, which are dominated by the cushion plant *Arenaria polytrichoides*, along an elevational gradient to, firstly, reveal the current and historical cushion individual distributions within communities using a landscape ecological conception and approach (Pickett and Cadenasso, 1995); after this, we determined the current cushion population age structure, density and reproductiveity. We predicted that cushion populations that experience climate warming (lower elevation) will become gradually fragmented (degenerated) because (i) they are particularly cold-adapted (Aubert et al., 2014; Boucher et al., 2016; Körner, 2003), thus sensitive to climate warming (Cranston et al., 2015), (ii) cushion plants' reproductive output is 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., 2020). Secondly, we elucidated the successional processes of cushion-dominated communities and the associated changes in plant composition and abundance. We predicted that species composition and community structure will dramatically change when cushion plants completely degenerate, because those species exclusively sustained by cushion plants may lose safe microsites and hence go secondly extinct (Losapio and Schöb, 2017). Finally, we determined the complex ecological factors that drive cushion population dynamics in consecutive life history stages. We predicted that both climate change and the associated changes in interspecific interactions simultaneously regulate the cushion-dominant community dynamics and hence species composition and plant diversity of these communities.

RESULTS

Cushion population dynamics

Cushion individual distribution within communities

Confirming the first prediction, the landscape metrics indicate that the distribution of cushion plants in lower-elevation communities that experience warmer temperatures is more fragmented than in higher-elevation communities that experience colder temperatures (Figure 1). Specifically, we found that four key metrics are ca. 40%–90% lower in lower-elevation communities than in higher-elevation communities (Table S1 in Supporting Information). Two are the total cushion patch area (CA) and the mean cushion patch area (Area_Mn), and 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 lower-elevation communities are ca. 30%–1,000% higher than these parameters in higher-elevation communities (Table S1 in Supporting Information). Additionally, a large proportion of the area of the lowest-elevation community was previously occupied by individual cushions (now traces of dead cushions), but this proportion decreases with increasing

elevation hence decreasing temperature, and no cushion traces were detected in the highest-elevation community (Figure 1). All the above results suggest that a large number of individual cushions in lower-elevation communities have been excluded in the past and their mortality rates increased, resulting in species turnover.

Current cushion age structure and density

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

Current cushion population reproductivity

Cushion population reproductivity varied among study communities ($DF=7$, $F=17.76$, $P<0.001$), and was highest for populations in Pujin pasture (Figure 2B). In Pujin pasture, the lowest-elevation population had significantly higher reproductivity than the other three populations, which did not significantly differ in this respect (Figure 2B). There were no significant differences in reproductivity between CM and PY populations, but the YL population had extremely low population reproductivity compared with all other populations (Figure 2B).

Community dynamics along with cushion plant dynamics

Beneficiary plants sequentially intrude into cushion surfaces, culminating in the exclusion of individual cushion plants (Figure S1 in Supporting Information). Specifically, in the early successional stage (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 are lower (Figure 3). Subsequently, at an intermediate successional stage (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 a stable community stage (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. Thus, from early successional stage to a stable community, the sequence of intruding beneficiary plants and the interactions between them and cushions both change. *Kobresia vidua*, *S. leontodontoides*, *P. macrophyllum* and *S. purpurea* 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 (Figure 3).

Ecological constraints on cushion population dynamics

Constraints on cushion seedling recruitment

Seed germination of *Arenaria polytrichoides* was significantly affected by temperature, water and light availability, as well as their interactions (Table S2 in Supporting Information). Seed germination percentage was lower at high (20/25°C) temperatures than at intermediate (10/15°C) temperatures; while at low temperatures (0/5°C), it was dependent on the water availability (Figure S3A in Supporting Information). In addition, high light availability (more than 50% of full light, with full light defined as 7,000 lx) could generally promote seed germination (Figure S3B in Supporting Information). Interestingly, it seemed that lower light availability could also promote seedling survival at low temperatures (Figure S4A in Supporting Information). However, once regardless of water and light availability, seedlings generally persisted longer at lower temperatures, and the higher water and light availability treatments also promoted their survival (Figure S4 in Supporting Information).

Simulated short-term extreme climate events significantly reduced the survival rate of seedlings younger than 60 days, but had weaker effects on seedlings that had grown for at least 90 days under the conditions of 10/15°C with full light availability (Figure 4A; Table S3 in Supporting Information). Older seedlings also had high tolerance to 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 to the long-term extreme climate treatment, and thus higher overwintering capacity. In other words, if extreme climate events become more frequent, older seedlings will have higher capacity to survive long extreme climate events, for example, a long cold and dry winter.

Germination rates of seeds buried in the field were relatively high (more than 60%) in the following May and July. Seeds buried at lower elevations generally showed lower frequencies of germination than those buried at higher elevation (Table S4 and Figure S5 in Supporting Information). No viable seeds remained in July, because if they did not germinate, seeds rotted in the soil (Figure S5 in Supporting Information). 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 in Supporting Information).

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 in Supporting Information). More specifically, in late September survival rates of seedlings transplanted into 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.

Constraints on cushion physiological status

Within a cushion individual, when leaves are covered by beneficiary plants, they express significantly lower specific leaf

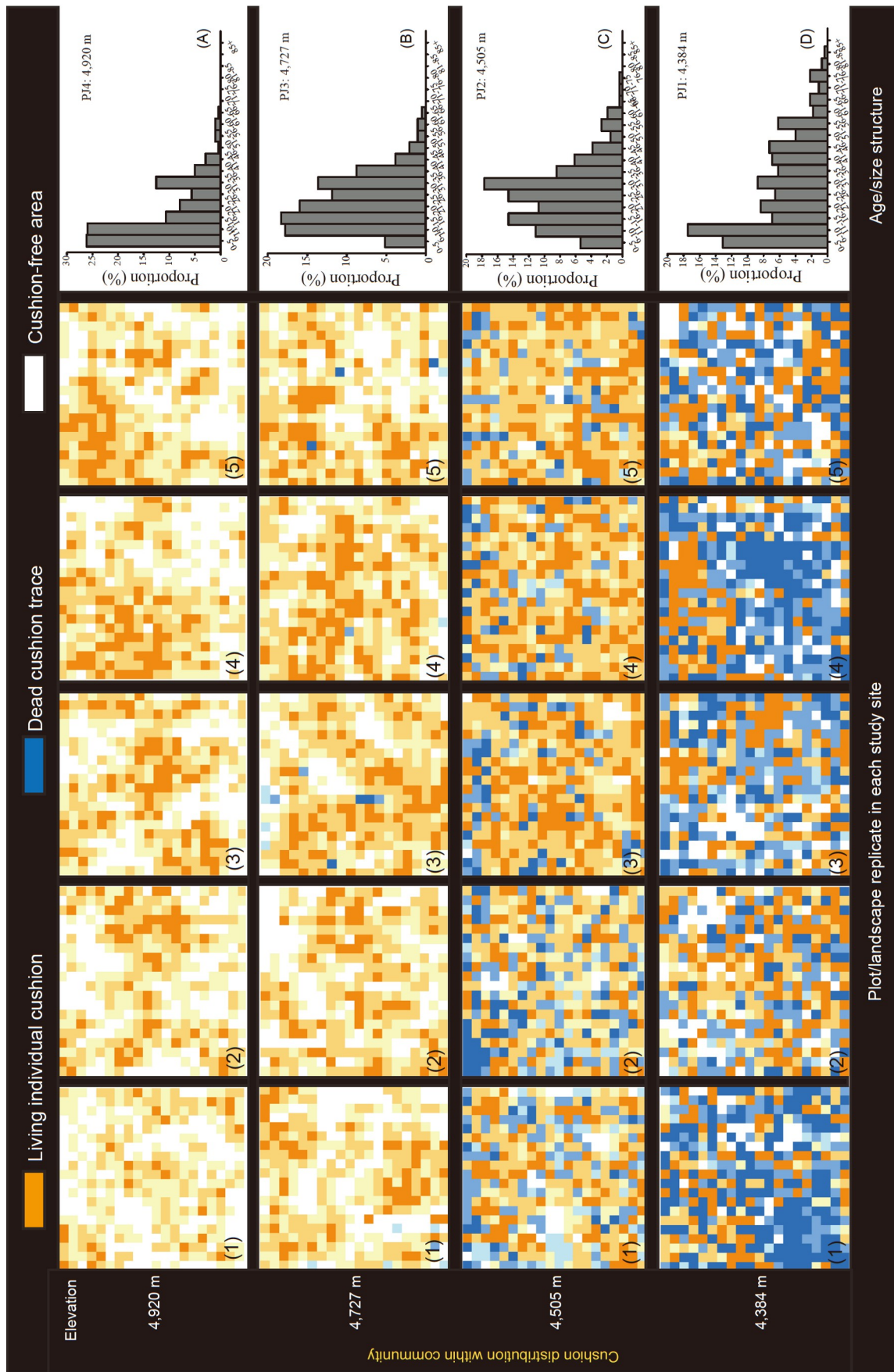


Figure 1. Distribution patterns of individual cushions (left) and age/size structure of populations of the *A. polytrichoides* cushion plant (right) in the four communities with increasing elevation in Pujin pasture. Orange, blue and white squares represent living individual cushions, dead cushion traces, 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.

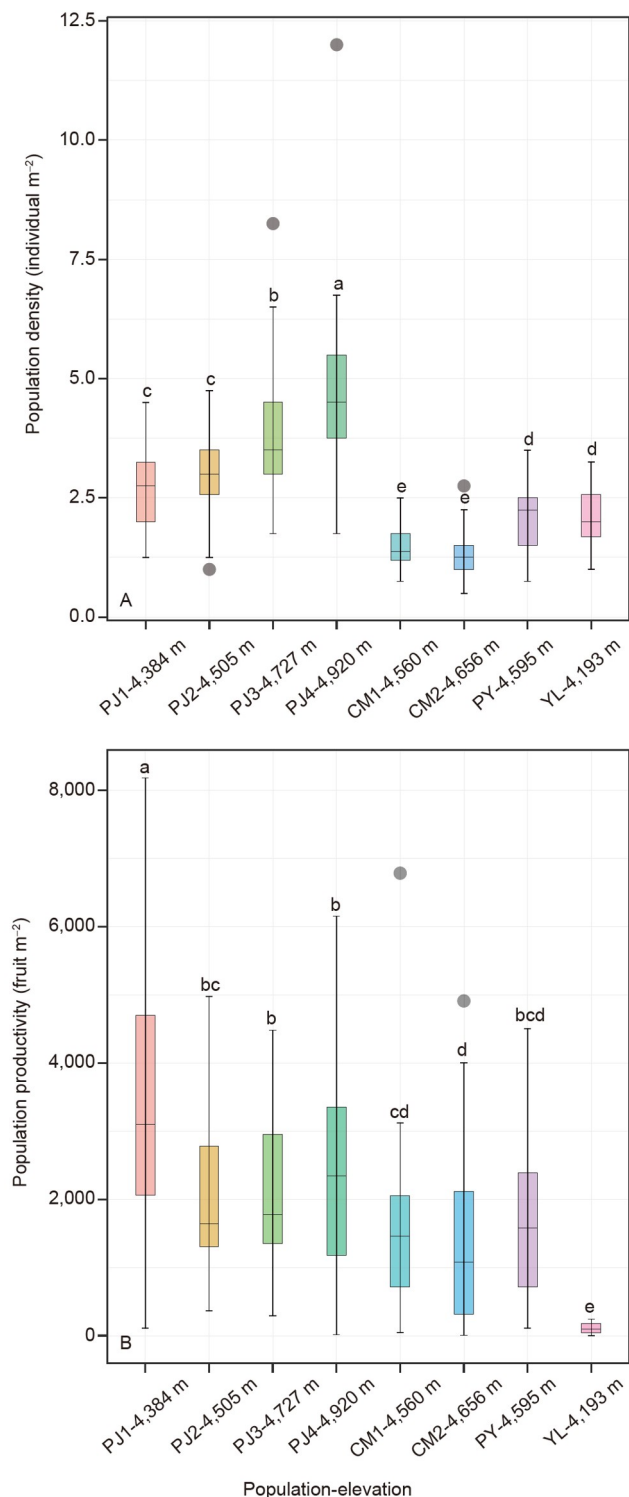


Figure 2. Population density (A) and productivity (B) of *A. polytrichoides* cushions at indicated study communities. Different letters indicate significant differences at the $\alpha < 0.05$ level (one-way ANOVA with Tukey HSD tests).

area (SLA) and leaf dry matter content (LDMC) compared with those leaves of individuals that are free from beneficiary cover (Figure S6A and C in Supporting Information). The effects were consistent in all study cushion populations and independent of the dominating beneficiary species (Figure S6A, C and Table S6

in Supporting Information). Such results indicate that the cushion surface areas (leaves) that are colonized hence covered by beneficiary plants indeed suffer some certain water- and/or light-associated stresses. However, when beneficiary plants' cover increased, both the average values of SLA and LDMC of involved cushion individuals significantly increased (Figure S6B and D in Supporting Information), indicating that the increasing beneficiary plant cover might inversely lower the relevant stresses.

Constraints on cushion reproduction and mortality

Beneficiary plant cover and cushion flower reproduction were not correlated in the CM1 population, weakly negatively correlated 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 reproduction. A significant negative correlation between beneficiary cover and fruit reproduction was also detected in the PY population (Figure 5G), but this relationship was neutral in the PJ3, CM1, CM2 and YL populations, and weakly negative in the others (PJ1, PJ2 and PJ4) (Figure 5). 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 communities (Figure 5I–K), indicating that increases in this variable can promote the mortality of cushion plants and accelerate their exclusion.

DISCUSSION

Foundation species, by virtue of their special structural or functional attributes, can create an entire ecological community or ecosystem, sustain community structures and hence 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). Accordingly, explicitly elucidating how foundation species respond to environmental change, and how the associated community changes, is crucial for robustly predicting changes in ecosystems, and thus their long-term sustainable management.

As typical foundation species, cushion plants sustain a prominent proportion of alpine biodiversity (Butterfield et al., 2013; Cavieres and Badano, 2009; 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 lower-elevation cushion populations now more fragmented than higher-elevation populations (Figure 1). This was supported by the fact that the lower-elevation cushion populations showed lower population density and older individuals than the higher-elevation populations (Figures 1A–D and 2A; Figure S2 in Supporting Information). This indicates a lower cushion demographic rate in communities that are experiencing warmer temperatures and higher vegetation coverage. Species composition, abundance and community structure gradually change with the process of cushion degeneration (Figure 3). After cushion exclusion from communities, the previously cushion-dominated communities gradually turned to relatively stable

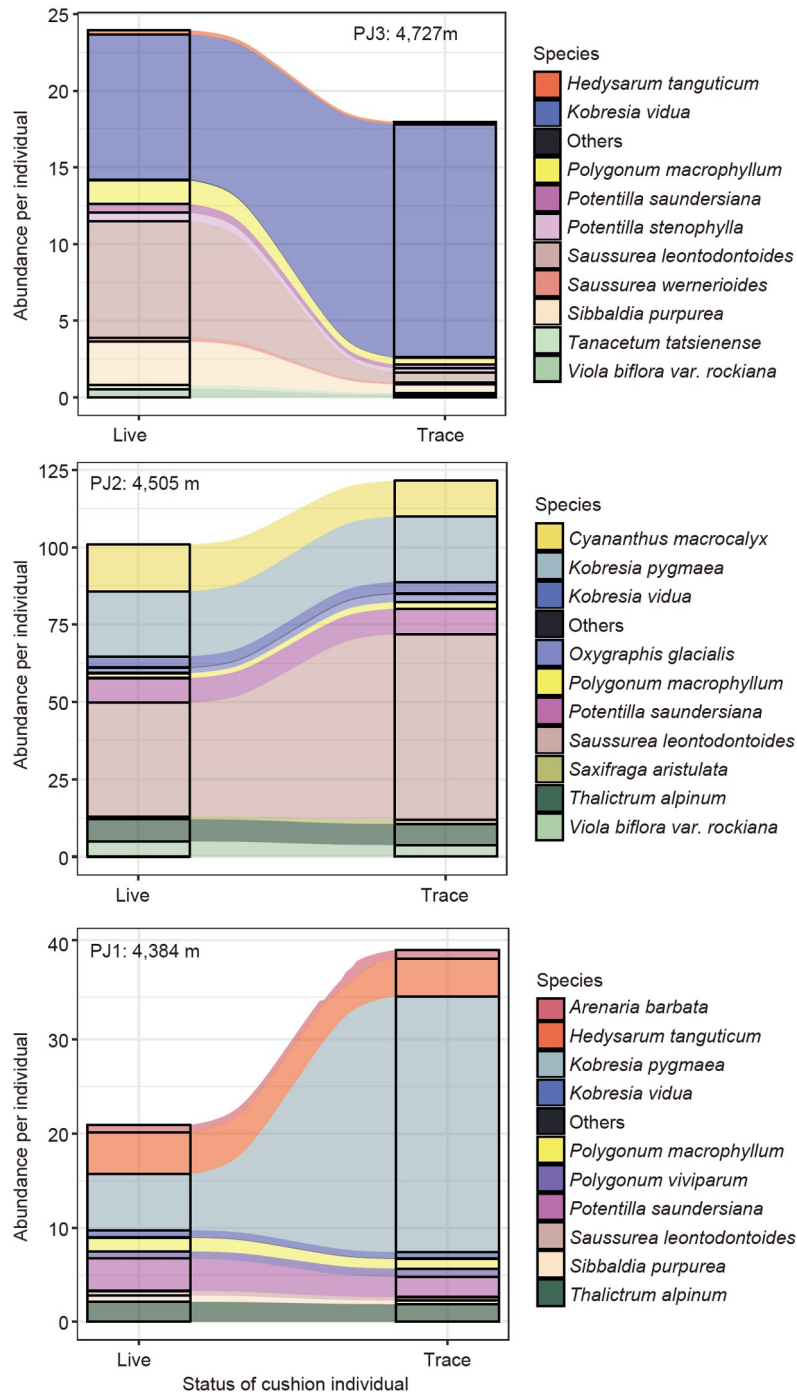


Figure 3. Successional processes and associated changes in species composition and abundance of cushion-dominated communities. Relative abundance of the top 10 beneficiary species associated with living individual cushions and dead cushion traces in communities from cold (high-elevation, PJ3) to warm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

communities that are overwhelmingly dominated by sedge species (Figure 3). All these results suggest that lower-elevation populations of the cushion *A. polytrichoides* that are experiencing warmer temperatures and higher vegetation coverage are simultaneously experiencing degeneration, while populations at higher elevations which are experiencing colder temperatures and lower vegetation coverage are maintaining recruitment and keep expanding (Chen et al., 2020).

Newly established cushion populations in high-elevation

habitats, especially those newly uncovered by glacial retreat (Baker and Moseley, 2007), could facilitate the establishment and survival of other species (Cavieres et al., 2007), thereby increasing local plant diversity (Cavieres and Badano, 2009). In contrast, population degeneration could potentially induce a thorough change in community structure and species composition (Figure 3). In our study region, the mean annual temperature in the past decades has increased at a rate of $0.06^{\circ}\text{C yr}^{-1}$, resulting in ca. 70 m upward shift in elevation of

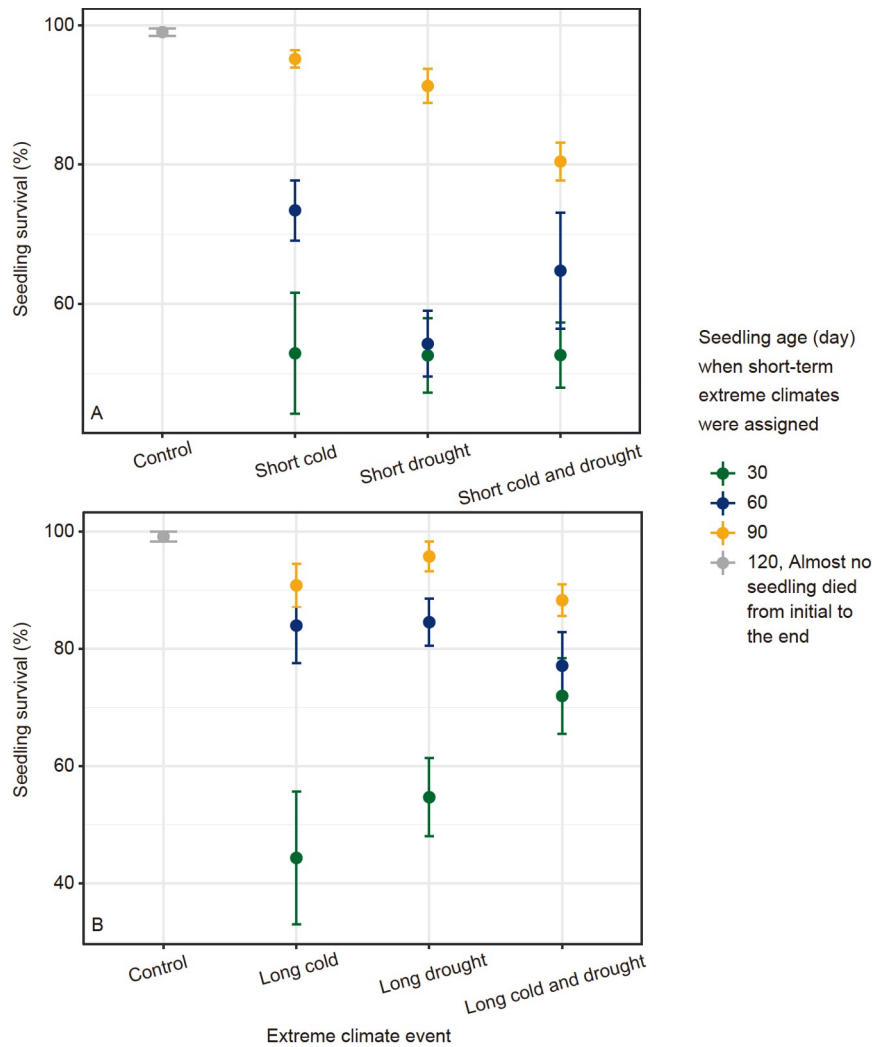


Figure 4. Effects of simulated extreme climate events on seedling survival. A, Survival rates of seedlings assigned to indicated short-term extreme climate events starting at indicated ages. B, Survival rates of seedlings that survived short-term extreme climate events subjected to indicated long-term extreme climate events after growth to 120 days in initial conditions (10/15°C with full light availability). $n=6$ (replicate pots with 30 initially sown seeds), data are mean and standard error (SE). Very few seedlings in the control group died from the start to the end of the experiment, so only their final survival rate is shown.

the treeline (Baker and Moseley, 2007), which could induce negative influences on high-elevation vegetation (Grabherr et al., 1994). Moreover, upward shifts of lowland species/vegetation induced by climate warming has been continuously proven in our study region (He et al., 2019; Liang et al., 2018; Zhao et al., 2011), which 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) and hence strong competition on cushion plants. Consequently, given that lowland vegetation will possibly keep continuously upward migrating due to future climate warming, those current high-elevation populations of the cushion plant *A. polytrichoides* would face the same challenges that low-elevation populations face now. Thus, in the long-term, low-elevation cushion 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 and Schöb, 2017). Furthermore, species interaction networks that are now mainly sustained by cushion plants (Losapio and Schöb,

2017; Losapio et al., 2019) would inevitably collapse.

Plants' dynamics are influenced by ecological factors at different life history stages (Giménez-Benavides et al., 2008; Oldfather et al., 2021). We found that all study cushion populations except the Yulong population produced sufficient seeds in a single growing season (Figure 2B), suggesting that the cushion population recruitment 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 population recruitment rates. We found that, generally, low light availability can delay seed germination and reduce final germination percentages (Figures S3B and S4 in Supporting Information), implying that the surrounding vegetation/litter may delay and/or reduce soil seed germination in the field. Moreover, low temperature could generally delay seed germination (Figure S4A in Supporting Information) and reduce seed germination percentage if water stress exists (Figure S3A in Supporting Information), implying that the frequently low temperature and drought in the early growing season (Wang, 2006) may also induce certain disadvantages in the seedling

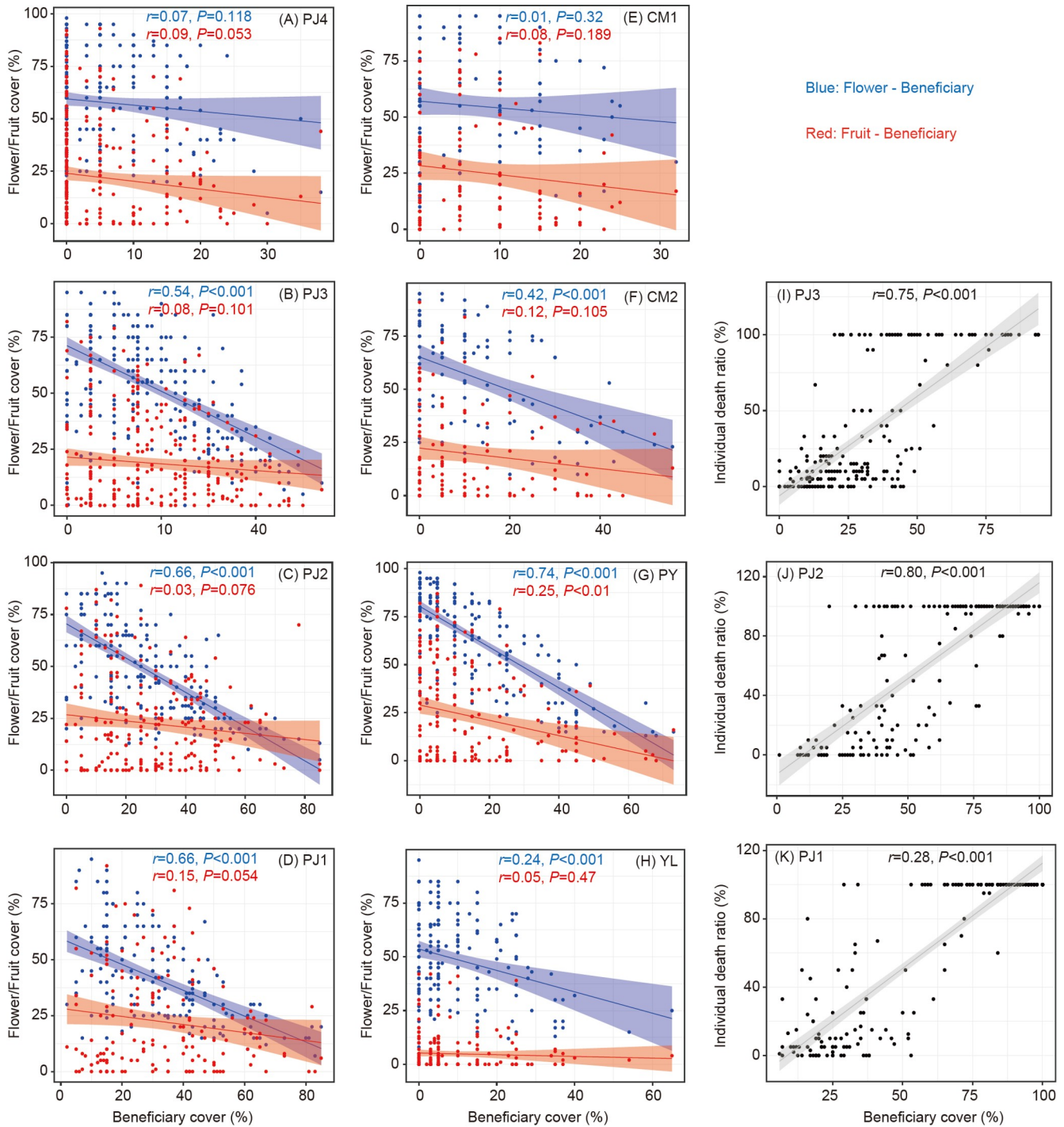


Figure 5. Pearson correlations between beneficiary cover and (A–H) cushion reproduction (flower and fruit), and (I–K) death ratio of individual cushions in the study populations.

recruitment. It was interesting that lower light availability seemed to promote seedling survival at low temperatures (Figure S4A in Supporting Information). However, considering that we had several factors in this experiment and all factors and their interactions have significant effects (Table S2 in Supporting Information), this result is hard to explain without further experiments. In addition, very few seedlings survived for 17 weeks (Figure S4 in Supporting Information) which equals the length of the growing season in their natural alpine ecosystems.

Taking together, although many factors act in concert to determine germination and seedling survival with sometimes even unpredictable exceptions, our 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 and Figure S5 in Supporting Information), 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 (90–120 days) significantly increases their ability to survive long-term extreme climate events (simulating a long winter; Figure 4; Table S3 in Supporting Information). 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 (Lüscher et al., 2001). The finding that all transplanted seedlings died by the end of the growing season (Table S5 in Supporting Information) corroborates this conclusion, possibly because the growing season was too short (ca. 60 days) for them to develop over-wintering capacity.

Our transplantation experiment implied that inter-specific competition can hinder seedlings' establishment. This could be because other competitive species can delay germination and accelerate the death of *A. polytrichoides* seedlings (Chen et al., 2020). Furthermore, competitive stress imposed by beneficiary plants plays a key role in the decay of previously established individual cushions. Beneficiary plant cover can significantly constrain the physiological status of the cushion plant, as indicated by the leaf traits (Figure S6A, C and Table S6 in Supporting Information), which point towards 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 (Ordoñez et al., 2009). Considering that the cover by beneficiary species can induce some certain shelter on the cushion surface which could further reduce light availability, the lower SLA is likely also a result of this shading (Figure S6A in Supporting Information). Thirdly, the plant cover by beneficiary species could generally reduce the LDMC of cushion leaves (Figure S6C in Supporting Information), indicating that they may stress cushion leaves partially through competition for water and associated stress (Cornelissen et al., 2003). However, it was interesting that at individual level, the average SLA increases but LDMC decreases with increases in beneficiary cover (Figure S6B and D in Supporting Information). A possible explanation is that increased soil nitrogen availability by benefactor species (Chen et al., 2015b) might outweigh the negative effects of the reductions in light availability on cushions' SLA. Nevertheless, the combined effects of high SLA and low LDMC induced by beneficiary species probably, at least partly, accelerate the competitive exclusion process of individual cushions (Figure 5I–K), for example, increasing the death areas (Figure S1 in Supporting Information) of a cushion individual, and hence degeneration of cushion populations.

Furthermore, beneficiary species could significantly reduce flower reproduction of cushion individuals, 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, which consequently reduced pollina-

tion efficiency and hence 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 defense traits (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 could show that when foundation species degenerate due to various ecological constraints that are possibly associated with climate warming, the associated species composition, relevant abundance and community structure dramatically change. How these changes affect alpine biodiversity, ecosystem functioning and the long-term sustainability of alpine ecosystems will be a challenging task for scientists and policy-makers. We therefore strongly recommend considering population dynamics of foundation species to effectively predict and conserve alpine biodiversity.

MATERIALS AND METHODS

Study systems

Arenaria polytrichoides Edgew. (Caryophyllaceae) is a long-lived cushion-forming plant with a gynodioecious sexual system. As an important foundation species, this species offers suitable microsites for both less stress-tolerant beneficiary plants and insects to colonize hence increasing and sustaining regional biodiversity (Chen et al., 2015a; Chen et al., 2015b, Chen et al., 2021; Yang et al., 2010).

Field experiments were conducted in northwestern Yunnan province, which locates in the core area of alpine plant diversity of the Himalaya-Hengduan Mountains, SW China (Sun et al., 2017; Zhang et al., 2021), one of the global biodiversity hotspots (Mittermeier et al., 1999). We selected four cushion-dominated communities along an altitudinal gradient in Pujin pasture of the Baima Snow Mountains (Figure S7 in Supporting Information), designated (from relatively low to high): PJ1 (N28°26'50.72", E98°59'52.25"; 4,384 m), PJ2 (N28°27'48.66", E99°00'00.34"; 4,505 m), PJ3 (N28°28'40.91", E99°00'04.21"; 4,727 m) and PJ4 (N28°28'49.77", E99°00'32.57"; 4,920 m). Dense alpine meadow with >95% cover and sedge species dominating the communities prevails in the PJ1 and PJ2 communities. The PJ3 community is in an alpine meadow-scrub transition zone (i.e., ecotone), with much lower vegetation cover (ca. 40%) than in the lower-elevation communities, and the vegetation type in the highest-elevation community (PJ4) is alpine scree with <15% cover. The differences in vegetation type and cover could be associated with a decrease in inter-specific competition with increases in elevation. In addition, the abiotic conditions, including soil nutrient contents, water availability and soil/air temperature, also become more inhospitable with increases in elevation (Chen et al., 2019; Chen et al., 2020; Wang, 2006). Hence, we chose these four communities to elucidate the cushion plant's population dynamics, the underlying mechanisms and the associated changes in plant composition, relevant abundance and community structure now and in response to anticipated climate change, in accordance with the "space-for-time" conception (Pickett, 1989).

We also selected four cushion-dominated communities in different mountain ranges to assess and compare current cushion

population dynamics at a larger scale and predict dynamics of cushion-dominated plant communities in alpine ecosystems more broadly (Figure S7 in Supporting Information). Two of these communities are situated on the Baima Snow Mountains ca. 7 km from the Pujin pasture. As they are close to an abandoned coal mine, we designated these two communities CM1 (N28°26'25.65", E99°01'43.68"; 4,560 m) and CM2 (N28°24'12.58", E99°01'54.13"; 4,656 m). The vegetation type in the CM1 community is shrub-sedge meadow (ca. 60% cover), while the vegetation type in the CM2 community is alpine scree (ca. 30% cover) with sporadically distributed *Rhododendron* shrubs. Another community, the Puyong community (PY hereafter; N28°24'42.09", E99°55'37.23"; 4,595 m) is situated on the Daxueshan Snow Mountains, ca. 57 km from the Baima Snow Mountains. This community is in typical alpine scree vegetation, with ca. 30% cover and sporadically distributed *Rhododendron* shrubs. The last community is situated on the summit of the Yulong Snow Mountains (YL hereafter; N27°01'59.72", E99°10'58.64"; 4,193 m) near Lijiang city, ca. 146 km from the Baima Snow Mountains. The vegetation type in the YL community is sparse grassland with ca. 40% vegetation cover and small, sparsely distributed scree areas.

Cushion population dynamics

Cushion individual distributions within communities

We selected the four communities in Pujin pasture to identify the current and historical distribution patterns of cushion individuals in their communities, by taking a landscape conception and approach (Pickett and Cadenasso, 1995). For this, we randomly established five 20 m×20 m quadrats and divided each quadrat into 400 1 m×1 m grid cells in each community. We counted the number of living cushions in each grid cell and assigned them to three categories according to their size (≤ 10 , 10–25 and > 25 cm surface diameter), which could simply represent juvenile, young and adult individuals (Chen et al., 2020), respectively. Additionally, some individual cushions had been completely excluded (i.e., died) before this study, but many had left apparent traces. In a preliminary investigation, we excavated more than 15 such traces to identify whether they were real cushion traces or not. Real traces commonly had decayed leaves/branches and tap roots 2–10 cm below the soil surface. If none of these vestiges were detected, we treated the apparent traces as original land (i.e., not cushion traces). Using the experience gained, we also counted the number of cushion traces and recorded their positions in each cell.

Current cushion age structure and density

To characterize the current cushion population structures within communities, we determined the age structure and density of cushion *A. polytrichoides* in each community. 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 (Benedict, 1989; Chen et al., 2020; Molau, 1997). For this, using PP bundling ropes we randomly established 25 sampling quadrats (2 m×2 m, with more than 2 m spacing) in each community in late August 2020, when *A. polytrichoides* was in a fruiting stage. In each quadrat, we counted the number of *A. polytrichoides* individuals and measured the length (L), width (W) and height (H) of each individual. The canopy surface of *A. polytrichoides* cushions is usually round or elliptical, so we simply

used the length (L) as a proxy for individual age. We also marked each cushion individual with an aluminum label to enable assignment of subsequent measurements to the correct individuals. Population density was calculated as the number of cushion individuals per square meter.

Current cushion population reproductivity

To characterize the overall reproductive output of cushion populations, each population's flower reproduction 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 SE), so rather than laboriously collecting and dissecting fruits we simply used fruit production as a proxy of population reproductivity in this study. We initially followed a previously published protocol (Zhang et al., 2020) to assess the flowering/fruiting ratio of 50 randomly chosen cushion individuals in each community, then by experience visually assessed the reproductive outputs of the remaining cushion individuals due to time constraints. Specifically, we spread a nylon net with 3 cm×3 cm mesh as evenly as possible on the surface of each individual. Then, we counted the squares that covered the entire surface of the individual and those that covered the flowering or fruiting area. Finally, the flowering or fruiting ratio was calculated as the ratio of the number of squares covering flowering or fruiting areas to the total number of squares covering the individual cushion surface.

Community dynamics along with cushion plant dynamics

In efforts to elucidate the dynamics of cushion-dominated communities and associated changes in species composition, relevant abundance and community structure, we randomly selected 90 living and 109 trace individual cushions of the PJ1 community, 98 and 94, respectively, of the PJ2 community, as well as 154 and 149, respectively, of the PJ3 community. The vegetation cover and number of individual cushion traces decrease and the population density increases with increases in elevation (see RESULTS in this study); the high-elevation communities currently experience colder soil and air temperatures (Chen et al., 2019) and the lowland plants are possibly experiencing upward shifting (He et al., 2019; Liang et al., 2018; Zhao et al., 2011). Based on these, it was reasonable to hypothesize that, in the long-term view, the cushion-dominated communities at higher elevations will possibly succeed to communities similar to the current low-elevation communities once the lowland vegetation continues to move upslope and results in increases in vegetation cover. Accordingly, for simplification of presentation, we arbitrarily considered PJ1 as a “relatively stable community”, PJ2 as an “intermediate successional community” and PJ3 as an “early successional community”. We counted and recorded all beneficiary species associated with each selected individual, and their abundance.

Ecological constraints on cushion population dynamics

Constraints on cushion seedling recruitment

To elucidate the effects of cushions' reproductive outputs on the subsequent population recruitment, we conducted a seed

germination and seedling culture experiment in the laboratory. Cushion seeds were collected from the populations in Pujin pasture in late September in 2020. In accordance with previous findings (Chen et al., 2020), the seed quality in terms of weight and germination percentage did not significantly differ between populations ($DF=7$, $F=1.71$, $P=0.13$ for 30-seed weight and $DF=7$, $F=0.491$, $P=0.835$ for germination percentage of seeds). Thus, we mixed all seeds from different populations for the subsequent experiments. To assess the effects of temperature, light and water availability on seed germination and subsequent seedling survival, we took a full factorial design (Figure S8 in Supporting Information) and 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. Peat soil was placed in 270 plastic pots (10 cm×10 cm×12 cm) with several holes in the bottom to allow passage of water, and 30 fully matured seeds were randomly sown in each pot. 90 randomly selected pots were assigned to each of the three chambers. We set the light availability in sections of each chamber to 0, 25%, 50%, 75% and 100% (7,000 lx) using polypropylene shading net (Chen et al., 2020). Three plastic saucers, each with six pots, were assigned to each level of light availability. One of each of these sets was watered sufficiently to avoid any water stress (once per week, “full water” hereafter), one sufficiently for slight water stress (once every two weeks, “half-water” hereafter) and the other was not watered at all, to subject the seedlings to extreme water stress. The number of germinated seeds was recorded every week until no new seedlings emerged for at least 10 days. This experiment lasted for ca. six months. No seeds under extreme water stress germinated, so we excluded material subjected to this treatment from further analyses.

Since extreme climate events, such as extreme cold and/or drought, frequently occur in the study region (Ning et al., 2012; Wang, 2006), a further aim was to elucidate their effects on the establishment of the cushion species’ seedlings. For this, we first cultured seedlings to certain days in the 10/15°C (night/day) conditions with full light availability, and then relevant extreme treatments were assigned. As mentioned above, we also took a full factorial design (Figure S9 in Supporting Information) for this experiment. Specifically, sets of 30-, 60-, 90- and 120-day-old seedlings (in six replicate pots for each seedling age, each with seedlings germinated from 30 seeds) were assigned to each of three extreme climate treatments. One was a short-term cold treatment (20 days at 0/5°C, with regular watering), the second was a short-term drought treatment (20 days at 10/15°C temperature regime, but no watering from a week before the start of this treatment), and the other was a short-term cold plus drought treatment (20 days at 0/5°C without watering). These short-term climate treatments were considered to simulate the frequent extreme climate events in the plant growing season. After each short-term climate event, all pots were returned to the initial conditions (10/15°C with full light and water), cultured to 120 days, and then exposed to a long-term (90 days) extreme climate treatment as before. The 120-day seedlings for previous short-term treatments were directly assigned to long-term treatments after relevant short-term treatments. These long-term extreme climate treatments were simulated as a long winter and were designed to test and compare the over-wintering capacity of seedlings that had, and had not, experienced extreme climate events during the growing season (i.e., short-term

treatment). The same number of pots (6) with the same number of seeds (30) were cultured under the conditions of 10/15°C with full light provided controls. Seedling survival (%) was recorded after each of these climate events. Since seedlings in the “control” treatment had a very high survival rate until the end of this experiment (see RESULTS), we took the final survival rate to do comparisons between control and relevant climatic treatments.

We also assessed seeds’ and seedlings’ performance in real natural conditions by subjecting them to burial and transplantation treatments. For the first, we buried seeds in soil at 2 cm depth in the PJ1, PJ3 and PJ4 communities; while for the latter, we transported seedlings cultured in laboratory to the field in PJ1 and PJ4 communities and transplanted them into two different micro-habitat types, i.e., bare ground and vegetation, in each community. See Text S1 in Supporting Information for details.

Constraints on cushion physiological status

Because the SLA (the ratio of fresh leaf area to leaf dry mass in $m^2 kg^{-1}$) and LDMC (the ratio of leaf dry mass to fully rehydrated fresh mass in $g kg^{-1}$) are directly related to the environmental stresses that plants experience (Ordoñez et al., 2009; Poorter et al., 2009; Wright et al., 2004), to assess the potential effects of beneficiary plants on the process of cushion population degeneration, we aimed to test the effects of beneficiary plants on the above two physiological traits (SLA and LDMC) of cushion plants. We only selected the PJ1, PJ2 and PJ3 cushion populations for this purpose, because the beneficiary plant cover on cushion surfaces is relatively low in the PJ4 population. Specifically, we collected leaves from individuals with beneficiary cover ratios ranging, in 10% increments, from 0 to 90%. We first randomly collected (regardless of being covered by beneficiaries or not) 10–20 healthy leaves from individuals of each of these categories, half from individuals mainly covered by *Kobresia pygmaea* and the other half from individuals mainly covered by *Saussurea leontodontoides*. Furthermore, to assess the specific stresses experienced by the leaves that were covered by beneficiary plants within a cushion individual, we randomly collected three healthy leaves from a beneficiary-covered area and three from beneficiary-free areas, respectively, of those cushion individuals of the above categories to determine their SLA and LDMC. Samples for determining SLA and LDMC were collected between 9.00 and 11.00 in the morning of a sunny day in mid-August 2020. The fresh mass of samples was determined immediately using an electronic balance after collection in the field. Their saturated mass was determined after 24 h of rehydration in totally dark conditions and dry mass after drying at 75°C for 48 h.

Constraints on cushion reproduction and mortality

A further aim was to elucidate the effects of beneficiary plants on cushions’ reproductive outputs. For this, during the assessment of cushion population reproduction (see above) we simultaneously assessed the beneficiary, flowering and fruiting cover ratio on each cushion individual in each previously established sampling quadrat (see above) for each community. Further, we selected the PJ1, PJ2 and PJ3 communities to assess potential effects of beneficiary species on the mortality process of individual cushions. Community PJ4 was not included because its cushion members have too low beneficiary cover ratios to induce individual mortality (personal observation). For this, in early August 2020, we randomly selected 199, 192 and 216 cushion

individuals in the PJ1, PJ2 and PJ3 communities, respectively. For each selected individual, we assessed and recorded the total beneficiary cover ratio and the death ratio (death area/total cushion surface area) of the individual cushions (Figure S1 in Supporting Information).

Data analyses

We applied a landscape ecological conception (Pickett and Cadenasso, 1995) to analyze the spatial distributions of current and historical cushion individuals within communities. For this, we used Fragstats4.2 software (McGarigal and Ene, 2013) to calculate six landscape metrics for cushion patches (Lustig et al., 2017; McGarigal and Ene, 2013; Wang et al., 2014), they are the total CA, ED, Area_Mn, CPLAND, NP, and PLADJ. See Text S2 and Box S1 in Supporting Information for the details. One-way ANOVA was applied to assess differences in these landscape metrics between populations, with the landscape metrics as dependent variables and community as the independent variable. Tukey HSD tests were applied to assess the significance of differences between populations. Raster graphics presenting the cushion patch distribution within communities were generated using Arcgis 10.2.

To illustrate the changes in species composition, relevant abundance and community structure 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 community ID includes information of the study community, including elevation and potential relevant microclimates, we applied one-way ANOVA to assess the differences in population density and reproductivity between cushion populations, with population density and reproductivity as dependent variables and community 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: (i) the effects of simulated environments 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; (ii) 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; (iii) 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; (iv) 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; (v) 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. 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 and 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 Development Core Team, 2021) was used for all the above analyses, the lme4 package 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.

Compliance and ethics

The author(s) declare that they have no conflict of interest.

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Supporting information

The supporting information is available online at <https://doi.org/10.1007/s11427-022-2383-6>. The supporting materials are published as submitted, without typesetting or editing. The responsibility for scientific accuracy and content remains entirely with the authors.

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