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# ECOGRAPHY

## Colonization and extinction lags drive non-linear responses to warming in mountain plant communities across the Northern Hemisphere

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Keywords:	climate warming, warming experiment, transplant experiment, elevation gradient, alpine plants, macroecology
Abstract:	<p>Global warming is changing plant communities due to the arrival of new species from warmer regions and declining abundance of cold-adapted species. However, experimentally testing predictions about trajectories and rates of community change is challenging because we normally lack an expectation for future community composition, and most warming experiments fail to incorporate colonization by novel species. To address these issues, we analyzed data from 44 whole-community transplant experiments along 22 elevational gradients across the Northern Hemisphere. In these experiments, high-elevation communities were transplanted to lower elevations to simulate warming, while also removing dispersal barriers for lower-elevation species to establish. We quantified the extent and pace at which warmed high-elevation communities shifted towards the taxonomic composition of lower elevation communities.</p> <p>High-elevation plant communities converged towards the composition of low-elevation communities, with higher rates under stronger experimental warming. Strong community shifts occurred in the first year after transplantation then slowed over time, such that communities remained distinct from both origin and destination control by the end of the experimental periods (3-9 years). Changes were driven to a similar extent by both new species colonization and abundance shifts of high-elevation species, but with substantial variation across experiments that could be partly explained by the magnitude and duration of experimental warming, plot size and functional traits.</p> <p>Our macroecological approach reveals that while warmed high-elevation communities increasingly resemble communities at lower elevations today, the slow pace of taxonomic shifts implies considerable colonization and extinction lags, where a novel taxonomic composition of both low- and high-elevation species could coexist for long periods of time. The important contribution of the colonizing species to community change also indicates that once dispersal barriers are overcome, warmed high-elevation communities are vulnerable to encroachment from lower elevation species.</p>

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### 3 4 **Abstract**

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8 normally lack an expectation for future community composition, and most warming experiments  
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28 both low- and high-elevation species could coexist for long periods of time. The important  
29 contribution of the colonizing species to community change also indicates that once dispersal  
30 barriers are overcome, warmed high-elevation communities are vulnerable to encroachment  
31 from lower elevation species.

### 32 **Introduction**

33 Changes in the composition of vegetation along steep elevation gradients reveal the role of  
34 climate as a powerful force in structuring plant communities (Giaccone et al. 2019, Chauvier et  
35 al. 2021), and now, climate warming is restructuring plant communities (Harrison 2020, IPBES  
36 2023). Climate change effects are especially prominent at higher elevations in mountains,  
37 where temperatures are rising faster than the global average (Pepin et al. 2022). The  
38 abundance and species composition of mountain plant communities are changing as extant  
39 populations respond to new environmental conditions and as species migrate upslope to track  
40 their preferred climate (Fig. 1B) (Lenoir et al. 2008, Rumpf et al. 2018). However, vegetation  
41 changes are strongly lagging behind expectations based on the pace of climate warming, due to  
42 lags in both local extinction (Rumpf et al. 2019) and colonization events (Zu et al. 2021). One  
43 expectation is that over time, these lags will be overcome and high-elevation plant communities

44 will increasingly resemble communities that are currently found at lower elevation (Jurasinski  
45 and Kreyling 2007, Savage and Vellend 2015). Alternatively, priority effects and novel plant-  
46 plant-climate interactions might set communities on alternative trajectories, yielding “no-analog”  
47 communities, as has occurred under past climatic changes (Overpeck et al. 1992, Leopold et al.  
48 2015, Staples et al. 2022) as well as during current climate warming (Roth et al. 2014). Insight  
49 into the trajectory and pace of changes in plant community composition will therefore be  
50 important to accurately forecast the impacts of climate change on biodiversity in mountainous  
51 regions.

52  
53 Since both the trajectory and pace of changes in community composition depend on the  
54 combined effects of colonization rates, local extinctions, and abundance shifts, we can gain  
55 insights into the relative importance of these processes by explicitly examining the response to  
56 warming of three distinct species pools (Lynn et al. 2021). Firstly, species that are restricted to  
57 high elevation (hereafter, “strictly high-elevation species”) are generally expected to respond  
58 negatively to warming and eventually become locally extinct (Geppert et al. 2023). This could  
59 happen either because they are poorly adapted to warmer conditions, or because they are  
60 poorer competitors for resources, such as light, that become increasingly limiting as warm-  
61 adapted, lower-elevation species arrive and increase in abundance (Alexander et al. 2015,  
62 Olsen et al. 2016). Secondly, species that occur in both high and low-elevation communities  
63 (hereafter, “overlapping species”), and thus that are adapted to a wider range of climatic and  
64 biotic conditions, might benefit from climate warming and increase in abundance (Lynn et al.  
65 2021). Finally, new species that migrate upslope from low elevation will establish in high-  
66 elevation communities and increase in abundance (hereafter, “colonizing species”). The relative  
67 contribution of these three local species pools – strictly high-elevation, overlapping, and  
68 colonizing species – to community shifts in response to climate change will depend on their  
69 reaction time (e.g., dispersal, establishment and extinction lags; Alexander et al. 2018) and the  
70 magnitude of warming. Disentangling responses of these different species pools can help  
71 anticipate the trajectory and rate of changes in high-elevation vegetation and the consequences  
72 for species’ range shifts under future climate.

73  
74 Manipulative experiments are key to studying possible long-term changes in community  
75 composition in response to climate warming. *In situ* warming experiments, for example using  
76 passive warming chambers, have been most commonly employed to reveal shifts in mountain  
77 plant communities towards assemblages more typical of lower elevations (Henry et al. 2022).  
78 However, *in situ* experiments do not capture the contribution of all species pools to community  
79 change, most notably that of colonizing species. This is because the pool of potential colonists  
80 is typically absent due to dispersal lags, unless this aspect is intentionally manipulated. Whole-  
81 community transplant experiments, which simulate climate change by moving plant communities  
82 with their soils to a new location representing possible future climate conditions, overcome this  
83 problem by simultaneously exposing communities to a change in climate and potential  
84 colonization by species from the destination transplant site (Fig. 1A). They thus offer a powerful  
85 way to examine the trajectory of mountain plant communities under future climate change, and  
86 how these trajectories are underlain by different species pools once dispersal barriers are lifted.  
87

88 Individual transplant experiments have already indicated shifts in species' population dynamics  
89 (Töpper et al. 2018), relative abundances (Yang et al. 2018, Block et al. 2020, Visakorpi et al.  
90 2022, Niu et al. 2023), colonization and extinction events (Vandvik et al. 2020, Schuchardt et al.  
91 2023a) and community assembly processes (Bektaş et al. 2023). Collectively, these studies  
92 suggest that under experimental climate change, transplanted high-elevation communities can  
93 restructure quickly and resemble lower-elevation communities. While the magnitude and pace of  
94 these shifts remain unknown, species pools driving changes in community composition can be  
95 region and experiment-dependent. For example, in a transplant experiment in Norway,  
96 transplanted turfs were rapidly colonized by low-elevation species, which negatively impacted  
97 high-elevation species within the community through novel competitive interactions (Vandvik et  
98 al. 2020) In contrast, an experiment in France, shifts in relative abundances within the existing  
99 communities drove the community reassembly (Bektaş et al. 2023). Furthermore, the functional  
100 strategies of individual plant species that benefit from climate change exhibit both general and  
101 region-specific responses. For example, taller species become more abundant under  
102 experimental warming in experiments from Switzerland (Visakorpi et al. 2022) and Norway  
103 (Guittar et al. 2016), where taller species have also lower extinction rates (Lynn et al. 2023). In  
104 addition, while species with slow resource acquisition were favored under warming in  
105 Switzerland (Visakorpi et al. 2022), species with fast resource acquisition strategies coming  
106 from warmer habitats colonized and increased their abundance more in colder sites in Norway  
107 (Lynn et al. 2023). These regional differences might arise from variations in limiting resources  
108 and how they are impacted by climate change, as well as from differences in the magnitude or  
109 duration of the experimental warming (Elmendorf et al. 2012). Consequently, it remains unclear  
110 whether we can make general predictions about the trajectory and pace of taxonomic responses  
111 to warming, and to what extent context-dependencies can be attributed to regional climatic or  
112 ecological or experimental differences.

113  
114 A macroecological experimental approach (Box 1) can allow us to identify general patterns in  
115 community composition change under climate change, while quantifying regional and  
116 experimental differences (Alexander et al. 2016). Here, we combine, for the first time, vegetation  
117 surveys spanning 2-9 years from a network of 44 whole-community downslope transplant  
118 experiments along 22 elevation gradients across the Northern Hemisphere to ask: i) To what  
119 extent does the species composition of warmed high-elevation communities diverge from the  
120 non-warmed high-elevation communities and converge towards that of low-elevation  
121 communities over time? ii) How do different species pools (strictly high-elevation, overlapping,  
122 or low-elevation colonizing species) contribute to divergence or convergence in plant community  
123 composition associated with climate change? iii) Is variation in overall rates of community  
124 change across experiments, as well as the average contribution of different pools to divergence  
125 or convergence, influenced by experimental design, the climate context of the study site, or  
126 plant functional trait composition?

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**Box 1: TransPlant Network**

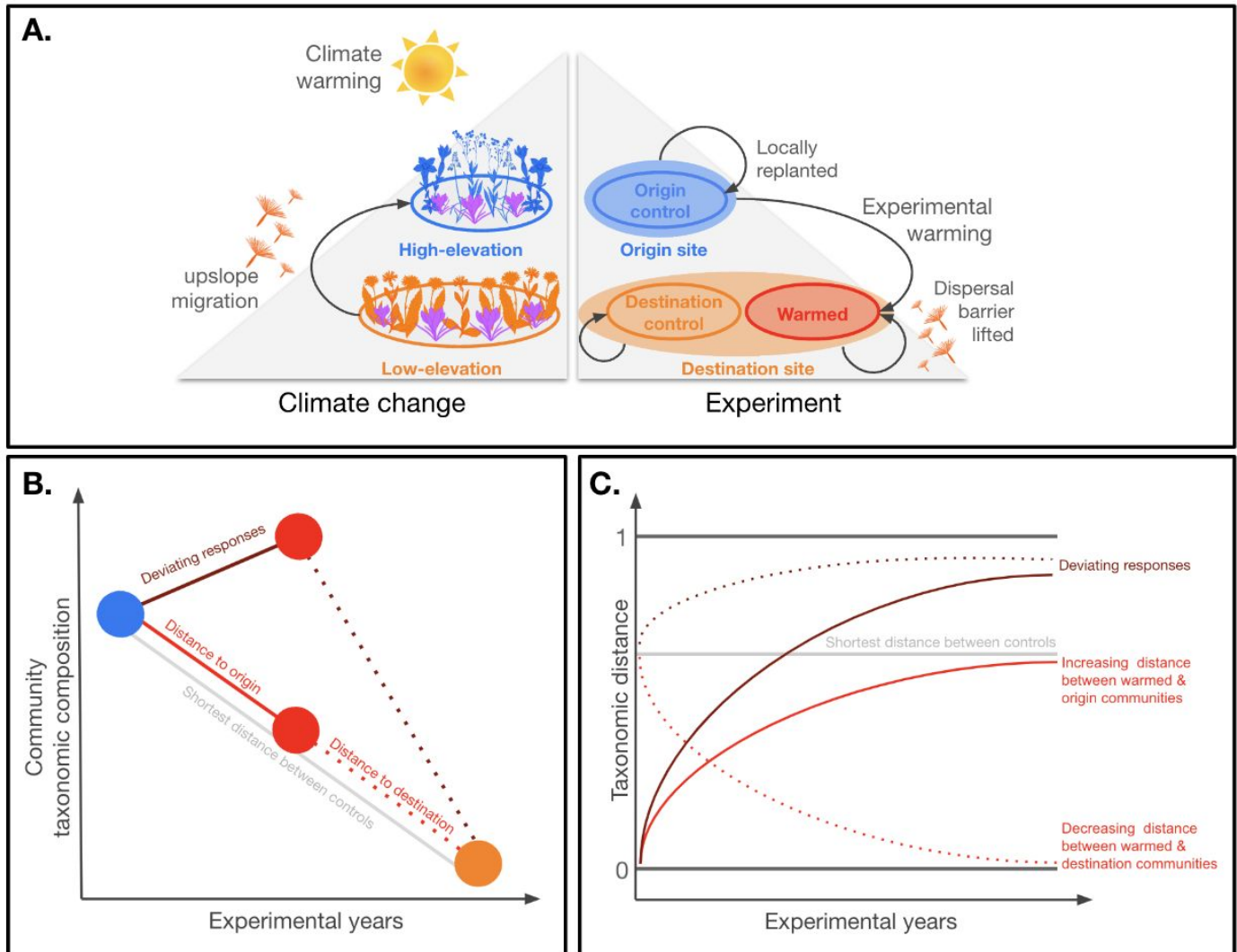
134 TransPlant is a network of 22 elevation gradients, distributed across 20 different mountainous  
135 regions of the Northern Hemisphere, where whole plant communities have been transplanted to  
136 lower elevations to simulate climate change (**Fig. 1-2, Table S1-2**). The basic design of the  
137 transplant experiments involve the transplantation of vegetation turfs (or “monoliths”) of whole  
138 plant communities with their soil from a higher (cooler) to a lower (warmer) elevation site to  
139 simulate climate warming (“warmed” treatment) (**Fig. 1A**). Moving plant communities to lower  
140 elevation in this way allows plants from the lower elevation site to quickly colonize transplanted  
141 turfs, also simulating the arrival of the novel species into high elevation communities that we  
142 expect to arrive following climate warming (**Fig. 1A**). For any given set of warmed turfs, there  
143 are “origin controls” (high-elevation turfs locally transplanted at their high-elevation site of origin)  
144 and “destination controls” (low-elevation turfs locally transplanted at the low-elevation site of  
145 destination) (**Fig.1A**). Thus, these controls make it possible to disentangle potential  
146 transplantation artifacts from the effects of experimental climate change. Along some  
147 TransPlant gradients, multiple experiments are conducted by transplanting the turfs from high to  
148 mid, mid to low, high to low elevations (**Fig. S1A**). We refer to a set of warmed, origin and  
149 destination control turfs within each gradient as an “experiment” (**Fig. 1A**), yielding a total of 40  
150 experiments because 12 gradients were composed of more than two sites (Table S1-2). The  
151 experiments were established between 2007 and 2017. Each experiment had 3-10 replicates of  
152 transplant and control turfs, and in total there were 668 turfs varying in sizes between 0.02 m<sup>2</sup>  
153 and 1 m<sup>2</sup> with a mean size of 0.3 m<sup>2</sup> across the 40 experiments. TransPlant Network data and  
154 experiment-specific results can be visualized on the dedicated Shiny app:  
155 <https://billurbektas.shinyapps.io/transplantsshiny-1/>

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157 **(End of Box 1)**

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**Fig. 1:** Overview of experimental designs in the TransPlant network, illustrating the ecological processes simulated through whole-community transplantation and the analytical framework used to study community shifts post-transplantation. **A)** Transplant experiments aim to simulate climate change by transplanting whole plant communities to putative future climates at lower elevation. This approach also lifts the dispersal barrier for colonizing species, thereby allowing colonization into the transplanted communities from the low-elevation site (colonizing species). We refer to the turfs transplanted from origin to destination sites as “warmed” communities (red circle), and to turfs locally replanted at origin and destination sites as “origin” (blue circle) and “destination” (orange circle) controls, respectively. **B)** Our expectation is that the warmed communities (red circle) will diverge in taxonomic composition from the origin controls (blue circle) and increasingly resemble the destination controls (orange circle), following the shortest distance between the controls over the years after transplantation. However, communities might deviate from this expected trajectory of resembling destination controls (red lines), showing deviating responses (pink lines). To quantify the degree of divergence from origin controls (solid lines) or convergence towards destination controls (dotted lines), we calculate the taxonomic distances of warmed



196 communities to either origin or destination controls, respectively. **C)** Over the experimental years, we  
197 expect that taxonomic distances between warmed and control communities change. If warmed  
198 communities follow the expected trajectory (red lines), the distance between warmed and origin control  
199 communities will increase (red solid line) and the distance between warmed and destination control  
200 communities will decrease (red dotted line). If the distance between warmed communities and origin  
201 controls reaches the maximum divergence determined by the distance between the controls, and if the  
202 distance to destination controls reduces to zero, indicating maximum convergence, then no lags remain in  
203 community shifts. However, warmed communities might deviate from this expected trajectory, increasing  
204 the taxonomic distances to both controls (pink lines), thereby maintaining lags in community shifts. Given  
205 that distances in warmed communities are constrained between zero and the shortest distance between  
206 controls for the expected trajectory, and between zero and one for the deviating trajectory, a logarithmic  
207 relationship is expected between experimental years and taxonomic distances. Note that the taxonomic  
208 distance between controls is expected to remain constant (gray line).

## 209 **Methods**

### 210 ***Climate data***

211 We extracted monthly mean daily air temperature ( $^{\circ}\text{C}$ ) and potential evapotranspiration (PET)  
212 (mm) data from the  $\sim 1$  km resolution CHELSA database (Karger et al. 2021) for each site. We  
213 calculated the average summer (June, July, August) temperature and annual PET for each site  
214 for each year of the experiment. We averaged the summer temperature and annual PET across  
215 all years for each experiment to calculate the origin and destination climates. To estimate the  
216 experimental climate warming experienced by warmed turfs, we calculated the average  
217 difference between destination and origin sites' summer temperature over the experimental  
218 years. Transplantation of turfs from high to low elevation simulated  $0.5\text{--}11.1$   $^{\circ}\text{C}$  (average of  $3.0$   
219  $^{\circ}\text{C}$ ) of experimental warming across all experiments, covering a range of climate change  
220 scenarios generated by the IPCC for the next 50 years (IPCC 2022a). The experiments aimed  
221 to simulate warming but other environmental changes, such as in PET, are also imposed by  
222 downward transplantation (Fig. 2B). However, due to the high spatio-temporal variability of  
223 precipitation, especially in mountainous regions, CHELSA model spatial projections convey  
224 more uncertainty than temperature projections (Prein and Gobiet 2017). This uncertainty may  
225 prevent us from accurately calculating the differences in PET between closely located origin and  
226 destination sites. Therefore, we only analyze the effect of PET at the destination sites rather  
227 than the difference between sites.

### 229 ***Plant relative abundances***

230 Vegetation surveys varied in timing, temporal resolution, and duration. Survey methodologies  
231 were also diverse, including percent cover estimates of all species in the turfs, point-intercept  
232 counts, or species-specific sorting of above-ground biomass. Some surveys did not record non-  
233 vascular plant categories, rock or bare soil. Thus, we removed inconsistent cover categories  
234 from the dataset and converted vascular plant species cover or count data into relative plant  
235 abundances to ensure comparability across experiments. The compiled data ranges from 1 to 9  
236 years, for 60635 observations of 967 identified species and 92 taxa identified only at genus  
237 level. We decomposed these species pools into strictly high-elevation, overlapping, or  
238 colonizing low-elevation species based on their presence/absence in the control communities  
239 for each experiment (Table S3, Fig. S3). By definition, strictly high-elevation species were only

240 found in the higher-elevation origin controls for each experiment, including high-elevation  
241 species relative to the experiment. We note that these are not necessarily alpine plants in a  
242 biogeographic sense (i.e., species found mainly above the treeline). The colonizing low-  
243 elevation species pool includes species that occur in destination controls but not in origin  
244 controls. Overlapping species are found both in origin and destination controls. Species that  
245 occur in warmed communities only but are absent from both sets of controls (i.e., on average,  
246 5% across all experiments, Fig. S3, Fig. S9) were excluded from the analysis. We limited our  
247 analysis to experiments with over two years of data, thus excluding US\_Colorado and  
248 IN\_Kashmir. We also excluded US\_Arizona due to its small high-elevation species pool of four  
249 species. Additionally, we excluded species found only once in a single turf to eliminate potential  
250 botanical identification errors. We square-root transformed species relative abundances in the  
251 analyses described below.

252

### 253 ***Plant functional traits***

254 We compiled five functional traits from the TRY database: vegetative height, leaf area (LA),  
255 seed mass, specific leaf area (SLA), and leaf nitrogen percentage (Kattge et al. 2020). These  
256 traits relate to plant size and resource use strategies that are relevant for plant responses to  
257 environmental change and their ability to compete for light, water and nutrients (Violle et al.  
258 2007, Díaz et al. 2016). We used a pre-processed version of the TRY dataset by (Walker et al.  
259 2023), filtered for trait values with an error risk < 4 according to the TRY database criterion  
260 (which measures the deviation from mean trait values within species, genus, family, or the entire  
261 dataset in standard deviation) and gap-filled using Bayesian hierarchical probabilistic matrix  
262 factorization imputation. This pre-processed dataset still had missing focal traits for certain  
263 species (vegetative height: 22%, SLA: 15%, LA: 31%, N-percent: 23%, seed mass: 29%) that  
264 we additionally gap-filled with miceRanger algorithm (Wilson in press). From these functional  
265 traits, we built a principal component analysis (PCA) with all the species from the TransPlant  
266 network (Fig. S2). Horn's parallel analysis retained two principal components (PC) to represent  
267 the variation in the trait space. LA (33%), vegetative height (26%), seed mass (23%) contributed  
268 primarily to PC1 followed by N-percent (9%) and SLA (8%). SLA (42%) and N-percent (38%)  
269 contributed the most to PC2 followed by vegetative height (9%), seed mass (9%) and LA (1%).  
270 Thus, we defined the first two PCs as denoting plant-size and resource acquisition-related traits,  
271 respectively, representing the two main axes of the global plant functional trait spectrum (Díaz  
272 et al. 2016). We calculated community-weighted means (CWMs) of PC1 and PC2 scores for  
273 each control community, reflecting plant size and resource acquisition strategies, respectively.

274

### 275 ***Quantifying plant community taxonomic divergence or convergence***

276 To quantify the plant community taxonomic change over time, we built principal response curves  
277 (PRC) (Van den Brink and Braak 1999). PRC, developed from redundancy analysis (RDA), is  
278 an ordination technique that quantifies the impact over time of several treatments on species  
279 relative abundances in experimental communities, relative to a reference community. It  
280 accounts specifically for the interaction between experimental years and treatment while  
281 controlling for the overall temporal trend in community composition. PRC allows for extracting i)  
282 taxonomic distances between the treatments and the reference over time as canonical

283 coefficients of the treatments and ii) species weights that quantify species' contributions to  
284 overall community taxonomic changes (Vandvik et al. 2014).

285  
286 We quantified the taxonomic distances of the warmed communities relative to the controls by  
287 constructing two PRCs for each experiment. The first PRC used the origin control as the  
288 reference community, with the warmed and destination control as treatments to quantify their  
289 taxonomic distance from the origin control. The second PRC used the destination control as the  
290 reference, with the warmed and origin control as treatments to quantify their taxonomic distance  
291 from the destination control (Table S4). Canonical coefficients ( $C_t$ ) from PRC axis 1 (hereafter,  
292 "PRC1") capture the most important taxonomic variation in differences between warmed and  
293 control communities for a given year  $t$ , quantifying warmed communities' divergence from the  
294 origin control and convergence towards the destination control. Canonical coefficients from PRC  
295 axis 2 (hereafter, "PRC2") capture the second most important variation, and most important  
296 deviation from the PRC1 (van den Brink et al. 2009). In PRCs, taxonomic distances between the  
297 origin and destination controls indicate the maximum expected divergence of warmed  
298 communities from origin controls and their maximum expected convergence towards destination  
299 controls (Fig. 1B-C). When canonical coefficients of the warmed communities exceed the  
300 canonical coefficients of the control communities in a given PRC, this can be interpreted as the  
301 communities deviating from the shortest trajectory between warmed communities and displaying  
302 a "deviating" response (Fig. 1B-C). We expect to see these responses mainly in PRC2 with  
303 higher values in PRC2 indicating stronger deviating responses.

### 304 305 **Quantifying species' contributions to taxonomic divergence or convergence**

306 To assess the species' contributions to the community taxonomic shifts, we calculated  
307 proportional relative abundance differences in warmed communities in comparison to the mean  
308 relative abundance in control communities following the expression  $b_k * c_t - 1$  for each species  
309  $k$ , with species weights  $b_k$  and canonical coefficient  $c_t$  of warmed communities at year  $t$  from  
310 both PRCs per experiment. Here, species weights  $b_k$  (i.e., constant over the years) allow us to  
311 obtain the fitted response curves for species  $k$  and quantifies the affinity of species  $k$  with the  
312 overall trajectory of the community (i.e., the higher the species' weights, the more likely it is that  
313 the species is aligned with the pattern of community change as quantified by PRC) (Van den  
314 Brink and Braak 1999). Interpreting this outcome as the species' contribution to a communities'  
315 taxonomic divergence and convergence provides several advantages to using raw relative  
316 abundance differences: i) disentangling species contributions to the most important variation  
317 (PRC1) from the second most important variation (PRC2, i.e., deviations from PRC1)  
318 community change, while ii) taking into account the noise in the data.

### 319 320 **Statistical analyses**

321 To address our first question, we assessed the rate of composition change in warmed  
322 communities along two primary axes: 1) divergence or convergence along PRC1, quantified by  
323 canonical coefficients, and 2) deviation from these trajectories along PRC2. We developed  
324 linear mixed effects models for each axis, considering both the warmed (red lines in Fig.1B-C)  
325 and control communities (gray lines in Fig.1B-C) relative to a reference community. These  
326 models used canonical coefficients as the response variable and included log-transformed

327 experimental year, distance type (to origin or destination control), experiment identity, and their  
328 three-way interactions as fixed effects. A random effect for gradient was included to adjust for  
329 non-independence across experiments due to regional variations like soil and habitat  
330 differences. We log-transformed the experimental year to fit a logarithmic regression because  
331 the distances between communities cannot surpass the maximum expected distance in the  
332 case of the divergence, or zero in the case of convergence. This transformation improved model  
333 fit, reducing AIC values by 121.39 and 153.20 for PRC1 and PRC2, respectively (df = 162). The  
334 slopes from these models provide estimates of the rates of divergence from origin controls,  
335 convergence towards destination controls, and deviations in composition across all experiments  
336 over the years.

337

338 To answer our second question, we estimated i) the proportional differences in relative  
339 abundances in warmed communities calculated from both PRC axes per species pool (strictly  
340 high-elevation, overlapping and colonizing) at the start (year = 1) and end (year = 9, projected  
341 for the short experiments) of experiments, and ii) the rate of changes in these proportional  
342 differences over time. We built linear mixed effects models for each axis and species pool with  
343 species' proportional differences in relative abundances in warmed communities as the  
344 response variable with experimental year (log-transformed), comparison type (to origin or  
345 destination control), experiment identity, and their three-way interactions as fixed effects. We  
346 included species nested in gradients as random effects. Here, we present the estimated  
347 proportional differences in relative abundances in warmed communities per species pool at the  
348 start and end of experiments, and the slopes (as rate of changes in relative abundances) from  
349 these species pool-level models for all experiments combined. When compared to origin  
350 controls, higher proportional relative abundance differences in warmed communities indicate  
351 greater climate change effects on relative abundances of that experiment and/or species pool.  
352 Also compared to origin controls, greater magnitudes of the slopes (absolute values) indicate  
353 faster changes in relative abundances. More precisely, higher positive rates indicate faster  
354 species gains, lower negative rates indicate faster losses. When compared to destination  
355 controls, i) higher proportional relative abundance differences in warmed communities indicate  
356 greater lags in relative abundances, while ii) larger magnitudes of the slopes (absolute values)  
357 indicate faster realization of the experimental climate change response and thus, declines in  
358 lags. More precisely, higher positive rates indicate faster decline in colonization lags (i.e.,  
359 realization of colonization events), lower negative rates indicate faster decline in extinction lags  
360 (i.e., realization of extinction events). Overall, changes in a species pool reflect overall changes  
361 in species' relative abundances in a given experimental community belonging to the species  
362 pool in question.

363

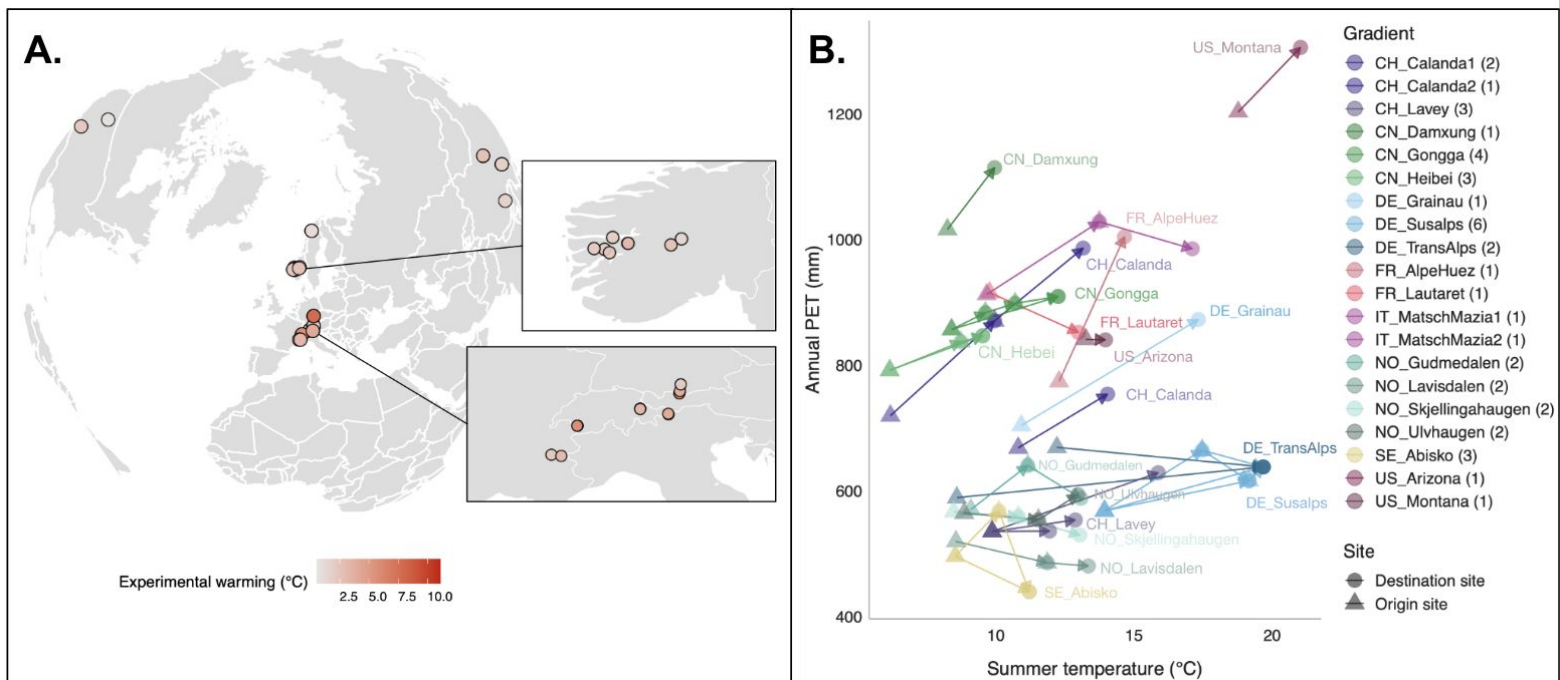
364 To answer our third question, we first extracted the slopes (i.e., rate of changes in distances  
365 between warmed and both control communities) and their standard errors for each experiment  
366 from the first-mentioned (community-level) model. Second, we extracted the initial and final  
367 proportional differences in relative abundances and slopes (i.e., rate of change in proportional  
368 differences in relative abundances) and their standard errors for each experiment from the  
369 second-mentioned (species pool-level) model. At community-level, we built two separate meta-  
370 regression models to accommodate each of the two distance types ( to origin or destination

371 control) with slopes as response variable. At species pool-level, we built 18 separate meta-  
 372 regression models to accommodate each of the two comparison types (to origin or destination  
 373 control) and three species pools with three response variables: i) slopes at species pool-level,  
 374 iii) initial and iii) final proportional differences in species-pool relative abundances. In these  
 375 models, experimental (turf size, experimental warming, duration), and climate factors (summer  
 376 temperature and annual PET of destination sites) and functional traits (CWM of plant size and  
 377 resource acquisition traits) were included as explanatory variables. Meta regression models  
 378 take into account the uncertainty in the response variables (Viechtbauer 2010). All explanatory  
 379 variables were standardized (i.e., z-score normalization).

380

381 We conducted the statistical analysis with R version 4.4.0 (R Core Team 2024) using the  
 382 following packages: emmeans (Lenth 2023), lme4 (Bates et al. 2015), vegan (Oksanen et al.  
 383 2022), MuMIn (Bartoń 2023), merTools (Knowles and Frederick 2024), metafor (Viechtbauer  
 384 2010).

385



386

387 **Fig. 2: A)** TransPlant experiments across the Northern Hemisphere. The color gradient indicates the magnitude of  
 388 experimental warming (°C) as the sum of temperature differences between the origin and destination sites across the  
 389 experimental years. **B)** Summer temperature (°C) and annual potential evapotranspiration (PET, mm) of TransPlant  
 390 sites (circle: Destination site, triangle: Origin Site). Different colors indicate gradients. The number of experiments in  
 391 each gradient is indicated in the color legend. Coloured arrows indicate the direction of the translocation for each  
 392 experiment. *Note:* We extracted temperature (°C) and PET (mm) from the ~1 km resolution CHELSA database for  
 393 each site (Karger et al. 2021).

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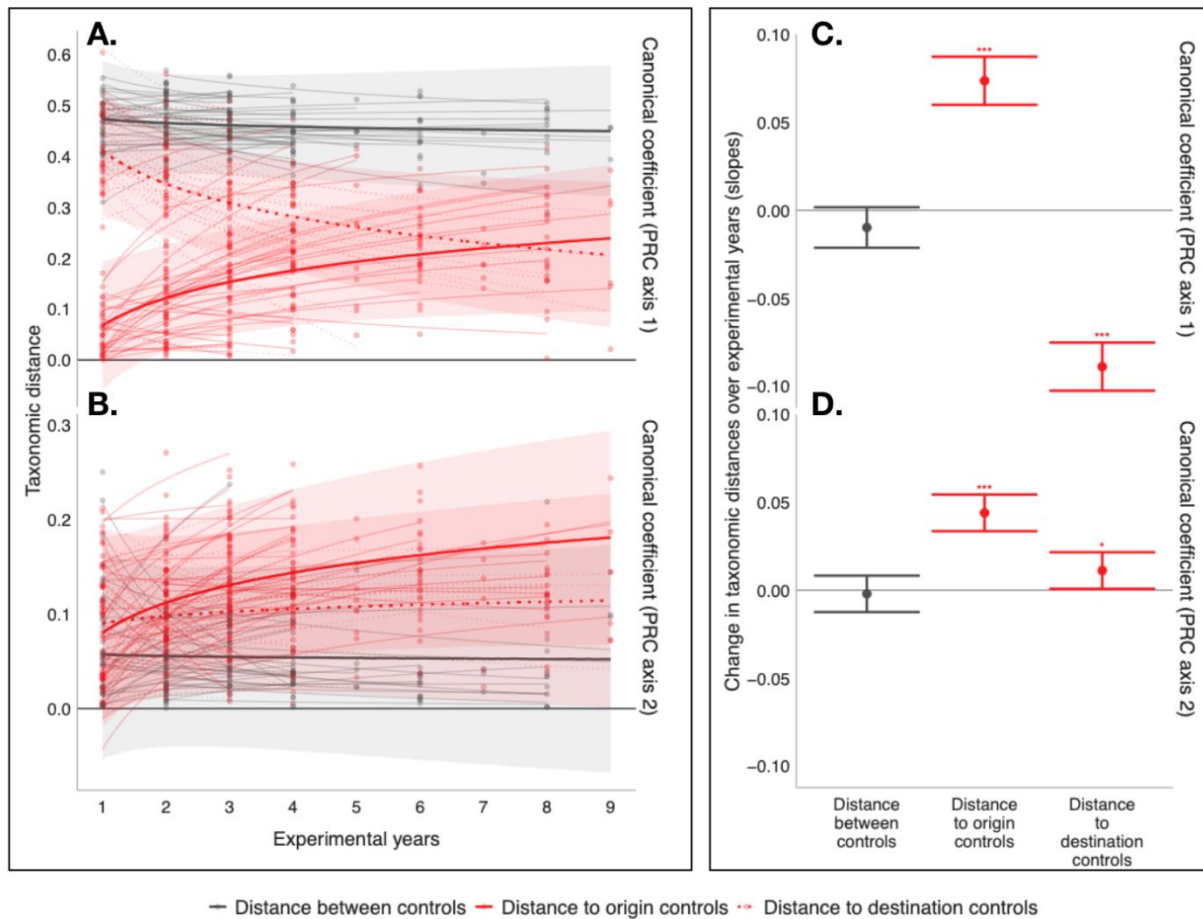
395



## 396 Results

## 397 To what extent does the species composition of warmed communities shift over time?

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399

400 **Fig. 3:** Community divergence and convergence in response to warming, reflected as the change in canonical  
 401 coefficients reflecting the taxonomic distances between experimental communities and their origin and destination  
 402 controls over time. **A-B)** Each panel reflects both divergence of the warmed communities from the origin control (solid  
 403 lines) and convergence towards the destination control (dotted lines). For divergence, the origin controls are set at  
 404 zero as the reference community and the plot shows the divergence of warmed communities (solid red line) and  
 405 destination controls (solid gray line) from the origin controls. For convergence, the destination controls are set at zero  
 406 and the plot shows the convergence of the warmed communities (dotted red line) and origin controls (solid gray line)  
 407 towards the destination controls. Distances between controls (gray lines) represent the expected taxonomic distance  
 408 if warmed communities fully converge (i.e., become identical to the destination community composition). Panels A  
 409 and B represent PRC axes 1 and 2, respectively. **C-D)** The rate of change in taxonomic distances (i.e. distance per  
 410 log-transformed experimental year) between control communities and between warmed communities and origin or  
 411 destination controls, as reflected in the analyses on A or B where the respective controls are set at zero as the  
 412 reference community. Panels C and D represent PRC axes 1 and 2, respectively. Canonical coefficients from PRC1  
 413 capture the most important variation in taxonomic distance, and represent the taxonomic divergence from the origin  
 414 control or convergence towards the destination control due to experimental warming. Canonical coefficients from  
 415 PRC2 capture the most important deviations from the PRC1, and so represent deviations in the trajectories of the  
 416 communities as they diverge or converge from/towards origin and destination controls, and thus give deviating  
 417 responses. Note that lines in A and B are from models fitted with log-transformed experimental years. Responses of  
 418 each experiment (fitted separately) and overall responses are shown in thin and thick lines respectively, with shading

419 indicating the 95% confidence interval for the overall effect. In C and D, significant slopes are indicated with \*:  
420 p.values <0.05, \*\*: p.values<0.01, \*\*\*: p.values<0.001

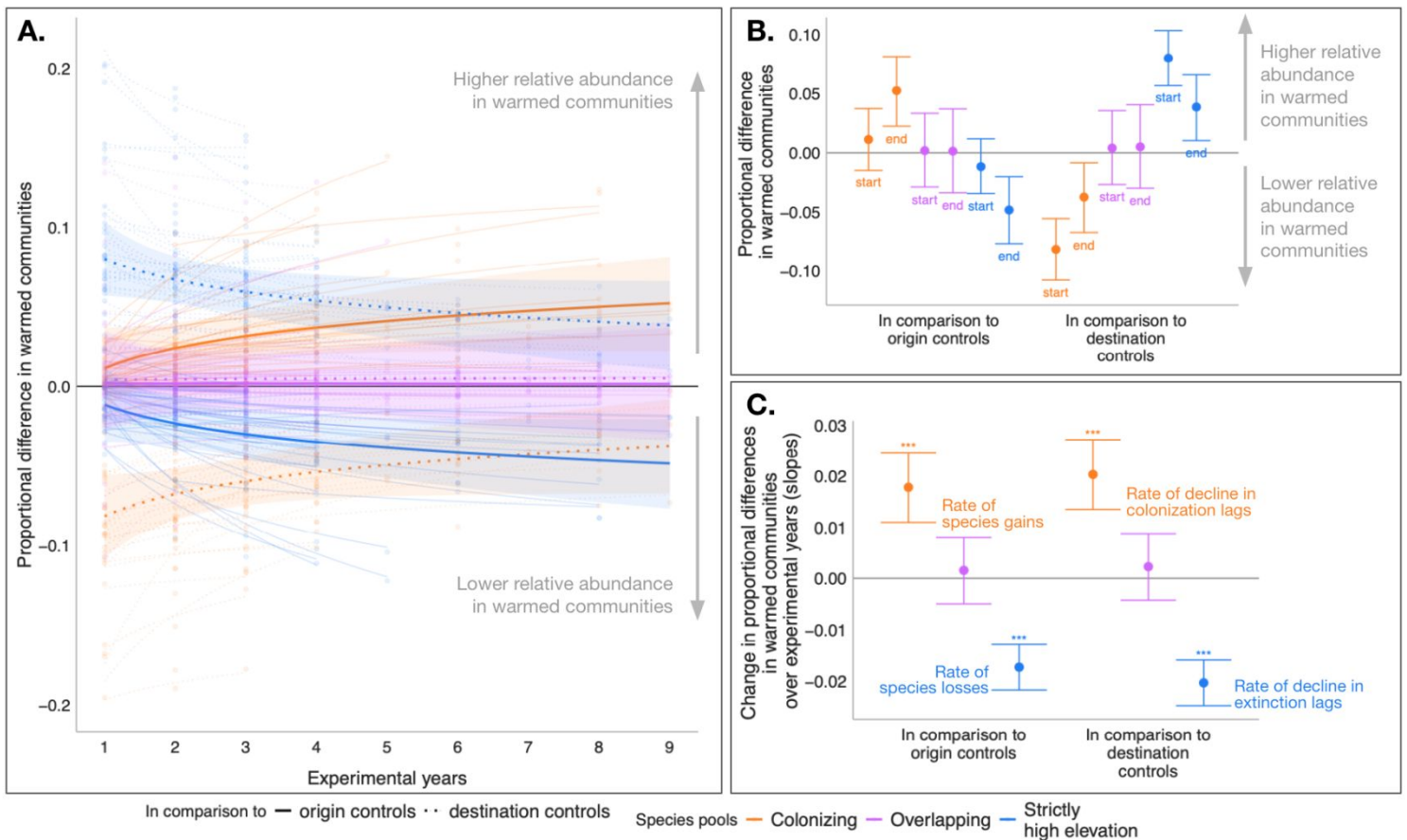
421  
422 Warmed communities taxonomically diverged from the high-elevation origin control communities  
423 (Fig. 3A red-solid lines; Table S5) and converged towards low-elevation destination control  
424 communities across all experiments (**Fig. 3A, red-dotted lines**). As expected, the distance  
425 between the two control communities remained constant on both PRC axes, indicating no  
426 significant directional change in composition in the controls (**Fig. 3 A-B, gray lines**). In the first  
427 year, warmed communities had already diverged on PRC1 by on average 14 %, and converged  
428 by on average 13 %, of the maximum expected distance (i.e., the distance between the two  
429 controls). If communities maintained this pace they would have reached zero taxonomic  
430 distance with destination controls at around 7 years, however, rates of divergence and  
431 convergence slowed down considerably over time. On average, (i.e., based on projections),  
432 48% and 54 % of taxonomic distance on PRC1 still remained, after 9 years, for communities to  
433 reach maximum divergence and convergence, respectively.

434  
435 However, variation in rates of composition change was observed across the 40 experiments  
436 (Fig. S5). First, warming led to divergence from origin controls only in 33 experiments.  
437 Conversely, in 7 experiments, warmed communities diverged from origin controls in the first  
438 year but they started to converge back towards origin controls over the years (Fig.3A, Fig. S5).  
439 The rates of change in taxonomic distances between warmed and origin control communities  
440 ranged from -0.053 to 0.215 (i.e., unitless change in taxonomic distance over the years scaled  
441 between -1 and 1, Fig. S5). Second, warming led to convergence with destination controls only  
442 in 36 experiments. Whereas in 4 experiments, warmed communities tended to diverge from the  
443 destination controls. The rates of change in taxonomic distances between warmed and  
444 destination controls ranged from -0.283 to 0.0584. In addition, taxonomic distances between  
445 warmed and control communities generally (**Fig. 3B solid and dotted red lines**) exceeded the  
446 distances between the controls (**Fig. 3B gray lines**) along PRC2. This indicates that warmed  
447 communities deviated from the expected trajectory of convergence. These deviations  
448 significantly increased over time (**Fig. 3B&D**).

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463 **How do different species pools contribute to divergence or convergence in plant**  
 464 **community composition?**



465 **Fig. 4:** Changes in different species pools in warmed communities in comparison to controls over time. **A)**  
 466 Proportional differences in relative abundances of each species pool in warmed communities in comparison to origin  
 467 controls (solid lines) and destination controls (dotted lines) calculated from PRC1. Positive values indicate higher  
 468 relative abundances in warmed communities, negative values indicate lower relative abundances in warmed  
 469 communities. **B)** Predicted proportional differences in relative abundances of different species pools in warmed  
 470 communities in comparison to controls at the start (year = 1) and end (year = 9, projected for shorter experiments) of  
 471 the experiments. **C)** Rate of changes in proportional differences in warmed communities over log-transformed  
 472 experimental years. When compared to origin controls, higher positive rates indicate faster species gains, lower  
 473 negative rates indicate faster losses. When compared to destination controls, higher positive rates indicate faster  
 474 decline in colonization lags (i.e., realization of colonization events), lower negative rates indicate faster  
 475 decline in extinction lags (i.e., realization of extinction events). Note that lines in A are from models fitted with log-transformed  
 476 experimental years. Responses of each experiment (fitted separately) and overall responses are shown in thin and  
 477 thick lines respectively, with shading indicating the 95% confidence interval for the overall effect. In C, significant  
 478 slopes are indicated with \*: p.values < 0.05, \*\*: p.values < 0.01, \*\*\*: p.values < 0.001  
 479  
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481 The divergence of warmed communities from origin controls was similarly driven by both the  
 482 decrease in relative abundances of strictly high-elevation species and the increase in colonizing  
 483 species. (Fig. 4A-B). However, both colonization and extinction lags remained after the 9-year  
 484 experimental period: On average, strictly high-elevation species remained more abundant and  
 485 colonizing species less abundant in warmed communities compared to destination controls (Fig.  
 486 4A-B). Besides having equal contributions to the overall shifts in warmed communities, rates of

487 species gains and losses over the years were similar, thus contributing equally to the rates of  
488 divergence from the origin controls and convergence towards destination controls (Fig. 4C).  
489 However, beyond these general trends, there was substantial variation across experiments (Fig.  
490 5A, thin lines, Fig. S5). In fact, the relative abundances of overlapping species across  
491 experiments showed both increasing and decreasing trends, which canceled each other out,  
492 resulting in no clear general trend.

493  
494 Taxonomic shifts away from the shortest trajectory between origin and destination controls in  
495 warmed communities were mainly driven by the colonizing species (Fig. S4). Interestingly, when  
496 predicted by PRC2, relative abundances of the colonizing species were increasingly higher in  
497 warmed communities in comparison to destination controls, indicating that some colonizing  
498 species were increasing their abundances more than expected (i.e., given their relative  
499 abundances in destination controls), contributing to the community-level deviating responses  
500 (Fig. S4).

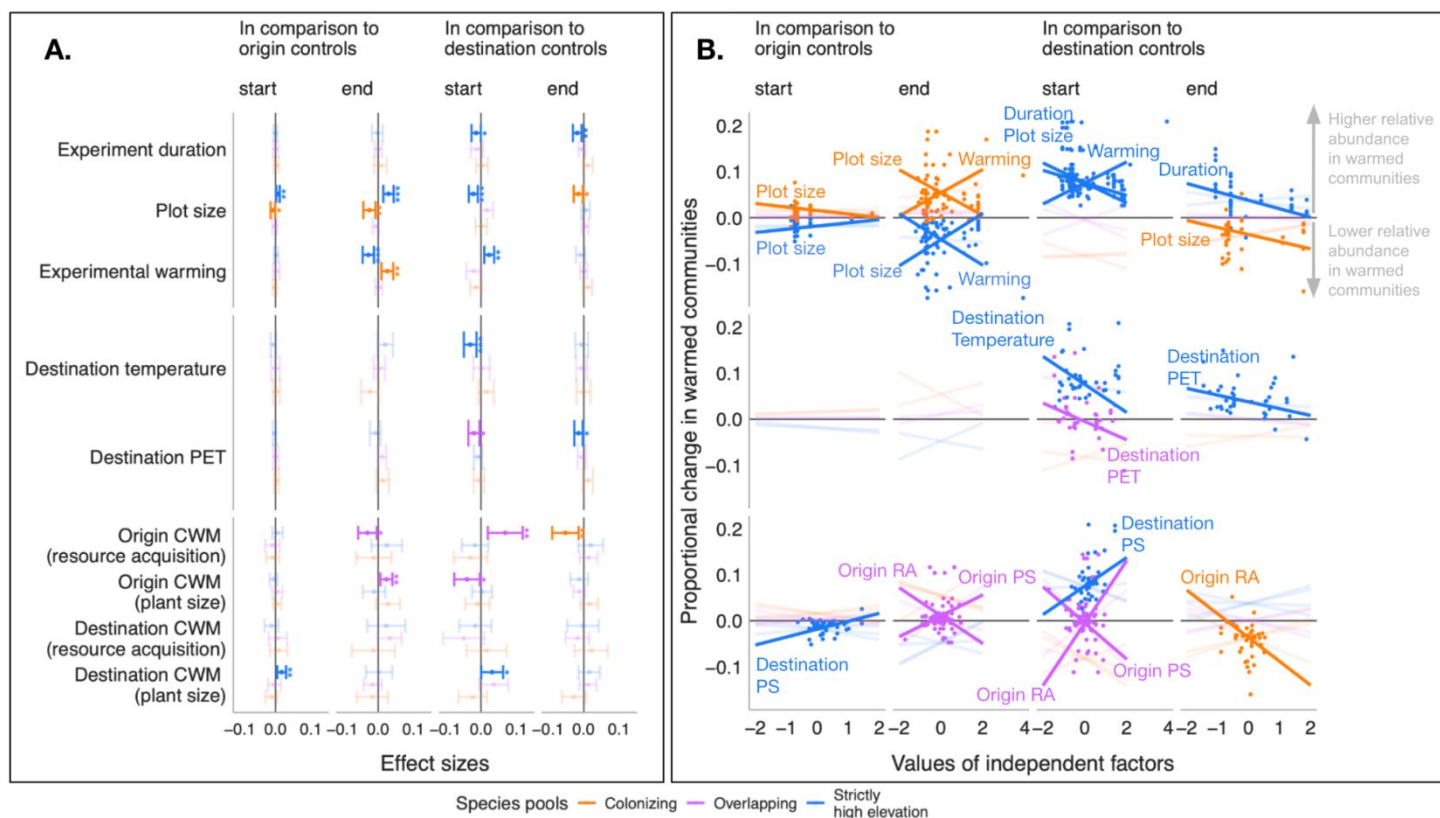
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502 **What influences the variation in overall rates of community change across experiments, as**  
503 **well as the contribution of different pools to divergence or convergence?**

504 Communities exposed to stronger warming, over longer periods, in smaller plots and  
505 transplanted to drier conditions diverged faster from origin controls (i.e., increasing taxonomic  
506 distances between warmed and origin control communities over time) (Fig. S6; Table S7). Also,  
507 communities exposed to stronger warming over longer periods converged faster towards  
508 destination controls (i.e., decreasing taxonomic distances between warmed and destination  
509 control communities over time) (Fig. S6; Table S7).

510  
511 Species pools' relative abundance differences in warmed communities compared to controls  
512 varied between the beginning and end of experiments (Fig. 5; Table S8). At the beginning of the  
513 experiments, species losses (i.e., decreases in the relative abundances of the strictly high-  
514 elevation species) in warmed communities were higher in experiments with smaller plots and  
515 when destination communities were dominated by smaller-sized plants. Similarly, extinction lags  
516 were greater in smaller plots, under stronger warming, in shorter experiments, when  
517 transplanted to cooler destinations where destination communities were dominated with taller-  
518 sized plants. Parallely, species gains (i.e., increases in the relative abundances of the colonizing  
519 species) in warmed communities were higher in smaller plots. Finally, overlapping species had  
520 higher relative abundances in warmed communities in comparison to destination controls when  
521 transplanted to a wetter destination (among other destination sites) and when they originated  
522 from smaller-sized and more resource-acquisitive communities.

523  
524 At the end of the experiments, species losses and gains were higher (Fig. 5) and faster (Fig. S7;  
525 Table S8) in smaller plots and under stronger warming. Whereas, extinction lags were higher in  
526 shorter experiments and when communities were transplanted to wetter conditions. Meanwhile,  
527 colonization lags were higher when the origin communities were dominated by more resource-  
528 acquisitive strategies. Finally, overlapping species had higher relative abundances in warmed  
529 communities than in origin controls when they originated from more conservative and taller-  
530 sized communities.

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**Fig. 5: A)** Magnitude of experimental, climatic and functional trait effects on the magnitude of species pool contributions (change in species pools' proportional relative abundance changes in warmed communities in comparison to controls) at the start (year = 1) and end (year = 9, projected for shorter experiments) of the experimental period **B)** Relationships in species pool contributions with experimental, climatic and functional trait factors. For experimental and climate effects, positive values indicate longer experiment duration, bigger turf sizes, stronger experimental warming, warmer and drier destination site. For functional trait effects, positive values indicate that on average communities are dominated by fast-growing resource-acquisitive (high SLA and leaf nitrogen) and taller species with wider leaves and heavier seeds (Fig. S2). When compared to origin controls, positive effect sizes indicate increases in relative abundances in warmed communities with the higher values of the explanatory factor for all species pools. When compared to destination controls, positive effect sizes still indicate higher relative abundances in warmed communities with increasing values of the explanatory factors but it can additionally be interpreted as higher extinction lags for strictly high-elevation species pool with the increasing values of the explanatory factors. For colonizing species, negative effect sizes indicate increasing colonization lags with increasing values of the explanatory factors. In B, only significant associations as quantified in A are shown and labeled. Linear metaregression models were built independently per species pool. All explanatory variables were standardized (i.e. z-score normalization).

## 549 Discussion

### 550 High-elevation plant community trajectories under climate warming

551 Ecologists are trying to understand the reconfigurations of plant communities due to abundance  
 552 and distribution shifts triggered by climate change. A “null hypothesis” is that when dispersal  
 553 limitations of warm-adapted species are overcome, the future composition of cool-adapted plant  
 554 communities converge on the composition of warm-adapted communities of today. Alternatively,

555 altered ecological interactions within warming communities might cause them to exhibit lagged  
556 responses or even follow alternative trajectories leading to novel community compositions. A  
557 network of transplant experiments provided us with the unique opportunity to examine the initial  
558 years of these trajectories under climate warming. As expected, the taxonomic composition of  
559 warmed communities shifted, converging towards their lower-elevation communities.  
560 Nonetheless, communities under warming did not fully converge on the low-elevation  
561 community composition, even up to nine years after transplantation. In addition, we found that  
562 warmed communities deviated significantly from the shortest trajectory of community shift  
563 between high- and low-elevation sites and rates of taxonomic convergence slowed over time.  
564 Together, these results suggest that even if high-elevation communities do eventually converge  
565 on today's low-elevation community composition, this will be a slow process characterized by  
566 significant colonization and extinction lags and transient dynamics leading to a prolonged period  
567 of novel community structures (Hastings et al. 2018). Such transient dynamics could be due to  
568 demographic lags (Alexander et al. 2018), feedbacks in plant-plant interactions (Alexander et al.  
569 2015, Vandvik et al. 2020, Bektaş et al. 2023), plant-soil nutrient pools (Khedim et al. 2022), or  
570 plant-microbial interactions (Zhang et al. 2014).

571  
572 Taxonomic changes were already large in the first year after transplantation. This might be an  
573 effect of the transplantation method, whereby the communities are exposed to an abrupt  
574 environmental change. Indeed, community responses to gradual warming might differ from  
575 those of abrupt climate manipulations, partly because individual species differ in their  
576 demographic responses to fast vs. slow warming altering the network of plant-plant interactions  
577 (Block et al. 2022). Nonetheless, the rapid responses to more intense warming and drying  
578 emphasize the crucial role of extreme events in driving community changes, triggering the loss  
579 of less resilient high-elevation species and facilitating swift colonizations by warm-adapted taxa.  
580 Even as taxonomic shifts appear to slow down over time, and warmed high-elevation  
581 communities stabilize, their vulnerability to extreme climatic events could further accelerate the  
582 rate of taxonomic changes, inducing a second wave of abrupt shifts. In fact, in transplant  
583 experiments in Switzerland and Austria, colonization of the low-elevation species started only  
584 three years after the transplantation, specifically after the drought in 2018, which led to  
585 significant species losses in transplanted high-elevation communities (Schuchardt et al. 2023b).  
586 With intense heatwaves and droughts becoming more common in mountainous areas (IPCC  
587 2022b), high-elevation communities may undergo multiple swift taxonomic changes, as  
588 evidenced by landscape-scale alterations following recent extreme events in the European Alps  
589 (Choler 2023).

590  
591 **Contributions of different species pools to changes in community composition**  
592 Changes in community composition under warming were influenced both by colonizing species from the  
593 destination site, and abundance shifts, including local extinctions, of strictly high-elevation species. On  
594 average, species gains from colonizing pools and losses from strictly high-elevation species pools, along  
595 with the rates of these changes, were of similar magnitude, albeit in opposite directions. This suggests that  
596 these two species pools contributed similarly to community changes. The large contributions of the  
597 strictly high-elevation species pool to the divergence of warmed communities from the high-elevation  
598 communities indicate that even after the first year of transplantation, decreasing relative abundances and



599 local extinction events of cold-adapted species under warming were important. Interestingly, a minority  
600 of experiments ( $n = 5$ ) displayed increasing relative abundance of this species pool over the years, which  
601 might be explained by a few species initially tolerating (or even benefiting from) climate change and/or  
602 altered plant-plant interactions under warming (Nomoto and Alexander 2021). Fewer losses from this  
603 species pool were detected in studies with shorter experimental durations. In longer-term experiments,  
604 despite overall losses, the strictly high-elevation species maintained enough abundance to significantly  
605 differentiate the warmed community from the destination controls even after nearly a decade. . In other  
606 words, many of these species appear able to persist for considerable periods of time under significant  
607 future warming. This is consistent with estimates of substantial extinction lags in alpine plant  
608 communities, especially when species continue to coexist with their original plant community via  
609 competition (Rumpf et al. 2019).

610  
611 Colonizing species also made large contributions to the difference in community composition between  
612 warmed and high-elevation communities over time, even though with substantial delays. This clearly  
613 demonstrates that under climate change, low-elevation species can colonize high-elevation plant  
614 communities if dispersal limitations are removed. This gives a first indication that the lags in range shifts  
615 observed in mountain floras (Rumpf et al. 2018, 2019) are at least partly explained by dispersal limitation,  
616 and that novel plant establishment should be expected once these limitations are overcome. Moreover,  
617 increasing colonizations in smaller plots, which have more exposure to the surrounding colonizing  
618 community at the edges due to a larger edge length ratio (e.g., 16 and 4 for 0.0625 and 1 m<sup>2</sup> plots,  
619 respectively), contradicts the expectation of colonist establishment from seeds, where larger plots should  
620 accommodate a higher probability of dispersal events. This implies that clonal growth may be a key factor  
621 facilitating the local expansion of low-elevation species once dispersal lags are overcome (Guittar et al.  
622 2016, Töpper et al. 2018). However, persisting colonization lags in our experiments even after almost a  
623 decade demonstrate that establishment lags play also a role in range shift dynamics, perhaps through  
624 plant-plant interactions within high-elevation communities (Meineri et al. 2020, Lyu and Alexander  
625 2022). Thus, future studies should explicitly investigate the biotic interactions between different species  
626 pools and their effects on plant demographic cycles.

627  
628 Overlapping species' contributions to community shifts were highly variable but on average close to zero.  
629 This does not imply that species in this pool were unaffected by warming. Instead, it suggests a spectrum  
630 of positive and negative responses across and within experiments: the overlapping species pool in each  
631 experiment contained a mixture of "winner" and "loser" species. Given that overlapping species  
632 demonstrate a larger niche in tolerating a broader range of environmental and biotic conditions at across  
633 elevations, their abundance change in the beginning of experiments may be stochastic. However, if  
634 originating from more resource-conservative communities, relative abundances of overlapping species  
635 increased more. Moreover, when in drier conditions than all other destinations, their relative abundances  
636 were lower than in destination controls. This indicates that responses to drought play a major role in  
637 mountain plant population dynamics and drought-tolerant species can be the winners of climate change in  
638 the mountains (Visakorpi et al. 2022).

#### 639 640 **Variation in responses across and within experiments due to biotic interactions?**

641 The large variation in magnitude and direction of species relative abundance changes, even within the  
642 same pool is typical for species-level responses to climate change (Rumpf et al. 2018, Töpper et al. 2018).

643 Only partly related to experimental design choices (e.g, plot size, duration, and climate context), much of  
644 the variation in species responses could be explained by destination or origin communities' functional  
645 traits. These traits, which indicate competitive abilities for acquiring light, water, and nutrients, suggest  
646 that plant-plant interactions and their temporal dynamics may play a role in the observed variation in  
647 population dynamics (Lynn et al. 2019, Meineri et al. 2020). For example, colonization lags persisted in  
648 warmed communities where resource-acquisitive plants were originally dominating. Perhaps, when high-  
649 elevation communities are competitive for resources such as soil nutrients and water, colonizers fail to  
650 establish. Moreover, we expected that warmed communities suffering competitive exclusion due to taller  
651 surrounding destination communities (Fig. S8). Yet, in destination sites dominated by taller-sized plants,  
652 species losses were lower and extinction lags were higher. This might suggest that biotic interactions  
653 between destination communities and strictly high-elevation species influence the population dynamics of  
654 the latter, possibly through tall and wide-leaved destination-species creating shade and thus, cooler  
655 microhabitats for intensely warmed high-elevation species. Finally, effects of functional traits were not  
656 consistent across the experimental period and they do not determine the rates of changes in communities  
657 and species contributions. This could indicate, on the one hand, initial stochastic losses and gains, on the  
658 other hand, plant-plant interactions needing time to adjust, being transient and leading to inconsistencies  
659 through feedback between them.

660

### 661 **Conclusions & Perspectives**

662 Our study underscores the dynamic shifts in high-elevation plant communities due to experimental  
663 climate warming, suggesting the formation and persistence of novel communities that complicate future  
664 predictions. While community taxonomic convergence towards lower elevations hints at a predictable  
665 trajectory under climate change, significant uncertainties due to local factors like climate and initial  
666 community composition highlight the need for localized studies. Future research should focus on the  
667 variability in temporal and spatial dynamics, investigate the causes of shifts in populations and  
668 communities, including the changes in biotic interactions. We encourage expanded collaborative  
669 macroecological experiments across diverse ecosystems to better understand plant community responses  
670 to climate change.

### 671 **Data Availability**

672 Raw and processed data are archived at Open Science Framework (OSF) under the following  
673 link [https://osf.io/9874t/?view\\_only=90e7bafd8eed40eb960a22ce3098c613](https://osf.io/9874t/?view_only=90e7bafd8eed40eb960a22ce3098c613)

674 Code to clean the raw data is available at: <https://github.com/Between-the-Fjords/TransPlant/>

675 Code to reproduce the analysis is available at:

676 [https://github.com/billurbektas/TransPlant\\_convergence\\_analysis/tree/review\\_V2](https://github.com/billurbektas/TransPlant_convergence_analysis/tree/review_V2)

677 Upon acceptance, the code will be published at Zenodo. TransPlant Network data and  
678 experiment-specific results can be visualized on the dedicated Shiny app:

679 <https://billurbektas.shinyapps.io/transplantshiny-1/>

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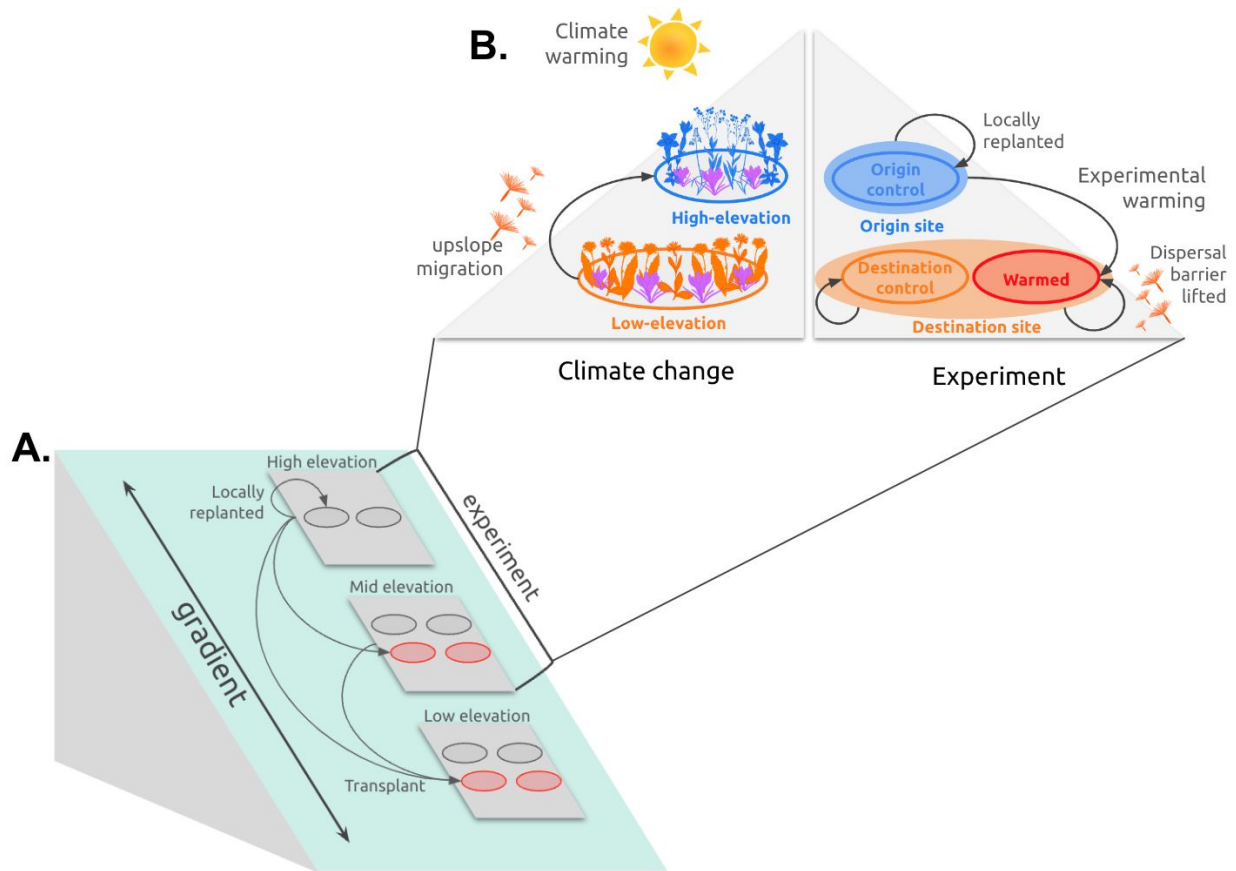
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3 **Fig. S1:** The general design of experiments included in the TransPlant network, indicating the  
 4 ecological processes simulated with whole-community transplant experiments. **A)** Each  
 5 TransPlant gradient comprises at least one pair of sites at high and lower elevation, which we  
 6 refer to as an “experiment”. **B)** Transplant experiments aim to simulate climate change by  
 7 transplanting whole plant communities to putative future climates at lower elevation. This  
 8 approach also lifts the dispersal barrier for colonizing species, thereby allowing colonization into  
 9 the transplanted communities from the low-elevation site (colonizing species). We refer to the  
 10 turfs transplanted from origin to destination sites as “warmed” communities (red circle), and to  
 11 turfs locally replanted at origin and destination sites as “origin” (blue circle) and “destination”  
 12 (orange circle) controls, respectively.

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21 **Table S1:** TransPlant Network experiments from different gradients across the Northern  
 22 Hemisphere. Mountain turfs were transplanted between high-elevation origin sites and low-  
 23 elevation destination sites. Coordinates are given in decimal degrees at the WGS84 projection  
 24 system. (CH: Switzerland, CN: China, DE: Germany, FR: France, IT: Italy, NO: Norway, SE:  
 25 Sweden, US: United States)  
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Gradient	Destination site	Origin site	Origin coordinates	Destination coordinates	Origin elevation	Destination elevation	Transplant year	Start of vegetation survey	Duration	Turf size (m <sup>2</sup> )	Number of replicates
CH_Calanda1	Nes	Cal	(46.89, 9.49)	(46.87,9.49)	2000	1400	2012	2013	6	0.75	10
CH_Calanda1	Cal	Pea	(46.89, 9.47)	(46.89,9.49)	2600	2000	2012	2013	6	0.75	10
CH_Calanda2	Nes	Cal	(46.89, 9.49)	(46.87,9.49)	2000	1400	2016	2017	4	1	10
CH_Lavey	CRE	RIO	(46.2, 7.06)	(46.22,7.05)	2200	1950	2016	2017	3	1	10
CH_Lavey	MAR	RIO	(46.2, 7.06)	(46.22,7.05)	2200	1750	2016	2017	3	1	10
CH_Lavey	PRA	RIO	(46.2, 7.06)	(46.22,7.04)	2200	1400	2016	2017	3	1	10
CN_Damxung	LOW	HIGH	(30.53, 91.05)	(30.5,91.06)	4800	4313	2013	2013	5	0.25	10
CN_Gongga	M	A	(29.89, 102.02)	(29.86,102.04)	3850	3500	2012	2012	4	0.06	7
CN_Gongga	A	H	(29.91, 102.01)	(29.89,102.02)	4100	3850	2012	2012	4	0.06	7
CN_Gongga	L	H	(29.91, 102.01)	(29.84,102.03)	4100	3000	2012	2012	4	0.06	7
CN_Gongga	L	M	(29.86, 102.04)	(29.84,102.03)	3500	3000	2012	2012	4	0.06	7
CN_Heibei	3200	3400	(37.67, 101.33)	(37.61,101.31)	3400	3200	2007	2007	9	1	3
CN_Heibei	3200	3800	(37.7, 101.37)	(37.61,101.31)	3800	3200	2007	2007	9	1	3
CN_Heibei	3400	3800	(37.7, 101.37)	(37.67,101.33)	3800	3400	2007	2007	9	1	3
DE_Grainau	LOW	HIGH	(47.44, 11.06)	(47.48,11.01)	1714	773	2013	2014	4	0.25	10
DE_Susalps	BT	EB	(47.52, 11.16)	(49.92,11.58)	1260	350	2016	2016	4	0.09	9
DE_Susalps	FE	EB	(47.52, 11.16)	(47.83,11.07)	1260	600	2016	2016	4	0.09	9
DE_Susalps	GW	EB	(47.52, 11.16)	(47.57,11.03)	1260	860	2016	2016	4	0.09	9

DE_Susalps	BT	FE	(47.83, 11.07)	(49.92,11.58)	600	350	2016	2016	4	0.09	9
DE_Susalps	BT	GW	(47.57, 11.03)	(49.92,11.58)	860	350	2016	2016	4	0.09	9
DE_Susalps	FE	GW	(47.57, 11.03)	(47.83,11.07)	860	600	2016	2016	4	0.09	9
DE_TransAlps	BT	FP	(46.58, 8.42)	(49.92,11.58)	2440	300	2016	2016	4	0.09	9
DE_TransAlps	BT	SP	(47.13, 11.31)	(49.92,11.58)	1850	300	2016	2016	4	0.09	9
FR_AlpeHuez	LOW	HIGH	(45.1, 6.06)	(45.09,6.04)	2072	1481	2014	2015	4	0.25	10
FR_Lautaret	L	G	(45.05, 6.4)	(45.04,6.42)	2450	1950	2016	2017	5	1	10
IT_MatschMazia1	Low	High	(46.69, 10.58)	(46.66,10.59)	1500	1000	2010	2010	3	0.25	3
IT_MatschMazia2	Low	High	(46.69, 10.59)	(46.69,10.58)	1950	1500	2010	2010	3	0.25	9
NO_Gudmedalen	Rambera	Gudmedalen	(60.83, 7.18)	(61.09,6.63)	1213	769	2009	2009	8	0.06	5
NO_Gudmedalen	Arhelleren	Rambera	(61.09, 6.63)	(60.67,6.34)	769	431	2009	2009	8	0.06	5
NO_Lavidalen	Vikesland	Hogsete	(60.88, 7.18)	(60.88,7.17)	700	474	2009	2009	8	0.06	5
NO_Lavidalen	Hogsete	Lavidalen	(60.82, 7.28)	(60.88,7.18)	1097	700	2009	2009	8	0.06	5
NO_Skjellingahaugen	Veskre	Skjellingahaugen	(60.93, 6.42)	(60.54,6.51)	1088	797	2009	2009	8	0.06	5
NO_Skjellingahaugen	Ovstedal	Veskre	(60.54, 6.51)	(60.69,5.96)	797	346	2009	2009	8	0.06	5
NO_Ulvhaugen	Fauske	Alrust	(60.82, 8.7)	(61.04,9.08)	815	589	2009	2009	8	0.06	5
NO_Ulvhaugen	Alrust	Ulvhaugen	(61.02, 8.12)	(60.82,8.7)	1208	815	2009	2009	8	0.06	5
SE_Abisko	Low	High	(68.29, 19.09)	(68.3,19.19)	1000	500	2012	2012	3	0.02	5
SE_Abisko	Mid	High	(68.29, 19.09)	(68.29,19.17)	1000	690	2012	2012	3	0.02	5
SE_Abisko	Low	Mid	(68.29, 19.17)	(68.3,19.19)	690	500	2012	2012	3	0.02	5
US_Arizona	PP	MC	(35.35, - 111.73)	(35.42,- 111.67)	2620	2344	2014	2014	4	0.09	7
US_Montana	Low	High	(45.31, - 111.5)	(45.31,- 111.5)	2185	1985	2013	2013	5	0.25	10



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**Table S2:** TransPlant Network experiments climatic conditions from different gradients across the Northern Hemisphere. Mountain turfs were transplanted between high-elevation origin sites and low-elevation destination sites. Coordinates are given in decimal degrees at the WGS84 projection system. We extracted temperature (°C) and Potential evapotranspiration PET (mm) from the ~1 km resolution CHELSA database for each site (Karger et al. 2021). We extracted monthly mean daily air temperature (°C) and potential evapotranspiration (PET) (mm) data from the ~1 km resolution CHELSA database (Karger et al. 2021) for each site. We calculated the average summer (June, July, August) temperature and annual PET for each site for each year of the experiment. We averaged the summer temperature and annual PET across all years for each experiment to calculate the origin and destination climates. (CH: Switzerland, CN: China, DE: Germany, FR: France, IT: Italy, NO: Norway, SE: Sweden, US: United States)

Gradient	Destination site	Origin site	Origin temperature (°C)	Destination temperature (°C)	Origin PET (mm)	Destination PET (mm)
CH_Calanda1	Nes	Cal	9.95	13.16	870.4	986.11
CH_Calanda1	Cal	Pea	6.18	9.95	719.43	870.4
CH_Calanda2	Nes	Cal	10.81	14.04	668.31	753.9
CH_Lavey	CRE	RIO	9.86	11.94	535.27	536.01
CH_Lavey	MAR	RIO	9.86	12.87	535.27	553.69
CH_Lavey	PRA	RIO	9.86	15.87	535.27	628.83
CN_Damxung	LOW	HIGH	8.24	9.95	1015.76	1114.02
CN_Gongga	M	A	9.62	10.69	883.35	898.22
CN_Gongga	A	H	8.39	9.62	856.57	883.35
CN_Gongga	L	H	8.39	12.25	856.57	909.2
CN_Gongga	L	M	10.69	12.25	898.22	909.2
CN_Heibei	3200	3400	8.73	9.52	837.13	846.76
CN_Heibei	3200	3800	6.15	9.52	791.59	846.76
CN_Heibei	3400	3800	6.15	8.73	791.59	837.13
DE_Grainau	LOW	HIGH	10.92	17.32	704.01	872.48
DE_Susalps	BT	EB	13.93	19.67	568.18	638.02
DE_Susalps	FE	EB	13.93	19.16	568.18	616.06
DE_Susalps	GW	EB	13.93	17.46	568.18	664.66

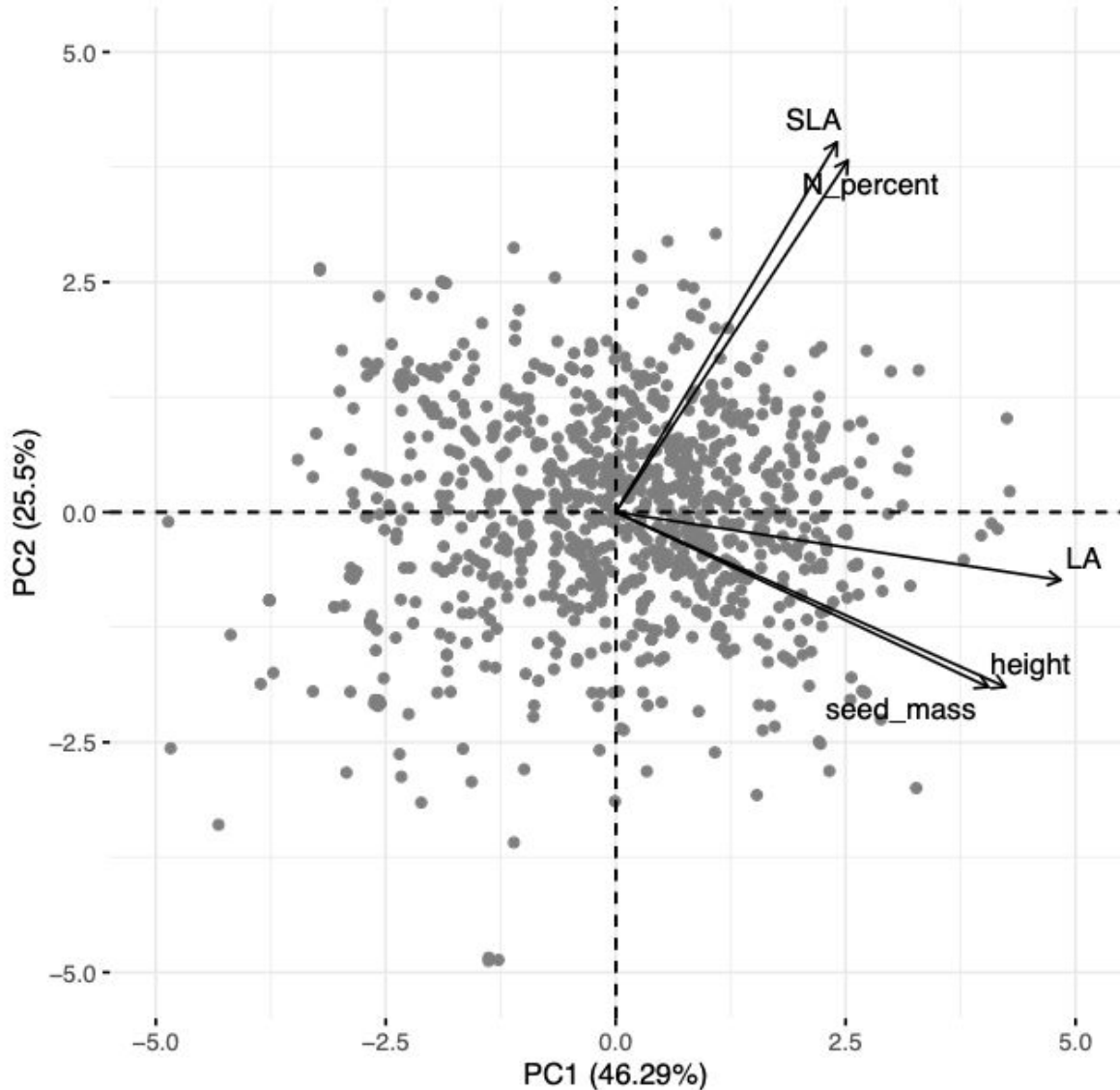


DE_Susalps	BT	FE	19.16	19.67	616.06	638.02
DE_Susalps	BT	GW	17.46	19.67	664.66	638.02
DE_Susalps	FE	GW	17.46	19.16	664.66	616.06
DE_TransAlps	BT	FP	8.58	19.67	589.13	638.02
DE_TransAlps	BT	SP	12.21	19.67	669.22	638.02
FR_AlpeHuez	LOW	HIGH	12.28	14.65	773.85	1004.04
FR_Lautaret	L	G	9.77	12.98	915.59	852.04
IT_MatschMazia1	Low	High	13.74	17.11	1028.07	984.98
IT_MatschMazia2	Low	High	9.66	13.74	912.37	1028.07
NO_Gudmedalen	Rambera	Gudmedalen	9.09	11.15	570.16	640.44
NO_Gudmedalen	Arhelleren	Rambera	11.15	13.07	640.44	588.12
NO_Lavidalen	Vikesland	Hogsete	11.86	13.34	485.61	480.45
NO_Lavidalen	Hogsete	Lavidalen	8.55	11.86	519.51	485.61
NO_Skjellingahau gen	Veskre	Skjellingahau gen	8.47	10.81	566.7	558.82
NO_Skjellingahau gen	Ovstedal	Veskre	10.81	13.03	558.82	529.71
NO_Ulvhaugen	Fauske	Alrust	11.54	12.96	553.81	593.94
NO_Ulvhaugen	Alrust	Ulvhaugen	8.85	11.54	564.58	553.81
SE_Abisko	Low	High	8.53	11.21	496.14	439.52
SE_Abisko	Mid	High	8.53	10.11	496.14	567.6
SE_Abisko	Low	Mid	10.11	11.21	567.6	439.52
US_Arizona	PP	MC	18.77	21.02	1203.18	1306.09
US_Montana	Low	High	13.25	13.96	841.12	840.17

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44 **Fig. S2:** Principal component analysis (PCA) of all TransPlant species' functional traits. Horn's  
 45 parallel analysis retained two principal components (PC) to represent the variation in the whole  
 46 functional trait space. LA (32%), vegetative height (22%), seed mass (22%) contributed the  
 47 most to the first PC followed by N-percent (14 %) and SLA (10%). SLA (43%) and N-percent  
 48 (29%) contributed the most to the second PC followed by vegetative height (16%), seed mass



49 (12%) and LA (1%). Thus, we defined the first two PCs as the plant-size and resource  
 50 acquisition related traits.

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56 **Table S3:** Number of unique species across all the years and percentages of each species  
 57 pools in experiments. By definition, strictly high-elevation species were only found in the higher-  
 58 elevation origin controls for each experiment, including high-elevation species relative to the  
 59 experiment. We note that these are not necessarily alpine plants in a biogeographic sense (i.e.,  
 60 species found mainly above the treeline). The colonizing low-elevation species pool includes

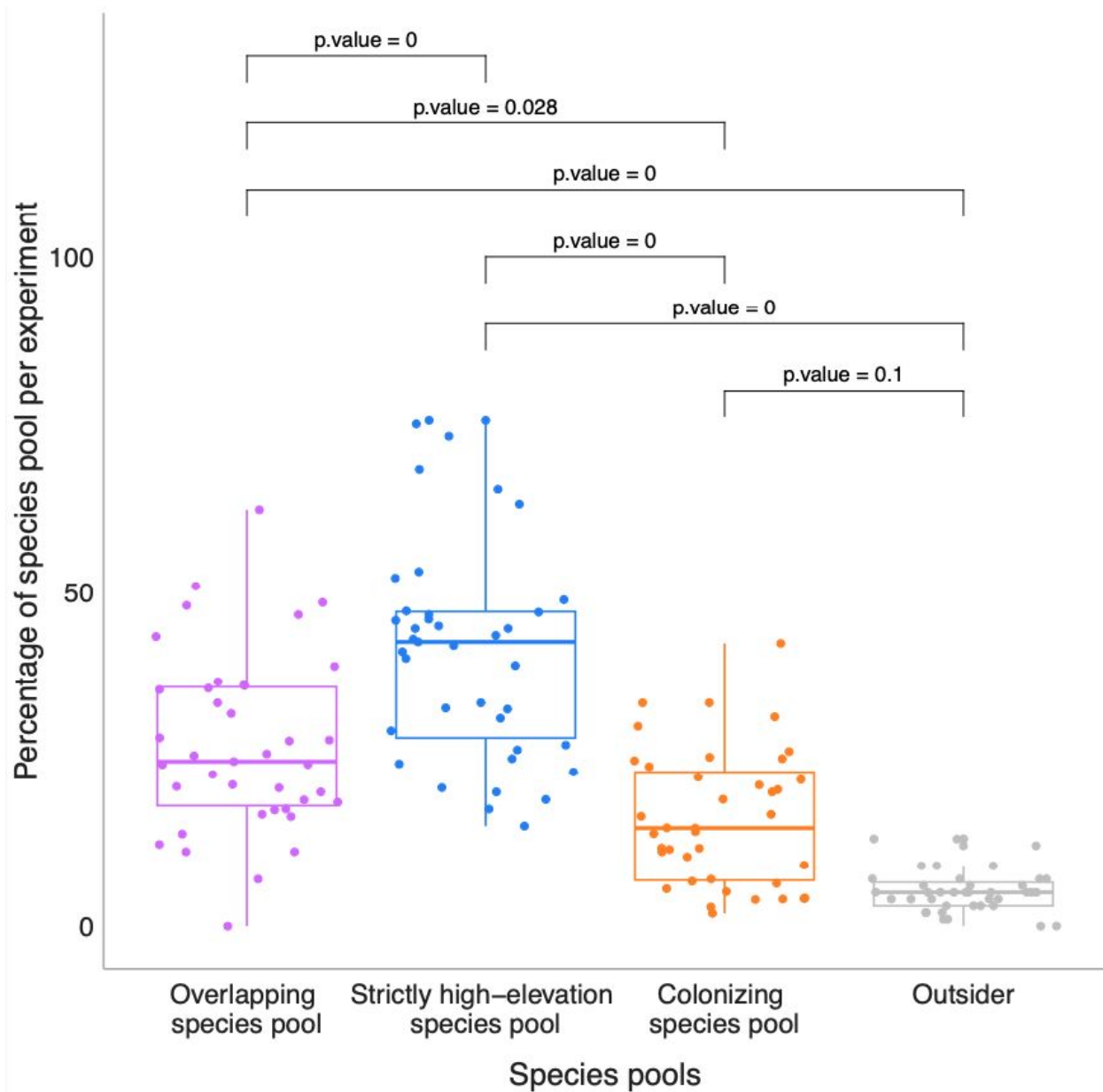
61 species that occur in destination controls but not in origin controls. Overlapping species are  
 62 found both in origin and destination controls. Species that occur in warmed communities only  
 63 (outsider species on the table), but are absent from both sets of controls, were excluded from  
 64 the analysis. Percentages of each species pool represent the proportion of species within the  
 65 total number of species in the experiment. Note that these percentages do not sum to 100%  
 66 because the experiments also include strictly low-elevation species, which are not investigated  
 67 in this study.  
 68

Region	Origin Site	Destination Site	Strictly high-elevation species (%)	Overlapping species (%)	Colonizing species (%)	Outsider species (%)	Number of species
NO_Ulvhaugen	Ulvhaugen	Alrust	43	28	21	3	76
NO_Ulvhaugen	Alrust	Fauske	17	51	22	5	63
NO_Lavidalen	Hogsete	Vikesland	27	43	19	4	37
NO_Lavidalen	Lavidalen	Hogsete	65	17	15	5	75
NO_Gudmedalen	Gudmedalen	Rambera	32	48	14	6	71
NO_Gudmedalen	Rambera	Arhelleren	47	28	22	3	64
NO_Skjellingahaugen	Skjellingahaugen	Veskre	26	36	25	7	76
NO_Skjellingahaugen	Veskre	Ovstedal	68	21	6	6	63
CH_Lavey	RIO	CRE	42	23	3	5	106
CH_Lavey	RIO	MAR	39	14	11	7	131
CH_Lavey	RIO	PRA	47	7	12	12	129
CH_Calanda	Pea	Cal	19	21	42	6	90
CH_Calanda	Cal	Nes	43	18	25	5	119
CH_Calanda2	Cal	Nes	42	26	2	5	105
US_Montana	High	Low	33	17	33	2	63
CN_Damxung	HIGH	LOW	73	12	15	2	41
CN_Gongga	A	M	40	25	20	4	55
CN_Gongga	H	A	41	25	16	4	61
CN_Gongga	H	L	63	11	20	7	54
CN_Gongga	M	L	49	36	5	5	39
CN_Heibei	3400	3200	24	62	9	4	66
CN_Heibei	3800	3200	21	37	24	3	63

CN_Heibei	3800	3400	15	39	30	9	67
DE_Grainau	HIGH	LOW	46	28	17	5	72
DE_Susalps	EB	GW	25	48	12	3	60
DE_Susalps	EB	BT	52	36	4	13	50
DE_Susalps	FE	BT	20	20	33	9	30
DE_Susalps	GW	BT	53	35	4	5	51
DE_Susalps	EB	FE	75	17	4	0	48
DE_Susalps	GW	FE	76	16	4	1	49
DE_TransAlps	FP	BT	46	0	26	9	46
DE_TransAlps	SP	BT	44	33	7	13	45
FR_AlpeHuez	HIGH	LOW	47	19	25	4	85
SE_Abisko	Mid	Low	31	24	14	2	29
SE_Abisko	High	Low	44	11	6	1	36
SE_Abisko	High	Mid	45	24	10	7	29
FR_Lautaret	G	L	23	32	11	5	126
IT_MatschMazia1	High	Low	33	47	7	0	43
IT_MatschMazia2	High	Low	29	21	31	5	48
US_Arizona	MC	PP	21	12	42	2	24

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71  
 72 **Figure S3:** Percentage of species pool per experiment over the total number of species across  
 73 all experimental years. By definition, strictly high-elevation species were only found in the  
 74 higher-elevation origin controls for each experiment, including high-elevation species relative to  
 75 the experiment. We note that these are not necessarily alpine plants in a biogeographic sense  
 76 (i.e., species found mainly above the treeline). The colonizing low-elevation species pool  
 77 includes species that occur in destination controls but not in origin controls. Overlapping species  
 78 are found both in origin and destination controls. Species that occur in warmed communities  
 79 only (outsider species on the table), but are absent from both sets of controls, were excluded  
 80 from the analysis.  
 81

82 **Table S4:** Principal response curve (PRC) results. Conditional, constrained, unconstrained and  
 83 PRC axes explained variances are in percentages. Conditional, constrained and unconstrained  
 84 explained variances are the percentages of total explained variance by the PRC. PRC axes  
 85 explained variances are the percentages of the constrained variances. PRC axis significances  
 86 are calculated by permuting the turfs freely across years 999 times. Significant axes: \*: p.values  
 87 <0.05, \*\*: p.values<0.01, \*\*\*: p.values<0.001 (CH: Switzerland, CN: China, DE: Germany, FR:  
 88 France, IT: Italy, NO: Norway, SE: Sweden, US: United States)  
 89

Region	Origin Site	Destination Site	Distance to	Conditional	Constrained	Unconstrained	PRC1	PRC2
NO_Ulvhaugen	Ulvhaugen	Alrust	Origin controls	3.83	37.4	58.76	76.68**	11.29
NO_Ulvhaugen	Alrust	Fauske	Origin controls	5.77	29.06	65.17	68.87**	15.65
NO_Lavidalen	Hogsete	Vikesland	Origin controls	8.46	23.77	67.77	59.59**	22.6
NO_Lavidalen	Lavidalen	Hogsete	Origin controls	4.94	42.29	52.77	75.48**	15.26*
NO_Gudmedalen	Gudmedalen	Rambera	Origin controls	2.44	27.31	70.25	70.48**	16.03
NO_Gudmedalen	Rambera	Arhelleren	Origin controls	3.92	27.28	68.8	67.61**	15.59
NO_Skjellinghaugen	Skjellinghaugen	Veskre	Origin controls	2.97	28.8	68.23	77.4**	10.86
NO_Skjellinghaugen	Veskre	Ovstedal	Origin controls	3.51	32.57	63.92	73.47**	14.9
CH_Lavey	RIO	CRE	Origin controls	6.82	57.67	35.51	82.75**	7.25**
CH_Lavey	RIO	MAR	Origin controls	5.8	59.24	34.96	79.42**	8.09**
CH_Lavey	RIO	PRA	Origin controls	9.56	57.54	32.9	74.41**	9.59**
CH_Calanda	Pea	Cal	Origin controls	2.57	48.13	49.3	86.77**	6.9**
CH_Calanda	Cal	Nes	Origin controls	5.7	49.22	45.07	76.25**	14.02*
CH_Calanda2	Cal	Nes	Origin controls	2.14	59.04	38.82	92.48**	4.68*
US_Montana	High	Low	Origin controls	3.89	30.12	65.99	84.05**	6.35
CN_Damxung	HIGH	LOW	Origin controls	16.76	51.31	31.93	69.73**	9.33**

CN_Gongga	A	M	Origin controls	3.6	37.45	58.94	80.6**	6.23
CN_Gongga	H	A	Origin controls	4.15	47.18	48.67	82.61**	6.31**
CN_Gongga	H	L	Origin controls	4.79	52.71	42.5	78.17**	10.9**
CN_Gongga	M	L	Origin controls	4.85	38.18	56.97	63.21**	23.61* *
CN_Heibei	3400	3200	Origin controls	33.13	38.14	28.73	59.82**	9.51**
CN_Heibei	3800	3200	Origin controls	32.61	48.2	19.19	50.67**	12.59* *
CN_Heibei	3800	3400	Origin controls	31.07	44.79	24.14	53.75**	14.68* *
DE_Grainau	HIGH	LOW	Origin controls	6.31	46.92	46.77	59.11**	25.8**
DE_Susalps	EB	GW	Origin controls	12.38	25.21	62.41	58.41**	25.49* *
DE_Susalps	EB	BT	Origin controls	7.23	30.06	62.71	66.28**	13.45* *
DE_Susalps	FE	BT	Origin controls	4.27	29.36	66.37	70.46**	15.67* *
DE_Susalps	GW	BT	Origin controls	4.51	30.22	65.26	58.55**	19.32* *
DE_Susalps	EB	FE	Origin controls	8.03	30.61	61.36	68.1**	15.27* *
DE_Susalps	GW	FE	Origin controls	4.7	31.87	63.43	59.71**	18.61* *
DE_TransAlps	FP	BT	Origin controls	3.68	41.67	54.65	68.69**	16.89* *
DE_TransAlps	SP	BT	Origin controls	4.99	28.04	66.98	64.49**	17.27* *
FR_AlpeHuez	HIGH	LOW	Origin controls	5.7	31.56	62.73	72.77**	9.48**
SE_Abisko	Mid	Low	Origin controls	1.79	28.31	69.91	71.85**	14.38
SE_Abisko	High	Low	Origin controls	1.36	32.39	66.25	81.24**	12.36
SE_Abisko	High	Mid	Origin controls	0.97	31.62	67.41	74.91**	19.42



FR_Lautaret	G	L	Origin controls	8.01	55.42	36.57	73.44**	11.7**
IT_MatschMazia 1	High	Low	Origin controls	8.56	35.58	55.86	54.5**	18.29*
IT_MatschMazia 2	High	Low	Origin controls	7.69	61.55	30.77	77.11**	12.2**
US_Arizona	MC	PP	Origin controls	8.87	28.77	62.37	61.63**	15.74*
NO_Ulvhaugen	Ulvhaugen	Alrust	Destination controls	3.83	37.4	58.76	76.68**	11.29
NO_Ulvhaugen	Alrust	Fauske	Destination controls	5.77	29.06	65.17	68.87**	15.65
NO_Lavidalen	Hogsete	Vikesland	Destination controls	8.46	23.77	67.77	59.59**	22.6
NO_Lavidalen	Lavidalen	Hogsete	Destination controls	4.94	42.29	52.77	75.48**	15.26*
NO_Gudmedalen	Gudmedalen	Rambera	Destination controls	2.44	27.31	70.25	70.48**	16.03
NO_Gudmedalen	Rambera	Arhelleren	Destination controls	3.92	27.28	68.8	67.61**	15.59
NO_Skjellingahaugen	Skjellingahaugen	Veskre	Destination controls	2.97	28.8	68.23	77.4**	10.86
NO_Skjellingahaugen	Veskre	Ovstedal	Destination controls	3.51	32.57	63.92	73.47**	14.9
CH_Lavey	RIO	CRE	Destination controls	6.82	57.67	35.51	82.75**	7.25**
CH_Lavey	RIO	MAR	Destination controls	5.8	59.24	34.96	79.42**	8.09**
CH_Lavey	RIO	PRA	Destination controls	9.56	57.54	32.9	74.41**	9.59**
CH_Calanda	Pea	Cal	Destination controls	2.57	48.13	49.3	86.77**	6.9**
CH_Calanda	Cal	Nes	Destination controls	5.7	49.22	45.07	76.25**	14.02*
CH_Calanda2	Cal	Nes	Destination controls	2.14	59.04	38.82	92.48**	4.68*
US_Montana	High	Low	Destination controls	3.89	30.12	65.99	84.05**	6.35
CN_Damxung	HIGH	LOW	Destination controls	16.76	51.31	31.93	69.73**	9.33**

CN_Gongga	A	M	Destination controls	3.6	37.45	58.94	80.6**	6.23
CN_Gongga	H	A	Destination controls	4.15	47.18	48.67	82.61**	6.31**
CN_Gongga	H	L	Destination controls	4.79	52.71	42.5	78.17**	10.9**
CN_Gongga	M	L	Destination controls	4.85	38.18	56.97	63.21**	23.61* *
CN_Heibei	3400	3200	Destination controls	33.13	38.14	28.73	59.82**	9.51**
CN_Heibei	3800	3200	Destination controls	32.61	48.2	19.19	50.67**	12.59* *
CN_Heibei	3800	3400	Destination controls	31.07	44.79	24.14	53.75**	14.68* *
DE_Grainau	HIGH	LOW	Destination controls	6.31	46.92	46.77	59.11**	25.8**
DE_Susalps	EB	GW	Destination controls	12.38	25.21	62.41	58.41**	25.49* *
DE_Susalps	EB	BT	Destination controls	7.23	30.06	62.71	66.28**	13.45* *
DE_Susalps	FE	BT	Destination controls	4.27	29.36	66.37	70.46**	15.67* *
DE_Susalps	GW	BT	Destination controls	4.51	30.22	65.26	58.55**	19.32* *
DE_Susalps	EB	FE	Destination controls	8.03	30.61	61.36	68.1**	15.27* *
DE_Susalps	GW	FE	Destination controls	4.7	31.87	63.43	59.71**	18.61* *
DE_TransAlps	FP	BT	Destination controls	3.68	41.67	54.65	68.69**	16.89* *
DE_TransAlps	SP	BT	Destination controls	4.99	28.04	66.98	64.49**	17.27* *
FR_AlpeHuez	HIGH	LOW	Destination controls	5.7	31.56	62.73	72.77**	9.48**
SE_Abisko	Mid	Low	Destination controls	1.79	28.31	69.91	71.85**	14.38
SE_Abisko	High	Low	Destination controls	1.36	32.39	66.25	81.24**	12.36
SE_Abisko	High	Mid	Destination controls	0.97	31.62	67.41	74.91**	19.42

FR_Lautaret	G	L	Destination controls	8.01	55.42	36.57	73.44**	11.7**
IT_MatschMazia 1	High	Low	Destination controls	8.56	35.58	55.86	54.5**	18.29*
IT_MatschMazia 2	High	Low	Destination controls	7.69	61.55	30.77	77.11**	12.2**
US_Arizona	MC	PP	Destination controls	8.87	28.77	62.37	61.63**	15.74* *

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**Table S5:** Results of linear mixed effects models to quantify the rate of divergence or convergence in community composition and the rate of deviance from their trajectories of divergence and convergence from the canonical coefficients of the warmed and control communities of the PRC axis 1 and axis 2, respectively. Linear mixed effects models were built for each axis and treatment group (warmed and control communities) with the experimental year (log-transformed), distance type (two-factor levels as distances between warmed-origin control and to warmed-destination control distances), experiment identity, and their three-way interactions as fixed effects, and gradient as a random effect. This table is complementary to the Fig. 3 in the main text.

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axis	treatment	Distance to	Slope estimate	SE	df	Lower CL	Upper CL	t.ratio	p.value	$R^2$ marginal	$R^2$ conditional
PRC1	control	Destination controls	-0.01	0.006	182	-0.021	0.002	-1.679	0.095	0.482	0.618
PRC1	control	Origin controls	-0.01	0.006	182	-0.021	0.002	-1.681	0.095	0.482	0.618
PRC1	warmed	Destination controls	-0.089	0.007	182	-0.103	-0.075	12.815	0	0.902	0.903
PRC1	warmed	Origin controls	0.074	0.007	182	0.06	0.087	10.62	0	0.902	0.903
PRC2	control	Destination controls	-0.002	0.005	182	-0.012	0.008	-0.398	0.691	0.452	0.672
PRC2	control	Origin controls	-0.002	0.005	182	-0.012	0.008	-0.398	0.691	0.452	0.672
PRC2	warmed	Destination controls	0.011	0.005	182	0.001	0.022	2.119	0.035	0.651	0.706
PRC2	warmed	Origin controls	0.044	0.005	182	0.034	0.054	8.322	0	0.651	0.706

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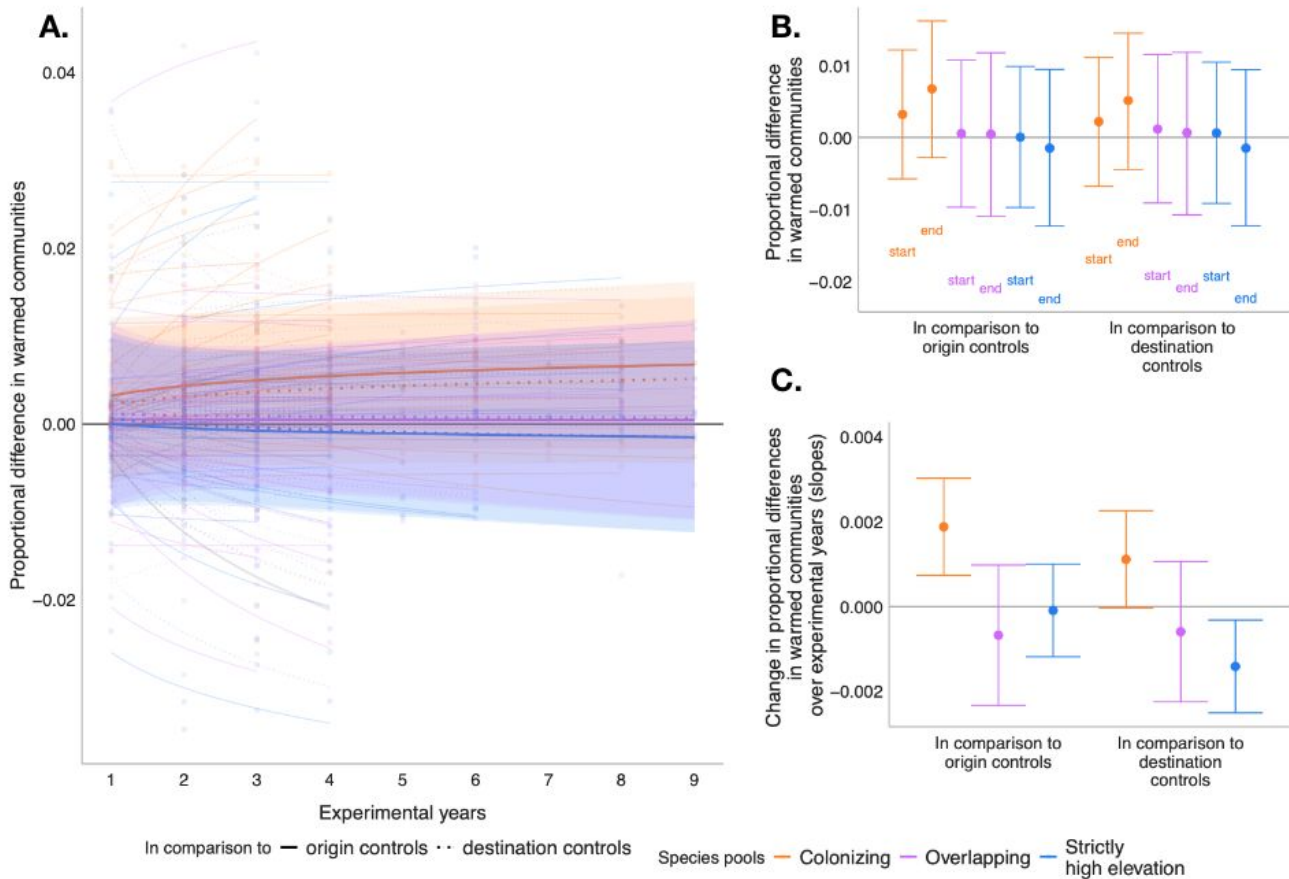
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109 **Table S6:** Results of linear mixed effects models to quantify the rate of changes proportional  
 110 differences in relative abundances in warmed communities in comparison to destination or  
 111 origin controls. Models were built for each axis and species pool with species' proportional  
 112 differences in relative abundances in warmed communities as the response variable with  
 113 experimental year (log-transformed), comparison type (to origin or destination control),  
 114 experiment identity, and their three-way interactions as fixed effects. We included species  
 115 nested in gradients as random effects. This table relates to Fig. 4 in the main text and Fig. S4 in  
 116 Appendix.  
 117

axis	treatment	pool	In comparison to	Slope estimate	SE	df	Lower CL	Upper CL	t.ratio	p.value	R <sup>2</sup> marginal	R <sup>2</sup> conditional
PRC1	warmed	overlapping	Destination controls	0.002	0.003	5253.055	0.004	0.009	0.682	0.495	0.078	0.14
PRC1	warmed	overlapping	Origin controls	0.002	0.003	5253.055	0.005	0.008	0.465	0.642	0.078	0.14
PRC1	warmed	strictly_high_elevation	Destination controls	-0.02	0.002	4467.229	0.025	0.016	-9.025	0	0.547	0.595
PRC1	warmed	strictly_high_elevation	Origin controls	-0.017	0.002	4467.229	0.022	0.013	-7.681	0	0.547	0.595
PRC1	warmed	colonizing	Destination controls	0.02	0.003	3366.971	0.013	0.027	5.826	0	0.54	0.566
PRC1	warmed	colonizing	Origin controls	0.018	0.003	3366.971	0.011	0.025	5.106	0	0.54	0.566
PRC2	warmed	overlapping	Destination controls	-0.001	0.001	5207.755	0.002	0.001	-0.706	0.48	0.066	0.555
PRC2	warmed	overlapping	Origin controls	-0.001	0.001	5207.755	0.002	0.001	-0.803	0.422	0.066	0.555
PRC2	warmed	strictly_high_elevation	Destination controls	-0.001	0.001	4453.13	0.003	0.000	-2.534	0.011	0.121	0.788
PRC2	warmed	strictly_high_elevation	Origin controls	0	0.001	4453.13	0.001	0.001	-0.168	0.867	0.121	0.788
PRC2	warmed	colonizing	Destination controls	0.001	0.001	3348.056	0.000	0.002	1.903	0.057	0.1	0.836
PRC2	warmed	colonizing	Origin	0.002	0.000	3348.	0.000	0.000	3.214	0.001	0.1	0.836

			controls		1	056	1	3				
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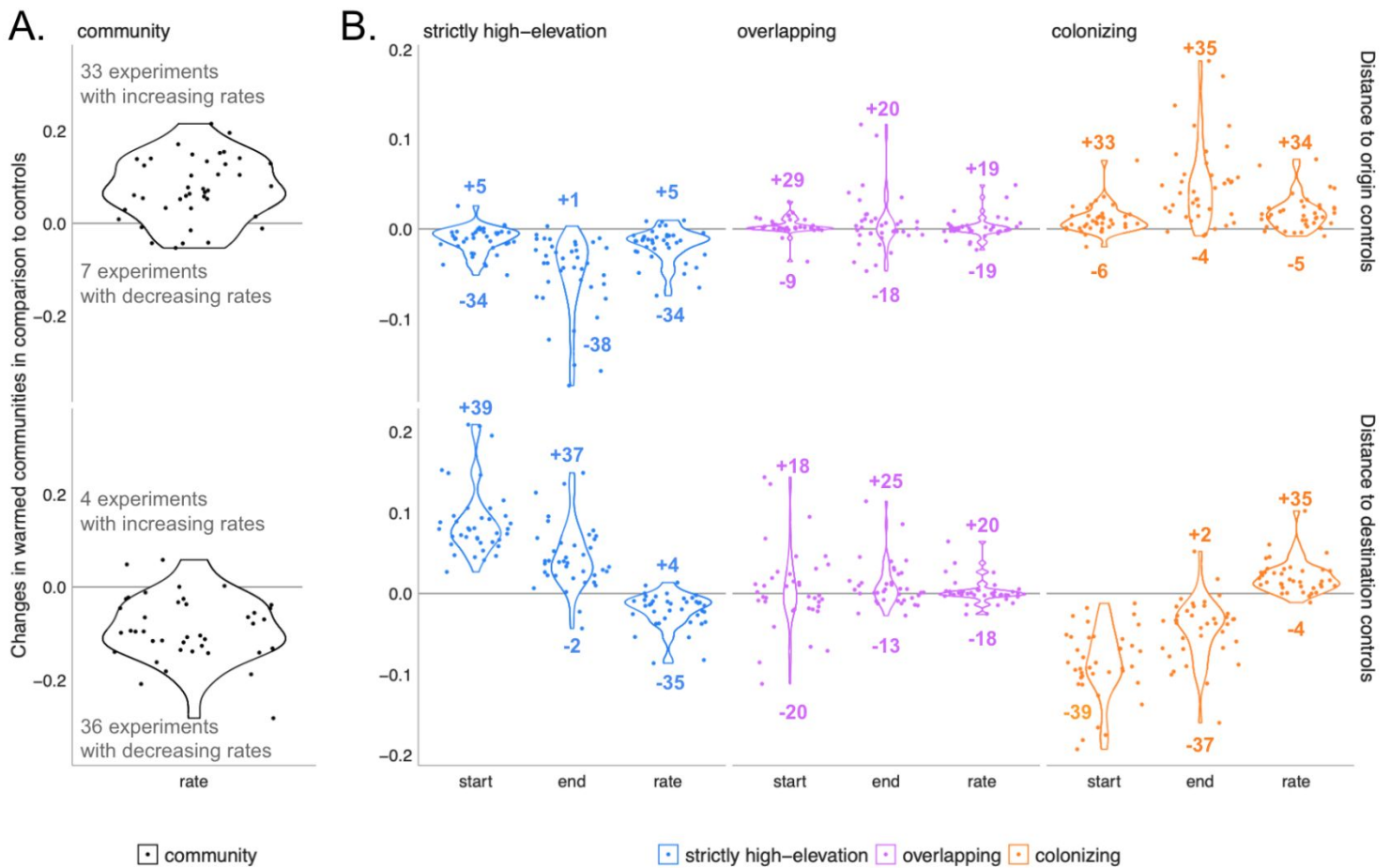
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125 **Fig. S4:** Changes in different species pools in warmed communities in comparison to controls over time. **A)**  
126 Proportional differences in relative abundances of each species pool in warmed communities in comparison to origin  
127 controls (solid lines) and destination controls (dotted lines) calculated from PRC2. Positive values indicate higher  
128 relative abundances in warmed communities, negative values indicate lower relative abundances in warmed  
129 communities. **B)** Predicted proportional differences in relative abundances of different species pools in warmed  
130 communities in comparison to controls at the start (year = 1) and end (year = 9, projected for shorter experiments) of  
131 the experiments. **C)** Rate of changes in proportional differences in warmed communities over log-transformed  
132 experimental years. When compared to origin controls, higher positive rates indicate faster species gains, lower  
133 negative rates indicate faster losses. When compared to destination controls, higher positive rates indicate faster  
134 decline in colonization lags (i.e., realization of colonization events), lower negative rates indicate faster decline  
135 in extinction lags (i.e., realization of extinction events). Note that lines in A are from models fitted with log-transformed  
136 experimental years. Responses of each experiment (fitted separately) and overall responses are shown in thin and  
137 thick lines respectively, with shading indicating the 95% confidence interval for the overall effect.  
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**Fig. S5:** Experimental variation in rates of changes in community and species pool levels calculated from PRC1. A) Rates of changes in distances between warmed and control communities. B) Proportional differences in relative abundances of different species pools in warmed communities in comparison to controls at the start and end (year = 9, projected estimates) of experiments and rates of proportional changes. Number experiments with increasing and decreasing values are indicated on the figure.

**Table S7:** Meta-regression model to reveal the effects of experimental, climatic and functional trait factors on the rates of community divergence and convergence. We built two separate meta-regression models to accommodate each of the two distance types ( to origin or

157 destination control) with rate of changes in community divergence or convergence as response  
 158 variable. These are slopes from the models described at S4 and visualized on Fig. 3 on the  
 159 main text. The effect sizes of different explanatory variables (moderators) from these models  
 160 are visualized on Fig. S6. Meta-regression modeling approach takes into account the  
 161 uncertainty around the response variables. In these models, experimental (turf size,  
 162 experimental warming, duration), and climate factors (summer temperature and annual PET of  
 163 destination sites) and functional traits (CWM of plant size and resource acquisition traits) were  
 164 included as explanatory variables.

165  $I^2$  : (residual heterogeneity / unaccounted variability)

166  $H^2$ : (unaccounted variability / sampling variability)

167  $\tau^2$ : (estimated amount of residual heterogeneity)  $\tau^2$  should be reduced as moderators added.

168 Q-test: Test for residual heterogeneity. Q-test is significant if the response variable is different  
 169 across studies.

170 Q-M-test: Test of moderators. Q-M-test is significant if the moderators can explain the variability  
 171 across studies.

172

Distance to	pool	type	$I^2$	$H^2$	$\tau^2$	SE $\tau^2$	Q-test	Q-test p.value	Q-M-test	Q-M-test p.value	df.residual
Destination controls	overall	rate	58.01	2.38	0.0	0.0	70.16	0	17.39	0.04	30
Origin controls	overall	rate	45.32	1.83	0.0	0.0	53.89	0	27.18	0	30

173

174 **Table S8:** Meta-regression model to reveal the effects of experimental, climatic and functional  
 175 trait factors on the starting, ending and rates of proportional changes in relative abundances of  
 176 the species pools in warmed communities in comparison controls. At species pool-level, we built  
 177 18 separate meta-regression models to accommodate each of the two comparison types (to  
 178 origin or destination control) and three species pools with three response variables: i) slopes at  
 179 species pool-level, ii) initial and iii) final proportional differences in species-pool relative  
 180 abundances. In these models, experimental (turf size, experimental warming, duration), and  
 181 climate factors (summer temperature and annual PET of destination sites) and functional traits  
 182 (CWM of plant size and resource acquisition traits) were included as explanatory variables. The  
 183 effect sizes from these models are given on Fig.5 on the main text and on Fig. S7 in Appendix.

184  $I^2$  : (residual heterogeneity / unaccounted variability)

185  $H^2$ : (unaccounted variability / sampling variability)

186  $\tau^2$ : (estimated amount of residual heterogeneity)  $\tau^2$  should be reduced as moderators added.

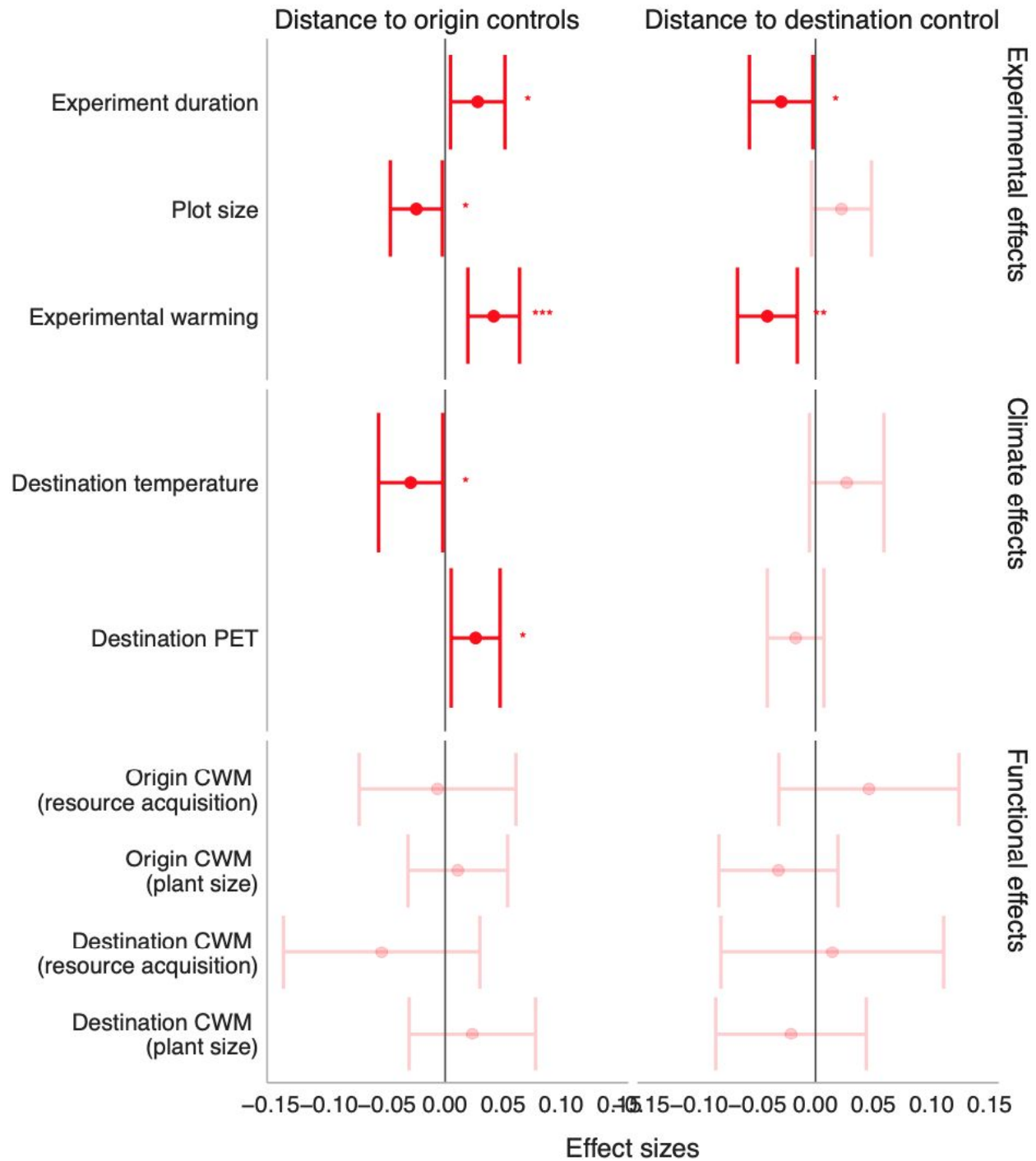
187 Q-test: Test for residual heterogeneity. Q-test is significant if the response variable is different  
 188 across studies.

189 Q-M-test: Test of moderators. Q-M-test is significant if the moderators can explain the variability  
 190 across studies.

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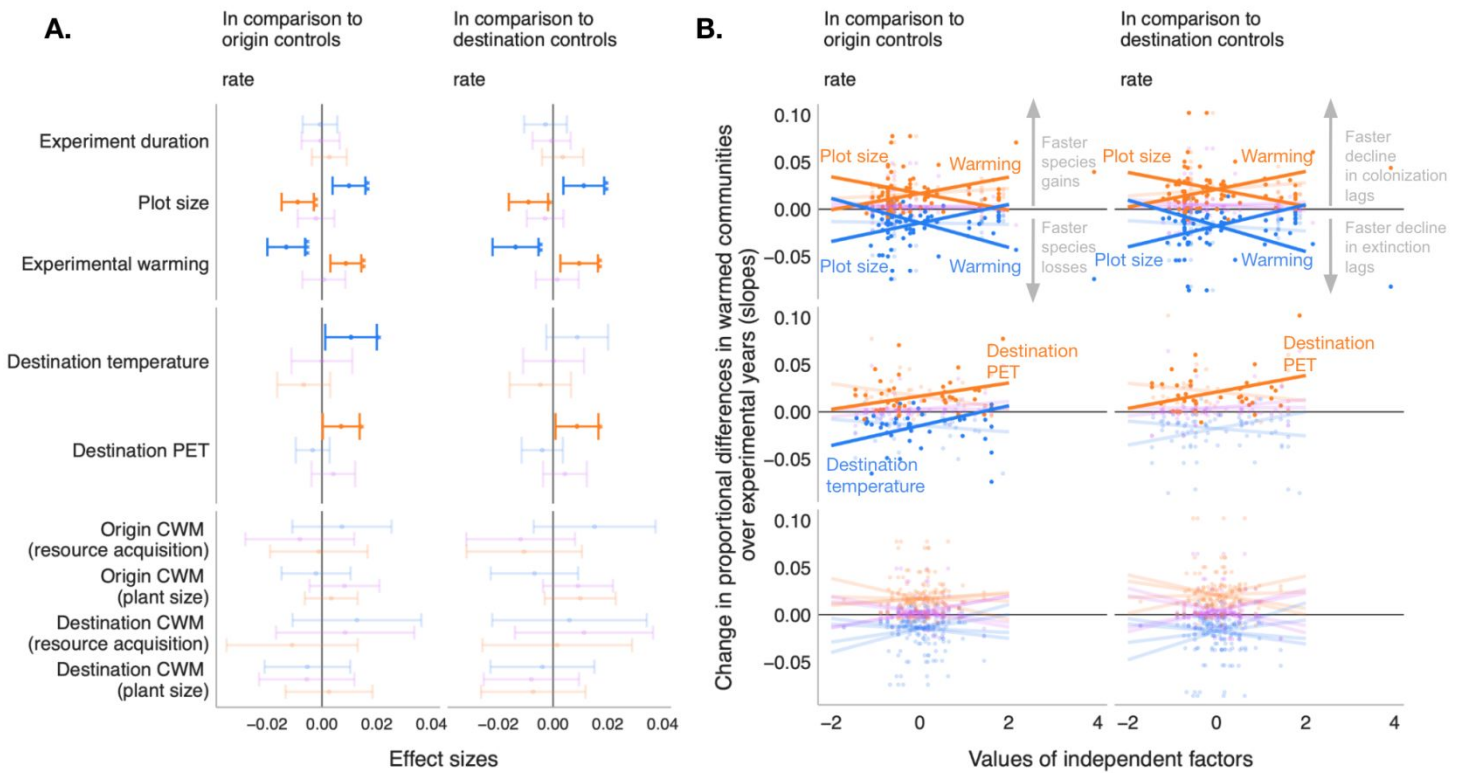
Distance to	pool	type	$I^2$	$H^2$	$\tau^2$	SE $\tau^2$	Q-test	Q-test p.value	Q-M-test	Q-M-test p.value	df.residual
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Destination controls	overlapping	rate	0	1	0	0	12.03	1	5.53	0.79	28
Origin controls	overlapping	rate	0	1	0	0	8.22	1	4.18	0.9	28
Destination controls	strictly high-elevation	rate	59.74	2.48	0	0	67.99	0	21.17	0.01	29
Origin controls	strictly high-elevation	rate	39.37	1.65	0	0	46.63	0.02	26.06	0	29
Destination controls	colonizing	rate	25.46	1.34	0	0	37.63	0.13	17.14	0.05	29
Origin controls	colonizing	rate	0	1	0	0	27.28	0.56	18.83	0.03	29
Destination controls	overlapping	start	79.65	4.91	0	0	116.18	0	22.43	0.01	28
Destination controls	overlapping	end	0	1	0	0	21.75	0.79	7.54	0.58	28
Origin controls	overlapping	start	0	1	0	0	5.47	1	1.56	1	28
Origin controls	overlapping	end	0	1	0	0	26.09	0.57	18.83	0.03	28
Destination controls	strictly high-elevation	start	82.89	5.84	0	0	164.75	0	46.22	0	29
Destination controls	strictly high-elevation	end	69.86	3.32	0	0	79.13	0	20.96	0.01	29
Origin controls	strictly high-elevation	start	2.84	1.03	0	0	26.2	0.61	30.17	0	29
Origin controls	strictly high-elevation	end	81.17	5.31	0	0	128.84	0	29.96	0	29
Destination controls	colonizing	start	81.53	5.41	0	0	126.61	0	9.97	0.35	29
Destination controls	colonizing	end	58	2.38	0	0	57.97	0	16.79	0.05	29
Origin controls	colonizing	start	0	1	0	0	18.87	0.92	12.44	0.19	29
Origin controls	colonizing	end	77.17	4.38	0	0	102.8	0	19.52	0.02	29

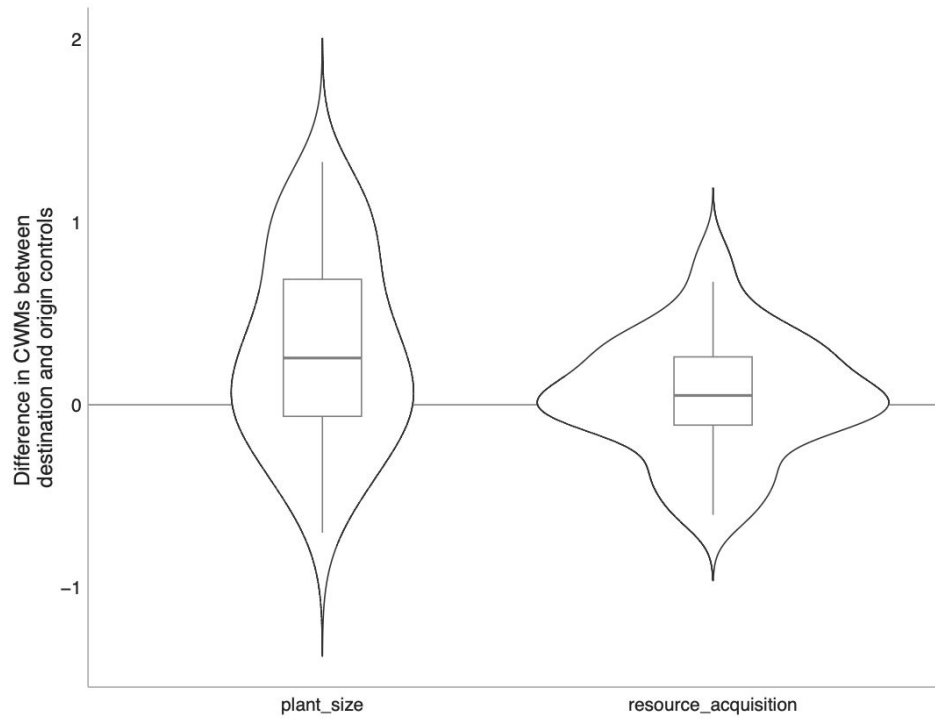


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**Fig. S6:** Effect sizes of experimental, climate and functional effects on the rate of changes in taxonomic distances. For experimental and functional effects, positive effect sizes indicate longer experiment duration, bigger plot sizes, stronger experimental warming, warmer and drier destination site. For functional effects, positive effect sizes indicate origin and destination control communities dominated on average by fast-growing (high SLA and leaf nitrogen) and taller species with wider leaves and heavier seeds (Fig. S1).



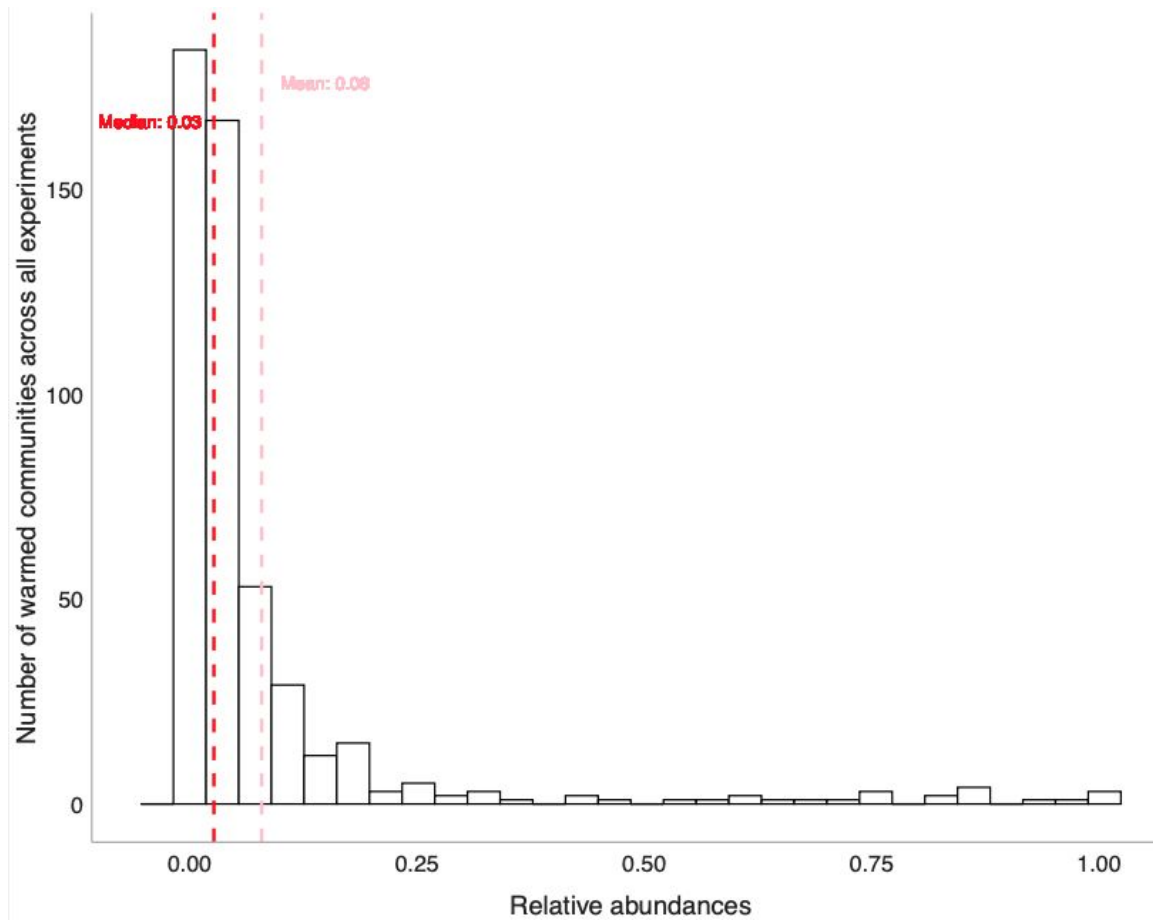
202 **Fig. S7: A)** Magnitude of experimental, climatic and functional trait effects on the rates of changes in species pool  
 203 contributions (change in species pools' proportional relative abundance changes in warmed communities in  
 204 comparison to controls) **B)** Relationships in species pool rates of changes with experimental, climatic and functional  
 205 trait factors. In B, only significant associations as quantified in A are shown and labeled. Linear metaregression  
 206 models were built independently per species pool. All explanatory variables were standardized (i.e. z-score  
 207 normalization).  
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**Fig. S8:** Differences in community weighted means in plant size (PC1 from the functional traits PCA Fig. S2) and resource-acquisition (PC2 from the functional traits PCA) related traits between destination and origin controls. Positive values indicate higher CWMs in destination control communities than in origin control communities.





234 **Fig. S9:** Distribution of relative abundances within a warmed community of outsider species  
235 (i.e., Species that occur in warmed communities only but are absent from both sets of controls)  
236 across all experiments and all years.

1 **Title:** Colonization and extinction lags drive non-linear responses to warming in mountain plant  
2 communities across the Northern Hemisphere

### 4 **Abstract**

5 Global warming is changing plant communities due to the arrival of new species from warmer  
6 regions and declining abundance of cold-adapted species. However, experimentally testing  
7 predictions about trajectories and rates of community change is challenging because we  
8 normally lack an expectation for future community composition, and most warming experiments  
9 fail to incorporate colonization by novel species. To address these issues, we analyzed data  
10 from 44 whole-community transplant experiments along 22 elevational gradients across the  
11 Northern Hemisphere, ~~where~~. In these experiments, high-elevation communities were  
12 transplanted to lower elevations to simulate warming, while also removing dispersal barriers ~~to~~  
13 establishment by lower ~~-~~ elevation species to establish. We quantified the extent and pace at  
14 which warmed high-elevation communities shifted towards the taxonomic composition of lower  
15 elevation communities.

16  
17 High-elevation plant communities converged towards the composition of low-elevation  
18 communities, with higher rates under stronger experimental warming. Strong community shifts  
19 occurred in the first year after transplantation then slowed over time, such that communities  
20 remained distinct from ~~either~~both origin ~~or~~and destination control by the end of the experimental  
21 periods (3-9 years). Changes were driven to a similar extent by both new species colonization  
22 and abundance shifts of high-elevation species, but with substantial variation across  
23 experiments that could be partly explained by the magnitude and duration of experimental  
24 warming, plot size and functional traits.

25  
26 Our macroecological approach reveals that while warmed high-elevation communities  
27 increasingly resemble communities at lower elevations today, the slow pace of taxonomic shifts  
28 implies considerable colonization and extinction lags, where a novel taxonomic composition of  
29 both low- and high-elevation species could coexist for long periods of time. The important  
30 contribution of the colonizing species to community change also indicates that once dispersal  
31 barriers are overcome, warmed high-elevation communities are vulnerable to encroachment  
32 from lower elevation species.

### 33 **Introduction**

34 Changes in the composition of vegetation along steep elevation gradients reveal the role of  
35 climate as a powerful force in structuring plant communities (Giaccone et al. 2019, Chauvier et  
36 al. 2021), and now, climate warming is restructuring plant communities (Harrison 2020, IPBES  
37 2023). Climate change effects are especially prominent at higher elevations in mountains,  
38 where temperatures are rising faster than the global average (Pepin et al. 2022). The  
39 abundance and species composition of mountain plant communities are changing as extant  
40 populations respond to new environmental conditions and as species migrate upslope to track  
41 their preferred climate (Fig. 1B) (Lenoir et al. 2008, Rumpf et al. 2018). However, vegetation  
42 changes are strongly lagging behind expectations based on the pace of climate warming, due to  
43 lags in both local extinction (Rumpf et al. 2019) and colonization events (Zu et al. 2021). One

44 expectation is that over time, these lags will be overcome and high-elevation plant communities  
45 will increasingly resemble communities that are currently found at lower elevation (Jurasinski  
46 and Kreyling 2007, Savage and Vellend 2015). Alternatively, priority effects and novel plant-  
47 plant-climate interactions might set communities on alternative trajectories, yielding “no-analog”  
48 communities, as has occurred under past climatic changes (Overpeck et al. 1992, Leopold et al.  
49 2015, Staples et al. 2022) as well as during current climate warming (Roth et al. 2014). Insight  
50 into the trajectory and pace of changes in plant community composition will therefore be  
51 important to accurately forecast the impacts of climate change on biodiversity in mountainous  
52 regions.

53

54 Since both the trajectory and pace of changes in community composition depend on the  
55 combined effects of colonization rates, local extinctions, and abundance shifts, we can gain  
56 insights into the relative importance of these processes by explicitly examining the response to  
57 warming of three distinct species pools (Lynn et al. 2021). Firstly, species that are restricted to  
58 high elevation (hereafter, “strictly high-elevation species”) are generally expected to respond  
59 negatively to warming and eventually become locally extinct (Geppert et al. 2023). This could  
60 happen either because they are poorly adapted to warmer conditions, or because they are  
61 poorer competitors for resources, such as light, that become increasingly limiting as warm-  
62 adapted, lower-elevation species arrive and increase in abundance (Alexander et al. 2015,  
63 Olsen et al. 2016). Secondly, species that occur in both high and low-elevation communities  
64 (hereafter, “overlapping species”), and thus that are adapted to a wider range of climatic and  
65 biotic conditions, might benefit from climate warming and increase in abundance (Lynn et al.  
66 2021). Finally, new species that migrate upslope from low elevation will establish in high-  
67 elevation communities and increase in abundance (hereafter, “colonizing species”). The relative  
68 contribution of these three local species pools – strictly high-elevation, overlapping, and  
69 colonizing species – to community shifts in response to climate change will depend on their  
70 reaction time (e.g., dispersal, establishment and extinction lags; Alexander et al. 2018) and the  
71 magnitude of warming. Disentangling responses of these different species pools can help  
72 anticipate the trajectory and rate of changes in high-elevation vegetation and the consequences  
73 for species’ range shifts under future climate.

74

75 Manipulative experiments are key to studying possible long-term changes in community  
76 composition in response to climate warming. *In situ* warming experiments, for example using  
77 passive warming chambers, have been most commonly employed to reveal shifts in mountain  
78 plant communities towards assemblages more typical of lower elevations (Henry et al. 2022).  
79 However, *in situ* experiments do not capture the contribution of all species pools to community  
80 change, most notably that of colonizing species. This is because the pool of potential colonists  
81 is typically absent due to dispersal lags, unless this aspect is intentionally manipulated. Whole-  
82 community transplant experiments, which simulate climate change by moving plant communities  
83 with their soils to a new location representing possible future climate conditions, overcome this  
84 problem by simultaneously exposing communities to a change in climate and potential  
85 colonization by species from the destination transplant site (Fig. 1A). They thus offer a powerful  
86 way to examine the trajectory of mountain plant communities under future climate change, and  
87 how these trajectories are underlain by different species pools once dispersal barriers are lifted.

88  
89 Individual transplant experiments have already indicated shifts in species' population dynamics  
90 (Töpper et al. 2018), relative abundances (Yang et al. 2018, Block et al. 2020, Visakorpi et al.  
91 2022, Niu et al. 2023), colonization and extinction events (Vandvik et al. 2020, Schuchardt et al.  
92 2023a) and community assembly processes (Bektaş et al. 2023). Collectively, these studies  
93 suggest that under experimental climate change, transplanted high-elevation communities can  
94 restructure quickly and resemble lower-elevation communities. While the magnitude and pace of  
95 these shifts remain unknown, species pools driving changes in community composition can be  
96 region and experiment-dependent. For example, in a transplant experiment in Norway,  
97 transplanted turfs were rapidly colonized by low-elevation species, which negatively impacted  
98 high-elevation species within the community through novel competitive interactions (Vandvik et  
99 al. 2020) In contrast, an experiment in France, shifts in relative abundances within the existing  
100 communities drove the community reassembly (Bektaş et al. 2023). Furthermore, the functional  
101 strategies of individual plant species that benefit from climate change exhibit both general and  
102 region-specific responses. For example, taller species become more abundant under  
103 experimental warming in experiments from Switzerland (Visakorpi et al. 2022) and Norway  
104 (Guittar et al. 2016), where taller species have also lower extinction rates (Lynn et al. 2023).  
105 However In addition, while species with slow resource acquisition were favored under warming  
106 in Switzerland (Visakorpi et al. 2022), species with fast resource acquisition strategies coming  
107 from warmer habitats colonized and increased their abundance more in colder sites in Norway  
108 (Lynn et al. 2023). These regional differences might arise from variations in limiting resources  
109 and how they are impacted by climate change, as well as from differences in the magnitude or  
110 duration of the experimental warming (Elmendorf et al. 2012). Consequently, it remains unclear  
111 whether we can make general predictions about the trajectory and pace of taxonomic responses  
112 to warming, and to what extent context-dependencies can be attributed to regional climatic or  
113 ecological or experimental differences.

114  
115 A macroecological experimental approach (Box 1) can allow us to identify general patterns in  
116 community composition change under climate change, while quantifying regional and  
117 experimental differences (Alexander et al. 2016). Here, we combine, for the first time, vegetation  
118 surveys spanning 2-9 years from a network of 44 whole-community downslope transplant  
119 experiments along 22 elevation gradients across the Northern Hemisphere to ask: i) To what  
120 extent does the species composition of warmed high-elevation communities diverge from the  
121 non-warmed high-elevation communities and converge towards that of low-elevation  
122 communities over time? ii) How do different species pools (strictly high-elevation, overlapping,  
123 or low-elevation colonizing species) contribute to divergence or convergence in plant community  
124 composition associated with climate change? iii) Is variation in overall rates of community  
125 change across experiments, as well as the average contribution of different pools to divergence  
126 or convergence, influenced by experimental design, the climate context of the study site, or  
127 plant functional trait composition?

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### Box 1: TransPlant Network

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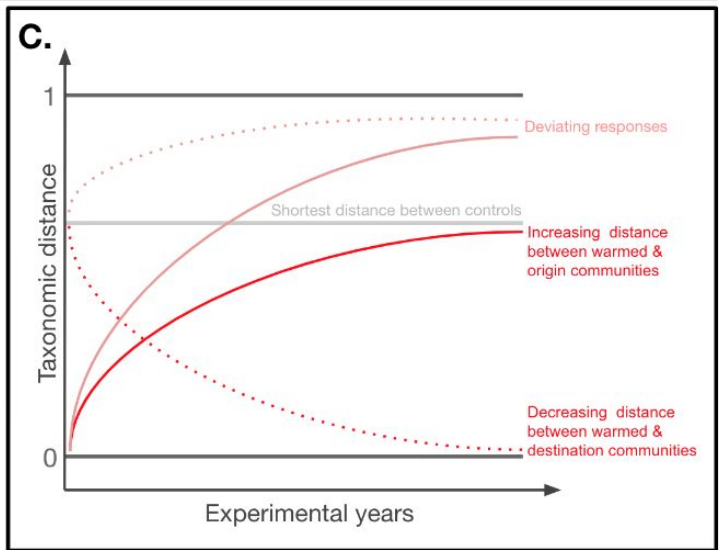
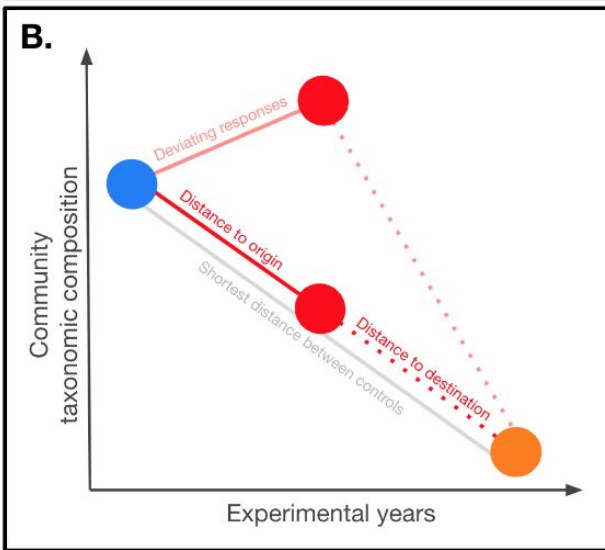
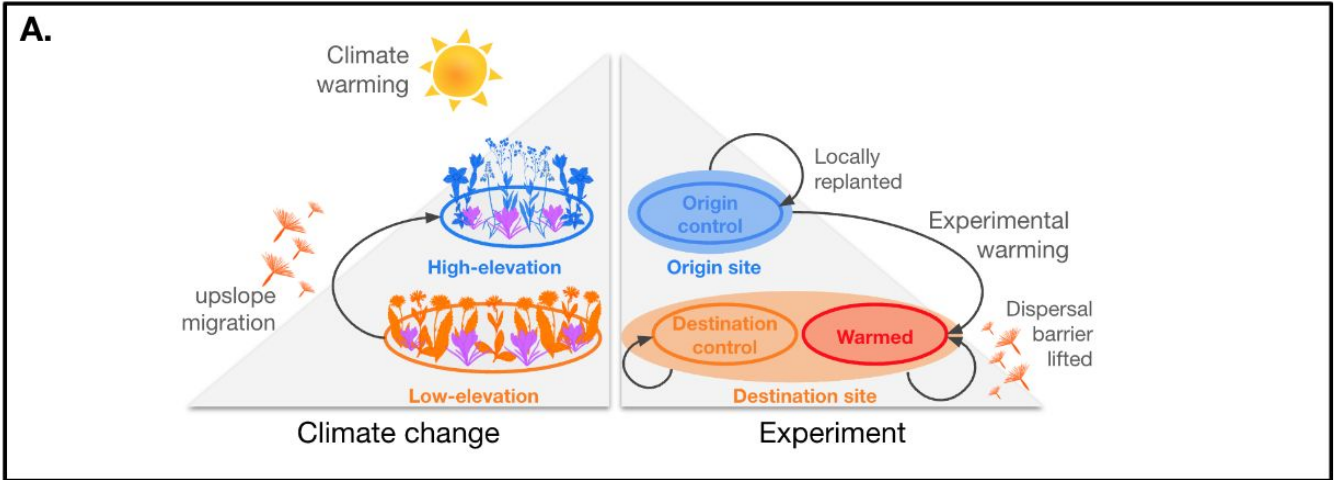
TransPlant is a network of 22 elevation gradients, distributed across 20 different mountainous regions of the Northern Hemisphere, where whole plant communities have been transplanted to lower elevations to simulate climate change (**Fig. 1-2, Table S1-2**). The basic design of the transplant experiments involve the transplantation of vegetation turfs (or “monoliths”) of whole plant communities with their soil from a higher (cooler) to a lower (warmer) elevation site to simulate climate warming (“warmed” treatment) (**Fig. 1A**). Moving plant communities to lower elevation in this way allows plants from the lower elevation site to quickly colonize transplanted turfs, also simulating the arrival of the novel species into high elevation communities that we expect to arrive following climate warming (**Fig. 1A**). For any given set of warmed turfs, there are “origin controls” (high-elevation turfs locally transplanted at their high-elevation site of origin) and “destination controls” (low-elevation turfs locally transplanted at the low-elevation site of destination) (**Fig.1A**). Thus, these controls make it possible to disentangle potential transplantation artifacts from the effects of experimental climate change. Along some TransPlant gradients, multiple experiments are conducted by transplanting the turfs from high to mid, mid to low, high to low elevations (**Fig. S1A**). We refer to a set of warmed, origin and destination control turfs within each gradient as an “experiment” (**Fig. 1A**), yielding a total of 40 experiments because 12 gradients were composed of more than two sites (Table S1-2). The experiments were established between 2007 and 2017. Each experiment had 3-10 replicates of transplant and control turfs, and in total there were 668 turfs varying in sizes between 0.02 m<sup>2</sup> and 1 m<sup>2</sup> with a mean size of 0.3 m<sup>2</sup> across the 40 experiments. TransPlant Network data and experiment-specific results can be visualized on the dedicated Shiny app: <https://billurbektas.shinyapps.io/transplantshiny-1/>

(End of Box 1)

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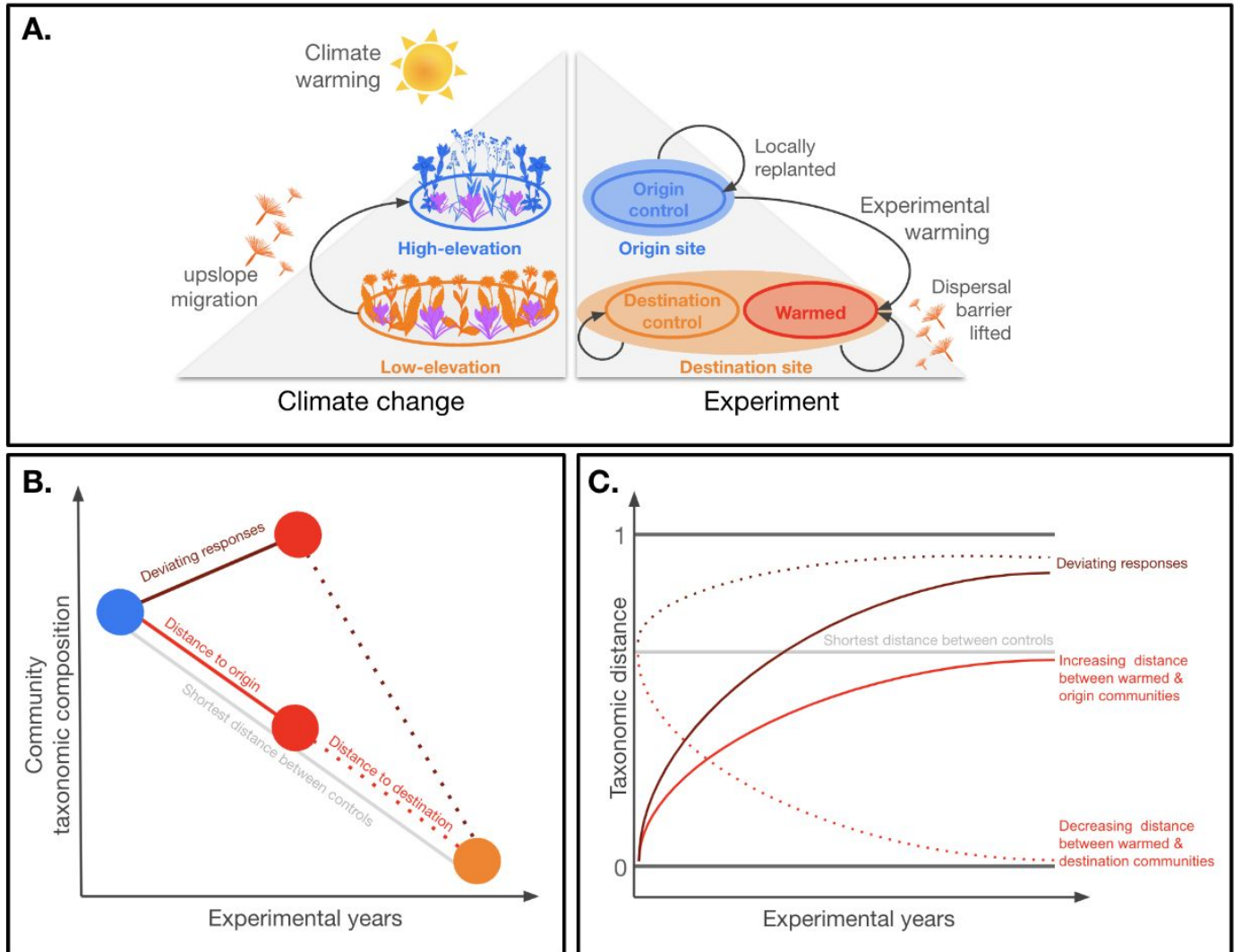
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**Fig. 1:** Overview of experimental designs in the TransPlant network, illustrating the ecological processes simulated through whole-community translocation and the analytical framework used to study community shifts post-transplantation. **A)** Transplant experiments aim to simulate climate change by transplanting whole plant communities to putative future climates at lower elevation. This approach also lifts the dispersal barrier for colonizing species, thereby allowing colonization into the transplanted communities from the low-elevation site (colonizing species). We refer to the turfs transplanted from origin to destination sites as “warmed” communities (red circle), and to turfs locally replanted at origin and

215 destination sites as “origin” (blue circle) and “destination” (orange circle) controls, respectively. **B)** Our  
216 expectation is that the warmed communities (red circle) will diverge in taxonomic composition from the  
217 origin controls (blue circle) and increasingly resemble the destination controls (orange circle), following  
218 the shortest distance between the controls over the years after transplantation. However, communities  
219 might deviate from this expected trajectory of resembling destination controls (red lines), showing  
220 deviating responses (pink lines). To quantify the degree of divergence from origin controls (solid lines) or  
221 convergence towards destination controls (dotted lines), we calculate the taxonomic distances of warmed  
222 communities to either origin or destination controls, respectively. **C)** Over the experimental years, we  
223 expect that taxonomic distances between warmed and control communities change. If warmed  
224 communities follow the expected trajectory (red lines), the distance between warmed and origin control  
225 communities will increase (red solid line) and the distance between warmed and destination control  
226 communities will decrease (red dotted line). If the distance between warmed communities and origin  
227 controls reaches the maximum divergence determined by the distance between the controls, and if the  
228 distance to destination controls reduces to zero, indicating maximum convergence, then no lags remain in  
229 community shifts. However, warmed communities might deviate from this expected trajectory, increasing  
230 the taxonomic distances to both controls (pink lines), thereby maintaining lags in community shifts. Given  
231 that distances in warmed communities are constrained between zero and the shortest distance between  
232 controls for the expected trajectory, and between zero and one for the deviating trajectory, a logarithmic  
233 relationship is expected between experimental years and taxonomic distances. Note that the taxonomic  
234 distance between controls is expected to remain constant (gray line).

## 235 **Methods**

### 236 ***Climate data***

237 We extracted monthly mean daily air temperature (°C) and potential evapotranspiration (PET)  
238 (mm) data from the ~1 km resolution CHELSA database (Karger et al. 2021) for each site. We  
239 calculated the average summer (June, July, August) temperature and annual PET for each site  
240 for each year of the experiment. We averaged the summer temperature and annual PET across  
241 all years for each experiment to calculate the origin and destination climates. To estimate the  
242 experimental climate warming experienced by warmed turfs, we calculated the average  
243 difference between destination and origin sites' summer temperature over the experimental  
244 years. Transplantation of turfs from high to low elevation simulated 0.5–11.1 °C (average of 3.0  
245 °C) of experimental warming across all experiments, covering a range of climate change  
246 scenarios generated by the IPCC for the next 50 years (IPCC 2022a). The experiments aimed  
247 to simulate warming but other environmental changes, such as in PET, are also imposed by  
248 downward transplantation (Fig. 2B). However, due to the high spatio-temporal variability of  
249 precipitation, especially in mountainous regions, CHELSA model spatial projections convey  
250 more uncertainty than temperature projections (Prein and Gobet 2017). This uncertainty may  
251 prevent us from accurately calculating the differences in PET between closely located origin and  
252 destination sites. Therefore, we only analyze the effect of PET at the destination sites rather  
253 than the difference between sites.

### 254 ***Plant relative abundances***

256 Vegetation surveys varied in timing, temporal resolution, and duration. Survey methodologies  
257 were also diverse, including percent cover estimates of all species in the turfs, point-intercept  
258 counts, or species-specific sorting of above-ground biomass. Some surveys did not record non-  
259 vascular plant categories, rock or bare soil. Thus, we removed inconsistent cover categories

260 from the dataset and converted vascular plant species cover or count data into relative plant  
261 abundances to ensure comparability across experiments. The compiled data ranges from 1 to 9  
262 years, for 60635 observations of 967 identified species and 92 taxa identified only at genus  
263 level. We decomposed these species pools into strictly high-elevation, overlapping, or  
264 colonizing low-elevation species based on their presence/absence in the control communities  
265 for each experiment (Table S3, Fig. S3). By definition, strictly high-elevation species were only  
266 found in the higher-elevation origin controls for each experiment, including high-elevation  
267 species relative to the experiment. We note that these are not necessarily alpine plants in a  
268 biogeographic sense (i.e., species found mainly above the treeline). The colonizing low-  
269 elevation species pool includes species that occur in destination controls but not in origin  
270 controls. Overlapping species are found both in origin and destination controls. Species that  
271 occur in warmed communities only but are absent from both sets of controls (i.e., on average,  
272 5% across all experiments, Fig. S3, Fig. S9) were excluded from the analysis. We limited our  
273 analysis to experiments with over two years of data, thus excluding US\_Colorado and  
274 IN\_Kashmir. We also excluded US\_Arizona due to its small high-elevation species pool of four  
275 species. Additionally, we excluded species found only once in a single turf to eliminate potential  
276 botanical identification errors. We square-root transformed species relative abundances in the  
277 analyses described below.

278

### 279 ***Plant functional traits***

280 We compiled five functional traits from the TRY database: vegetative height, leaf area (LA),  
281 seed mass, specific leaf area (SLA), and leaf nitrogen percentage (Kattge et al. 2020). These  
282 traits relate to plant size and resource use strategies that are relevant for plant responses to  
283 environmental change and their ability to compete for light, water and nutrients (Violle et al.  
284 2007, Díaz et al. 2016). We used a pre-processed version of the TRY dataset by (Walker et al.  
285 2023), filtered for trait values with an error risk < 4 according to the TRY database criterion  
286 (which measures the deviation from mean trait values within species, genus, family, or the entire  
287 dataset in standard deviation) and gap-filled using Bayesian hierarchical probabilistic matrix  
288 factorization imputation. This pre-processed dataset still had missing focal traits for certain  
289 species (vegetative height: 22%, SLA: 15%, LA: 31%, N-percent: 23%, seed mass: 29%) that  
290 we additionally gap-filled with miceRanger algorithm (Wilson in press). From these functional  
291 traits, we built a principal component analysis (PCA) with all the species from the TransPlant  
292 network (Fig. S2). Horn's parallel analysis retained two principal components (PC) to represent  
293 the variation in the trait space. LA (33%), vegetative height (26%), seed mass (23%) contributed  
294 primarily to PC1 followed by N-percent (9%) and SLA (8%). SLA (42%) and N-percent (38%)  
295 contributed the most to PC2 followed by vegetative height (9%), seed mass (9%) and LA (1%).  
296 Thus, we defined the first two PCs as denoting plant-size and resource acquisition-related traits,  
297 respectively, representing the two main axes of the global plant functional trait spectrum (Díaz  
298 et al. 2016). We calculated community-weighted means (CWMs) of PC1 and PC2 scores for  
299 each control community, reflecting plant size and resource acquisition strategies, respectively.

300

### 301 ***Quantifying plant community taxonomic divergence or convergence***

302 To quantify the plant community taxonomic change over time, we built principal response curves  
303 (PRC) (Van den Brink and Braak 1999). PRC, developed from redundancy analysis (RDA), is

304 an ordination technique that quantifies the impact over time of several treatments on species  
 305 relative abundances in experimental communities, relative to a reference community. It  
 306 accounts specifically for the interaction between experimental years and treatment while  
 307 controlling for the overall temporal trend in community composition. PRC allows for extracting i)  
 308 taxonomic distances between the treatments and the reference over time as canonical  
 309 coefficients of the treatments and ii) species weights that quantify species' contributions to  
 310 overall community taxonomic changes (Vandvik et al. 2014).

311  
 312 We quantified the taxonomic distances of the warmed communities relative to the controls by  
 313 building constructing two PRCs perfor each experiment: one with. The first PRC used the origin  
 314 control as the reference community, with the warmed and ~~the other with the~~ destination control,  
 315 ~~using warming and the other control~~ as treatments to quantify their taxonomic distance from the  
 316 origin control. The second PRC used the destination control as the reference, with the warmed  
 317 and origin control as treatments to quantify their taxonomic distance from the destination control  
 318 (Table S4). Canonical coefficients ( $C_t$ ) from PRC axis 1 (hereafter, "PRC1") capture the most  
 319 important taxonomic variation in differences between warmed and control communities for a  
 320 given year  $t$ , quantifying warmed communities' divergence from the origin control and  
 321 convergence towards the destination control. Canonical coefficients from PRC axis 2 (hereafter,  
 322 "PRC2") capture the second most important variation, and most important deviation from the  
 323 PRC1 (van den Brink et al. 2009). In PRCs, taxonomic distances between the origin and  
 324 destination controls indicate the maximum expected divergence of warmed communities from  
 325 origin controls and their maximum expected convergence towards destination controls (Fig. 1B-  
 326 C). When canonical coefficients of the warmed communities exceed the canonical coefficients  
 327 of the control communities in a given PRC, this can be interpreted as the communities deviating  
 328 from the shortest trajectory between warmed communities and displaying a "deviating" response  
 329 (Fig. 1B-C). We expect to see these responses mainly in PRC2 with higher values in PRC2  
 330 indicating stronger deviating responses.

### 331 332 **Quantifying species' contributions to taxonomic divergence or convergence**

333 To assess the species' contributions to the community taxonomic shifts, we calculated  
 334 proportional relative abundance differences in warmed communities in comparison to the mean  
 335 relative abundance in control communities following the expression  $b_k * c_t - 1$  for each species  
 336  $k$ , with species weights  $b_k$  and canonical coefficient  $c_t$  of warmed communities at year  $t$  from  
 337 both PRCs per experiment. Here, species weights  $b_k$  (i.e., constant over the years) allow us to  
 338 obtain the fitted response curves for species  $k$  and quantifies the affinity of species  $k$  with the  
 339 overall trajectory of the community (i.e., the higher the species' weights, the more likely it is that  
 340 the species is aligned with the pattern of community change as quantified by PRC) (Van den  
 341 Brink and Braak 1999). Interpreting this outcome as the species' contribution to a communities'  
 342 taxonomic divergence and convergence provides several advantages to using raw relative  
 343 abundance differences: i) disentangling species contributions to the most important variation  
 344 (PRC1) from the second most important variation (PRC2, i.e., deviations from PRC1)  
 345 community change, while ii) taking into account the noise in the data.

### 346 347 **Statistical analyses**

348 To address our first question, we assessed the rate of composition change in warmed  
349 communities along two primary axes: 1) divergence or convergence along PRC1, quantified by  
350 canonical coefficients, and 2) deviation from these trajectories along PRC2. We developed  
351 linear mixed effects models for each axis, considering both the warmed (red lines in Fig.1B-C)  
352 and control communities (gray lines in Fig.1B-C) relative to a reference community. These  
353 models used canonical coefficients as the response variable and included log-transformed  
354 experimental year, distance type (to origin or destination control), experiment identity, and their  
355 three-way interactions as fixed effects. A random effect for gradient was included to adjust for  
356 non-independence across experiments due to regional variations like soil and habitat  
357 differences. We log-transformed the experimental year to fit a logarithmic regression because  
358 the distances between communities cannot surpass the maximum expected distance in the  
359 case of the divergence, or zero in the case of convergence. This transformation improved model  
360 fit, reducing AIC values by 121.39 and 153.20 for PRC1 and PRC2, respectively (df = 162). The  
361 slopes from these models provide estimates of the rates of divergence from origin controls,  
362 convergence towards destination controls, and deviations in composition across all experiments  
363 over the years.

364  
365 To answer our second question, we estimated i) the proportional differences in relative  
366 abundances in warmed communities calculated from both PRC axes per species pool (strictly  
367 high-elevation, overlapping and colonizing) at the start (year = 1) and end (year = 9, projected  
368 for the short experiments) of experiments, and ii) the rate of changes in these proportional  
369 differences over time. We built linear mixed effects models for each axis and species pool with  
370 species' proportional differences in relative abundances in warmed communities as the  
371 response variable with experimental year (log-transformed), comparison type (to origin or  
372 destination control), experiment identity, and their three-way interactions as fixed effects. We  
373 included species nested in gradients as random effects. Here, we present the estimated  
374 proportional differences in relative abundances in warmed communities per species pool at the  
375 start and end of experiments, and the slopes (as rate of changes in relative abundances) from  
376 these species pool-level models for all experiments combined. When compared to origin  
377 controls, higher proportional relative abundance differences in warmed communities indicate  
378 greater climate change effects on relative abundances of that experiment and/or species pool.  
379 Also compared to origin controls, greater magnitudes of the slopes (absolute values) indicate  
380 faster changes in relative abundances. More precisely, higher positive rates indicate faster  
381 species gains, lower negative rates indicate faster losses. When compared to destination  
382 controls, i) higher proportional relative abundance differences in warmed communities indicate  
383 greater lags in relative abundances, while ii) larger magnitudes of the slopes (absolute values)  
384 indicate faster realization of the experimental climate change response and thus, declines in  
385 lags. More precisely, higher positive rates indicate faster decline in colonization lags (i.e.,  
386 realization of colonization events), lower negative rates indicate faster decline in extinction lags  
387 (i.e., realization of extinction events). Overall, changes in a species pool reflect overall changes  
388 in species' relative abundances in a given experimental community belonging to the species  
389 pool in question.

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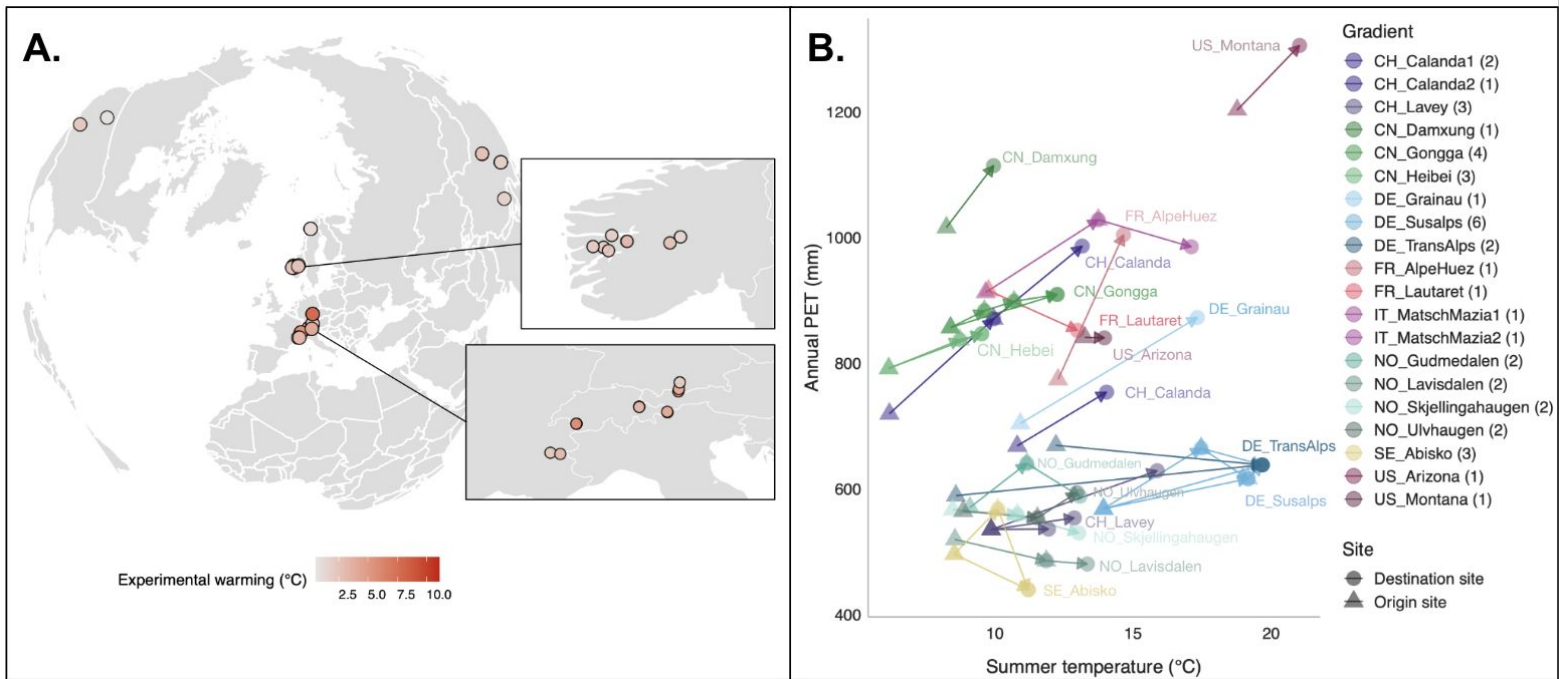


391 To answer our third question, we first extracted the slopes (i.e., rate of changes in distances  
392 between warmed and both control communities) and their standard errors for each experiment  
393 from the first-mentioned (community-level) model. Second, we extracted the initial and final  
394 proportional differences in relative abundances and slopes (i.e., rate of change in proportional  
395 differences in relative abundances) and their standard errors for each experiment from the  
396 second-mentioned (species pool-level) model. At community-level, we built two separate meta-  
397 regression models to accommodate each of the two distance types ( to origin or destination  
398 control) with slopes as response variable. At species pool-level, we built 18 separate meta-  
399 regression models to accommodate each of the two comparison types (to origin or destination  
400 control) and three species pools with three response variables: i) slopes at species pool-level,  
401 iii) initial and iii) final proportional differences in species-pool relative abundances. In these  
402 models, experimental (turf size, experimental warming, duration), and climate factors (summer  
403 temperature and annual PET of destination sites) and functional traits (CWM of plant size and  
404 resource acquisition traits) were included as explanatory variables. Meta regression models  
405 take into account the uncertainty in the response variables (Viechtbauer 2010). All explanatory  
406 variables were standardized (i.e., z-score normalization).

407  
408 We conducted the statistical analysis with R version 4.4.0 (R Core Team 2024) using the  
409 following packages: emmeans (Lenth 2023), lme4 (Bates et al. 2015), vegan (Oksanen et al.  
410 2022), MuMIn (Bartoń 2023), merTools (Knowles and Frederick 2024), metafor (Viechtbauer  
411 2010).

412





413

414 **Fig. 2: A)** TransPlant experiments across the Northern Hemisphere. The color gradient indicates the magnitude of  
 415 experimental warming (°C) as the sum of temperature differences between the origin and destination sites across the  
 416 experimental years. **B)** Summer temperature (°C) and annual potential evapotranspiration (PET, mm) of TransPlant  
 417 sites (circle: Destination site, triangle: Origin Site). Different colors indicate gradients. The number of experiments in  
 418 each gradient is indicated in the color legend. Coloured arrows indicate the direction of the translocation for each  
 419 experiment. *Note:* We extracted temperature (°C) and PET (mm) from the ~1 km resolution CHELSA database for  
 420 each site (Karger et al. 2021).

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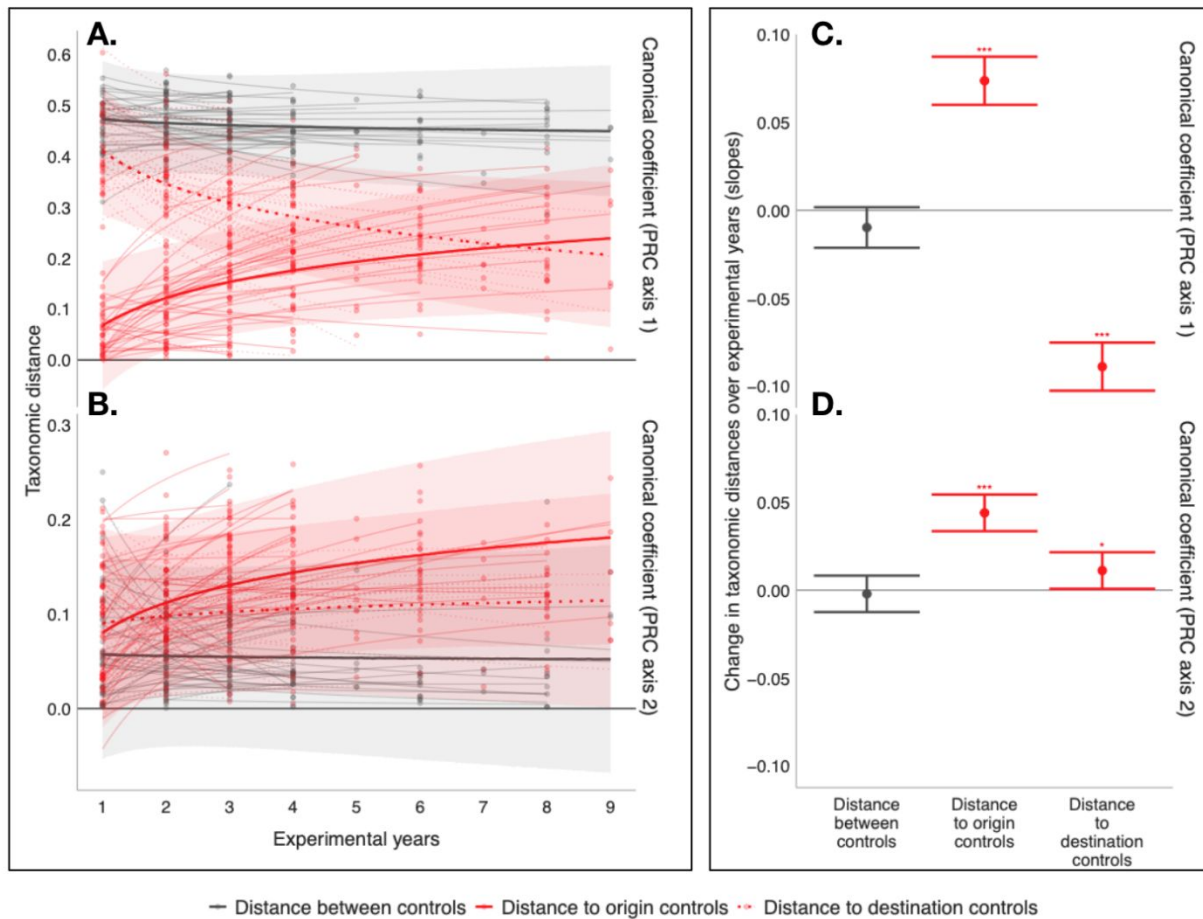
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## 436 Results

## 437 To what extent does the species composition of warmed communities shift over time?

438



439

440 **Fig. 3:** Community divergence and convergence in response to warming, reflected as the change in canonical  
 441 coefficients reflecting the taxonomic distances between experimental communities and their origin and destination  
 442 controls over time. **A-B)** Each panel reflects both divergence of the warmed communities from the origin control (solid  
 443 lines) and convergence towards the destination control (dotted lines). For divergence, the origin controls are set at  
 444 zero as the reference community and the plot shows the divergence of warmed communities (solid red line) and  
 445 destination controls (solid gray line) from the origin controls. For convergence, the destination controls are set at zero  
 446 and the plot shows the convergence of the warmed communities (dotted red line) and origin controls (solid gray line)  
 447 towards the destination controls. Distances between controls (gray lines) represent the expected taxonomic distance  
 448 if warmed communities fully converge (i.e., become identical to the destination community composition). Panels A  
 449 and B represent PRC axes 1 and 2, respectively. **C-D)** The rate of change in taxonomic distances (i.e. distance per  
 450 log-transformed experimental year) between control communities and between warmed communities and origin or  
 451 destination controls, as reflected in the analyses on A or B where the respective controls are set at zero as the  
 452 reference community. Panels C and D represent PRC axes 1 and 2, respectively. Canonical coefficients from PRC1  
 453 capture the most important variation in taxonomic distance, and represent the taxonomic divergence from the origin  
 454 control or convergence towards the destination control due to experimental warming. Canonical coefficients from  
 455 PRC2 capture the most important deviations from the PRC1, and so represent deviations in the trajectories of the  
 456 communities as they diverge or converge from/towards origin and destination controls, and thus give deviating  
 457 responses. Note that lines in A and B are from models fitted with log-transformed experimental years. Responses of  
 458 each experiment (fitted separately) and overall responses are shown in thin and thick lines respectively, with shading

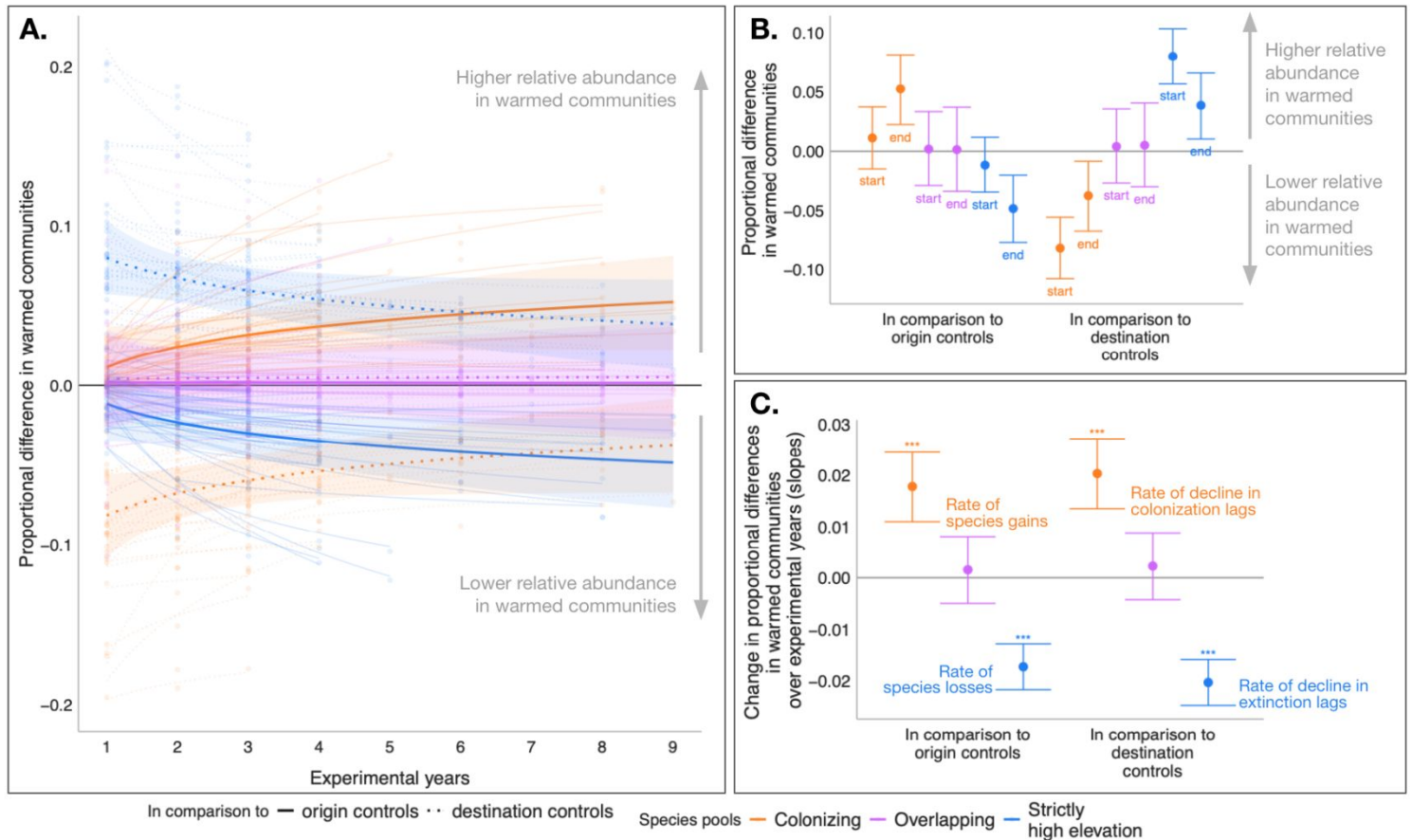
459 indicating the 95% confidence interval for the overall effect. In C and D, significant slopes are indicated with \*:  
460 p.values <0.05, \*\*: p.values<0.01, \*\*\*: p.values<0.001

461  
462 Warmed communities taxonomically diverged from the high-elevation origin control communities  
463 (Fig. 3A red-solid lines; Table S5) and converged towards low-elevation destination control  
464 communities across all experiments (**Fig. 3A, red-dotted lines**). As expected, the distance  
465 between the two control communities remained constant on both PRC axes, indicating no  
466 significant directional change in composition in the controls (**Fig. 3 A-B, gray lines**). In the first  
467 year, warmed communities had already diverged on PRC1 by on average 14 %, and converged  
468 by on average 13 %, of the maximum expected distance (i.e., the distance between the two  
469 controls). If communities maintained this pace they would have reached zero taxonomic  
470 distance with destination controls at around 7 years, however, rates of divergence and  
471 convergence slowed down considerably over time. On average, (i.e., based on projections),  
472 48% and 54 % of taxonomic distance on PRC1 still remained, after 9 years, for communities to  
473 reach maximum divergence and convergence, respectively.

474  
475 However, variation in rates of composition change was observed across the 40 experiments  
476 (Fig. S5). First, warming led to divergence from origin controls only in 33 experiments.  
477 Conversely, in 7 experiments, warmed communities diverged from origin controls in the first  
478 year but they started to converge back towards origin controls over the years (Fig.3A, Fig. S5).  
479 The rates of change in taxonomic distances between warmed and origin control communities  
480 ranged from -0.053 to 0.215 (i.e., unitless change in taxonomic distance over the years scaled  
481 between -1 and 1, Fig. S5). Second, warming led to convergence with destination controls only  
482 in 36 experiments. Whereas in 4 experiments, warmed communities tended to diverge from the  
483 destination controls. The rates of change in taxonomic distances between warmed and  
484 destination controls ranged from -0.283 to 0.0584. In addition, taxonomic distances between  
485 warmed and control communities generally (**Fig. 3B solid and dotted red lines**) exceeded the  
486 distances between the controls (**Fig. 3B gray lines**) along PRC2. This indicates that warmed  
487 communities deviated from the expected trajectory of convergence. These deviations  
488 significantly increased over time (**Fig. 3B&D**).

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503 **How do different species pools contribute to divergence or convergence in plant**  
 504 **community composition?**



505 **Fig. 4:** Changes in different species pools in warmed communities in comparison to controls over time. **A)**  
 506 Proportional differences in relative abundances of each species pool in warmed communities in comparison to origin  
 507 controls (solid lines) and destination controls (dotted lines) calculated from PRC1. Positive values indicate higher  
 508 relative abundances in warmed communities, negative values indicate lower relative abundances in warmed  
 509 communities. **B)** Predicted proportional differences in relative abundances of different species pools in warmed  
 510 communities in comparison to controls at the start (year = 1) and end (year = 9, projected for shorter experiments) of  
 511 the experiments. **C)** Rate of changes in proportional differences in warmed communities over log-transformed  
 512 experimental years. When compared to origin controls, higher positive rates indicate faster species gains, lower  
 513 negative rates indicate faster losses. When compared to destination controls, higher positive rates indicate faster  
 514 decline in colonization lags (i.e., realization of colonization events), lower negative rates indicate faster  
 515 decline in extinction lags (i.e., realization of extinction events). Note that lines in A are from models fitted with log-transformed  
 516 experimental years. Responses of each experiment (fitted separately) and overall responses are shown in thin and  
 517 thick lines respectively, with shading indicating the 95% confidence interval for the overall effect. In C, significant  
 518 slopes are indicated with \*: p.values < 0.05, \*\*: p.values < 0.01, \*\*\*: p.values < 0.001  
 519  
 520

521 The divergence of warmed communities from origin controls was similarly driven by both the  
 522 decrease in relative abundances of strictly high-elevation species and the increase in colonizing  
 523 species. (Fig. 4A-B). However, both colonization and extinction lags remained after the 9-year  
 524 experimental period: On average, strictly high-elevation species remained more abundant and  
 525 colonizing species less abundant in warmed communities compared to destination controls (Fig.  
 526 4A-B). Besides having equal contributions to the overall shifts in warmed communities, rates of

527 species gains and losses over the years were similar, thus contributing equally to the rates of  
528 divergence from the origin controls and convergence towards destination controls (Fig. 4C).  
529 However, beyond these general trends, there was substantial variation across experiments (Fig.  
530 5A, thin lines, Fig. S5). In fact, the relative abundances of overlapping species across  
531 experiments showed both increasing and decreasing trends, which canceled each other out,  
532 resulting in no clear general trend.

533  
534 Taxonomic shifts away from the shortest trajectory between origin and destination controls in  
535 warmed communities were mainly driven by the colonizing species (Fig. S4). Interestingly, when  
536 predicted by PRC2, relative abundances of the colonizing species were increasingly higher in  
537 warmed communities in comparison to destination controls, indicating that some colonizing  
538 species were increasing their abundances more than expected (i.e., given their relative  
539 abundances in destination controls), contributing to the community-level deviating responses  
540 (Fig. S4).

541  
542 **What influences the variation in overall rates of community change across experiments, as**  
543 **well as the contribution of different pools to divergence or convergence?**

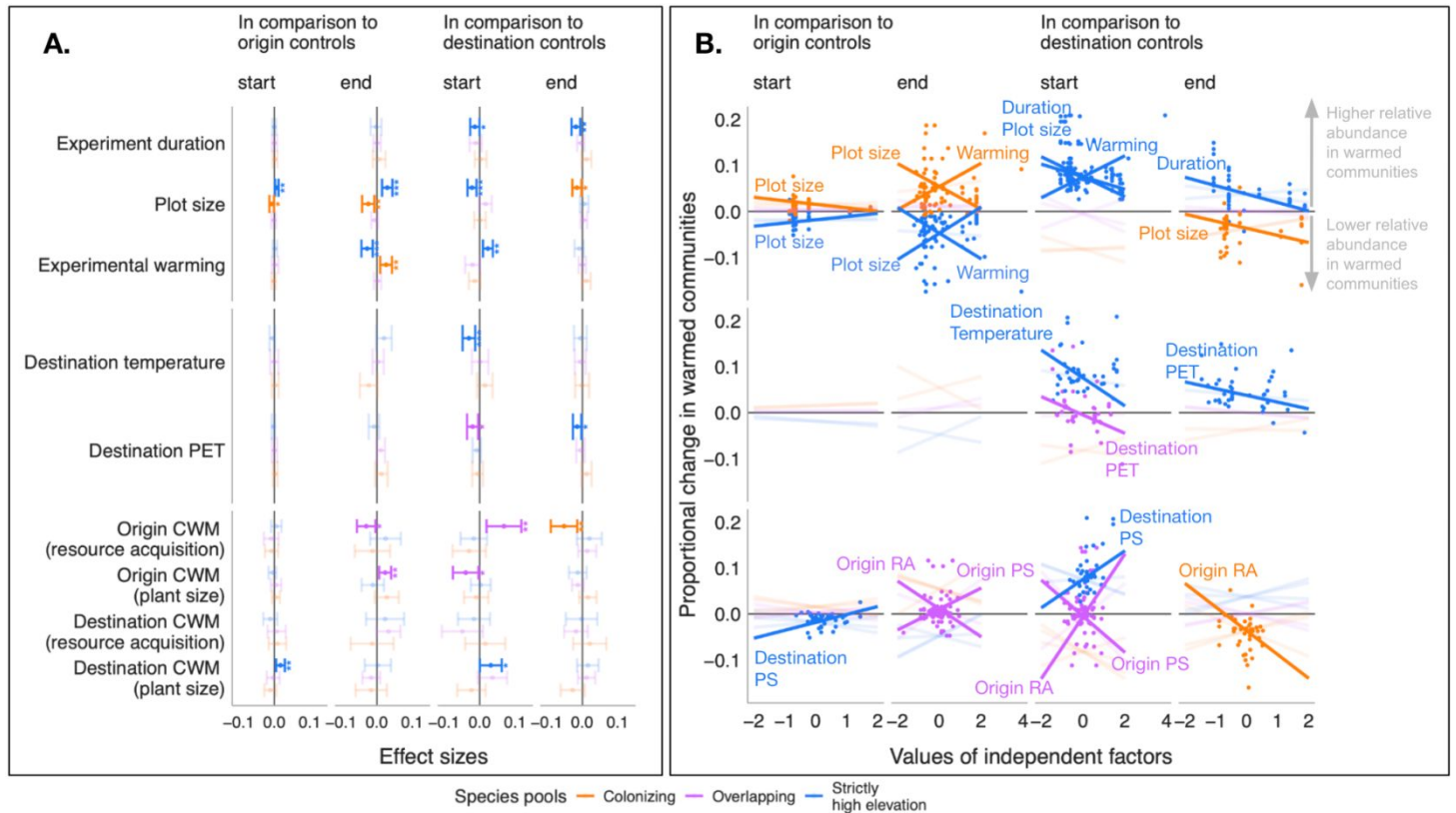
544 Communities exposed to stronger warming, over longer periods, in smaller plots and  
545 transplanted to drier conditions diverged faster from origin controls (i.e., increasing taxonomic  
546 distances between warmed and origin control communities over time) (Fig. S6; Table S7). Also,  
547 communities exposed to stronger warming over longer periods converged faster towards  
548 destination controls (i.e., decreasing taxonomic distances between warmed and destination  
549 control communities over time) (Fig. S6; Table S7).

550  
551 Species pools' relative abundance differences in warmed communities compared to controls  
552 varied between the beginning and end of experiments (Fig. 5; Table S8). At the beginning of the  
553 experiments, species losses (i.e., decreases in the relative abundances of the strictly high-  
554 elevation species) in warmed communities were higher in experiments with smaller plots and  
555 when destination communities were dominated by smaller-sized plants. Similarly, extinction lags  
556 were greater in smaller plots, under stronger warming, in shorter experiments, when  
557 transplanted to cooler destinations where destination communities were dominated with taller-  
558 sized plants. Parallely, species gains (i.e., increases in the relative abundances of the colonizing  
559 species) in warmed communities were higher in smaller plots. Finally, overlapping species had  
560 higher relative abundances in warmed communities in comparison to destination controls when  
561 transplanted to a wetter destination (among other destination sites) and when they originated  
562 from smaller-sized and more resource-acquisitive communities.

563  
564 At the end of the experiments, species losses and gains were higher (Fig. 5) and faster (Fig. S7;  
565 Table S8) in smaller plots and under stronger warming. Whereas, extinction lags were higher in  
566 shorter experiments and when communities were transplanted to wetter conditions. Meanwhile,  
567 colonization lags were higher when the origin communities were dominated by more resource-  
568 acquisitive strategies. Finally, overlapping species had higher relative abundances in warmed  
569 communities than in origin controls when they originated from more conservative and taller-  
570 sized communities.



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**Fig. 5: A)** Magnitude of experimental, climatic and functional trait effects on the magnitude of species pool contributions (change in species pools' proportional relative abundance changes in warmed communities in comparison to controls) at the start (year = 1) and end (year = 9, projected for shorter experiments) of the experimental period **B)** Relationships in species pool contributions with experimental, climatic and functional trait factors. For experimental and climate effects, positive values indicate longer experiment duration, bigger turf sizes, stronger experimental warming, warmer and drier destination site. For functional trait effects, positive values indicate that on average communities are dominated by fast-growing resource-acquisitive (high SLA and leaf nitrogen) and taller species with wider leaves and heavier seeds (Fig. S2). When compared to origin controls, positive effect sizes indicate increases in relative abundances in warmed communities with the higher values of the explanatory factor for all species pools. When compared to destination controls, positive effect sizes still indicate higher relative abundances in warmed communities with increasing values of the explanatory factors but it can additionally be interpreted as higher extinction lags for strictly high-elevation species pool with the increasing values of the explanatory factors. For colonizing species, negative effect sizes indicate increasing colonization lags with increasing values of the explanatory factors. In B, only significant associations as quantified in A are shown and labeled. Linear metaregression models were built independently per species pool. All explanatory variables were standardized (i.e. z-score normalization).

## 589 Discussion

### 590 High-elevation plant community trajectories under climate warming

591 Ecologists are trying to understand the reconfigurations of plant communities due to abundance  
 592 and distribution shifts triggered by climate change. A “null hypothesis” is that when dispersal  
 593 limitations of warm-adapted species are overcome, the future composition of cool-adapted plant  
 594 communities converge on the composition of warm-adapted communities of today. Alternatively,



595 altered ecological interactions within warming communities might cause them to exhibit lagged  
596 responses or even follow alternative trajectories leading to novel community compositions. A  
597 network of transplant experiments provided us with the unique opportunity to examine the initial  
598 years of these trajectories under climate warming. As expected, the taxonomic composition of  
599 warmed communities shifted, converging towards their lower-elevation communities.  
600 Nonetheless, communities under warming did not fully converge on the low-elevation  
601 community composition, even up to nine years after transplantation. In addition, we found that  
602 warmed communities deviated significantly from the shortest trajectory of community shift  
603 between high- and low-elevation sites and rates of taxonomic convergence slowed over time.  
604 Together, these results suggest that even if high-elevation communities do eventually converge  
605 on today's low-elevation community composition, this will be a slow process characterized by  
606 significant colonization and extinction lags and transient dynamics leading to a prolonged period  
607 of novel community structures (Hastings et al. 2018). Such transient dynamics could be due to  
608 [demographic lags \(Alexander et al. 2018\)](#), feedbacks in plant-plant interactions (Alexander et al.  
609 2015, Vandvik et al. 2020, Bektaş et al. 2023), plant-soil nutrient pools (Khedim et al. 2022), or  
610 plant-microbial interactions (Zhang et al. 2014).

611  
612 Taxonomic changes were already large in the first year after transplantation. This might be an  
613 effect of the transplantation method, whereby the communities are exposed to an abrupt  
614 environmental change. Indeed, community responses to gradual warming might differ from  
615 those of abrupt climate manipulations, partly because individual species differ in their  
616 demographic responses to fast vs. slow warming altering the network of plant-plant interactions  
617 (Block et al. 2022). Nonetheless, the rapid responses to more intense warming and drying  
618 emphasize the crucial role of extreme events in driving community changes, triggering the loss  
619 of less resilient high-elevation species and facilitating swift colonizations by warm-adapted taxa.  
620 Even as taxonomic shifts appear to slow down over time, and [warmed](#) high-elevation  
621 communities stabilize, their vulnerability to extreme climatic events could further accelerate the  
622 rate of taxonomic changes, inducing a second wave of abrupt shifts. In fact, in transplant  
623 experiments in Switzerland and Austria, colonization of the low-elevation species started only  
624 three years after the transplantation, specifically after the drought in 2018, which led to  
625 significant species losses in transplanted high-elevation communities (Schuchardt et al. 2023b).  
626 With intense heatwaves and droughts becoming more common in mountainous areas (IPCC  
627 2022b), high-elevation communities may undergo multiple swift taxonomic changes, as  
628 evidenced by landscape-scale alterations following recent extreme events in the European Alps  
629 (Choler 2023).

### 630 **Contributions of different species pools to changes in community composition**

631  
632 Changes in community composition under warming were influenced both by colonizing species  
633 from the destination site, and [decrease in relative abundances abundance shifts](#), including local  
634 extinctions, of strictly high-elevation species. On average, species gains from colonizing pools  
635 and losses from strictly high-elevation species pools, along with the rates of these changes,  
636 were of similar magnitude, albeit in opposite directions. This suggests that these two species

637 pools contributed similarly to community changes. The large contributions of the strictly high-  
638 elevation species pool to the divergence of warmed communities from the high-elevation  
639 communities indicate that even after the first year of transplantation, decreasing relative  
640 abundances and local extinction events of cold-adapted species under warming were important.  
641 Interestingly, a minority of experiments ( $n = 5$ ) displayed increasing relative abundance of this  
642 species pool over the years, which might be explained by a few species initially tolerating (or  
643 even benefiting from) climate change and/or altered plant-plant interactions under warming  
644 (Nomoto and Alexander 2021). Fewer losses from this species pool were detected in studies  
645 with shorter experimental durations. In longer-term experiments, despite overall losses, the  
646 strictly high-elevation species maintained enough abundance to significantly differentiate the  
647 warmed community from the destination controls even after nearly a decade. . In other words,  
648 many of these species appear able to persist for considerable periods of time under significant  
649 future warming. This is consistent with estimates of substantial extinction lags in alpine plant  
650 communities, especially when species continue to coexist with their original plant community via  
651 competition (Rumpf et al. 2019).

652  
653 Colonizing species also made large contributions to the difference in community composition  
654 between warmed and high-elevation communities over time, even though with substantial  
655 delays. This clearly demonstrates that under climate change, low-elevation species can colonize  
656 high-elevation plant communities if dispersal limitations are removed. This gives a first indication  
657 that the lags in range shifts observed in mountain floras (Rumpf et al. 2018, 2019) are at least  
658 partly explained by dispersal limitation, and that novel plant establishment should be expected  
659 once these limitations are overcome. Moreover, increasing colonizations in smaller plots, which  
660 have more exposure to the surrounding colonizing community at the edges due to a larger edge  
661 length ratio (e.g., 16 and 4 for 0.0625 and 1 m<sup>2</sup> plots, respectively), contradicts the expectation  
662 of colonist establishment from seeds, where larger plots should accommodate a higher  
663 probability of dispersal events. This implies that clonal growth may be a key factor facilitating the  
664 local expansion of low-elevation species once dispersal lags are overcome (Guittar et al. 2016,  
665 Töpfer et al. 2018). However, persisting colonization lags in our experiments even after almost

666 a decade demonstrate that establishment lags play also a role in range shift dynamics, perhaps  
667 through plant-plant interactions within high-elevation communities (Meineri et al. 2020, Lyu and  
668 Alexander 2022). Thus, future studies should explicitly investigate the biotic interactions  
669 between different species pools and their effects on plant demographic cycles.

670  
671 Overlapping species' contributions to community shifts were highly variable but on average  
672 close to zero. This does not imply that species in this pool were unaffected by warming. Instead,  
673 it suggests a spectrum of positive and negative responses across and within experiments: the  
674 overlapping species pool in each experiment contained a mixture of "winner" and "loser"  
675 species. Given that overlapping species demonstrate a larger niche in tolerating a broader  
676 range of environmental and biotic conditions at across elevations, their abundance change in  
677 the beginning of experiments may be stochastic. However, if originating from more resource-  
678 conservative communities, relative abundances of overlapping species increased more.  
679 Moreover, when in drier conditions than all other destinations, their relative abundances were  
680 lower than in destination controls. This indicates that responses to drought play a major role in  
681 mountain plant population dynamics and drought-tolerant species can be the winners of climate  
682 change in the mountains (Visakorpi et al. 2022).

683

#### 684 **Variation in responses across and within experiments due to biotic interactions?**

685 The large variation in magnitude and direction of species relative abundance changes, even  
686 within the same pool is typical for species-level responses to climate change (Rumpf et al. 2018,  
687 Töpper et al. 2018). Only partly related to experimental design choices (e.g. plot size, duration,  
688 and climate context), much of the variation in species responses could be explained by  
689 destination or origin communities' functional traits. These traits, ~~indicative of which indicate~~  
690 competitive abilities for acquiring light, water, and ~~nutrient acquisition~~ nutrients, suggest that  
691 plant-plant interactions and their temporal dynamics ~~might contribute to~~ may play a role in the  
692 observed variation in population dynamics (Lynn et al. 2019, Meineri et al. 2020). For example,  
693 colonization lags persisted in warmed communities where resource-acquisitive plants were  
694 originally dominating. Perhaps, when high-elevation communities are competitive for resources

695 such as soil nutrients and water, colonizers fail to establish. Moreover, we expected that  
696 warmed communities suffering competitive exclusion due to taller surrounding destination  
697 communities (Fig. S8). Yet, in destination sites dominated by taller-sized plants, species losses  
698 were lower and extinction lags were higher. This might suggest that biotic interactions between  
699 destination communities and strictly high-elevation species influence the population dynamics of  
700 the latter, possibly through tall and wide-leaved destination-species creating shade and thus,  
701 cooler microhabitats for intensely warmed high-elevation species. Finally, effects of functional  
702 traits were not consistent across the experimental period and they do not determine the rates of  
703 changes in communities and species contributions. This could indicate, on the one hand, initial  
704 stochastic losses and gains, on the other hand, plant-plant interactions needing time to adjust,  
705 being transient and leading to inconsistencies through feedback between them.

706

## 707 **Conclusions & Perspectives**

708 Our study underscores the dynamic shifts in high-elevation plant communities due to  
709 experimental climate warming, suggesting the formation and persistence of novel communities  
710 that complicate future predictions. While community taxonomic convergence towards lower  
711 elevations hints at a predictable trajectory under climate change, significant uncertainties due to  
712 local factors like climate and initial community composition highlight the need for localized  
713 studies. Future research should focus on the variability in temporal and spatial dynamics,  
714 investigate the causes of shifts in populations and communities, including the changes in biotic  
715 interactions. We encourage expanded collaborative macroecological experiments across  
716 diverse ecosystems to better understand plant community responses to climate change.

## 717 **Data Availability**

718 Raw and processed data are archived at Open Science Framework (OSF) under the following  
719 link [https://osf.io/9874t/?view\\_only=90e7bafd8eed40eb960a22ce3098c613](https://osf.io/9874t/?view_only=90e7bafd8eed40eb960a22ce3098c613)

720 Code to clean the raw data is available at: <https://github.com/Between-the-Fjords/TransPlant/>

721 Code to reproduce the analysis is available at:

722 [https://github.com/billurbektas/TransPlant\\_convergence\\_analysis/tree/review\\_V2](https://github.com/billurbektas/TransPlant_convergence_analysis/tree/review_V2)

723 Upon acceptance, the code will be published at Zenodo. TransPlant Network data and

724 experiment-specific results can be visualized on the dedicated Shiny app:

725 <https://billurbektas.shinyapps.io/transplantshiny-1/>

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899

For Review Only

Dear Editor Dr. Freestone,

We thank you and the reviewers for the suggestions to improve our manuscript, ECOG-07378.R1. We are pleased to submit the revised version of our manuscript.

Please find our point-by-point responses below.

Thank you very much for your consideration.

Kind regards,

On behalf of the co-authors, Billur Bektas

L9-13 I think this sentences would be clearer if split into two sentences - this would better highlight the scale of the study and the strength of turf transplant studies for global change biology

We splitted the sentences.

L19 Should 'either' be 'both'?

Corrected.

L86 The phrase "how these are underlain by..." is difficult to follow, I would suggest adding 'trajectories' to be clearer what 'these' is referring to

Added.

L104 - 107 This sentence seems to be set-up to have the two examples contrast with each other, however these two examples are not in contrast to each other.

Corrected.

Figure 1 - The difference between the red and pink lines are hard to decipher, I would pick a different color for the deviating response lines

Corrected.

L286 - 288 Although I can now follow what the two PRC analyses are doing, this sentence still could be clearer. As these PRC comparison are key for the majority of the results in the manuscript I think the specific comparisons need to be laid out as two separate sentences (i.e., The first PCR compares X and Y. The second PCR compares X and Z). Or at least resolve the sentence to modify 'and the other control as treatments'. It is especially difficult to follow which comparisons are being made in this part of the sentence.

We clarified at L286-291 as follows: "We quantified the taxonomic distances of the warmed communities relative to the controls by constructing two PRCs for each experiment. The first PRC used the origin control as the reference community, with the warmed and destination control as treatments to quantify their taxonomic distance from the origin control. The second PRC used the destination control as the reference, with the warmed and origin control as treatments to quantify their taxonomic distance from the destination control (Table S4)."

L337 It may be useful to remind readers what the three species pools are, perhaps in parenthetical.

Added.

L346-353 In the explanation of how to interpret this analysis the focus is largely on relative abundance changes and the lags in those changes of relative abundance. However in the results (e.x., Fig. 4 caption L478 - 481) the rates (and lags) of extinction and colonization is also discussed. To me, the difference in interpretation is dependent on which species pools is being focused on. I think this point about how interpretation changes for the different species pool results needs to be made clear in the section on how to interpret this specific analysis.

To clarify we added “More precisely, higher positive rates indicate faster species gains, lower negative rates indicate faster losses.” at L353 and “More precisely, higher positive rates indicate faster decline in colonization lags (i.e., realization of colonization events), lower negative rates indicate faster decline in extinction lags (i.e., realization of extinction events).” at L358.

L572 - These transient dynamics could also be driven by demographic lags as well as species-specific responses to disturbance and dispersal dynamics

We added the demographic lags as one of the reasons.

L585 - Does 'high elevation communities' refer to experimentally warmed turfs?

Added that they are the warmed communities.

L598 - It is not clear what part of the sentence 'abundance shifts' refers to.

We replaced it with “decrease in relative abundances” to be more precise.

L655 - 656 This sentence is difficult to follow, I think this might just be a grammatical issue.

We tried to correct the sentence grammatically.