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Drivers of local extinction risk in alpine plants under warming climate

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Abstract

The scarcity of local plant extinctions following recent climate change has been explained by demographic inertia and lags in the displacement of resident species by novel species, generating an “extinction debt”. We established a transplant experiment to disentangle the contribution of these processes to local extinction risk of four alpine plants in the Swiss Alps. Projected population growth (λ) derived from integral projection models was reduced by 0.07/°C of warming on average, while novel species additionally decreased λ by 0.15 across warming levels. Effects of novel species on predicted extinction time were greatest at warming <2°C for two species. Projected population declines under both warming and with novel species were primarily driven by increased mortality. Our results suggest that extinction debt can be explained by a combination of demographic inertia and lags in novel species establishment, with the latter being particularly important for some species under low levels of warming.

Keywords

Climate change; competition; demography; elevation gradient; extinction risk; integral projection models; novel species; population growth rate; population-dynamics; transplant experiment

Introduction

Climate warming is impacting ecological communities around the world and is increasing the local extinction risk of many species (Thomas et al., 2004; Cahill et al., 2013; Warren et al., 2018). Yet so far, most studies show limited, or even positive, effects of climate change on local scale species richness (Vellend et al., 2013; Dornelas et al., 2014; Suggitt et al., 2019). This has been interpreted as reflecting an ‘extinction debt’ (Tilman et al., 1994; Dullinger et al., 2012; Rumpf et al., 2019), caused by a lag in the rate of local extinctions

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Authorship

JMA designed the experiment. HAN and JMA collected data, HAN performed analyses and wrote the first draft of the manuscript, which JMA and HAN subsequently edited.

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relative to the pace of changing climate (Kuussaari et al., 2009). For example in mountains, which are considered particularly vulnerable to warming (Thuiller et al., 2005; Lenoir et al., 2008), plant extinctions have only occasionally been documented, even in time-series data spanning over a century of climate warming (Pauli et al., 2012; Wipf et al., 2013; Steinbauer et al., 2018). Rather, local plant species richness has in general increased as species spread upwards to track warming climate (Walther et al., 2005; Steinbauer et al., 2018). While it is assumed that these increases in biodiversity are transient (Jackson & Sax, 2010; Svenning & Sandel, 2013; Alexander et al., 2018), the existence and causes of extinction debt in plant populations faced by both warming and novel species from lower elevations have to our knowledge not been quantified directly.

Two hypotheses have been proposed to explain extinction debt of alpine plants faced with climate warming. Firstly, warming may have a negative impact on population dynamics, but the decline in population growth is small and/or initial population sizes are large, such that populations drift only slowly to extinction and temporarily persist in climatically unfavourable areas (Kissling et al., 2010; Talluto et al., 2017). This process of demographic inertia (Malhi et al., 2009) can be expected in long-lived species, including many alpine plants (De Witte et al., 2012), which can persist through long periods of unsuitable climatic conditions while failing to reproduce and recruit new individuals to the population (Svenning & Sandel, 2013).

A second explanation proposed for extinction debt is that alterations of non-climatic factors, such as biotic interactions, drive extinction as indirect effects of warming, but their effects lag behind the pace of climate warming itself. In mountains, competitively dominant species from lower elevations can strongly reduce the performance of alpine plants when growing in a warmer climate (Alexander et al., 2015), and the upward movement of low elevation species has been suggested to drive range retractions of alpine plants in the European Alps (Rumpf et al., 2018; Steinbauer et al., 2018). Yet so far, few studies have observed replacement occurring in mountain plant communities (however see Kudo et al., 2011; Rixen & Wipf, 2017), and thus it has been argued that novel species have not yet reached sufficient densities at high elevation to competitively replace alpine plants (Kudo et al., 2011; Steinbauer et al., 2018).

To evaluate the risk of local extinction faced by plants under a warming climate, it is necessary to quantify how both warming and the additional effect of novel species impact plant demography. Time-series data typically reveal changes in the presence or cover of species, but are often unsuitable to predict ongoing demographic changes, whereas the available data often preclude the evaluation of changing species interactions under warming (e.g. Klanderud & Birks, 2003; Gottfried et al., 2012; Steinbauer et al., 2018). Using manipulative experiments, it is easier to directly quantify effects of warming on population growth, and to disentangle effects of climate and biotic interactions, for example by growing focal plants in the presence or absence of neighbouring plants. Such studies have revealed that competition can play an important role in determining population growth under warming, for example demonstrating a shift from facilitation to competition under warming (Olsen et al., 2016). Yet so far, experiments that test the impact of novel species on resident plants experiencing warming (Alexander et al., 2015) have not estimated population

growth rates and hence could not disentangle the contribution of changing climate and novel species to local extinction risk. As well as predicting overall population trends, a demographic approach makes it possible to identify the specific vital rates underlying population changes (Caswell, 2001). This can provide greater mechanistic insight into the impacts of climate change on population dynamics (Souther & McGraw, 2014; Olsen et al., 2016; Cui et al., 2018; Iler et al., 2019) and potentially guide strategies to manage populations at risk of local extinction (Toräng et al., 2010; Hylander & Ehrlén, 2013). Moreover, direct effects of warming and indirect effects of novel species may have either opposing or reinforcing effects on vital rates, which might influence approaches to manage populations of conservation concern.

Here, we use a whole-community transplant experiment along an elevation gradient in the Swiss Alps (Fig. 1) to estimate the contribution of warming and the establishment of novel species to local extinction risk in four alpine plants. Elevation gradients in mountains are useful model-systems to simulate future climates by transplanting plants downhill (Nooten & Hughes, 2017; Tito et al., 2020), where they experience warmer climate as well as changes in other abiotic and biotic factors like precipitation or pollinator communities. While sometimes complicating the interpretation of direct temperature effects (Nooten & Hughes, 2017), these correlated changes often also mimic expected future environments (National Centre for Climate Services, 2018), and provide clear expectations for which novel species will interact with higher elevation plants in the future (Alexander et al., 2015; Descombes et al., 2020; Richman et al., 2020). Given the limited local extinctions of mountain plants despite approximately 2 °C of warming in the Swiss Alps over the last 150 years (National Centre for Climate Services, 2018), we hypothesise (1) that the combination of interactions with novel species and simulated warming contribute more strongly to declines in population growth than warming alone, due to compounding negative effects of warming and increased competition from species that are better adapted to warmer conditions. We also identify the underlying vital rates driving local extinction under simulated warming, hypothesising (2) that different vital rates drive population declines when plants are faced by warming than when faced by warming in combination with novel species. For example, previous studies lead us to predict that warming increases extinction risk primarily through mortality (Olsen et al., 2016; Cui et al., 2018; Panetta et al., 2018) as a consequence of drought stress (Orsenigo et al., 2014), whereas interactions with novel species increase extinction risk both by increased mortality (Alexander et al., 2015) and by suppressing growth (Huenneke & Thomson, 1995; Williams & Crone, 2006). Overall, we hypothesise (3) that while the predicted time to local extinction will be shortened by increasing levels of warming, these effects will be amplified when alpine plants face competition from low elevation species.

Materials Methods

Study-system

In September 2016, we established a whole-community transplant experiment along an elevational gradient in the Swiss Alps (46°13'08N, 7°03'13E), including four sites situated at 2200, 1950, 1750 and 1400 m. The sites represent a temperature gradient ranging from 9.5

to 14.3 °C during the growing season (May-September) over the course of the experiment (2016-2019; Fig. 1; Table S1). We selected as focal species four perennial alpine forbs with different growth forms and functional types that are abundant in the study area and widespread in the alpine zone of Switzerland (Table S2): *Plantago alpina* (Plantaginaceae), *Anthyllis vulneraria* ssp. *Alpestris* (Fabaceae, hereafter *A. alpestris*), *Trifolium badium* (Fabaceae) and *Campanula scheuchzeri* (Campanulaceae). All species are abundant above 2000 m in our study area and were absent from the field sites below 2200 m (except *P. alpina*, found occasionally at 1950 and 1750 m sites), though isolated individuals can sometimes be observed below 1500 m (Atlas de la Flore Vaudois).

Experimental design

Our experiment was designed to simulate two scenarios: (1) a scenario in which alpine plants experience different levels of climate warming, but continue to interact with the plant community found at high elevation today ('current species'); (2) a scenario in which at each level of warming, focal alpine plants interact with lower-elevation plants that could migrate upwards to track warming climate ('novel species'; Fig. 1). We simulated gradual climate warming by transplanting alpine plants from 2200 m to the three lower sites, corresponding to warming of growing season (May-September) temperatures of between 1.65 and 4.85 °C during the period of the experiment (Fig. 1, Table S1). The simulated warming is within the range of expected temperature increases in Switzerland over the coming century (National Centre for Climate Services, 2018).

To simulate scenario 1, we transplanted 1 m² turfs containing intact plant communities and soil to a depth of approximately 20 cm from the 2200 m site to each lower elevation site (n = 10 turfs per site), plus 10 turfs replanted at the 2200 m site as 'no warming' controls (Fig. S1). Focal individuals of each species were then planted into the transplanted turfs. To simulate scenario 2, we excavated ten replicate turfs at each of the three lower elevation sites (1400, 1750, 1950 m) containing the local plant communities (Figs S2 and S3), planted them back into the site from which they came (but at different locations), and then planted individuals of our focal species into the turfs (Fig. 1). Soil from each of the sites was transplanted among the sites according to the same design as for the turfs to evaluate effects of soil origin (high/low elevation soil) on plant demography. At each site, each treatment (high and low elevation turfs/soils) was assigned at random to four positions (plots) within ten blocks, yielding 140 plots across the whole experiment (40 at each lower site and 20 at the highest site; Fig. S1). The sites were fenced to avoid disturbance from livestock, but at the end of each season turfs were clipped to c. 15 cm to simulate biomass removal by grazers. Bare-soil plots were weeded frequently during the growing season.

Adult individuals were collected from near to the 2200 m site within an area of approximately 0.27 km², by excavating plugs containing a single ramet (hereafter 'individual'; 'Supplementary Methods'). At the end of September 2016, five individuals of each species were planted into each plot at randomly selected positions 13 cm apart within a regular grid (i.e. 50 individuals per species, treatment and site; in total N = 2800 individuals at the start of the experiment). In October 2017, individuals of *P. alpina* (n = 45),

A. alpestris (n = 70) and *T. badium* (n = 52) that had died during the first season were also replaced.

Assessments of vital rates

Vital rates were monitored over three growing seasons (2017–2019; i.e. two annual transitions). Leaf number served as a proxy for plant size, which correlated more strongly with aboveground biomass (mean $r = 0.68$ across the four species) than other traits that we tested (Table S3). Leaf number and seed production (estimation of number of viable seeds produced per individual; Supplementary Methods) were recorded towards the end of the growing season (August–September). Flowering was monitored weekly during the growing season (mid–April–September), whereas survival was determined at the end of the growing season (September). Recruitment probability and recruit size were evaluated with a separate experiment in 2019 (Supplementary Methods; Fig S5). We were unable to collect sufficient seeds to estimate recruitment success and recruit size for *C. scheuchzeri*, so instead represented these vital rates in our models as constants across all community and warming treatments (Supplementary Methods).

Statistical Analyses

Modelling population growth

To estimate projected population growth rates (λ ; hereafter, population growth), we compiled demographic data over two censuses (2017–2018 and 2018–2019) and used these to parameterise size-structured integral projection models (IPMs; Rees et al., 2014). We used R version 3.6.3 (R Core Team, 2020) to build separate IPMs for each species, warming level and surrounding community identity, as well as separate IPMs for each species and soil origin (see Supplementary Methods for further details of the modelling approach; Fig. S4). Leaf number was used as the state variable describing demographic processes represented by survival, growth, reproduction and recruitment (Fig. S6). We pooled data across years (2017–2019) into a single dataset with interannual transitions and fit linear models to estimate parameters for growth, survival and reproduction of each species as functions of plant size, warming level, plant community identity and their interactions. Seed production and recruitment probability were implemented as size-independent constants, with separate estimates for each plant community and site, whereas recruit sizes (\pm SD) per species were implemented as constants at the site level due to low recruitment for separate treatments across the experiment (Fig. S5; Supplementary Methods). We evaluated the uncertainty around λ by performing 5000 parametric bootstraps of each vital rate estimate and refitting IPMs to obtain 95% confidence intervals around λ for each species, warming level and community origin. We used the bootstrap values to test the effects of community origin on population growth at each warming level. To do so, we performed 5000 pairwise comparisons of bootstrapped λ values between community origins at each warming level, with an effect considered significant when it was observed in 95% of comparisons (following Cui et al., 2018).

Estimating times to local extinction

We additionally estimated the time to local extinction under warming and with novel species using a simple exponential population growth model:

$$N_t = N_0 \times \lambda^t$$

The model assumes that the λ values we obtained are representative of the natural populations and ignores demographic stochasticity, since this can only be reliably accounted for in longer time-series (Metcalf et al., 2015). While estimates of predicted local extinction time should therefore be interpreted with caution given the limited duration of the experiment, the purpose of this analysis was to compare effects of warming and community origin. Specifically, we estimated the time (t) predicted for the population size (N_t) of our focal species to fall below 1 with current or novel species across the gradient of climate warming. We fitted the model based on estimates of each species' current population size (N_0) at high elevation (49 000, 146 800, 50 100 and 228 000 for *P. alpina*, *A. alpestris*, *T. badium* and *C. scheuchzeri* respectively; Supplementary Methods) and our observed estimates of λ . We also visualised effects of community origin on predicted extinction times by estimating extinction times from fitted values of linear regressions of observed λ on temperature (for each 0.1 °C of warming between 1.65 and 5 °C) for each species and community origin. Extinction times were also calculated for the 5000 bootstrapped λ values (excluding $\lambda > 0.99$) to estimate uncertainty, with inference of significant differences between treatments based on the same method as previously described for λ .

Vital rate contributions to λ

We used Life Table Response Experiments (LTRE; Caswell 2001) to quantify the contribution of underlying vital rates to changes in λ . LTREs decompose differences in λ between two IPMs into contributions from each vital rate and can be used to indicate how vital rates contribute to differences in λ between two treatments. We used an IPM based on a 'midkernel' (Caswell 2001) that was constructed by combining vital-rate parameters obtained from (1) individuals growing at the 2200 m site, interacting with the current high-elevation plant community (representing a control), and (2) individuals experiencing different levels of warming and interacting with either current or novel species (representing a treatment). We produced LTREs for each warming level and surrounding community identity. This enabled us to test how vital rates contribute to changes in λ under warming with current species, and whether different vital rates drive changes in λ when warming is combined with novel species. We performed a second set of LTREs to isolate effects of novel species when averaged across warming levels. To do so, we used an IPM based on a mid-kernel that combined individuals interacting with current species (control) and novel species (treatment) at each elevation. We replicated this second set of LTRE analyses for plants growing on high (control) and low (treatment) elevation soil, to identify which vital rates drove differences in λ between high and lower elevation soils. In all cases, we calculated the sensitivities of λ to vital rates by perturbing vital rates by 0.001 for the IPM based on the mid-kernel (Caswell 2001). The sensitivities were multiplied by the differences in vital rate parameters between the treatment and the control to obtain the LTRE

contribution to λ for a given vital rate. We standardised LTREs for each temperature scenario and surrounding community identity to facilitate comparisons of the relative contribution of vital rates to changes in λ between community and warming treatments (Supplementary Methods).

Results

Effects of warming and novel species on population growth rate

Population growth rates (λ) decreased for all species when experiencing warming in combination with their current community (Fig. 2). Warming decreased λ by 0.07/°C on average across species (linear regression of λ on temperature), with stronger responses to warming for *T. badium* ($-0.16 \lambda/^\circ\text{C}$) than for *P. alpina*, *A. alpestris* and *C. scheuchzeri* (-0.03 , -0.05 and $-0.05 \lambda/^\circ\text{C}$ for *P. alpina*, *A. alpestris* and *C. scheuchzeri* respectively).

Interactions with novel species additionally suppressed λ by 0.11, 0.32, 0.12 and 0.06 on average for *P. alpina*, *A. alpestris*, *T. badium* and *C. scheuchzeri*, respectively, although these effects varied depending on warming level (Fig. 2). Across focal species, novel species had a larger impact on population growth at higher levels of warming ($\lambda -0.30$ on average across species at 4.85 °C warming; Fig. 2) than at lower levels of warming ($\lambda -0.20$ on average across species at 1.65 °C warming). The negative impact of novel species on λ was significant at 4.85 °C of warming for all species (marginally significant for *C. scheuchzeri*; $P = 0.07$) and additionally at 1.65 °C for *A. alpestris* and *T. badium*. Soil origin had no overall effect on λ of *P. alpina* and *C. scheuchzeri*, but λ values of *A. alpestris* and *T. badium* were higher when growing on high elevation soil ($\lambda -2.3$ and -0.42 for *A. alpestris* and *T. badium* respectively; Fig. S7).

Effects of warming and novel species on time to local extinction

Increasing warming caused exponential declines in predicted times to population extinction, and hence largest effects of warming from 1.65 to 3.05 °C (Fig. 3). *A. alpestris* and *T. badium* were predicted to persist under low levels of warming while interacting with current species, while predicted to go extinct at temperatures exceeding 1.65 °C. Novel species consequently had the strongest impact on predicted local extinction time for these species at low levels of warming, with populations predicted to go extinct when interacting with novel species under all warming levels (Fig. 3). At warming > 3 °C, novel species accelerated predicted extinction time, significantly so for three species at 4.85 °C, yet the relative magnitude of novel species effects was small.

Vital rate contributions to population growth with warming and novel species

Survival was the most important vital rate contributing to declines in λ when plants experienced warming in combination with current species, with recruitment also contributing substantially in *A. alpestris* and *T. badium* (Fig. 4). Growth for *P. alpina* and *T. badium* acted to increase λ under warming, whereas increasing seed production and flowering also buffered declines in λ for *A. alpestris* and *T. badium*.

Novel species in general had a negative effect on most vital rates, with the exception of recruitment success (Fig. 4, Fig. S8). Novel species had a pronounced negative effect on survival of *A. alpestris*, growth of *P. alpina* and growth, survival and reproduction of *T. badium*, and minimal effects on *C. scheuchzeri* (Fig. 4, Fig. S8). Differences in λ on lower vs. high elevation soil were driven by different vital rates, primarily by lower survival for *P. alpina* and *T. badium* and by lower reproduction for *A. alpestris* (Fig. S8). Where a positive effect of vital rates on λ under warming with current species was found, the effect was always smaller when growing with novel species (Fig. 4). In contrast, recruitment success was greater with novel species (excluding *C. scheuchzeri*, for which these data were not available), which buffered negative effects of warming (Fig. 4) and partially offset negative effects of novel species (Fig. S8) on λ .

Discussion

Despite over a century of climate warming, substantial local extinctions of mountain plants are still relatively rarely documented (Pauli et al., 2012; Wipf et al., 2013; Rixen & Wipf, 2017; Steinbauer et al., 2018). Our experiment suggests that, at least for some species, this ‘extinction debt’ can be explained by a combination of demographic inertia and lags in alpine plant replacement by novel species spreading upwards from lower elevation. While climate warming depressed population growth rates for all focal species, novel species had the most consistent impact on declines in population growth at high levels of warming (+4.85 °C). Nonetheless, because predicted extinction time decreases exponentially with the declining population growth rate, relative effects of novel species on extinction time were small at the highest level of warming. Indeed, we saw that impacts of novel species on predicted extinction time were greatest at lower levels of warming for two focal species, *A. alpestris* and *T. badium*, for which persistence under moderate warming (< 2 °C) was contingent on the presence of novel species. These results are in line with our hypotheses that the combination of interactions with novel species and simulated warming contribute more strongly to declines in population growth than warming alone, and that novel species can amplify the acceleration of local extinction risk of alpine plants faced by warming. In general, these results lead to the expectation that novel species establishment will have the greatest impact on populations whose growth rates are still close to replacement. Since the lowest level of warming simulated in this study is similar to the warming of 2.1 °C observed in Switzerland over the last 150 years (National Centre for Climate Services, 2018), we propose that lags in novel species establishment at high elevations might be an important explanation for extinction debt of some alpine plants up to now. However, with more substantial warming expected towards the end of this century, novel species effects will likely add little to direct effects of warming on rates of local extinction for our study species.

The impact of warming and the establishment of novel species on population growth varied for different focal species. As for many mountain plants (Dullinger et al., 2003; Lembrechts et al., 2017), all four focal species can occasionally be found at lower elevation in the study area in disturbed areas such as along roads and tracks. This can be partly explained by the steep terrain and correspondingly short dispersal distances, but also indicates that the species do have the potential to grow under warmer climates, especially when sheltered from competition. Moreover, the species that responded most negatively to warming (*T. badium*)

was never observed below approximately 1700 m. Also, the only focal species to be found occasionally at low cover in the 1750 and 1950 m sites, *P. alpina*, also showed very weak responses to community identity in these sites. Together, these observations suggest that outlier occurrences at the fringes of a species' distribution might contain information about their potential responses to changes in climate. Analyses involving a greater number of species are needed to understand whether species attributes might be useful to predict these responses (Estrada et al., 2016).

Species-specific responses to factors other than temperature that varied across the elevation gradient might also explain some of the observed variation in responses across our focal species. For instance precipitation also declines with decreasing elevation, although this is consistent with projections for climate change in Switzerland (National Centre for Climate Services, 2018), whereas elevational changes in UV radiation are considered to have negligible impacts on alpine plant growth (Körner, 2003). Differences in soil across elevation gradients can also affect potential responses to changing climate (Ford & HilleRisLambers, 2020). For two of our species, we also observed benefits in terms of λ for plants growing on alpine soil, compared to soil of the lower elevation sites (Fig. S7). This might have resulted from differences between soils in terms of their chemical, physical or biotic properties, for example due to an absence of beneficial or greater abundance of pathogenic soil microbiota in low elevation soils (van der Putten et al., 2013). However, different vital rates drove the responses of λ to low elevation soils and vegetation (Fig. S8). Therefore, while soils might have contributed to impacts of novel species on the performance of two of our focal plants, soil and vegetation effects acted at least partially independently. Finally, some of the variation we observed in effects of novel species might be explained by differences in the functional composition of background species at each site (Alexander et al., 2015). For example the notably small differences in effects of current and novel species on population growth at the 1750 m site could be related to the lower dominance of graminoids, and higher relative cover of lower-stature forbs, at this site (Fig. S3), since graminoids have previously been implicated as drivers of population declines of other alpine plants under warming (Klanderud & Totland, 2005; Olsen et al., 2016).

As we hypothesised, survival most consistently contributed to declining population growth under warming, although other vital rates were important in some species (Fig. 4). Survival has previously been shown to play an important role in determining the population growth of alpine plants under climate change (Olsen et al., 2016), where temperature-driven drought can have severe effects on mortality rates in high elevation plants (Orsenigo et al., 2014). In our experiment, temperatures in early July often reached 35 °C, whereas precipitation remained low during the same time period at the two lower sites. Drought stress during summer may therefore have led to increased mortality and declining population growth under simulated warming. Our findings suggest that monitoring mortality could provide a proxy for population trends in other species faced by climate change, and that conservation efforts might be most effectively invested in promoting adult survival (Toräng et al., 2010; Hylander & Ehrlén, 2013).

By transplanting focal plants to lower elevations, they were also exposed to more diverse and abundant pollinator communities (Arroyo et al., 1982; Totland, 2001), which they are

also expected to encounter as climate warms and pollinators migrate to higher elevations (Konvicka et al., 2003; Forister et al., 2010; Richman et al., 2020). Improved seed production of *A. alpestris* and *T. badium* under warming could therefore have arisen through a reduction of pollinator limitation, as well as direct effects of warming (but see Richman et al., 2020). Previous studies have also shown that initially positive effects of warming on some vital rates may stabilise or even increase population size, despite the deterioration of other vital rates (van Mantgem et al., 2009; Doak & Morris, 2010; Vilellas et al., 2015). The positive contributions through seed production, flowering and growth were, however, far from enough to outweigh the general decline in λ across all species that was driven by increasing mortality.

Consistent with previous studies (Alexander et al., 2015), we found that novel species from lower elevations suppressed the performance of alpine plants by decreasing growth, survival and flowering probability. Interestingly, however, recruitment was the only vital rate to show the opposite pattern, with less negative contributions to λ under warming when interacting with novel vs. with current species. Germination rate estimated at the beginning of the season (data not shown) did not differ substantially from recruitment success, indicating that germination, rather than the survival of seedlings during the growing season, was greater with novel species. A possible explanation for this is that the high density of tussock-forming graminoids and dwarf shrubs (Table S1, Fig. S3) and correspondingly thick litter and necromass layers reduce germination success in the high elevation community under warming (Pitelka et al., 1997; Graae et al., 2011). Few previous studies have quantified recruitment success of mountain plants under field conditions to understand its role in driving population-level responses to climate warming (but see Shevtsova et al., 2009; Cui et al., 2018), possibly because large sample sizes are needed to account for the generally low recruitment success (Körner, 2003; Graae et al., 2011). Our results should also be interpreted with caution, since recruitment in alpine plants can vary greatly across years (Diemer, 1992) and data obtained here only represented one season (2019). Nonetheless, they emphasise that recruitment should not be neglected in studies addressing plant community dynamics, as it may not only influence successful colonisation of new areas under warming (Pitelka and Plant Migration Workshop, 1997; Graae et al., 2009), but also contribute to population persistence as environments change.

Overall, our results show that when established at high densities, novel species can amplify negative effects of climate warming on resident plant populations. The increased species richness observed today on mountain summits (Steinbauer et al., 2018) and potentially also in lowland ecosystems (Vellend et al., 2013; Suggitt et al., 2019) thus likely reflects a transient stage that will be followed by increasing extinction under continued warming and as novel species increase in abundance. These predictions assume that evolutionary adaptation will not mediate local extinction risk and enable longer term persistence (Hoffmann & Sgrò, 2011). In evaluating this possibility, a demographic approach can reveal which vital rates are likely targets of selection from warming climate and novel species. Moreover, our experiment only simulated two extreme scenarios where alpine plants interact with current vs. novel species, whereas over time they will face a temporally dynamic community including both novel and current species (Alexander et al., 2018). Important questions still remain, including how quickly novel species can reach high density once

established, at what density they start to significantly impact resident species, and which species have the largest effect. These questions should be targets for future work, for example using experiments designed to estimate per capita effects of novel species under warming climate.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Data Availability Statement

Data used for analyses are archived in Dryad (<https://doi.org/10.5061/dryad.w3r2280q4>) and code used for analyses are archived in Zenodo (<https://doi.org/10.5281/zenodo.4555809>).

Data accessibility statement

Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository such as Dryad or Figshare and the data DOI will be included at the end of the article.

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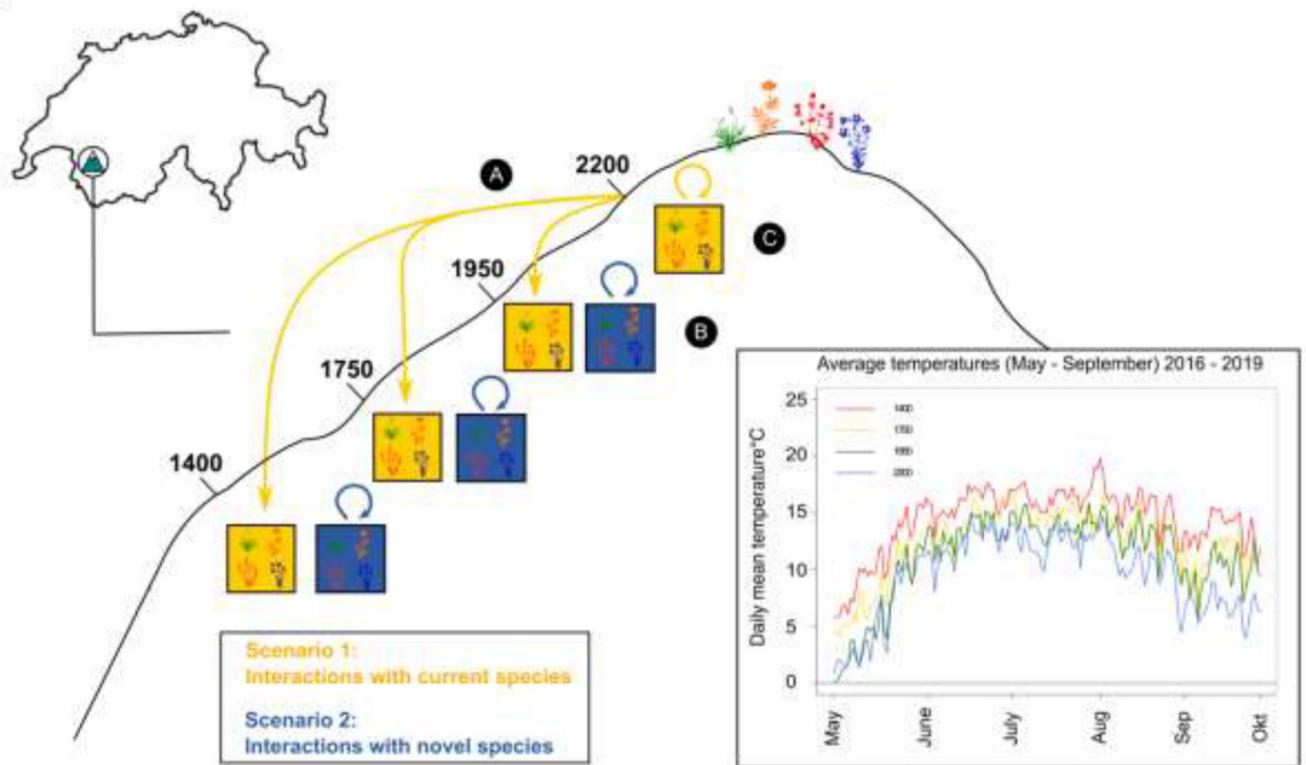


Fig. 1. Transplant experiment design.

Turfs from 2200 m containing plants and soil were transplanted to three lower elevation sites (1950, 1750, 1400 m) to simulate climate warming of, respectively, 1.65, 3.05 and 4.85 °C average growing season (May-September) temperatures during the experiment (2017-2019; inset) (a). By planting individuals of four alpine plants into the high elevation community turfs at the lower elevation sites, we tested the response to climate warming while individuals continue to interact with high elevation species currently found at 2200 m. At each of the low elevation sites, turfs containing local communities were also excavated and planted back into the site from which they came (b). By planting individuals into the low elevation communities, we tested their response to climate warming when interacting with novel species from low elevation. Individuals were transplanted into high elevation turfs and soil at 2200 m to evaluate the performance of individuals in their current environment (c)

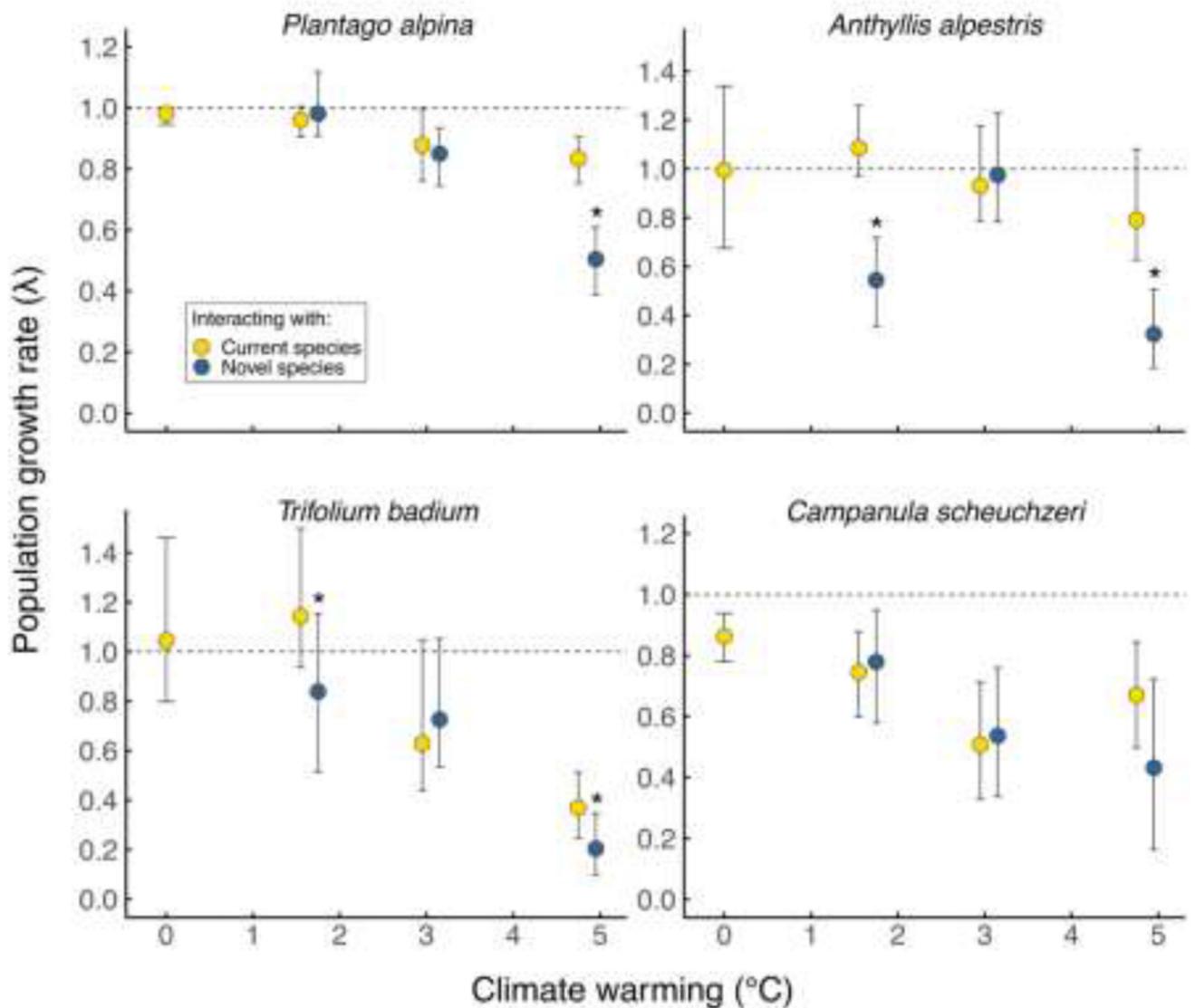


Fig. 2. Effects of warming and novel species on predicted population growth rate (λ). Estimates of λ from IPMs of four focal alpine species when growing with current or novel species across a temperature gradient simulated by transplantation from a high elevation (2200 m) to three lower elevation sites. Elevations are expressed as degrees of warming following transplantation (see Fig. 1). The dashed horizontal lines represent zero population growth (i.e. replacement). Error bars indicate 95% bias corrected confidence intervals based on 5000 bootstrapped λ values. Significant differences (*) between treatments were obtained from the pairwise comparisons of bootstrapped λ values (see Methods). $n = 50$ individuals per site/treatment/species/year before mortality

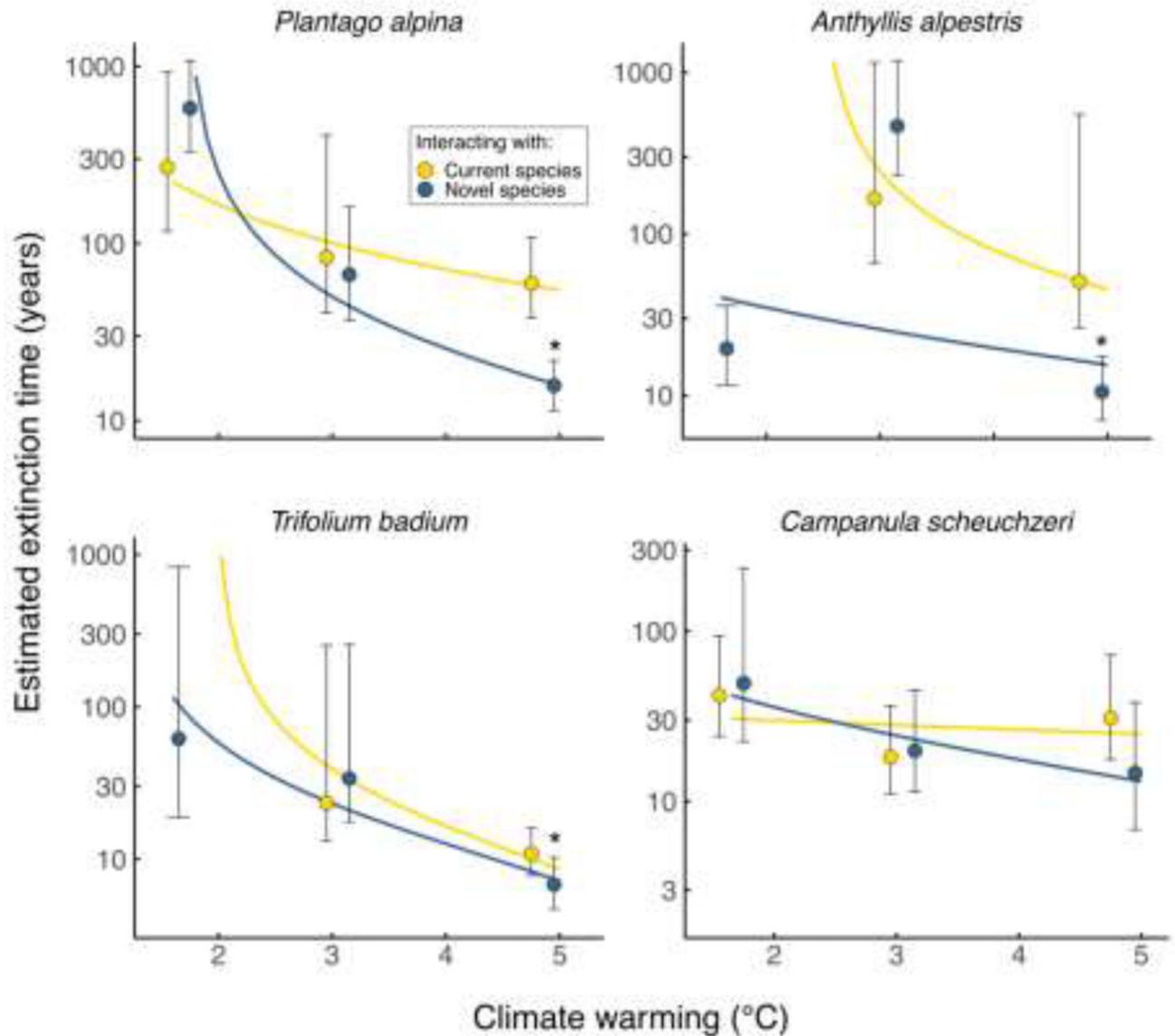


Fig. 3. Estimates of extinction time under warming with current or novel species.

Estimated time to extinction based on a population growth model (see Methods) assuming initial population sizes of 49 000, 147 000, 51 000 and 228 000 for *P. alpina*, *A. alpestris*, *T. badium* and *C. scheuchzeri* respectively. Predicted extinction times are shown for observed λ values (points) for focal plants experiencing different levels of climate warming and interacting either with current or novel species. Significant differences (*) were obtained from pairwise comparisons of 5000 predicted times to extinction obtained bootstrapped λ values. Trendlines indicate predicted extinction times from fitted values of linear regressions of λ on warming between 1.65 and 5 °C. Note the logarithmic scale of the y-axes

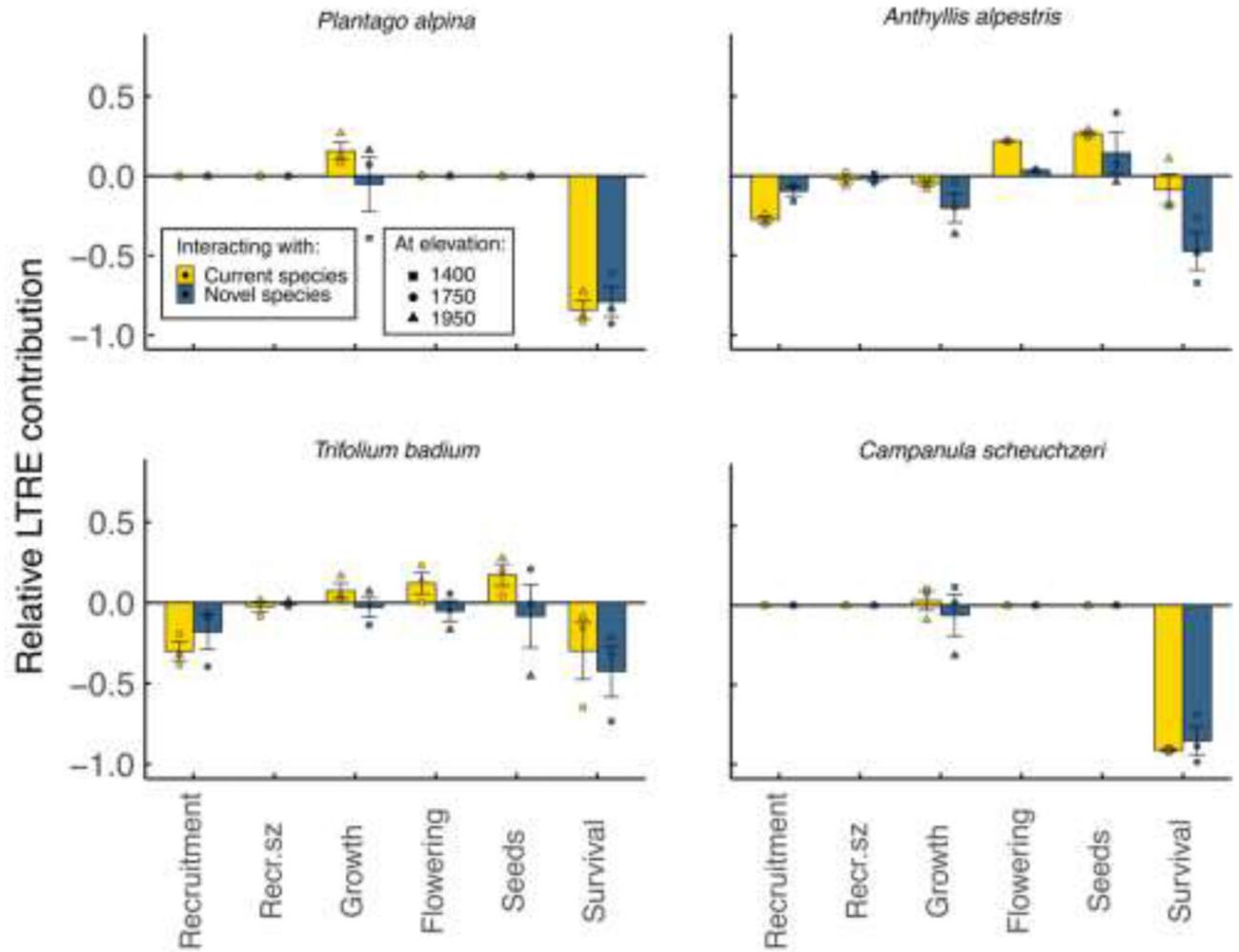


Fig. 4. Relative Life Table Response Experiment (LTRE) contributions of each vital rate to λ under warming and with novel species.

The figure shows average responses (\pm SE) to the surrounding community identities across warming treatments, with the relative LTRE contribution for each level of warming (elevation) shown by symbols