

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

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21

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24 survey vegetation with input from SB and JML. SB and MJM collected and processed the data. SB
25 analyzed the data and lead the writing of the manuscript, with input from all coauthors.

26

27 **Data availability statement:** All code and data needed to reproduce our results will be deposited in
28 Zenodo upon acceptance of the manuscript.

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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.

57 **Introduction**

58 Climate change has already altered the distribution of species, the composition of communities, and
59 the functioning of ecosystems around the world (Parmesan & Yohe 2003; Walther 2010). These
60 changes are likely to accelerate, posing a growing threat to global biodiversity and ecosystem services
61 (Urban 2015). While we have increasingly reliable forecasts of the trajectory of climate change under
62 alternative greenhouse gas emission scenarios (Kirtman *et al.* 2013), we generally lack forecasts of
63 the trajectory of ecosystem change under these climate scenarios (Klein *et al.* 2014; Urban *et al.*
64 2016). This is because when climate change is rapid, we do not expect the properties of ecosystems to
65 be in equilibrium with their current climate. While species' physiology can respond almost
66 immediately to changing climatic conditions, it takes time for demographic and ecological processes
67 to translate physiological responses into changes in species' equilibrium abundances and distributions
68 (Alexander *et al.* 2018). As a result, ecosystem change lags climate change. During this century of
69 rapid warming, ecosystems globally are undergoing transient dynamics, approaching climate-driven
70 equilibria which are themselves in continuous flux.

71

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

82

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

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

106

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

113 to those of a “no lag” simulated community that stays in equilibrium with its annual climatic
114 conditions. Similar to mechanistic niche models (Briscoe *et al.* 2019), this approach is empirically
115 challenging, since it requires exposing replicated communities to different climates and quantifying
116 the effects on species’ demography and interactions. While not feasible in many communities, the
117 compact turf structure and high species density of many alpine grasslands enables the transplantation
118 of replicated, multi-species communities to lower elevations, where climatic and biotic conditions
119 already resemble the conditions expected at alpine regions with future climate change (Tito *et al.*
120 2020).

121

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

134

135 **Materials and Methods**

136 *Transplant experiment*

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

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

142

143 We selected transplantation sites in pastures at five different elevations (1000, 1400, 1600, 1800, and
144 2000 m), which are between ca. 0 to over 5.5 K warmer than the focal site at 2050-m, based on the
145 adiabatic lapse rate of temperature. This encompasses the range of climatic conditions that the focal
146 plant community may experience over different scenarios of 21st century climate change (CH2018
147 2018). We selected the sites to resemble the focal site as much as possible other than in their climate
148 and associated biotic environment. The sites are only a few kilometers apart and have similar
149 topography, soil depth (> 20 cm), and calcareous bedrock.

150

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

158

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

163

164 *Climate along the elevational gradient*

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

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

173

174 *Plant community surveys*

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

189

190 *Defining and tracking ramets to quantify demographic rates*

191 All the shoots of a given taxon rooted in a single 25-cm² quadrant were considered a 'ramet' or
192 'individual' of that taxon. Shoots rooted in adjacent quadrants were counted as different ramets
193 (creeping species in the genera *Thymus* and *Helianthemum*, which have multiple adventitious roots
194 and are thus difficult to assign to a single location, were excluded from the analyses). Since most
195 species in the community are clonal, ramets were the demographic units in subsequent analyses. We

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

201

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

206

207 *Climate- and density-dependent demographic models*

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

223

224 We fit all the models following a Bayesian approach, using weakly regularizing priors (McElreath
225 2020) and sampling the posterior distribution of the parameters with adaptive Hamiltonian Monte
226 Carlo, as implemented in Stan 2.17 (Carpenter *et al.* 2017; Stan Development Team 2018). We
227 specified and analyzed the models in R (R Core Team 2019) using the package *rethinking* (version
228 2.0, McElreath 2020). We ran four chains per model, with 500 iterations for warmup and between
229 1000 and 5000 iterations for sampling, and assessed their mixing and convergence with the R-hat
230 criterion. The R code for the exact model implementation is available in Supporting Information 2 and
231 the entire workflow will be maintained on GitHub at <https://github.com/blockecology/lagging->
232 meadows.

233

234 We attempted to fit models for all 34 perennial, flowering plant taxa with at least 1,000 observations
235 across all years and sites. Of these, we successfully fitted all models for 24 taxa (table S1.3, details
236 about sampling problems in Supporting Information 1.4). To test whether the fitted models could
237 reproduce the species' responses observed in the transplant experiment, we simulated the dynamics of
238 these 24 taxa across experimental turfs using mean parameter values. With the 2017 turf maps as the
239 starting point (from all elevations but 1800 m), we projected three years of community dynamics
240 under the simulated time series of weather conditions and compared the predicted versus observed
241 log-transformed ratio of final to initial cover of each taxon in each turf (Fig. S1.4; turfs from the
242 1800-m site were excluded from this comparison since they were transplanted until the Autumn of
243 2018 and first mapped the following summer). Downstream simulations only included the 11 taxa for
244 which the sum of squared residuals from our model predictions was 80% or less of that from a null
245 model expecting no changes in cover. These were generally the most abundant taxa in the community,
246 and together account for 44 % of total cover across years and experimental turfs. We compared the
247 trajectories of observed and predicted dynamics of these 11 taxa in different turfs with a Principal
248 Coordinate Analysis based on Euclidean distances using the R package *ecodist* (Goslee & Urban
249 2007), and compared the trajectories of taxon diversity with Shannon index ($H' = -\sum_{i=1}^S p_i * \ln(p_i)$,
250 where p_i is the relative cover of taxon i and S is the total number of taxa).

251

252 *Climate change scenarios*

253 We used the CH2018 climate change scenarios for Switzerland, which are based on downscaling of
254 EURO-CORDEX climate projections under three contrasting greenhouse gas scenarios (or
255 Representative Concentration Pathways, RCP): RCP2.6, RCP4.5, and RCP8.5 (CH2018 Project Team
256 2018), corresponding to optimistic, realistic, and worst-case climate futures, respectively. We used
257 scenarios for the Chur weather station (i.e., the nearest station to our experimental sites) to predict
258 mean summer temperature at our 2000 m study site throughout the century (details in Supporting
259 Information 1.7).

260

261 *Projecting community dynamics with an individual-based model*

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

266

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

274

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

280

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

286

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

292

293 **Results**

294 *Reproducing responses to experimental climate change with demographic models*

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

304

305 *Simulated responses to 21st century climate change*

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

308 change scenarios (RCP 2.6, 4.5, and 8.5), mean summer temperatures at 2000 m increase only
309 modestly during the first two decades of simulations. After year 2040, warming differences between
310 scenarios become clear. While temperature stabilizes after mid-century in RCP 2.6, warming
311 continues throughout the century in RCP 4.5 and even more rapidly in RCP 8.5 (Fig 2A). These
312 different rates and magnitudes of warming resulted in contrasting trajectories of species diversity (Fig.
313 2B). After an initial decline during the first half of the century in all scenarios, diversity stabilized in
314 RCP 2.6 but rebounded to nearly its initial levels in RCP 4.5. Since our simulations did not include
315 immigration, this diversity rebound was driven solely by increasing evenness of species abundances
316 (mainly due to the mid-century rise of *Alchemilla xanthochlora*). The rebound also happened in RCP
317 8.5, albeit nearly 30 years later than in RCP 4.5, and it was followed by a precipitous decline towards
318 the end of the century.

319

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

331

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

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

346

347 *Simulated responses to gradual and abrupt climate change*

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

357

358 *Combined effects of demographic and competitive lags*

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

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

370

371

372 **Discussion**

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

387

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

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

401

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

419 not about their long-term equilibria, at least in communities of long-lived organisms where
420 demographic and interaction lags can be particularly strong (Duncan 2021).
421

422 We have shown that beyond delaying responses to climate change, demographic and competitive lags
423 can alter the trajectory and, under special circumstances, even the outcome of responses. In our
424 simulations, lags buffered the decline of *Alchemilla xanthochlora* during the first decades of relatively
425 cool climate, preventing it from going extinct (Fig. 3A) and thereby completely altering future
426 community trajectories and their eventual endpoint (Fig. 4A). While this result might stem partly from
427 our models underestimating *Alchemilla*'s performance under cold climate (Fig. S1.4), demographic
428 lags are essential for populations to persist through periods of unfavourable conditions (Warner &
429 Chesson 1985). Lags also delayed the extinction of other taxa by multiple decades (Fig. 3), thereby
430 generating an extinction debt by mid-century (Dullinger *et al.* 2012). Indeed, long-lived perennial
431 species, like those in our simulations, are typically buffered from inter-annual variability in weather
432 conditions (Morris *et al.* 2008; Compagnoni *et al.* 2021), and this tends to stabilize the diversity of
433 perennial communities (Adler *et al.* 2010).
434

435 Several caveats need to be considered when interpreting our results. First, by fencing out cows from
436 the experimental sites, we altered the normal grazing regime. Thus, our data reflect the dynamics of
437 alpine plant communities in a warmer future, albeit one without cows. Still, because cows were
438 excluded at all sites, and climate differed across these sites, our models do effectively isolate climate
439 effects on species' demography and interactions. Second, our approach depends on projecting an
440 individual based model forward in time. And though the model does a reasonable job at predicting
441 three years of observed change in the community, how well it does over multiple decades is uncertain.
442 This uncertainty, however, comes with all approaches predicting species' responses to end of century
443 climate change.
444

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

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

457

458

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467

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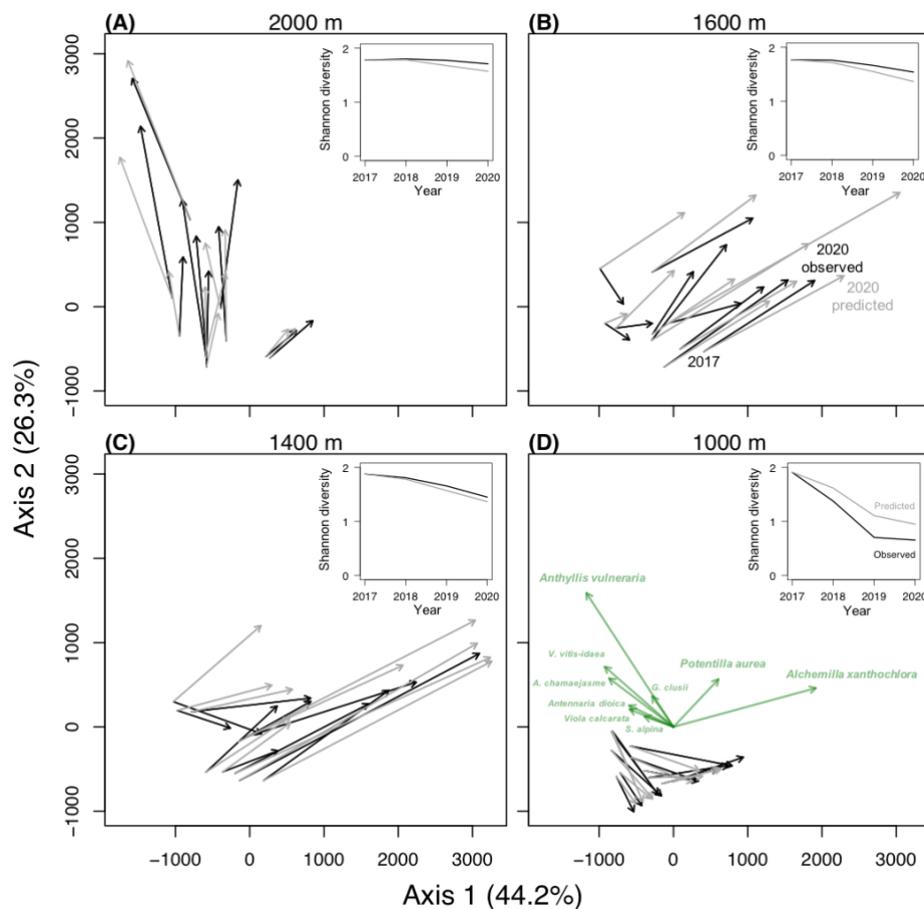
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606 **Figure 1. Trajectories of alpine plant communities transplanted to different elevations in the Swiss**607 **Alps to simulate climate change.** The communities originated from a site at 2050 m and were

608 transplanted to sites at (A) 2000 m, (B) 1600 m, (C) 1400 m, or (D) 1000 m (which correspond to

609 approximately 0, 2.2, 3.3, and 5.5 °C of warming, respectively). Panels show a Principal Coordinates

610 Analysis ordination based on Euclidean distances of all observed and simulated turfs from 2017 to 2020.

611 The arrows show the observed (black) and predicted (gray) changes in community structure of each turf. In

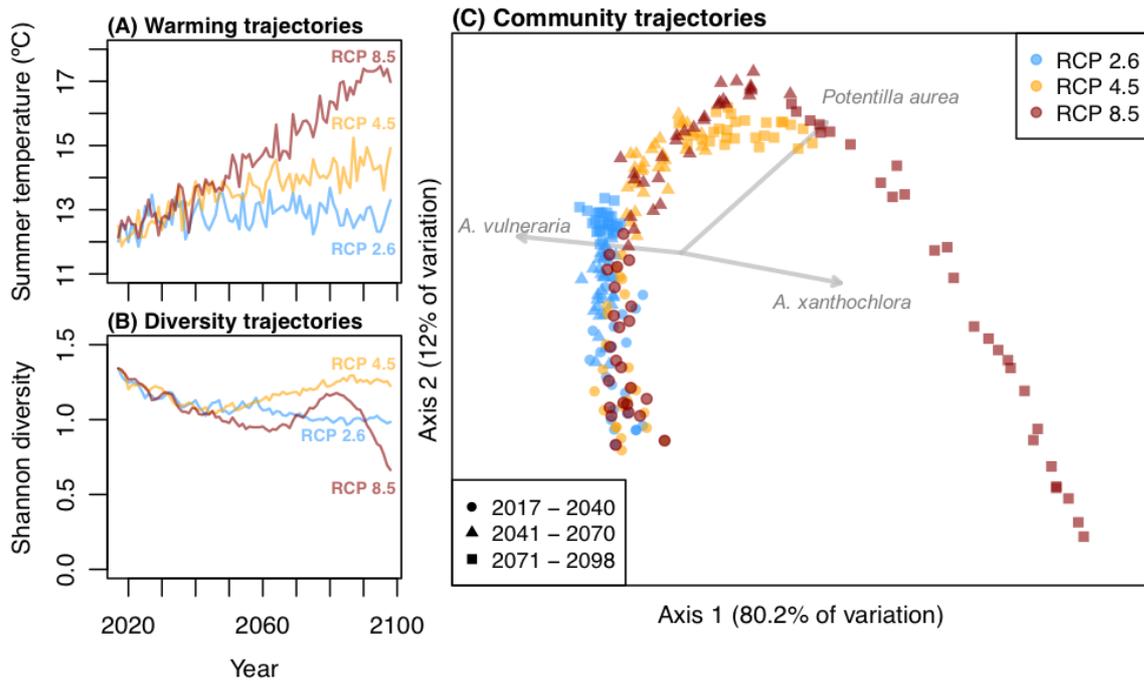
612 panel D, the thicker green arrows starting from the origin show the taxa for which the first two ordinations

613 axes explain at least 20% of their cover variation. The inset plots within each panel show the mean

614 observed (black) and predicted (gray) Shannon diversity across the ten turfs transplanted to each elevation.

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618 **Figure 2. Trajectories of alpine plant community responses to contrasting climate change scenarios**

619 **for the 21st century.** (A) Depending on future greenhouse gas emissions, this region of the Alps could

620 experience contrasting climate futures, warming from 0.5 (in RCP 2.6, solid line) to 2.3 (in RCP 4.5,

621 dashed line) and potentially even 4.8 °C (in RCP 8.5, dotted line) by the end of the century relative to the

622 experimental period (2017 to 2020). (B) Increases in temperature under the contrasting climate change

623 scenarios led to non-monotonic changes in the diversity of the simulated alpine community. (C) Principal

624 coordinates ordination based on Euclidean distances showing the trajectory of simulated alpine

625 communities under the different climate change scenarios between years 2017 and 2098 (each point

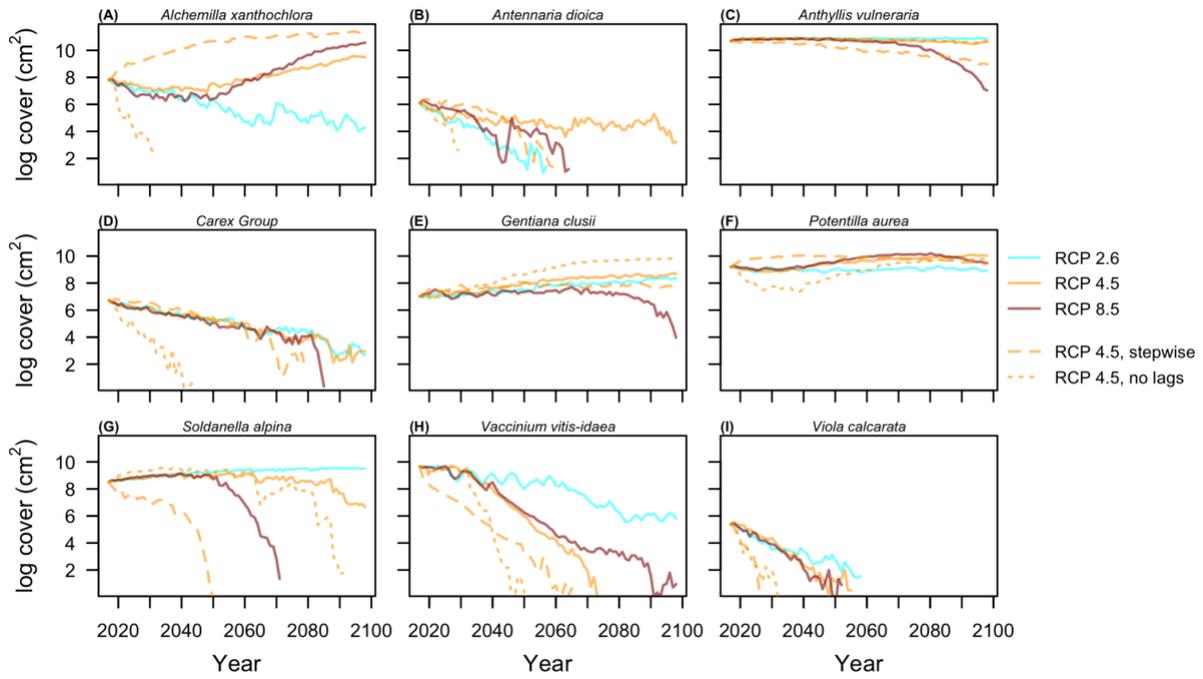
626 corresponds to a year in one scenario). The gray arrows are vectors of taxa for which ordination axes

627 explained more than 90% of variation in abundance through time.

628

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632 **Figure 3. Cover dynamics of alpine plant species under contrasting climate change scenarios RCP 2.6**

633 (cyan), RCP 4.5 (purple), and RCP 8.5 (red). Lines show the natural logarithm of the sum of the cover of

634 all ramets in each year of the climate change simulations. The trajectories of summer temperatures in the

635 region under these scenarios are shown in figure 2A. For scenario RCP 4.5, dotted lines show dynamics

636 with a reduced influence of demographic and competitive lags, while dashed lines show dynamics

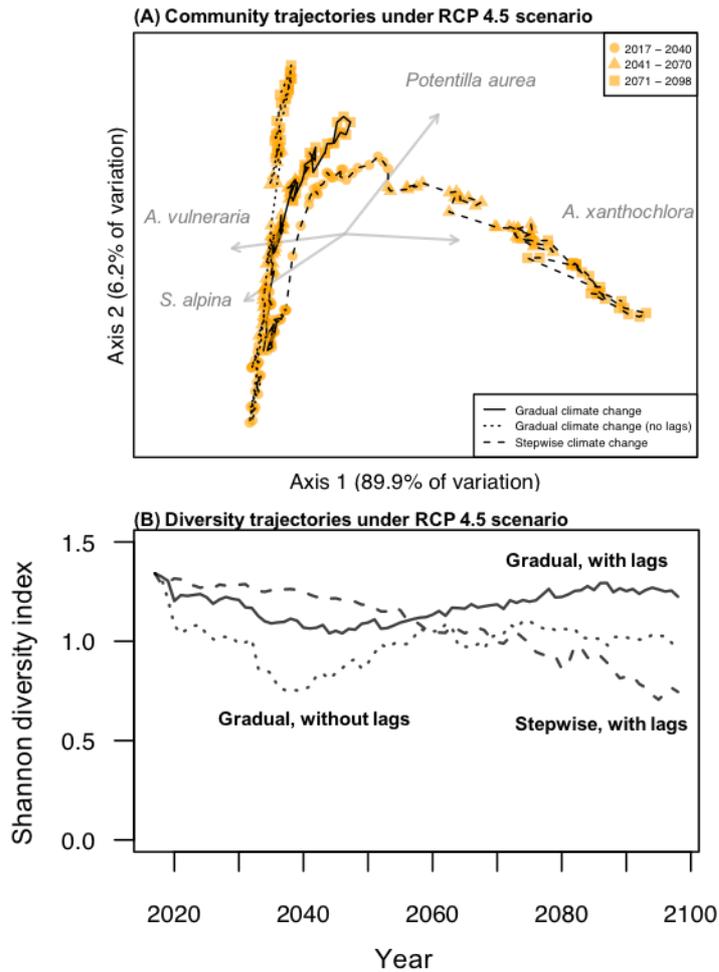
637 following a stepwise change in climate to conditions expected by the end of the century (mean conditions

638 between 2088 and 2098).

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

650