

Demographic and interaction lags govern the pace and outcome of plant community responses to 21st century climate change

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Abstract

Forecasting the trajectories of species assemblages in response to ongoing climate change requires quantifying the time lags in the demographic and ecological processes through which climate impacts species' abundances. Since experimental climate manipulations are typically abrupt, the observed species responses may not match their responses to gradual climate change. We addressed this problem by transplanting alpine grassland turfs to lower elevations, recording species' demographic responses to climate and competition, and using these data to parameterize community dynamics models forced by scenarios of gradual climate change. We found that shifts in community structure following an abrupt climate manipulation were not simply accelerated versions of shifts expected under gradual warming, especially when they missed the rise of species benefiting from moderate warming. Time lags in demography and species interactions controlled the pace and trajectory of changing species' abundances under simulated 21st century climate change, and thereby prevented immediate diversity loss.

Introduction

Climate change has already altered the distribution of species, the composition of communities, and the functioning of ecosystems around the world (Parmesan & Yohe 2003; Walther 2010). These changes are likely to accelerate, posing a growing threat to global biodiversity and ecosystem services (Urban 2015). While we have increasingly reliable forecasts of the trajectory of climate change under alternative greenhouse gas emission scenarios (Kirtman *et al.* 2013), we generally lack forecasts of the trajectory of ecosystem change under these climate scenarios (Klein *et al.* 2014; Urban *et al.* 2016). This is because when climate change is rapid, we do not expect the properties of ecosystems to be in equilibrium with their current climate. While species' physiology can respond almost immediately to changing climatic conditions, it takes time for demographic and ecological processes to translate physiological responses into changes in species' equilibrium abundances and distributions (Alexander *et al.* 2018). As a result, ecosystem change lags climate change. During this century of rapid warming, ecosystems globally are undergoing transient dynamics, approaching climate-driven equilibria which are themselves in continuous flux.

The pace and trajectory of ecosystem dynamics under climate change are shaped by time lags in demographic, ecological, and evolutionary processes. For example, long-lived individuals may persist at locations long after climate becomes unsuitable for recruitment (i.e., extinction debt; Dullinger *et al.* 2012), whereas, due to slow dispersal and demography, some species' ranges are still expanding into locations which became suitable after the end of the last glaciation (Johnstone & Chapin 2003; Svenning & Skov 2004). Ecological lags arise when species that initially benefit from a change in climate, later suffer when their competitors rise in abundance (Suttle *et al.* 2007). Finally, evolutionary lags may cause populations that initially decline to later recover once they adapt to their novel environment (Carlson *et al.* 2014). Understanding and quantifying these lags will be necessary to accurately forecast the impacts of climate change on the diversity and composition of ecosystems.

Current approaches to studying the biological impacts of climate change fail to quantify the processes underlying lags, and are thus insufficient to forecast how much and how fast ecosystems will change

over the coming decades. Space-for-time substitutions (e.g., climate niche models) rely on extrapolating current correlations between climate and species' distributions, assuming the two variables are (and will remain) in equilibrium (Elith & Leathwick 2009). By neglecting the role of lags (Alexander *et al.* 2018), space-for-time substitutions may at best inform us about the potential long-term equilibrium state of a community under a given climate (Elmendorf *et al.* 2015), but not about the rate or trajectory of change. Manipulative experiments can be used to expose species to the novel climatic and biotic conditions they might experience in the future (Alexander *et al.* 2015; Descombes *et al.* 2020), but necessarily impose abrupt changes in environmental conditions which do not reflect the more gradual trajectories of real climate change (De Boeck *et al.* 2015). Whether abrupt climatic changes simply lead to accelerated responses relative to what we would expect under gradual climate change, or instead lead to different transient trajectories or even different equilibrium outcomes, remains poorly understood. Moreover, since most experiments only last a few years, or decades at most, the results rarely reflect the equilibrium states we can expect under novel climates (Epstein *et al.* 2004). Indeed, the initial, short-term responses of plant communities to climate manipulations can be modified (Hollister *et al.* 2005; Andresen *et al.* 2016) or even reversed (Zhang *et al.* 2017) due to indirect effects of climate change mediated by changing species interactions (Suttle *et al.* 2007; Shi *et al.* 2015). These indirect effects can arise either from changes in the abundance (Suttle *et al.* 2007) or identity (Nomoto & Alexander 2021) of interacting species, or from changes in the nature of their interactions (Olsen *et al.* 2016). Despite their potential importance, lags in changing species interactions remain poorly understood and their impacts on community trajectories under climate change are rarely quantified.

Combining the complementary strengths of experiments and models can generate better informed forecasts of community dynamics under climate change (Kotta *et al.* 2019). Experiments can be used to quantify how climate affects species' demography and their interactions with other species. In turn, models of climate-dependent community dynamics, parameterized with the experimental data, can predict community responses to the trajectories of climatic change forecasted by general circulation models. The effect of time lags can then be quantified by comparing the trajectory of these responses

to those of a “no lag” simulated community that stays in equilibrium with its annual climatic conditions. Similar to mechanistic niche models (Briscoe *et al.* 2019), this approach is empirically challenging, since it requires exposing replicated communities to different climates and quantifying the effects on species’ demography and interactions. While not feasible in many communities, the compact turf structure and high species density of many alpine grasslands enables the transplantation of replicated, multi-species communities to lower elevations, where climatic and biotic conditions already resemble the conditions expected at alpine regions with future climate change (Tito *et al.* 2020).

Here, we use high-resolution maps of alpine plant community change when transplanted along an elevational gradient in the Swiss Alps to quantify climate’s impact on species’ demography and interactions with neighbors. The key innovation is that, while climate-induced changes in competitive population dynamics may involve multi-year time lags, these lags arise from climate effects on the demography and sensitivity to competition of individual plants which are measurable in a short-term experiment. With such experimental data, we parameterized models to project the dynamics of the community under alternative scenarios of 21st century climate change, and aimed to answer the following questions: (1) How will the diversity and composition of alpine plant communities respond to contrasting climate change scenarios? (2) How do responses to gradual climate change differ from responses to abrupt climate change typical of experimental manipulations? And (3) how does the combined effect of demographic and competitive lags affect the pace, trajectory, and outcome of community responses to climate change?

Materials and Methods

Transplant experiment

We conducted a whole-community transplant experiment along the south-facing slope of the Calanda mountain in the eastern Swiss Alps. The focal community was an alpine grassland on a ridge at 2050 m elevation, dominated by perennial forbs and grasses. At this elevation, the snow-free period

typically lasts from early May to early November. Plant growth peaks during summer (June to August), when the mean daily air temperature is 12.3 °C (mean from 2019 to 2020, see below).

We selected transplantation sites in pastures at five different elevations (1000, 1400, 1600, 1800, and 2000 m), which are between ca. 0 to over 5.5 K warmer than the focal site at 2050-m, based on the adiabatic lapse rate of temperature. This encompasses the range of climatic conditions that the focal plant community may experience over different scenarios of 21st century climate change (CH2018 2018). We selected the sites to resemble the focal site as much as possible other than in their climate and associated biotic environment. The sites are only a few kilometers apart and have similar topography, soil depth (> 20 cm), and calcareous bedrock.

In mid-October of 2016, we identified three transplant source areas within the focal meadow community at 2050 m, all within 220 m of each other, with similar community composition, and with low grass abundance. Across these three areas, we haphazardly selected 50, 1-m² turfs, avoiding rocky areas. We excavated turfs to a depth of ca. 15 cm and transplanted 10 to each elevation following a stratified random design. We lined the sides of the transplanted turfs with a root barrier to prevent encroachment from the surrounding vegetation. We also weeded recruits of lowland species from the turfs during subsequent plant community surveys.

After the summer of 2018, lush growth of the plants transplanted to the 1800-m site revealed that soil fertility at this site was much higher than at other sites, making it incomparable. We therefore selected a different site at the same elevation into which we transplanted 10 more 1-m² turfs from the same source sites in September 2018.

Climate along the elevational gradient

To measure climatic conditions along the elevational gradient, we deployed air temperature (DECAGON ECH₂O Temperature/RH) and soil moisture sensors (DECAGON ECH₂O TE Moisture/Temp/EC) at the five experimental sites from late May to early October in 2019 and 2020.

With these weather data, we fit models of each site's air temperature and soil moisture as a function of weather conditions at the nearby meteorological station in the city of Chur (weather data available from Swiss Federal Office of Meteorology and Climatology portal IDAWEB, <https://gate.meteoswiss.ch/idaweb/>). We then used those models to predict weather conditions at the different sites during the entire experimental period (details in Supporting Information 2.1.1.3).

Plant community surveys

To monitor community dynamics and quantify plant demography under climate change in a way that allowed us to parameterize models, we made detailed surveys of the spatial distribution of canopy cover of plant species in the transplanted turfs. To this end, soon after snowmelt in the spring after transplantation, we fixed a metallic grid subdivided into $0.1\text{ m} \times 0.1\text{ m}$ cells to each transplanted turf. Every summer for the next four years (2017 to 2020), we subdivided each grid cell into four $5\text{ cm} \times 5\text{ cm}$ quadrants and surveyed the inner 256 quadrants of each transplanted turf (leaving a 10-cm unsurveyed buffer from the turf edge). In each quadrant, we visually estimated the canopy cover of each species present using an ordinal scale (Table S1.2). We started surveys at the lowest site (1000 m) in mid-June and moved up the mountain over the summer in an attempt to map turfs at a similar stage of phenological development, close to the peak of the growing season at each site (Fig S1.3). While we tried to identify plants as close to the species level as possible, time constraints during the field season forced us to clump some species into groups varying in taxonomic hierarchy and functional meaning (Table S1.1). Hereafter, we use 'taxa' to refer to both individual species and the various groups used in the surveys.

Defining and tracking ramets to quantify demographic rates

All the shoots of a given taxon rooted in a single 25-cm^2 quadrant were considered a 'ramet' or 'individual' of that taxon. Shoots rooted in adjacent quadrants were counted as different ramets (creeping species in the genera *Thymus* and *Helianthemum*, which have multiple adventitious roots and are thus difficult to assign to a single location, were excluded from the analyses). Since most species in the community are clonal, ramets were the demographic units in subsequent analyses. We

used an algorithm to track ramets from one year to the next, accounting for potential small changes in location due to re-sprouting and observation error (see details Supporting Information 2.1.3). If a ramet could not be tracked into the following year, it was noted as a death. Ramets that could not be linked with previous-year ramets were classified as new recruits. The change in a surviving ramet's cover from one year to the next quantified its growth.

Ramets that were declared dead in the vicinity (< 5 cm) of areas of the turf affected by vole activity during winter and spring were excluded from the data used to fit demographic models. Also, approximately one quarter of each turf at the 2000-m and 1400-m sites was excluded due to physical disturbance by other measurements made on those turfs.

Climate- and density-dependent demographic models

We fit statistical models that quantified how a taxon's three demographic rates from the plant community surveys – survival, growth, and recruitment – related to climate and crowding from neighbors. Crowding was a distance-weighted sum of neighbors' cover, according to a Gaussian interaction kernel (Adler *et al.* 2010) parameterized so that most crowding was exerted by neighbors within a 10-cm radius. As detailed in the Supporting Information 1.3, the probabilities of ramet survival and recruitment were modeled as logistic hierarchical functions of temperature and crowding, while ramet growth was a linear hierarchical function of these variables. In the fitted models, a taxon's intrinsic demographic rates and response to crowding by conspecific and heterospecific neighbors were both functions of temperature. Specifically, the intrinsic survival rate was a sigmoidal function of temperature with an inflection point dependent on soil moisture (to reflect the role of aridity in warming-related plant mortality). Instead, the intrinsic growth rate was a Gaussian function of temperature with parameters determining the optimum temperature for growth and the thermal niche breadth. Finally, recruitment probability in each previously unoccupied quadrant was an increasing function of conspecific crowding (conspecifics being the source of new propagules) and a decreasing function of heterospecific crowding (reflecting competition).

We fit all the models following a Bayesian approach, using weakly regularizing priors (McElreath 2020) and sampling the posterior distribution of the parameters with adaptive Hamiltonian Monte Carlo, as implemented in Stan 2.17 (Carpenter *et al.* 2017; Stan Development Team 2018). We specified and analyzed the models in R (R Core Team 2019) using the package *rethinking* (version 2.0, McElreath 2020). We ran four chains per model, with 500 iterations for warmup and between 1000 and 5000 iterations for sampling, and assessed their mixing and convergence with the R-hat criterion. The R code for the exact model implementation is available in Supporting Information 2 and the entire workflow will be maintained on GitHub at <https://github.com/blockecology/lagging-meadows>.

We attempted to fit models for all 34 perennial, flowering plant taxa with at least 1,000 observations across all years and sites. Of these, we successfully fitted all models for 24 taxa (table S1.3, details about sampling problems in Supporting Information 1.4). To test whether the fitted models could reproduce the species' responses observed in the transplant experiment, we simulated the dynamics of these 24 taxa across experimental turfs using mean parameter values. With the 2017 turf maps as the starting point (from all elevations but 1800 m), we projected three years of community dynamics under the simulated time series of weather conditions and compared the predicted versus observed log-transformed ratio of final to initial cover of each taxon in each turf (Fig. S1.4; turfs from the 1800-m site were excluded from this comparison since they were transplanted until the Autumn of 2018 and first mapped the following summer). Downstream simulations only included the 11 taxa for which the sum of squared residuals from our model predictions was 80% or less of that from a null model expecting no changes in cover. These were generally the most abundant taxa in the community, and together account for 44 % of total cover across years and experimental turfs. We compared the trajectories of observed and predicted dynamics of these 11 taxa in different turfs with a Principal Coordinate Analysis based on Euclidean distances using the R package *ecodist* (Goslee & Urban 2007), and compared the trajectories of taxon diversity with Shannon index ($H' = -\sum_{i=1}^S p_i \cdot \ln(p_i)$), where p_i is the relative cover of taxon i and S is the total number of taxa).

Climate change scenarios

We used the CH2018 climate change scenarios for Switzerland, which are based on downscaling of EURO-CORDEX climate projections under three contrasting greenhouse gas scenarios (or Representative Concentration Pathways, RCP): RCP2.6, RCP4.5, and RCP8.5 (CH2018 Project Team 2018), corresponding to optimistic, realistic, and worst-case climate futures, respectively. We used scenarios for the Chur weather station (i.e., the nearest station to our experimental sites) to predict mean summer temperature at our 2000 m study site throughout the century (details in Supporting Information 1.7).

Projecting community dynamics with an individual-based model

Having parameterized functions describing how species' demography depended on climate and on interactions with neighbors, we used those functions to project the demographic fate of individual ramets (and the emergent community dynamics) under different scenarios of climate change (details in Supporting Information 1.8).

To isolate the effects of climate change on community dynamics from potential side effects of the experimental manipulation or imprecision in model descriptions of demography, we first simulated community dynamics under constant climatic conditions (i.e., mean summer temperature at the 2000-m site between 2017 and 2020) allowing the abundances of each taxon to quasi-equilibrate (defined as either a total cover growth rate < 0.05 or a total cover change $< 320 \text{ cm}^2$, equivalent to 0.5 % of turf total area, between two subsequent years). This quasi-equilibrium community was the starting point of our simulations of community dynamics under future climate change.

Using climate time series corresponding to different RCP scenarios, we forecasted community dynamics from 2017 to 2098. At every time step, we recorded the diversity of the simulated community with Shannon's index. To visualize the trajectories of community dynamics under the different climate change scenarios, we conducted a Principal Coordinates Analysis based on Euclidean distances.

To compare the trajectories of community responses to gradual change versus the stepwise change simulated by most climate change experiments, we ran simulations of community dynamics under climate conditions that from the beginning of the simulations (after the communities equilibrated to current climate) had the same mean and variance as conditions expected between 2088 and 2098 under the RCP4.5 scenario.

Finally, to assess the degree to which the trajectories of community change depend on the combined effects of demographic and competitive lags, we ran additional simulations with no such lags. In these simulations, we let the community equilibrate with the climatic conditions experienced each year (using the same quasi-equilibrium condition as in the pre-climate change simulations) before projecting the next time step.

Results

Reproducing responses to experimental climate change with demographic models

The cover of most taxa declined sharply after transplantation to the lowest site (where summers are *ca.* 5°C warmer than at the original elevation), but responses to moderate climate change were more variable (Fig. S1.4). While some taxa declined monotonically with increasing warming (e.g., *Vaccinium vitis-idaea* and *Androsace chamaejasme*), others benefitted when transplanted to intermediate elevations (e.g., *Alchemilla xanthochlora* and *Potentilla aurea*). Our individual-based model simulations of community dynamics predicted taxa's observed cover changes with varying success (Fig. S1.4), but broadly reproduced observed changes in community structure and diversity among the subset of 11 taxa which were included in simulations of dynamics under future climate change (Fig. 1).

Simulated responses to 21st century climate change

We projected community dynamics under the climate change trajectories expected at the 2000-m site (near the elevation of the original community) under different RCP scenarios. Under all climate

change scenarios (RCP 2.6, 4.5, and 8.5), mean summer temperatures at 2000 m increase only modestly during the first two decades of simulations. After year 2040, warming differences between scenarios become clear. While temperature stabilizes after mid-century in RCP 2.6, warming continues throughout the century in RCP 4.5 and even more rapidly in RCP 8.5 (Fig 2A). These different rates and magnitudes of warming resulted in contrasting trajectories of species diversity (Fig. 2B). After an initial decline during the first half of the century in all scenarios, diversity stabilized in RCP 2.6 but rebounded to nearly its initial levels in RCP 4.5. Since our simulations did not include immigration, this diversity rebound was driven solely by increasing evenness of species abundances (mainly due to the mid-century rise of *Alchemilla xanthochlora*). The rebound also happened in RCP 8.5, albeit nearly 30 years later than in RCP 4.5, and it was followed by a precipitous decline towards the end of the century.

Species compositional change followed a common trajectory for all three warming scenarios, with the scenarios differing in how far they moved along that trajectory (Fig. 2C). Most (80.2 %) of the variation in community structure across time in the different simulations was captured by the first axis of the Principal Coordinates Analysis. This axis was positively correlated with the abundance of *Alchemilla xanthochlora*, which increased with warming (Fig 2C). Thus, the severity of warming scenarios dictated how far simulated communities moved towards the positive side of the first ordination axis. In contrast, movement along the second ordination axis was not monotonic. Instead, under modest to moderate warming, simulated communities moved towards more positive values along the second ordination axis, but this trend eventually reversed under the severe warming of the second half of the century in scenario RCP 8.5 (Fig. 2C, to better visualize the trajectories through time, see interactive results in [Supporting Material 6](#)).

A closer look at the dynamics of different taxa sheds light on the nature of these contrasting community trajectories (Fig. 3). First of all, our models did not predict stable community dynamics under current climatic conditions. Thus, some taxa went completely extinct during the pre-climate change burn-in period (*Leontodon* Group), or soon after starting the climate change simulations

(*Androsace chamejasme*), while others increased sharply in abundance (namely *Anthyllis vulneraria*, *Soldanella alpina* and *Vaccinium vitis-idaea*, Fig. S1.5). After the equilibrating burn-in period, moderate warming till mid-century (RCP 2.6) led to minor changes in community structure, namely the extinction of *Viola calarata* by mid-century, and a gradual decline in the cover of *Vaccinium* and *Alchemilla xanthochlora*. In contrast, warming unabated throughout the century (RCP 4.5) began with similar trends as RCP 2.6, but eventually reverses *Alchemilla*'s declining trend, and accelerates *Vaccinium*'s. More severe warming (RCP 8.5) led to a faster rise in *Alchemilla* after 2050 and to the synchronous sharp decline of the initially dominant legume *Anthyllis vulneraria*. Moreover, *Potentilla aurea*, which benefitted from moderate warming, declined towards the end of the century in RCP 8.5 after nearly five decades of increasing cover.

Simulated responses to gradual and abrupt climate change

When we projected community dynamics following the common experimental approach of a stepwise change to RCP 4.5 end-of-century climate, the community changed more rapidly than predicted under a gradual approach to the same climate endpoint (Fig. 4). More surprisingly, these two trajectories to RCP 4.5 end-of-century climate also differed in their species compositional endpoint. Stepwise change led to a rapid rise in the cover of *Alchemilla*, which precipitated a decline in the cover of taxa which would have otherwise remained abundant throughout the century, such as *Anthyllis vulneraria*, *Potentilla aurea* and *Soldanella alpina* (cf. solid and dashed orange lines, Fig. 3). This also resulted in a slower, but constant, diversity decline following stepwise warming, as opposed to a faster initial decline followed by a rebound under gradual warming (Fig. 4B).

Combined effects of demographic and competitive lags

Demographic and competitive lags had a profound influence on not only the timescale but also the compositional endpoint of community responses to climate change (Fig. 4). Namely, during the first (and cooler) decade of simulated community dynamics without demographic and competitive lags, the relatively thermophilic *Alchemilla* went extinct. This prevented its eventual rise to dominance, as seen when lags enabled it to persist through the initial cooler period and into warmer conditions later

in the century. Reduced lags also precipitated the extinction of *Viola*, *Antennaria*, and *Carex* Group, although this had a much smaller influence on future dynamics. Later in the century, as temperatures continued to rise, removing lags led to a much faster decline in the cover of *Vaccinium* and *Soldanella*, species intolerant of the warmer climate. These amplified responses of species to climate in the absence of lags led to a sharper decline in diversity during the first two decades of climate change simulations, which never completely recovered (Fig. 4B).

Discussion

Transplanting alpine plant communities to lower elevations, where environmental conditions resemble those expected in the alpine zone in the coming decades, led to large, non-linear changes in community structure and diversity. Despite a tendency for errors to propagate across time steps in projections of community dynamics (Adler *et al.* 2010), our simulations based on demographic models reproduced the trajectories of the community-level changes observed during the experiment (Fig. 1), as well as the taxon-level cover dynamics of most dominant forbs. Assuming that these taxa are representative of the rest of the community, our experimentally parameterized models of community dynamics offer an unprecedented tool to explore the trajectory of community dynamics under future climate change scenarios. Overall, our simulations demonstrate that (1) the fate of alpine community diversity and composition is tightly linked to the severity of climate change over the coming decades, (2) responses to abrupt climate manipulations shortcut transient community trajectories expected under gradual climate change, with lasting consequences and (3) demographic and interaction lags govern the pace, trajectory, and even the outcome of community responses to climate change.

Severe warming during the second half of the 21st century expected under worst-case scenarios of climate change (e.g., RCP 8.5) could profoundly reshape patterns of plant diversity in mountains (Engler *et al.* 2011). According to climate niche modeling, such a warming scenario could cause nearly half of European mountain plant species to lose 80% of their ranges by the end of the century

(Engler *et al.* 2011). Consistent with these predictions, our projections of local community dynamics under RCP 8.5 revealed a sharp loss of local species diversity by the end of the century (Fig. 2B), with most taxa either extinct or declining towards extinction (Fig. 3, Dullinger *et al.* 2012). However, while a recent space-for-time substitution study found that most species in high latitude communities are likely to face dangerous warming around 2050 (Trisos *et al.* 2020), we found that the timing of population decline varied by multiple decades across taxa in this alpine community (Fig. 3). Some of this variation could emerge from taxon-specific lags in demographic and ecological processes, which impact the timing of population dynamic responses to climate change (Dullinger *et al.* 2012; Alexander *et al.* 2018).

While stepwise climate manipulations can reveal how species' demography and ecological interactions respond to future conditions, our simulations show that they are prone to mischaracterizing the trajectory of non-monotonic population dynamics (Fig. 3 and Fig S.2). How prone, however, depends on the mechanism behind the non-monotonic dynamics. If a species' demographic performance peaks at intermediate levels of warming, gradual warming may lead to an initial increase in the species' abundance followed by a decline once the optimal temperature is surpassed, whereas stepwise warming beyond the optimal temperature would lead to an immediate decline (e.g., *Soldanella alpina* in our simulations, Fig. 3G and Fig. S5.3). Given that the growth of alpine species often increases with warming only until water becomes limiting (Dolezal *et al.* 2020), this situation might be common in experiments imposing severe stepwise warming. Instead, if the initial population trend is reversed due to lagged changes in the abundance of competitors (Suttle *et al.* 2007), stepwise manipulations could detect the non-monotonic trajectory (as long as dynamics are followed for enough time). In our simulations, *Potentilla aurea* exemplified this situation: its cover increased immediately after stepwise change, but later decreased due to competition with the increasing *Alchemilla xanthochlora* (Fig. 3). Nonetheless, our simulations show that community dynamics following an abrupt change in climate can take multiple decades to stabilize (Fig. 4). Thus, experiments may give useful clues as to the direction of community responses to climate change, but

not about their long-term equilibria, at least in communities of long-lived organisms where demographic and interaction lags can be particularly strong (Duncan 2021).

We have shown that beyond delaying responses to climate change, demographic and competitive lags can alter the trajectory and, under special circumstances, even the outcome of responses. In our simulations, lags buffered the decline of *Alchemilla xanthochlora* during the first decades of relatively cool climate, preventing it from going extinct (Fig. 3A) and thereby completely altering future community trajectories and their eventual endpoint (Fig. 4A). While this result might stem partly from our models underestimating *Alchemilla*'s performance under cold climate (Fig. S1.4), demographic lags are essential for populations to persist through periods of unfavourable conditions (Warner & Chesson 1985). Lags also delayed the extinction of other taxa by multiple decades (Fig. 3), thereby generating an extinction debt by mid-century (Dullinger *et al.* 2012). Indeed, long-lived perennial species, like those in our simulations, are typically buffered from inter-annual variability in weather conditions (Morris *et al.* 2008; Compagnoni *et al.* 2021), and this tends to stabilize the diversity of perennial communities (Adler *et al.* 2010).

Several caveats need to be considered when interpreting our results. First, by fencing out cows from the experimental sites, we altered the normal grazing regime. Thus, our data reflect the dynamics of alpine plant communities in a warmer future, albeit one without cows. Still, because cows were excluded at all sites, and climate differed across these sites, our models do effectively isolate climate effects on species' demography and interactions. Second, our approach depends on projecting an individual based model forward in time. And though the model does a reasonable job at predicting three years of observed change in the community, how well it does over multiple decades is uncertain. This uncertainty, however, comes with all approaches predicting species' responses to end of century climate change.

We conclude by highlighting important questions for future research. First, phenomenological models like the ones we used to describe the climate-dependency of species' demography and interactions do

not reveal the underlying mechanisms. Thus, more mechanistic modeling approaches based on eco-physiology could provide complementary insights (e.g., Trugman *et al.* 2018). Second, this study focused on alpine community dynamics driven by the changing abundances of the current resident species of the alpine. An important goal of future research is to compare the timescale of the arrival of novel competitors to the timescale of the dynamics of the resident species. The fast community change we observed in our experiment and in our simulations, despite the influence of demographic and competitive lags, suggests that alpine plant communities may experience substantial change even before novel competitors arrive. An important but largely untested question, asks how the types of changes to the alpine communities we forecast here will influence the arrival of novel competitors from lower elevation.

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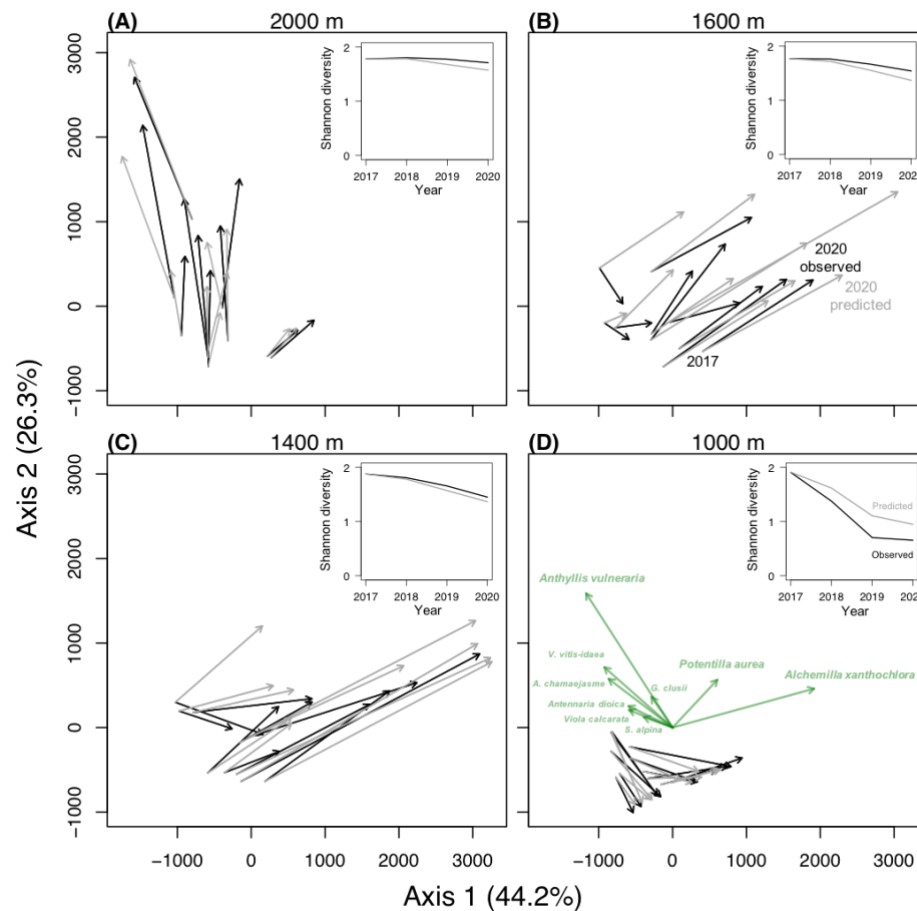


Figure 1. Trajectories of alpine plant communities transplanted to different elevations in the Swiss Alps to simulate climate change. The communities originated from a site at 2050 m and were transplanted to sites at (A) 2000 m, (B) 1600 m, (C) 1400 m, or (D) 1000 m (which correspond to approximately 0, 2.2, 3.3, and 5.5 °C of warming, respectively). Panels show a Principal Coordinates Analysis ordination based on Euclidean distances of all observed and simulated turfs from 2017 to 2020. The arrows show the observed (black) and predicted (gray) changes in community structure of each turf. In panel D, the thicker green arrows starting from the origin show the taxa for which the first two ordination axes explain at least 20% of their cover variation. The inset plots within each panel show the mean observed (black) and predicted (gray) Shannon diversity across the ten turfs transplanted to each elevation.

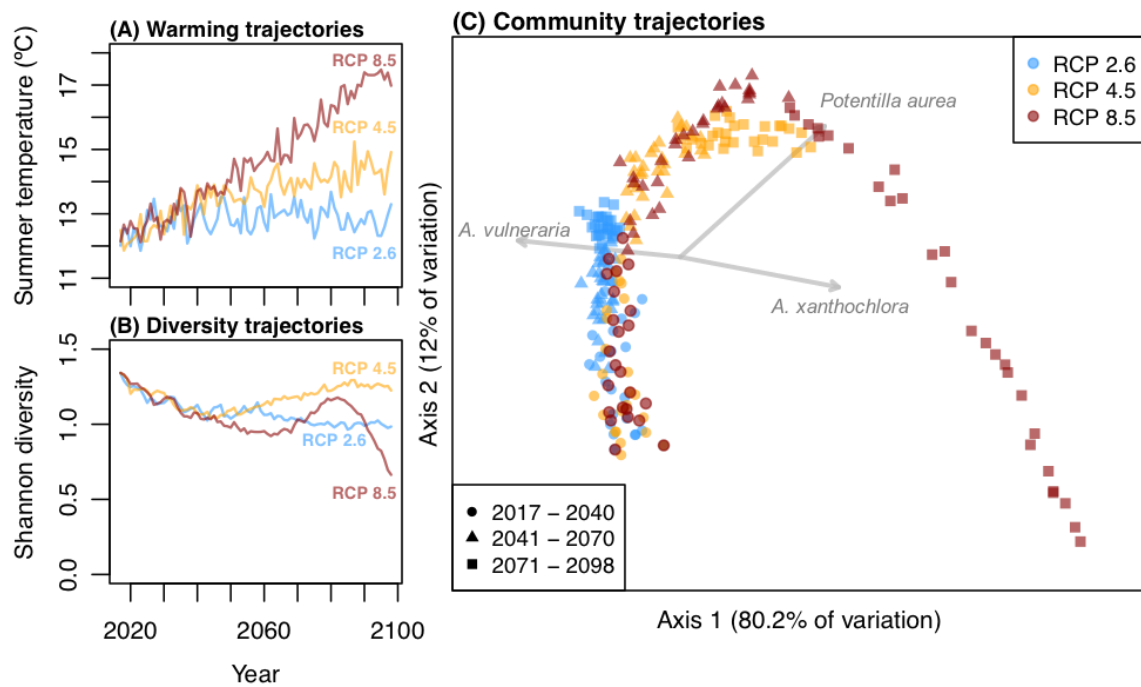


Figure 2. Trajectories of alpine plant community responses to contrasting climate change scenarios for the 21st century. (A) Depending on future greenhouse gas emissions, this region of the Alps could experience contrasting climate futures, warming from 0.5 (in RCP 2.6, solid line) to 2.3 (in RCP 4.5, dashed line) and potentially even 4.8 °C (in RCP 8.5, dotted line) by the end of the century relative to the experimental period (2017 to 2020). (B) Increases in temperature under the contrasting climate change scenarios led to non-monotonic changes in the diversity of the simulated alpine community. (C) Principal coordinates ordination based on Euclidean distances showing the trajectory of simulated alpine communities under the different climate change scenarios between years 2017 and 2098 (each point corresponds to a year in one scenario). The gray arrows are vectors of taxa for which ordination axes explained more than 90% of variation in abundance through time.

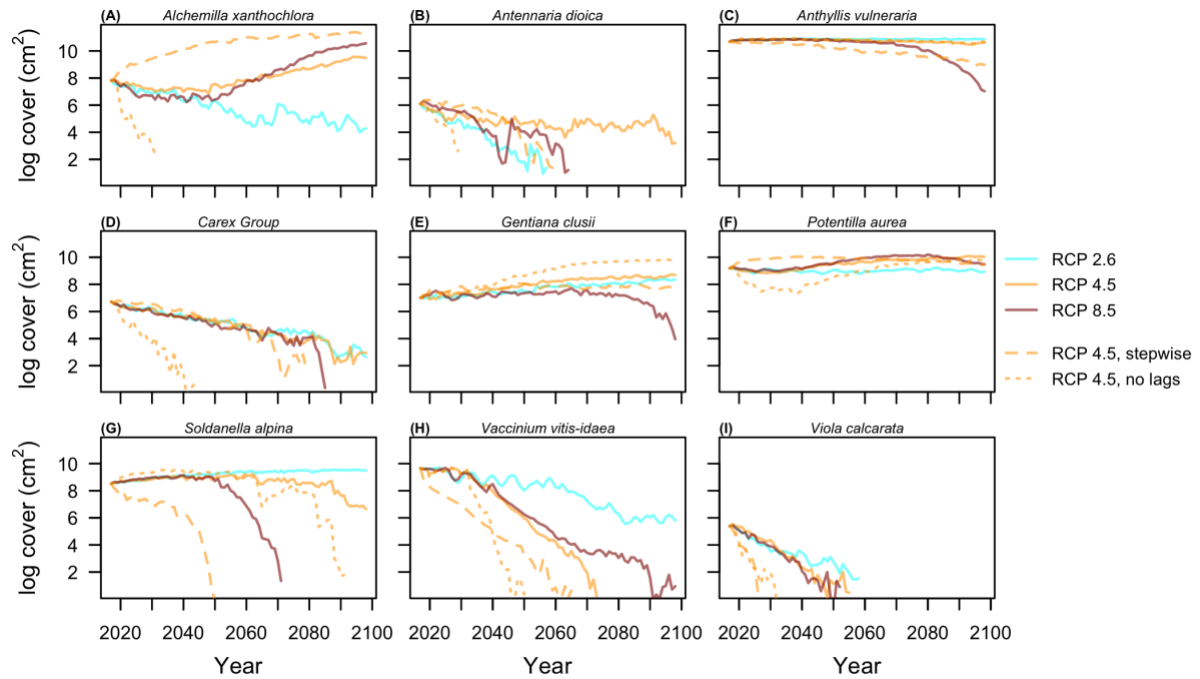


Figure 3. Cover dynamics of alpine plant species under contrasting climate change scenarios RCP 2.6 (cyan), RCP 4.5 (purple), and RCP 8.5 (red). Lines show the natural logarithm of the sum of the cover of all ramets in each year of the climate change simulations. The trajectories of summer temperatures in the region under these scenarios are shown in figure 2A. For scenario RCP 4.5, dotted lines show dynamics with a reduced influence of demographic and competitive lags, while dashed lines show dynamics following a stepwise change in climate to conditions expected by the end of the century (mean conditions between 2088 and 2098).

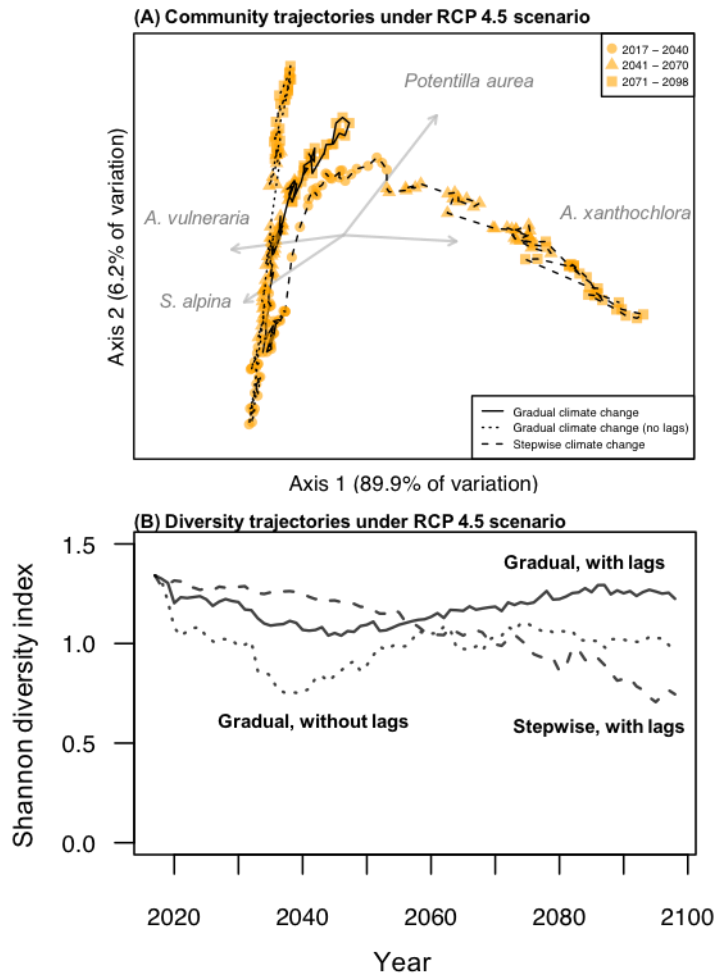


Figure 4. Alpine community responses to gradual vs stepwise climate change. (A) Principal coordinates analysis ordination based on Euclidean distances showing the trajectory of simulated alpine communities under stepwise (dashed line) vs gradual climate change (RCP 4.5), with either full (solid line) or reduced (dotted line) influence of demographic and competitive lags. Each point corresponds to a year. The gray arrows are vectors of taxa for which ordination axes explained more than 90% of variation in abundance through time. (B) Trajectories of Shannon diversity based on taxa's total cover in simulated communities.