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RESEARCH ARTICLE

Taxonomic and functional changes in mountain meadow communities four years after transplantation to a lowland environment

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Abstract

Aims: Climate warming at high altitudes occurs at an above-average rate. Due to short geographical distances, warm-adapted species might establish rapidly in mountain communities, while cold-adapted specialists are likely to locally disappear, sometimes after a lag phase. Here, we investigate changes not only of the community composition of species-rich mountain meadows, but also resulting alterations of their functional identity and diversity. Thereby, we hypothesize that transplantation to a warmer lowland environment leads to a shift towards a more acquisitive resource-use strategy, caused by the immigration of lowland species. Temporarily this leads to an increase in functional diversity through the lagged extinction of high-altitude species with conservative resource-use strategies.

Location: European Alps, Germany.

Methods: Using a space-for-time substitution, we conducted a community transplant experiment at a high- and low-elevation common garden site, where we compared the development of highland communities transplanted to the warmer low-elevation site and control plant communities locally replanted at both sites over a period of 4 years after transplantation. In situ, we collected functional leaf morphological and biochemical traits based on which we calculated community weighted mean traits as well as community functional richness and functional divergence.

Results: Species richness of the communities transplanted to the low-elevation site increased over time, resulting from more species invasions than disappearances. This led to increasing similarity between transplanted highland communities and local lowland communities, and to greater functional richness and divergence 4 years after transplantation, although mean community traits did not diverge yet.

Conclusions: Although the exposure to warmer temperatures did not immediately lead to the extinction of typical mountain meadow species, substantial community changes are expected through immigration of warm-adapted species. Resulting changes in the functional characteristics of mountain communities are likely to modify competition regimes within these communities, which might accelerate the local extinction of mountain specialists.

KEYWORDS
climate warming, community composition, functional changes, functional diversity, high-elevation communities, mountain grasslands, species richness, taxonomic diversity, translocation experiment, transplantation experiment

1 | INTRODUCTION

Mountains are recognized hotspots of biodiversity (Körner, 2004; Nagy & Grabherr, 2009). In particular, montane meadows harbor a wealth of plant species and valuable plant communities (MacDonald et al., 2000; Bohner et al., 2019). However, high-elevation ecosystems are under particular threat through global climate change because warming in mountains takes place at higher rates compared to lowlands (Nogués-Bravo et al., 2007; Gobiet et al., 2014; Pepin et al., 2015, 2022). A well-documented consequence of climate warming is the upslope movement of plants. One of the most prominent examples is the upward shift of >500 m of the upper vegetation limit on Chimborazo in Ecuador since Alexander von Humboldt's visit in the year 1802 (Morueta-Holme et al., 2015). Such upslope shifts have been observed on all continents and in different climatic zones (e.g. Lenoir et al., 2008; Jump et al., 2012; Rumpf, Hülber, Zimmermann, & Dullinger, 2019b). Consequently, the number of more warm-adapted species from lower elevations increases—a phenomenon called thermophilization (Gottfried et al., 2012). In contrast, plant species adapted to cold conditions are unlikely to survive under warmer temperatures in the long-run (Rumpf et al., 2018; Rumpf, Hülber, Wessely, et al., 2019a). However, species extinctions often lag behind the observed increase in temperature, because the typically long-lived plants at high elevation might be able to persist vegetatively, without reproduction for a substantial period of time (Alexander et al., 2018). Both the invasion of lowland species and the local extinction of cold-adapted species lead to changes in plant community composition. Because of the immediate invasion of new species, but delayed disappearance of high-elevation specialists, community change might temporarily go along with an increase of species richness (Steinbauer et al., 2018; Rumpf, Hülber, Wessely, et al., 2019a).

Climate warming is also supposed to alter the functional identity and diversity of high-elevation plant communities. Such communities typically follow a more conservative resource-allocation strategy (Wright et al., 2004; Díaz et al., 2016; Ratier Backes et al., 2023), and plants are characterized by a small stature and slow growth, thick leaves (low specific leaf area, high leaf dry matter content) and low leaf nutrient concentrations but a high leaf carbon to nitrogen ratio (Körner, 2003; Ordoñez et al., 2009; de Bello et al., 2013; Midolo et al., 2019). In contrast, species coming from lower elevations follow a more acquisitive resource-allocation strategy (tall plants with fast growth, high specific leaf area and leaf nutrient concentrations, and low leaf dry matter content and carbon to nitrogen ratio), and their functional trait syndromes are associated with higher competitive ability (Wright et al., 2004; Alexander et al., 2015). Species turnover due to temperature warming should thus lead to communities following a more acquisitive growth strategy because of invading acquisitive lowland species, but also because the most conservative species are most likely those that go extinct first. The pace of species turnover might accelerate because invading acquisitive species from the lowland increase the level of competition in the high-elevation communities—in particular competition for light because lowland species are typically of taller stature and produce more biomass. Consequently, cold-adapted species are likely to go extinct not only because of the direct effect of climate warming, but also because of changes in biotic interactions (Alexander et al., 2015).

Functional diversity is typically low at high elevations because strong environmental filters require that plants possess similar traits to survive (Cornwell et al., 2006; Ratier Backes et al., 2023). Climate warming removes this temperature filter, making trait specificity less important. Consequently, we expect that the trait space occupied by high-elevation communities expands through invading lowland species, which add very different trait expressions. The peak of functional diversity should be reached before high-elevation specialists go extinct, thus paralleling the expected temporary increase in species richness.

In this paper, we simultaneously address changes in highland plant communities regarding their taxonomic and functional composition in response to warmer temperatures. We report on a community transplant experiment between a high- and a low-elevation common garden site in the European Alps. We compared the development of highland communities transplanted to the warmer low-elevation site and control plant communities locally replanted at both sites over a period of 4 years. Specifically, we addressed the following hypotheses:

1. (a) Species richness of the highland communities transplanted to warmer climate increases due to the immigration of lowland species and the lagged extinction of cold-adapted species. (b) Extinction mostly affects species, which do not locally occur at low elevation, and which are characterized by a conservative resource-allocation strategy.
2. Over time, species composition of the transplanted highland communities increasingly diverges from locally replanted highland communities and becomes more similar to locally replanted lowland communities.
3. Through lagged extinction of conservative high-elevation species and invasion of more acquisitive lowland species (a) functional composition of the transplanted highland communities shifts from a more conservative to a more acquisitive resource-allocation strategy, and (b) functional diversity increases in the transplanted communities.

2 | METHODS

2.1 | Study sites

We established two experimental sites (hereafter 'sites') with an elevational distance of nearly 1000 m in the German part of the European Alps. The low-elevation site in the village of Grainau (758 m a.s.l.; 47°28′34.29″ N, 11°00′40.45″ E) was located in a typical species-rich, montane hay meadow that is usually mown two or three times per year. The plant community at the low-elevation site was characterized by the occurrence of species such as *Anthoxanthum odoratum*, *Pimpinella major* and *Trifolium repens*. The high-elevation site at Hochalm (1737 m a.s.l.; 47°26′29.12″ N, 11°03′42.26″ E) was part of a larger alpine pasture, which is grazed by young cattle for 1–2 weeks per year. Such low intensity grazing leads to high species richness and gives these ecosystems high conservation value. Here, herbaceous species dominated, and characteristic species included *Agrostis tenuis*, *Leontodon hispidus*, *Poa alpina*, *Ranunculus montanus*, and occasionally *Festuca rubra*. During the experiment, both sites were fenced to exclude large animals, and mown at the end of the growing season to simulate the previous management regimes. The study sites are characterized by a temperate climate with the majority of precipitation falling during summer (Appendix S1). Based on our own measurements from May 2014 to June 2015, mean annual temperature of the low-elevation site was 8.1°C, of the high-elevation site 4.9°C. Both sites receive high amounts of rainfall, 1348 mm at the low-elevation site and 2130 mm at the high-elevation site. The sites did not significantly differ in soil pH, both being in the neutral range around 6.6. Own laboratory analyses revealed higher amounts of soil carbon, nitrogen and phosphorus at the high-elevation site, which is not surprising assuming higher biomass accumulation and slower decomposition. The soil carbon to nitrogen ratio was around 12 for both sites, not indicating an excess of nitrogen.

2.2 | Experimental design and vegetation surveys

In September 2013, to simulate climate warming, we transplanted ten turfs with whole highland plant communities from the high- to the low-elevation site. We locally replanted an additional ten turfs with control plant communities at both sites (Figure 1). The square turfs had a side length of 50 cm and were excavated to a depth of 15–20 cm. The resultant holes served as planting locations for the transplanted and replanted turfs. At the low-elevation site, we established ten blocks, which had at least 1 m distance from each other and each received one transplanted highland community turf and one locally replanted lowland community control turf. At the high-elevation site, the locally replanted control turfs were excavated at a spacing of at least 1 m and randomly distributed among the resultant holes. Individual turfs were not replanted into the same holes from which they had been extracted. Right after trans- and replanting, the turfs were watered extensively to aid establishment at their new location. In the years 2014–2017, we annually surveyed the vegetation in the transplanted and locally replanted turfs at the peak of the vegetation period, which was in May at the low-elevation site and June–July at the high-elevation site. Nomenclature followed Müller et al. (2021). For each species, we recorded projection cover in each turf applying 13 cover classes (<1%; 1%; 2%–5%; 6%–10%; 11%–20%; 21%–30%; 31%–40%; 41%–50%; 51%–60%; 61%–70%; 71%–80%; 81%–90%; 91%–100%). Class means were used for statistical analysis.

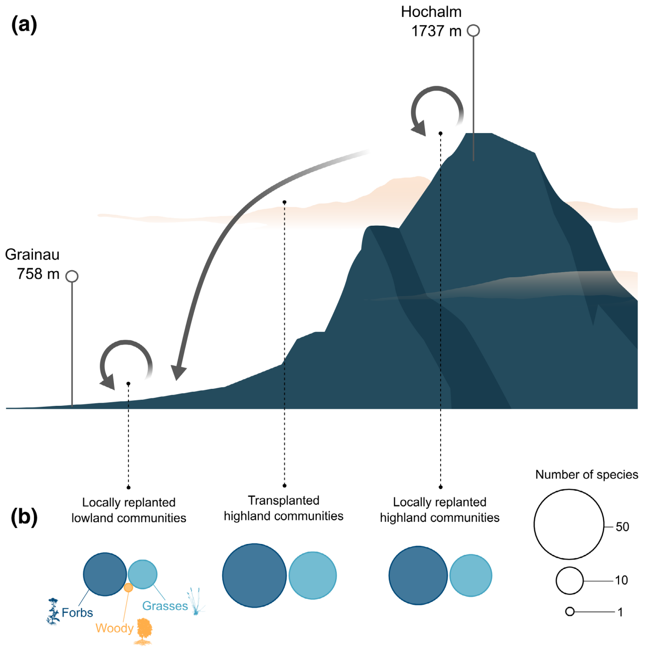


FIGURE 1 Design of the transplantation experiment with highland grassland communities transplanted to a low-elevation common garden to simulate climate warming, and locally replanted communities at both the low- and the high-elevation common garden (a). Colored circles indicate the number of species found in each treatment, separately for different life forms (b).

Such a translocation experiment to investigate potential effects of future climate change has both advantages and limitations compared to other methodical approaches. By carefully selecting the sites, it is possible to determine the temperature increase with relatively high precision. The higher temperatures are automatically correlated with a decrease in the proportion of precipitation as snow and an increase in the concentration of CO_2 (De Boeck & Nijs, 2017). Compared to other experimental methods, soil conditions, particularly soil temperature, do not differ between transplanted turfs and the surrounding environment (unlike, e.g., in lysimeter approaches), and plant communities are not influenced by artefacts resulting from warming constructions, such as open top chambers, where reduced wind speed, differences in snow melt or reduced pollinator visits might occur. Additionally, translocation experiments allow the invasion of local neighbours and therefore include the effects of changing biotic interactions (Yang et al., 2018). However, by excavating the turfs, plant roots are inevitably cut, which might affect plants' performance after transplantation (De Boeck & Nijs, 2017), and the amount of temperature increase has been criticized as representing unrealistic scenarios (Korell et al., 2020). In our case, the average difference between the high- and the low-elevation site was 3.3°C (Appendix S1). For a majority of mountain regions worldwide it was observed that the strongest increase in temperature happens in the highest elevational belt (Nigrelli & Chiarle, 2023), and from Switzerland decadal trends of up to 0.47°C were recorded between 1970 and 2011 (Ohmura, 2012). Hence, our warming scenario likely corresponds to what can be expected to occur in this region before the end of the century.

2.3 | Functional trait measurements

In 2019 at peak season, we collected leaf material for 66 out of the 77 species recorded during the course of the experiment, at both sites and in their surroundings. Leaves were taken from several individuals per species and pooled for further analysis. The fresh leaf samples were weighed, and leaf area was measured using the software WinFOLIA (Regent Instruments, Quebec, Canada). After drying for 72 h at 80°C, the samples were weighed again, and we calculated leaf dry matter content (LDMC = dry weight/fresh weight) and specific leaf area (SLA = leaf area/dry weight) (Perez-Harguindeguy et al., 2013). After milling the samples to fine powder, we measured total carbon and total nitrogen concentration (leaf C and leaf N) gas-chromatographically with the Dumas method (Vario EL Cube, Elementar Analysensysteme, Langenselbold, Germany). From this, we calculated the leaf carbon to nitrogen ratio (leaf C:N).

Trait values were averaged per species across both sites. We decided on this approach because the proportion of sampled species to all species was significantly smaller for the transplanted turfs compared to the turfs relocated within each site. This was because some species originating from the high-elevation site and not present at the low-elevation site had disappeared during the course of the experiment, and generally we did not want to sample within the transplanted turfs to avoid any impact on future development of the transplanted communities. Still, we are convinced that our species mean traits are more suitable for our analyses than trait measurements extracted from databases, potentially originating from other geographic regions.

For each plot and for each year of our experiment, we calculated the community weighted mean of SLA, LDMC, leaf C:N, and leaf N (Garnier et al., 2004):

$$\mathrm{CWM} = \sum_{i=1}^{N} p_i \mathrm{trait}_i. \qquad (1)$$

Thereby, p_i reflects the relative cover of species i in the community, and trait_i represents this species' trait value.

Additionally, for the same four leaf traits, we calculated multi-trait functional richness (FRic) and functional divergence (FDiv) to assess changes of community functional diversity. FRic represents the volume of the functional space occupied by the species of a community and is calculated as the convex hull volume (Mouchet et al., 2010). A decreasing trait space might point to an increase of environmental filters (Villéger et al., 2008). A comparison of different metrics of functional diversity revealed that FRic reached the highest power values to identify community assembly rules (Mouchet et al., 2010). In our study, FRic was used to reveal the assumed change from environmental filtering at high elevation to limiting similarity at low elevation. However, FRic is positively correlated with species richness, which must be taken into account when interpreting the results. In contrast, FDiv is generally independent of species richness and integrates information on species abundance (Villéger et al., 2008). FDiv is calculated as the species deviance from the mean distance to the center of gravity in the trait space, weighted by the relative abundance of the species (Mouchet et al., 2010). Values of FDiv approaching 1 mean that species with high abundances tend to be close to the outer margins of the functional space and are therefore very dissimilar and weakly competing with each other. This indicates a high degree of niche differentiation between the species of a community (Mouchet et al., 2010). Being generally independent of each other, these two metrics represent two important facets of functional diversity (Mason et al., 2005).

All calculations were performed using the dbFD function in the FD package (Laliberté & Legendre, 2010; Laliberté et al., 2014) in the R statistical environment (version 4.0.3; R Core Team, 2020). Trait values were standardized to a mean of 0 and unit variance prior to the analysis of FRic and FDiv. For the interpretation of our results, it is important to remember that changes in CWMs and functional diversity are caused by a shift in the species' cover and/or by species turnover, but not by within-species trait adaptations, which were not measured in this study.

2.4 | Statistical analyses

All statistical analyses were performed in the R statistical environment (version 4.0.3; R Core Team, 2020). To evaluate changes in the communities' species richness (H1a), functional composition (H3a) and functional diversity (H3b) during the 4 seasons (2014–2017) following replanting and transplantation, respectively, we applied two types of models that compared changes in community characteristics of high-elevation turfs transplanted to the low-elevation common-garden site with the two different controls: (model 1) locally replanted high-elevation turfs, and (model 2) locally replanted low-elevation turfs. The response variables comprised species richness, the CWMs of LDMC, SLA, leaf C:N, and leaf N, and FRic and FDiv of these four traits together. Model 1 included the fixed effects of site, first and second order polynomials of time (years 2014–2017, as a continuous variable) and their interaction with site as fixed effects, whereas model 2 included community origin instead of site. Functional richness was $\log_e$ transformed in all models. We used linear mixed models (R package lme4, Bates et al., 2015) with block-ID as a random effect. Models were fitted with a maximum likelihood approach. Significance of the main effects was tested with Type III Wald *F* tests (Satterthwaite's method) except for main effects included in higher-order terms. To analyze how species extinction in the high-elevation turfs transplanted to the low-elevation site depended on species traits and local occurrence (H1b), we first regressed the presence of each species (coded as a binary presence-absence variable) against time (years 2014–2017) using a generalized linear model with a logistic link function. Based on the logistic regression results, we classified species as winners (at least marginally significant ($p < 0.1$) positive slope) and losers (at least marginally significant negative slope). Additionally, we considered those species as winners, which did not occur in any of the locally replanted highland communities at the high-elevation common garden, but were recorded at least twice in the highland communities following transplantation to the low-elevation site (and did not disappear again). We further considered those species as loser species, which were recorded at least twice in the transplanted highland communities in the beginning of the experiment, but then completely disappeared from all transplanted turfs and did also not occur in any of the lowland communities. Using the winner and loser species only, we ran linear models with their functional traits as response and success category ("winner"/"loser") as an explanatory variable. Significance was tested with *F*-tests.

To test how the community composition within the transplanted and locally replanted turfs changed over time (H2), we performed a canonical correspondence analysis (CCA; R package "vegan", Oksanen et al., 2018), with the year as constraining variable on the first ordination axis.

3 | RESULTS

In our repeated vegetation surveys, we recorded 50 forb species, 26 graminoid species and one tree seedling (Appendix S2). While the proportion of forbs and graminoid species was similar for the locally replanted communities at the low- and high-elevation site and for the transplanted communities, the number of species recorded in each treatment differed strongly. Fewest species were found in the locally replanted communities at the low-elevation site (40 species), the locally replanted communities at the high-elevation site harbored 56 species, and 62 species were observed in the transplanted communities. Twenty-one species were present in all treatments, 34 species only occurred in the locally replanted highland communities, and 18 species were recorded only at the low-elevation site (Appendix S2).

3.1 | Community composition

The CCA shows that highland and lowland communities at their original sites strongly differ from each other (Figure 2). While over the course of the experiment, locally replanted communities kept their dissimilarity, highland communities transplanted to the low-elevation site became increasingly similar to the lowland communities but diverged from the locally replanted highland communities

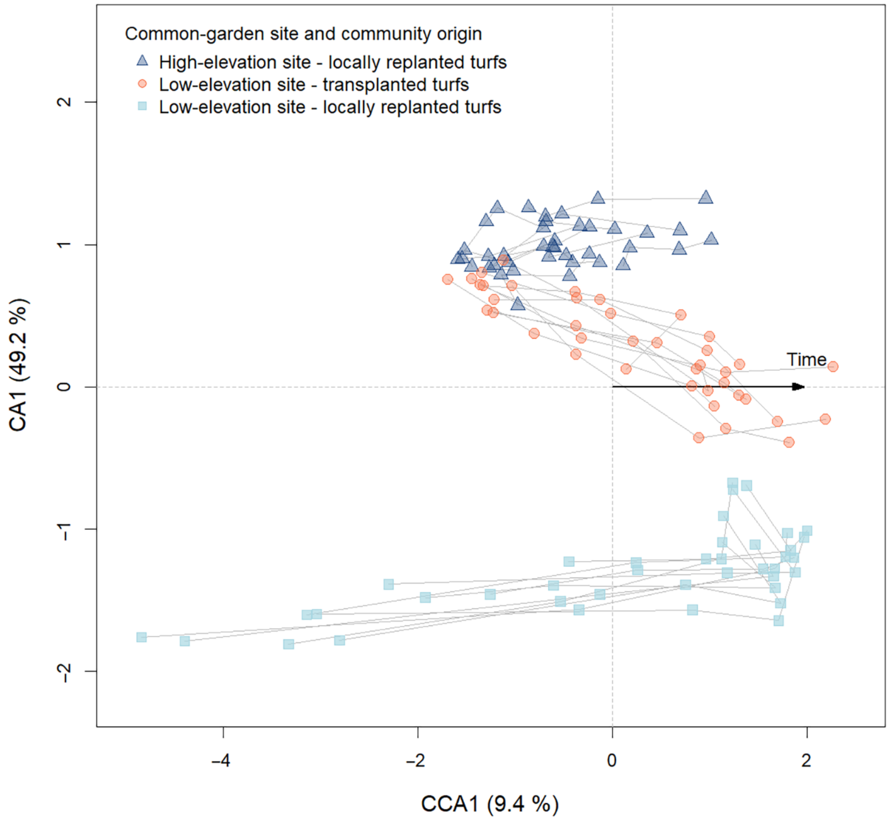


FIGURE 2 Results of the canonical correspondence analysis (CCA) with the year as constraining variable on the first ordination axis to analyze the change of community composition over time. The highland communities transplanted to the low-elevation site are represented by red circles.

(Figure 2). Community change over time was also observed for the locally replanted communities, especially during the first couple of years at the low-elevation site. Overall, time accounted for 9.4% of the variation in community composition. A permutation test with 999 iterations revealed a very good fit of the model ($p < 0.001$).

3.2 | Species richness

Species richness of the transplanted communities significantly increased over time, however, this effect was less pronounced towards the end of the experiment (Figure 3a,b; Table 1). An increase of species richness was also observed for locally replanted communities at the high-elevation site (Figure 3a), but not for locally replanted communities at the low-elevation site (significant origin-by-year interaction; Figure 3b; Table 1). In the first year of the experiment, at the low-elevation site, species richness of the transplanted highland communities was lower compared to locally replanted lowland communities, but this difference disappeared in the following years.

3.3 | Functional diversity

Functional richness (FRic) of the transplanted communities continuously increased over time (Figure 3c,d; Table 1). An overall increase of FRic was also observed for locally replanted communities at the high-elevation site, mainly resulting from higher FRic in the last year of the experiment (Figure 3c). For locally replanted communities at the low-elevation site, FRic was rather constant over time (significant origin-by-year interaction; Figure 3d; Table 1). While in the first year of the experiment, FRic of the transplanted communities was lower compared to locally replanted lowland communities, both community origins were similar in FRic in the fourth year.

Functional divergence (FDiv) of the transplanted communities decreased directly after transplantation, but increased during the second half of the experiment, to reach after 4 years the level of the first year (Figure 3e,f; Table 1). In contrast, FDiv of locally replanted communities at the high-elevation site continuously decreased, so that the greatest difference in FDiv of highland communities at both sites was observed in the last year of the experiment (significant site-by-year interaction; Figure 3e; Table 1). At the low-elevation site, highland and lowland communities showed contrasting temporal changes of FDiv, with locally replanted communities' FDiv peaking in the middle of the experiment (significant origin-by-year interaction; Figure 3f; Table 1).

3.4 | Winners and losers

Of all 62 species recorded in the transplanted communities, we identified 15 “winner” species and 12 “loser” species (Appendices S2, S3 and S4). Among the winner species, nine species were not found in any of the locally replanted highland communities (*Alopecurus pratensis*, *Brachypodium pinnatum*, *Colchicum autumnale*, *Geum rivale*, *Heracleum sphondylium*, *Knautia arvensis*, *Lolium perenne*, *Plantago lanceolata*, *Vicia cracca*), making it likely that these species established in the transplanted highland communities only after the transplantation event. All loser species were highland species and occurred only in the locally replanted communities at the high-elevation site and in the transplanted highland communities. *Poa alpina* and *Carex ferruginea* showed the strongest decline, with species records in the first year of the experiment in all ten (*P. alpina*) and nine transplanted communities (*C. ferruginea*), respectively, and only one observation in the fourth year. There were no significant differences between winner and loser species with regard to SLA, LDMC, leaf N and leaf C:N (Figure 4).

3.5 | Community weighted means

For the transplanted communities, the community weighted means (CWM) of SLA, leaf N and leaf C:N showed a consistent pattern, with communities shifting towards a more conservative resource-use strategy in the first 2 years of the experiment (lower values for SLA and leaf N, but higher values for leaf C:N), followed by a shift towards a more acquisitive resource-use strategy in the last 2 years (Figure 5; Table 1). The opposite pattern was observed for the CWM of LDMC, with a decrease (i.e., more acquisitive strategy) followed by an increase. For locally replanted highland communities, the CWM of leaf N and leaf C:N followed a similar trend as the transplanted communities, while the CWM of SLA and LDMC of replanted highland communities were constant over time (Figure 5a,c,e,g). At the low-elevation site, the temporal trend of the CWM of SLA, leaf N and leaf C:N of the locally replanted communities did not deviate from that of the transplanted communities (Figure 5b,d,h). In contrast, the CWM of LDMC for locally replanted lowland communities increased significantly over time, reflecting a shift towards a more conservative resource-use strategy (Figure 5f).

At the low-elevation site, the CWM of SLA and leaf N were lower for the transplanted communities compared to the locally replanted communities (marginally significant in the case of SLA), while the CWM of LDMC and leaf C:N were significantly higher. Except for

FIGURE 3 Changes in species richness and functional diversity over the years 2014–2017 (indicated as years 1–4 on the x-axis). The left column presents diversity changes in highland plant community turfs locally replanted within the high-elevation common garden (high-elevation control, dark blue) versus transplanted turfs to the low-elevation common garden (red). Plots in the right column compare changes in highland plant community turfs transplanted to the low-elevation garden (red) with lowland community turfs locally replanted within the same low-elevation garden (low-elevation control, light blue). Panels represent (a,b) species richness, (c,d) functional richness, and (e,f) functional divergence. Lines represent predictions of the full models. Functional richness was $\log_e$ transformed in the models. Random noise has been added to the x-values.

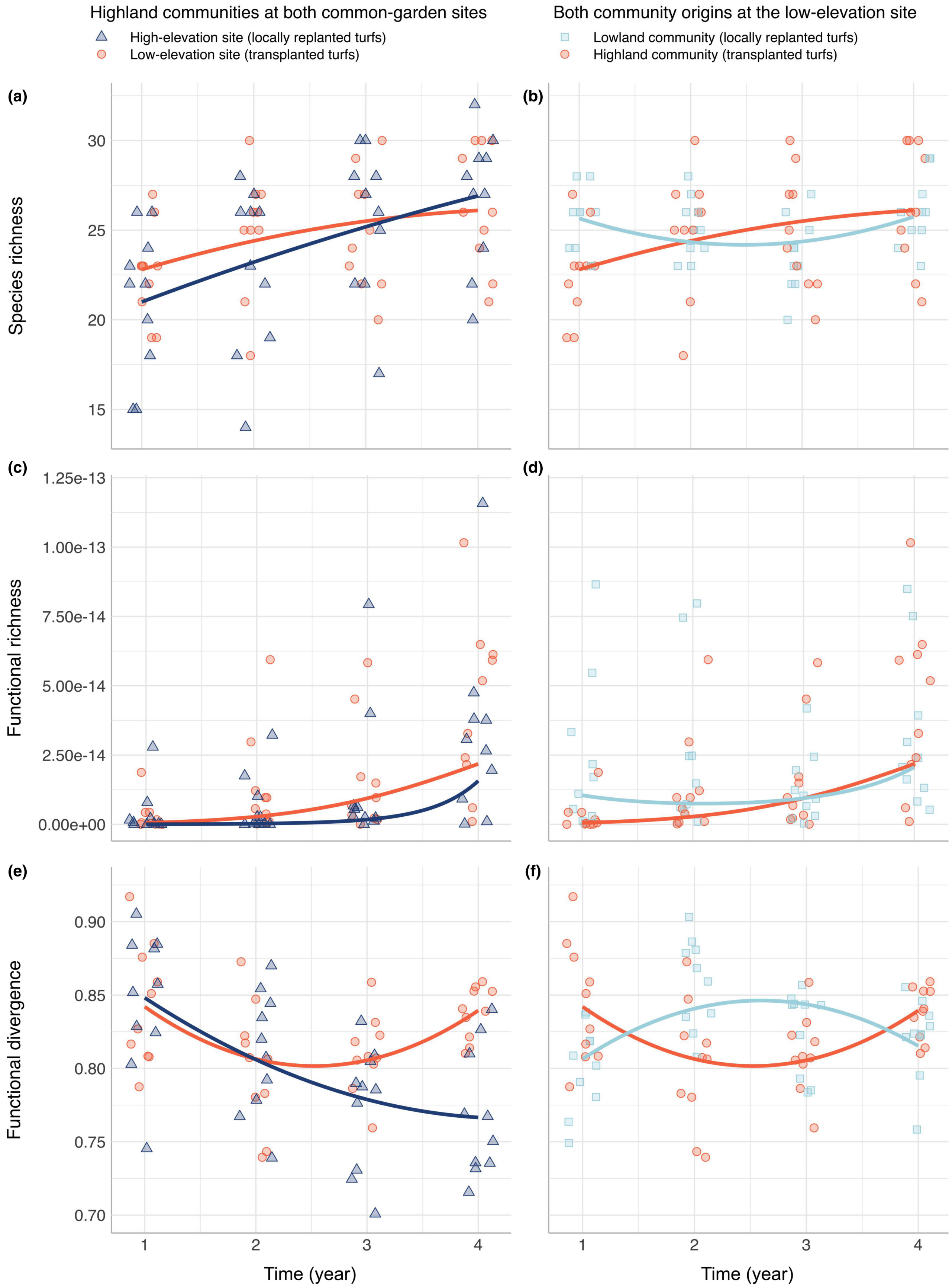

Highland communities at both common-garden sites
△ High-elevation site (locally replanted turfs)
○ Low-elevation site (transplanted turfs)
Both community origins at the low-elevation site
□ Lowland community (locally replanted turfs)
○ Highland community (transplanted turfs)
(a)
(b)
Species richness
15
20
25
30
(c)
(d)
Functional richness
0.00e+00
2.50e-14
5.00e-14
7.50e-14
1.00e-13
1.25e-13
(e)
(f)
Functional divergence
0.70
0.75
0.80
0.85
0.90
1
2
3
4
Time (year)
1
2
3
4
Time (year)

TABLE 1 Analyses of changes in community diversity and mean functional traits over time (years since experimental set-up) in the community transplant experiment.

Response variables		Community diversity								
		Species richness			Functional richness			Functional divergence		
Explanatory variable	**df**	**Est**	***F***	***p***	**Est**	***F***	***p***	**Est**	***F***	***p***
Model 1										
Intercept	—	24.075	—	—	−34.755	—	—	0.8	—	—
Site (low-elevation)	18;1	0.625	0.201	0.659	1.671	1.69	0.21	0.023	3.834	0.066
Year	—	19.7	high.ord.	high.ord.	18.762	high.ord.	high.ord.	−0.272	high.ord.	high.ord.
poly(Year, 2)	56;2	−1.118	**23.255**	**<0.001*** **	1.392	25.485	**<0.001*** **	0.067	15.393	**<0.001*** **
Site (low-elevation): Year	—	−8.7	high.ord.	high.ord.	−6.681	high.ord.	high.ord.	0.263	high.ord.	high.ord.
Site (low-elevation): poly(Year, 2)	56;2	−1.118	1.876	0.163	−3.041	1.443	0.245	0.089	9.289	**<0.001*** **
Model 2										
Intercept	—	24.7	—	—	−33.084	—	—	0.823	—	—
Origin (lowland)	18;1	0.325	0.194	0.665	0.956	3.778	0.068	0.003	0.086	0.773
Year	—	11	high.ord.	high.ord.	12.081	high.ord.	high.ord.	−0.008	high.ord.	high.ord.
poly(Year, 2)	56;2	−2.236	**3.189**	**<0.05* **	−1.649	**11.857**	**<0.001*** **	0.155	0.13	0.878
Origin (lowland) : Year	—	−10.7	high.ord.	high.ord.	−9.831	high.ord.	high.ord.	0.038	high.ord.	high.ord.
Origin (lowland) : poly(Year, 2)	56;2	8.274	**4.105**	**<0.05* **	4.148	**11.857**	**<0.01** **	−0.296	**17.334**	**<0.001*** **

Response variables		Community weighted means (CWMs) of functional traits					
		SLA			Leaf N		
Explanatory variable	**df**	**Est**	***F***	***p***	**Est**	***F***	***p***
Model 1							
Intercept	—	23.701	—	—	2.736	—	—
Site (low-elevation)	18;1	0.692	1.476	0.24	−0.011	0.055	0.818
Year	—	0.535	high.ord.	high.ord.	−0.201	high.ord.	high.ord.
poly(Year. 2)	56;2	0.591	**5.122**	**<0.01** **	0.173	**12.988**	**<0.001*** **
Site (low-elevation) : Year	—	−1.476	high.ord.	high.ord.	0.13	high.ord.	high.ord.
Site (low-elevation) : poly(Year, 2)	56;2	7.029	**3.909**	**<0.05* **	0.132	1.465	0.24

TABLE 1 (Continued)

		Community weighted means (CWMs) of functional traits					
Response variables		**SLA**			**Leaf N**		
Explanatory variable	**df**	**Est**	***F***	***p***	**Est**	***F***	***p***
Model 2							
Intercept	–	24.392	–	–	2.725	–	–
Origin (lowland)	18;1	0.679	4.182	0.056	0.092	**19.843**	**<0.001*****
Year	–	−0.941	high.ord.	high.ord.	−0.072	high.ord.	high.ord.
poly(Year, 2)	56;2	7.621	**29.565**	**<0.001*****	0.306	**16.158**	**<0.001*****
Origin (lowland) : Year	–	−1.572	high.ord.	high.ord.	−0.123	high.ord.	high.ord.
Origin (lowland) : poly(Year, 2)	56;2	−0.603	0.371	0.692	−0.142	1.966	0.15

		Community weighted means (CWMs) of functional traits					
Response variables		**LDMC**			**Leaf C:N**		
Explanatory variable	**df**	**Est**	***F***	***p***	**Est**	***F***	***p***
Model 1							
Intercept	–	251.25	–	–	16.572	–	–
Site (low-elevation)	18;1	9.746	**8.867**	**<0.01****	0.123	0.253	0.621
Year	–	10.129	high.ord.	high.ord.	1.735	high.ord.	high.ord.
poly(Year, 2)	56;2	10.128	**5.993**	**<0.01****	−0.776	**14.314**	**<0.001*****
Site (low-elevation) : Year	–	−22.916	high.ord.	high.ord.	−0.606	high.ord.	high.ord.
Site (low-elevation) : poly(Year, 2)	56;2	33.505	**0.408**	**<0.05***	−0.578	0.789	0.459
Model 2							
Intercept	–	251.254	–	–	16.695	–	–
Origin (lowland)	18;1	−20.927	**56.782**	**<0.001*****	−0.608	**22.612**	**<0.001*****
Year	–	−12.787	high.ord.	high.ord.	1.129	high.ord.	high.ord.
poly(Year, 2)	56;2	43.633	**13.27**	**<0.001*****	−1.354	**12.386**	**<0.001*****
Origin (lowland): Year	–	101.21	high.ord.	high.ord.	−0.278	high.ord.	high.ord.
Origin (lowland) : poly(Year, 2)	56;2	−50.02	**23.794**	**<0.001*****	0.474	0.421	0.659

Note: 'Model 1' analyzed the effects of time in interaction with site (high-elevation vs. low-elevation), whereas 'Model 2' included the interactive effects of time and community origin (highland vs. lowland). Quadratic effects (second order polynomials) of time were first included in all models, and the significance of linear effects of year were not tested if the higher order polynomial term was present (high. ord.), which was the case for all analyses presented here. Significance was tested with Type III *F*-Tests (Satterthwaite's method). Year: year of data collection; Site: low-elevation or high-elevation common-garden site; Community origin: lowland or highland turf. Significant effects are indicated in bold. Levels of significance: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

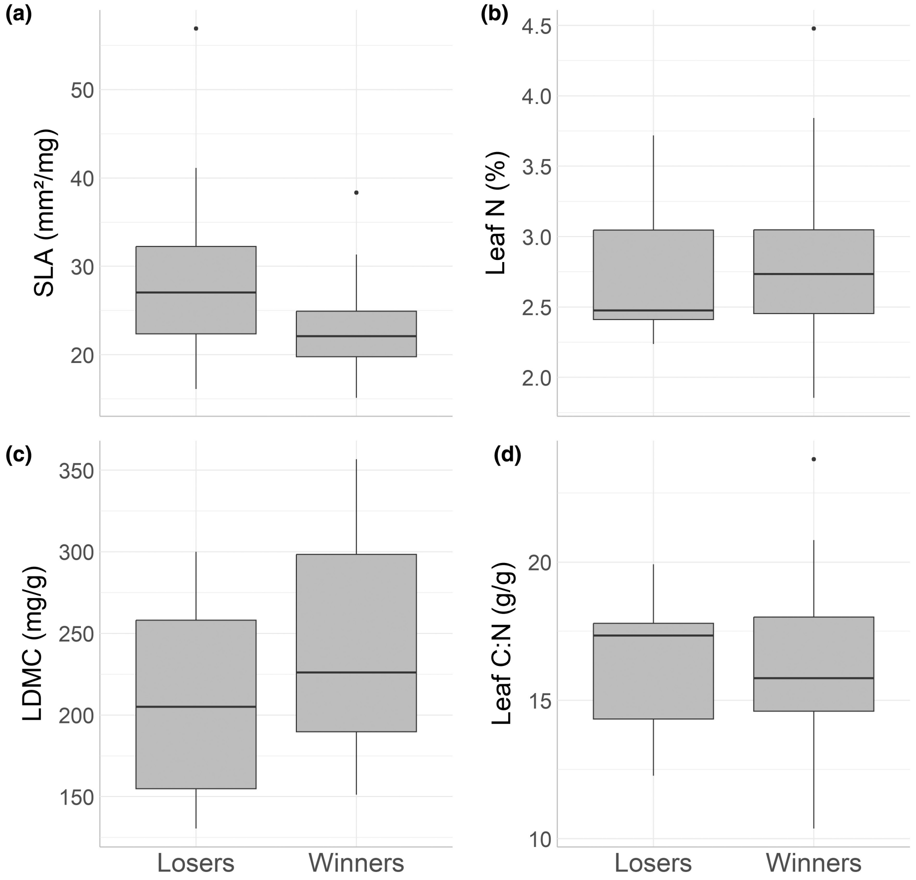


FIGURE 4 Differences in functional leaf traits of loser and winner species in highland plant community turfs transplanted to the low-elevation common garden. (a) specific leaf area (SLA), (b) leaf nitrogen concentration (leaf N), (c) leaf dry matter content (LDMC), and (d) leaf carbon to nitrogen ratio (leaf C:N). For classification criteria of loser and winner species please refer to Methods. *F*-tests did not show any significant differences between the two groups of species.

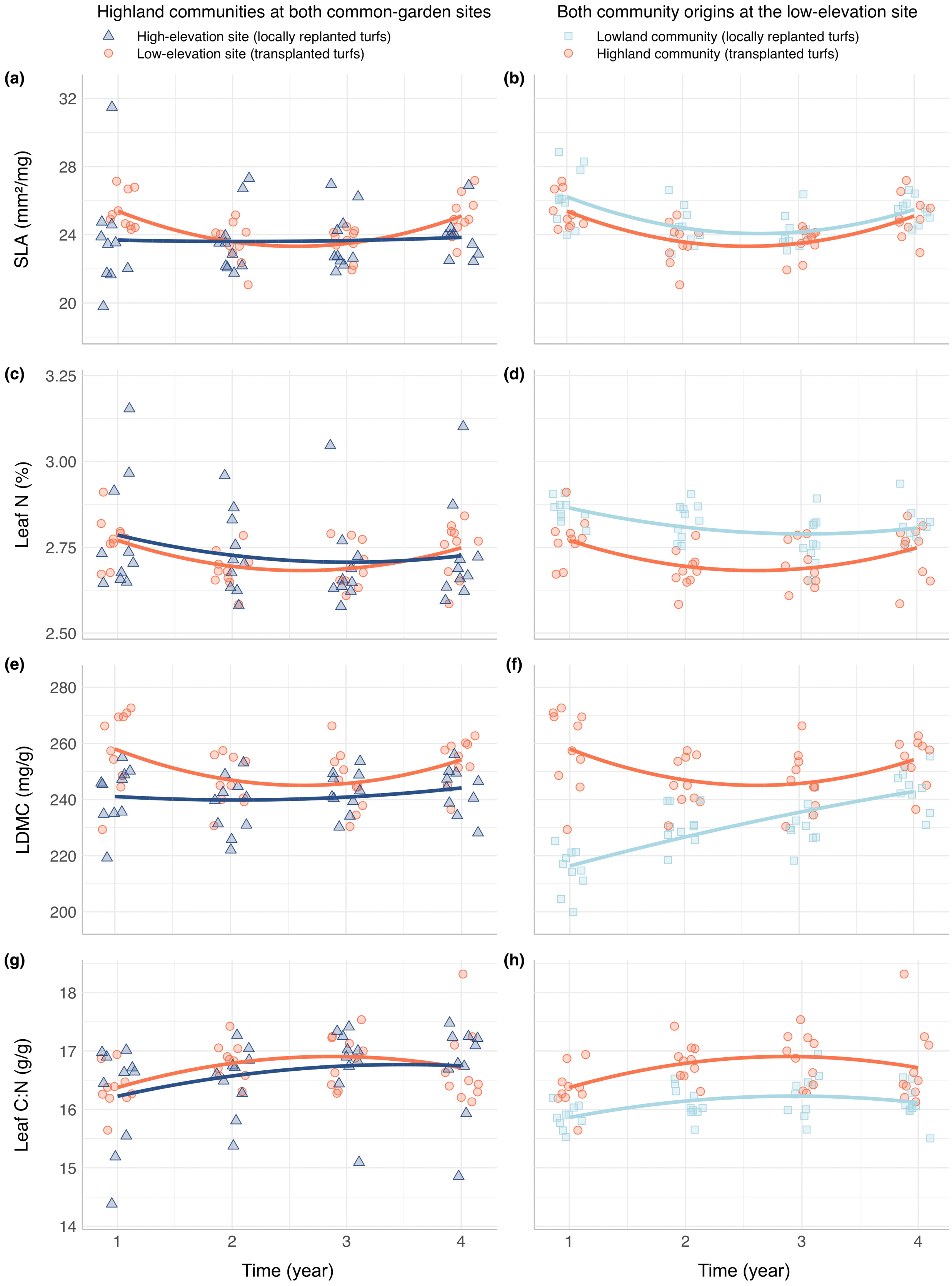
the CWM of LDMC (higher for transplanted compared to locally replanted communities), there was no difference between the highland communities at both common-garden sites.

4 | DISCUSSION

4.1 | Immediate species invasion, but lagged extinction after 4 years of warming

Species richness of the experimentally warmed communities increased over time, thus confirming hypothesis 1a. Such a warming-induced gain in species richness has been reported from numerous mountain regions (Pauli et al., 2012; Steinbauer et al., 2018; Rumpf, Hülber, Wessely, et al., 2019a) and seems to be particularly common for moist-temperate mountain areas, where communities become more productive through warming and where sources of new species are nearby (Harrison, 2020). However, for our transplanted highland communities, the increase of species richness slowed down over time. This indicates that invasion into the transplanted turfs happened directly after transplantation, while extinction does not seem to be immediate. This is an interesting finding, since most observational studies, which report increases in species richness through climate warming, were conducted at larger scales. Here, in our communities with a size of only 50 cm × 50 cm, we observed the same process. However, at such a small scale, species co-existence is limited, which might explain why the increase in species richness did not happen at a constant rate but slowed down over time. In our experiment, delayed extinction might

FIGURE 5 Changes in functional leaf traits over the years 2014–2017 (indicated as years 1–4 on the x-axis). The left column presents diversity changes in highland plant community turfs locally replanted within the high-elevation common garden (high-elevation control, dark blue) versus transplanted turfs to the low-elevation common garden (red). Plots in the right column compare changes in highland plant community turfs transplanted to the low-elevation garden (red) with lowland community turfs locally replanted within the same low-elevation garden (low-elevation control, light blue). Panels represent community weighted means (CWM) of (a,b) specific leaf area (SLA), (c,d) leaf nitrogen concentration, (e,f) leaf dry matter content (LDMC), and (g,h) leaf carbon to nitrogen ratio (Leaf C:N). Lines represent predictions of the full models. Random noise has been added to the x-values.



be explained primarily through the longevity of most species and the ability of mountain species to survive in relatively warm conditions for extended periods through their clonal reproduction strategies, while invasion is supported by the clonal spread of lowland species (Appendix S2). As expected in hypothesis 1b, it were the mountain species, which did not naturally occur at the low-elevation site, that went extinct in the transplanted communities. This aligns with the findings of an observational study from Italy, where over a period of 15 years primarily the cold-adapted species declined (Porro et al., 2019). However, contrary to our expectations, the 'loser' species were not characterized by more conservative trait expressions compared to the 'winner' species. This is despite the fact that winners were almost exclusively species that occur at the low-elevation site (*Carex pallescens* being the only high-elevation species, which increased in abundance) and losers were mostly high-elevation species. A possible explanation might be that high-elevation species had rather high foliar nutrient concentrations due to their small stature, while there is a dilution effect for tall lowland species (Körner, 1989; Smith et al., 1994). Further, high amounts of precipitation at both common-garden sites, and the resultant absence of water limitation, might diminish differences in leaf dry matter content between the species. This finding contradicts the expectation that a high specific leaf area is associated with high relative growth rates (Poorter & Remkes, 1990). Moreover, the species identified as losers in our experiment were mostly species restricted to higher elevations, where SLA is assumed to be lower as a consequence of colder temperatures and less nutrient-rich soils (Poorter & Remkes, 1990). However, SLA also strongly depends on light availability, with plants growing in full sunlight displaying lower SLA compared to plants growing in shade (Ryser & Wahl, 2001; Poorter et al., 2019). In our experiment, light might have been the dominant factor, and high-elevation species with a typically smaller stature were growing in shady conditions, which might explain the tendency of higher SLA of loser species. Additionally, SLA can be considered a competitive response trait, decreasing with increasing light depletion following from a plant's higher competitive ability (Violle et al., 2009; Kunstler et al., 2016). These findings emphasize that trait-environment relationships are complex and depend on the scale considered. While relationships between traits and macroclimate are well established (e.g. Swenson et al., 2012; Bruelheide et al., 2018; Šímová et al., 2018), it seems to be much more difficult to predict at local scales, which species are likely to benefit or suffer from climate warming (see also De Frenne et al., 2013).

Generally, local extinctions will be only partly driven by the direct impact of climate warming, and many of them will likely be caused by competition through invading lowland species with more vigorous growth compared to the typical slow-growing, stress-tolerant high-elevation species (Alexander et al., 2015, 2016).

Although there was only a slight annual increase in species richness from the third to the fourth year after transplantation, we could still observe changes in community composition, resulting from species turnover through invasions and local extinctions. For example, *Poa alpina* and *Carex ferruginea* were present in almost all transplanted turfs in the first year of the experiment but disappeared in all but one turf in the fourth year. Additionally, changes in community composition were caused by changes in species abundances within the communities. Especially, relative plot cover of the 'winner' species tended to be higher in the fourth year of observation compared to the first year, while it was the opposite for 'loser' species (Appendix S5). As a consequence, the transplanted communities diverged from the locally replanted communities at the high-elevation common garden and became more similar to the communities from the low-elevation site during the study period, hence supporting our second hypothesis. A loss of community dissimilarity across elevations and a conversion of species assemblages of high-elevations towards that of low-elevations was also observed in a 40-year study in a montane region in Canada and was attributed to climate warming over this time period (Savage & Vellend, 2015).

We also observed changes in species richness and/or community composition in the turfs locally replanted in the respective common garden. At the high-elevation site, the exclusion of the usual grazing through the fencing of our common garden is the most likely explanation for these changes. Although grazing intensity is low in the study area, it suppresses the vigorous growth of the plants, and does not allow species to become dominant. We visually observed that the lack of grazers seems to favor graminoid species abundance, while suppressing forb species, which are typically of smaller stature and therefore minor competitors in grass-dominated communities. At the low-elevation site, changes in mowing frequency and timing during the experiment might have led to a gradual change in species composition of the locally replanted communities (including both species turnover and changes in species abundance) without significantly affecting species richness.

4.2 | Increased functional diversity through invading species

As expected in hypothesis 3b, functional richness, i.e., the communities' volume of functional space, increased in the transplanted highland turfs over time. This aligns with our finding that new lowland species colonized the transplanted turfs immediately, which contributed trait syndromes beyond the trait range of the original highland community (de Bello et al., 2013; Rosbakh et al., 2015). We might speculate that after 4 years of transplantation, functional richness of the transplanted turfs has not reached its peak yet, but that the continuous invasion of lowland species, including a possible invasion of non-native lowland species, and the lagged extirpation of highland species may lead to a further increase of functional richness in the following years, before the loss of highland species will switch this trend.

Directly after transplantation, functional richness of the locally replanted turfs at the low-elevation site was higher compared to the turfs transplanted from high to low elevation. This finding reflects the stronger effect of environmental filtering at high elevations, where trait values are restricted by the environmental constraints and a large trait variation is not possible (Schellenberger Costa et al., 2017). Through transplantation to the warmer low-elevation site, these environmental constraints were lifted, supporting the increase in community trait space. This is in line with the tolerance hypothesis, which assumes that more sets of functional strategies can tolerate favorable compared to harsher environmental conditions (Harrison, 2020), also providing a mechanistic explanation behind the observed increase of species richness in the transplanted communities.

For the transplanted communities, we hypothesized functional divergence (FDiv) to increase as well (hypothesis 3b), but this trend was only observed in the last 2 years of the experiment. Higher FDiv points to a higher degree of species niche differentiation, which means that abundant species within a community occupy different functional niches (Mouchet et al., 2010). In the transplanted communities, invading and locally dominant lowland species are likely to possess very different functional traits compared to the most persistent (highland) species.

4.3 | Lack of community trait shifts

For the resource-use related traits leaf N, leaf C:N and SLA, we consistently found more conservative values for transplanted turfs compared to locally replanted turfs at the low-elevation site, which aligns with previous findings (Körner, 1989; Rosbakh et al., 2015; Ratier Backes et al., 2021). However, against our expectation (hypothesis 3a), the transplanted highland communities did not shift consistently towards a more acquisitive resource-use strategy under the warmer conditions at the low-elevation site compared to the high-elevation common garden, as observed in other studies (Cantarel et al., 2013; Guittar et al., 2016). Rather, trait changes over time were similar for all treatments, possibly reflecting general interannual fluctuations of weather conditions and/or the change in mowing and grazing, respectively.

Regarding LDMC, which is not only driven by temperature, but may also be related to water availability, we found transplanted highland communities to have a lower LDMC than both locally replanted highland and lowland communities, however, likely for different reasons. At the low-elevation site, the difference fits our expectation of lowland communities following a more acquisitive resource-use strategy, but since we did not find such responses for the other traits, it is more likely that lowland communities benefit from moister conditions in the loamy lowland soils compared to the rather stony highland soil. At the high-elevation site, the lower LDMC might be caused by higher precipitation amounts (Haider et al., 2022).

5 | CONCLUSIONS

After 4 years following transplantation to a lowland environment we found noticeable changes in the composition of highland plant communities, resulting from the invasion of lowland species and decrease of mountain specialists. These processes led to an increase of species richness and functional diversity, while community trait means have not shifted significantly yet. At the local scale, competitive interactions determine the number of co-existing species and will limit the number of new species. We therefore expect the higher community diversity to disappear over time, paralleling the loss of species adapted to cooler temperatures. Our findings emphasize that responses to warmer temperatures can happen very quickly and it is likely that the ongoing species turnover will also affect community traits in a direction towards a more acquisitive resource-use strategy with faster-growing and hence more competitive species. Such trait changes might then accelerate community changes, which is expected to be associated with a loss of taxonomic and functional diversity over time and space. It is noteworthy that results from small-scale experimental approaches might diverge from findings of large-scale observational studies. To better understand the consequences of climate warming on mountain plant communities, and the underlying processes, it is necessary to combine research across scales, to address both the effect of macroclimate change and the mediating role of local biotic and abiotic conditions. For example, while in our study area transplantation of highland communities to a lowland environment was not associated with a critical reduction of water or nutrient availability, these factors can interact and accelerate or strengthen the effects of climate warming (Wu et al., 2011; Cowles et al., 2018).

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DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Climate information of the study sites.
Appendix S2. Species list and functional traits.
Appendix S3. Species occurrence over time in transplanted communities.
Appendix S4. Heatmaps of species occurrence in different treatments.
Appendix S5. Relative plot cover of winner and loser species.

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