Networks, but not composition or commonness, capture early community responses to warming in alpine grassland

Abstract

Alpine regions are warming faster than the global average, yet mounting evidence suggests that alpine plant communities respond slowly, raising the question of whether this reflects ecological robustness or the accumulation of extinction debts. Resolving this question requires looking beyond community composition. Climate warming affects plant demography, and ultimately composition, but its effect on plant-plant interactions remains poorly understood because such interactions are difficult to detect and attribute to drivers. Recent statistical advances now allow inferring fine-scale spatial associations among species co-occurring in small, environmentally homogeneous communities from high-resolution mapping data, providing proxies for biotic interactions that can be combined in spatial associations networks. Using a whole-community transplant experiment of alpine grasslands and high-resolution mapping of plant-plant associations at ~10k pinpoints across small communities of 1 m^2, we assessed the effects of ~3 °C warming on plant-plant spatial association networks. After five years, species composition, the identity of the most common species and the commonness structure of alpine warmed communities showed only slight, non-significant shifts towards subalpine communities. In contrast to the apparent compositional stability, warming markedly restructured plant-plant spatial association networks. Network architecture shifted towards that of subalpine communities, with an almost complete turnover of species occupying the highly connected network core. Across treatments, almost all spatial associations detected were negative, and they increased markedly with warming, consistent with the stress-gradient hypothesis predicting more negative associations under more benign conditions. These findings underscore that climate change can rapidly reorganize species' ecological roles and interaction structure within alpine communities despite minimal short-term compositional change, potentially signalling ongoing community reassembly and the build-up of extinction debts. Focusing solely on compositional metrics may therefore provide a misleading sense of stability under climate change, overlooking early structural transformations with implications for long-term biodiversity and ecosystem resilience.

Keywords: alpine plants, biotic interactions, climate warming, competition, interaction networks, spatial associations, species dominance, transplant experiment

INTRODUCTION

Global warming is reshaping plant community demography, composition and structure, particularly in alpine environments where temperatures are rising faster than the global average (Pepin et al. 2022; IPCC 2023). Warming is increasing the frequency of summer droughts, advancing snowmelt, lengthening growing seasons and elevating the risk of freezing damage (IPCC 2023; Choler et al. 2021; Vorkauf et al. 2021). These climatic changes are driving upward range shifts in some plant species (Vitasse et al. 2021), increasing summit biodiversity (Steinbauer et al. 2018), altering community composition and changing biotic interactions (Gilman et al. 2010; Suttle et al. 2007). However, despite the emergence of these novel communities, how climate change reorganizes biotic interactions remains poorly understood. This knowledge gap is important because the network of biotic interactions in a community underpins key ecosystem functions, including resistance to invasion (Mitchell et al. 2006), resilience to disturbance (Lajaaiti et al. 2026) and decomposition (Wang et al. 2025).

Climate warming is expected to affect biotic interactions both directly and indirectly. First, changing climatic conditions can change how species interact with each other. For example, the stress-gradient hypothesis predicts that under increasingly benign conditions biotic interactions can shift from facilitative to increasingly competitive interactions (Bertness & Callaway 1994; Choler et al. 2001; He & Bertness 2014). Second, climate warming changes interaction partners with the arrival of colonizers, and this could indirectly create novel biotic interactions (Pellissier et al. 2018). Finally, laboratory and removal experiments show that the presence of one species can significantly alter another's response to warming, showing that biotic interactions can modulate warming responses (Verlinden et al. 2014; Klanderud 2005). However, the understanding of the effects of climate change on biotic interactions is still very limited, especially for real-world communities out of experimental settings. This is partly due to the inherent difficulty of identifying biotic interactions in the field. Indeed, direct biotic interactions cannot be observed without complex methodologies (Blanchet et al. 2020; Delalandre & Montesinos-Navarro 2018). Experiments tailored to detect species interactions have provided insights under controlled conditions, but are limited to a few species and therefore cannot be generalized to study biotic interactions at the scale of very rich grasslands (Verlinden et al. 2014; Klanderud 2005). Approaches at the community level have used the comparison of community diversity patterns to null models to detect signals of competition (Münkemüller et al. 2020; Bektaş et al. 2023). However, this assumes that all species contribute to the interaction network and that a single interaction type dominates. This method therefore cannot distinguish between the different roles species may play in the community and may thus miss to represent the interaction networks of communities.

To go beyond these limitations, proxy approaches to infer pairwise interactions from field data are more and more used (Blanchet et al. 2020; Morales-Castilla et al. 2015), with analyses of spatial associations becoming particularly popular (Chillo et al. 2021; Losapio et al. 2018; Losapio et al. 2021; Saiz et al. 2018). Here, we use such a novel statistical approach (Rohr et al. 2026; Wendling & Galiez 2026) that builds on the spatial-explicit sampling of pinpoints at which individuals actually touch each other, in small-scale communities (here $1m^2$) where species co-occur in homogeneous environmental conditions. The approach tests whether

species are more or less associated at pinpoints than expected from their co-occurrence in the community given the environmental filters. In this framework, co-occurence in the community means that the species share environmental preferences. Under the assumption that environmental conditions in community plots are homogeneous, spatial aggregation at the pinpoint would hint to positive biotic interactions and spatial segregation to negative interactions (Freilich et al. 2018). By combining this information on pairwise spatial associations within a community across all species and multiple communities, we can build species association network, in which species that constrain each other's distributions (structuring species) are represented as nodes and their positive or negative associations as signed links (Losapio et al. 2019). Network theory then provides a powerful framework for quantifying emergent network properties (e.g., size, order, and centralization) and relating them to community functioning (Delmas et al. 2019), independently of species identity. Networks also allow identifying keystone species that we define here as common species that shape the spatial distribution of other species, in contrast to common species with no effects on other species (Avolio et al. 2019). These keystone species are essential because they will shape ecosystem functioning and services under future climatic conditions (Smith et al. 2020).

Because community composition, commonness and interaction structure are tightly intertwined, it remains unclear which component responds first to climate warming and subsequently drives changes in the other two. Two alternative mechanisms can be expected. On one hand, climate warming could primarily alter community composition, thereby indirectly modifying biotic interactions through species turnover and novel interaction pairs (Gravel et al. 2016; Vellend 2010). On the other hand, warming could also first reshape biotic interactions, and ultimately drive subsequent changes in community composition (Mod et al. 2014; Gilman et al. 2010; Alexander et al. 2015). Distinguishing between these alternative pathways remains a major challenge in community ecology. It is particularly important for predicting how alpine plant communities will reorganize under warming and whether early responses to climate change are best detected through changes in species composition or through the reorganization of species interactions.

In response to the call for more in-situ experiments in climate warming research (Alexander et al. 2016), here we used a whole community transplant experiment to simulate warming effects on alpine plant communities (Fig. 1a). Combining the experiment with high-resolution vegetation surveys allowed us to infer spatial association networks (Wendling & Galiez 2026) for each of the three treatments (i.e. warmed communities, control communities at the original colder site, control communities at the destination warmer site). Building on this, we investigated how climate warming affects alpine grassland communities through changes in species composition, community commonness structure, and species interaction structure. Specifically, we asked:
(1) How did the composition and the community commonness structure change under climate warming (Hypothesis H1 in Fig. 1)?
(2) Were the common species also the most important in plant spatial association networks?
(3) Did the association network change under warming (or did only non-structuring species change, H2), and if so, via changes in structuring species (H3) or via changes in spatial associations (H4)?
(4) What firstly shift in the communities: its composition, its commonness structure or its network?

METHODS

Experimental design

The transplantation experiment was conducted in September 2016 in the French Alps, between the alpine site 'Galibier' (45°05'44"N 06°40'06"E; 2,450 m) and the subalpine site 'Lautaret' (45°04'00"N 06°41'90"E; 1,920 m). The sites share similar orientation, bedrock, and soil (Bektaş et al. 2021), differing mainly in temperature and growing season length. During the data collection (2017, 2018, and 2021), the subalpine site exhibited a mean annual soil temperature 3.53 °C higher than the alpine site, a mean July soil temperature 3.11 °C higher, and a snow-free period longer by 56 days.

To simulate warming effects on alpine grassland communities, we transplanted forty 1 m^2 homogeneous vegetation blocks from the alpine site to the subalpine site, including at least 20 cm of intact belowground components and surrounding soil ("alpine warmed" communities or treatment; Fig. 1a) (Bektaş et al. 2021). To control for transplantation stress, we also performed horizontal transplants: ten 1 m^2 blocks within the alpine site ("alpine" communities) and ten within the subalpine site ("subalpine" communities). The experimental sites were fenced during summer. Additional details on the experimental design are provided in Bektaş et al. (2021).

Vegetation surveys

At peak plant growth (July 2017, 2018 and 2021), we identified and recorded all individuals that touched a 4 mm metal stick (hereafter, pinpoint) across 100 equally spaced points (10 cm apart) for each of the warmed, alpine and subalpine communities. This design distinguishes *co-occurrence* within communities (species present in the same 1 m^2 plot) from fine-scale spatial associations (individual touching the same pinpoints).

All taxa were considered at the species level, individuals that could not be identified, or only at the genus level were excluded from the analysis (5% of the 40,011 individuals recorded). Across all three years of sampling, 98 species were recorded (see Supporting information, for the complete species list and associated abbreviations). We identified 22 *alpine specialist*, here defined as species occurring exclusively in alpine communities. The 19 species that were absent from the alpine communities but appear in the alpine warmed ones were classified as *colonizers*.

Commonness shift of communities under climate warming

To assess how climate warming affected community commonness structure, we considered both aspects of species commonness: relative abundance and occurrence frequency, using the Dominance Candidate index (equation 1) proposed by (Avolio et al. 2019).

$$DC_i = \frac{\bar{A} + F}{2} \tag{1}$$

With $\bar{A}$ representing the mean relative abundance of a species in the communities where it occurs, and F

its frequency of occurrence (the proportion of communities in which it occurs).

We defined the *common* species as those with DCi values in the top 10% for each treatment. To ensure that our results were not sensitive to this arbitrary threshold, we verified that our results on commonness were robust across alternative threshold definitions (top 5%, 10%, 15% and 20% ; Supporting information).

Spatial association networks

Tests of spatial associations within 1 m² communities

We tested whether the observed number of shared pinpoints (i.e., n_{ijs}) differed from a random spatial distribution of the individuals across the $N_s = 100$ pinpoints within each community s. Under such random distribution, with the hypothesis of environmental homogeneity within the 1 m² plot, n_{ijs} follows a hypergeometric distribution (equation 2).

$$n_{ijs} \sim HG(N_s, n_{is}, n_{js}) \tag{2}$$

where n_{is} and n_{js} are the numbers of pinpoints occupied by species i and j, respectively. We performed one-tailed Fisher exact tests for aggregation (H_{1s}^{+}) and segregation (H_{1s}^{-}), yielding two p-values (p_s^+ , p_s^-) per pair of species within each community s. Conceptually, this identifies species pairs that associate at the same pinpoints more (or less) often than expected under a random spatial distribution in a community. Under the assumption of homogeneous environmental conditions in small communities, the approach identifies associations that are independent of environmental filtering.

Combining evidence across communities of a treatment

The signal of spatial association may be weak within a given community, but once aggregated across multiple communities, it can become statistically robust. To combine evidence, we used the *Gamma Approximation of Stratified Truncated Exact test* (GASTE) method (Wendling & Galiez 2026), specifically designed for discrete-uniform p-value distributions such as those derived from the hypergeometric test. For each treatment and each species pair, we separately combined p-values for local aggregations (p_s^+) and local segregations (p_s^-) to obtain the two combined p-values (p^+, p^-).

This combination tests a global null hypothesis H_0, stating that for each pair i and j, species are spatially independent in every community where they co-occur. Rejection of H_0 indicates that at least one community exhibits significant aggregation or segregation (H_1^+, H_1^-), implying an overall significant association within a given treatment. We controlled the false discovery rate for all species pairs using the Benjamini–Hochberg procedure (Benjamini & Hochberg 1995) to adjust the combined p-values.

The combination of statistical signals across sampled communities implies that the number of detected associations depends on sample size, as aggregating more communities increases statistical power. Therefore, to ensure comparability among treatments, we constructed networks using data from the same number of communities: 10 alpine warmed communities (matching the 10 alpine and 10 subalpine), each sampled over three years. Using the additional communities available in the alpine warmed treatment (40 per year), we verified

that our conclusions were robust to variation in sample size and to the selection of communities included in the analysis. This analysis confirmed the robustness of all main results except for connectance, the ratio of observed links to all possible links (Delmas et al. 2019), which was therefore excluded from subsequent interpretation (Supporting information).

To maximise the statistical power of spatial association detection, we pre-filtered species pairs based on whether a spatial association could be detected given their abundances. Negative associations cannot be detected for locally rare species pairs, whereas positive associations cannot be detected for locally abundant pairs. For each co-occurring species pair, we computed, within each treatment, the minimum achievable p-value based on their abundances in the communities where they co-occurred. Only pairs with an adjusted minimum combined p-value below the significance threshold ($\alpha = 0.05$) were retained for further analysis.

To verify that this pre-filtering step did not bias our results, we repeated the analyses without it. This had no effect on our conclusions, except for network connectance, which was therefore excluded from subsequent interpretation (Supporting information).

Network analysis

For each treatment, we aggregated the significant association as an undirected signed network, with the species as nodes and the positive (aggregation) or negative (segregation) associations as links.

To compare network structure across treatments, we quantified the network order (O) and size (S) as the number of nodes (species involved in at least one significant association) and the number of links, respectively (Delmas et al. 2019). We also computed each species' degree as the number of links it shares with others, and plotted it against its DCi, fitting an exponential regression to the relationship.

For each network, we defined the *most structuring* species as the most connected species, corresponding to the top 10% of the degree distribution. Similarly to the definition of *common* species, we verified that our conclusions were robust to alternative threshold definitions (5%, 10%, 15% and 20% ; Supporting information).

We further defined *keystone* species as those that are both *common* and among the *most structuring* (species ranking in the top 10% for both DCi and degree).

Visualization of species features along the community composition gradient

To assess compositional differences between alpine and alpine warmed communities, we performed a correspondence analysis (CA) on the species abundance matrix including all alpine, alpine warmed, and subalpine communities. The ordination was computed using the prince package in Python.

To evaluate whether warming-induced community shift was reflected in species commonness, we projected the species-specific DCi values onto the first CA axis. For each species j, we computed a projected commonness score as its DCi (DCi_j, scaled by 100) multiplied by its coordinate on the first CA axis. These weighted projections were then used to construct species distributions along the first axis for the alpine, alpine warmed, and subalpine treatments. Differences among treatments were tested using weighted permutation tests with

10,000 permutations of DCis and their weights. Effect sizes for pairwise treatment differences were quantified using a pseudo-R^2:

$$\text{pseudo-}R^2 = \frac{\text{SS}_{\text{between}}}{\text{SS}_{\text{total}}}$$

where the total sum of squares (SS_{total}) is the variance of all weighted species projections from the two compared treatments, and the between-group sum of squares ($\text{SS}_{\text{between}}$) is the weighted sum of squared deviations of each treatment mean from the overall weighted mean.

Finally, to assess whether warming-induced changes in spatial association networks were driven by community shifts, we projected each species' degree onto the first CA axis by multiplying it by its coordinate. We then compared the distributions of these projections across the three treatments using the same weighted permutation tests as for DCi. The proportion of variation explained by community shifts was quantified using the same pseudo-R^2 as described above.

All analyses were performed in Python 3.12.3.

RESULTS

Did the composition of the most *common* species change after five years of warming?

There were no drastic shifts in the *common* species after five years of warming (Fig. 2a). We identified five *common* species in alpine communities, and seven in warmed communities. Four of the five alpine *common* species remained *common* after warming: *Poa alpina, Plantago alpina, Trifolium alpinum* and *Potentilla aurea* (Fig. 2a).

In contrast, *non-common* species exhibited much larger changes in their DCi values. *Alpine specialists*, in particular, were the most affected by warming: 75% of the species showing the strongest declines were *alpine specialists*, and eight (44%) *alpine specialists* became locally extinct under warming, compared with only three (7%) *non-specialist* species. Conversely, 15 *colonizers* emerged, but none became *common* after five years. Nevertheless, several initially rare species increased substantially in DCi, including *Meum athamanticum*, which became *common* (Fig. 2a).

Shifts in commonness showed a clear temporal progression, being minor after two years and nearly absent after one year (Supporting information).

We used the DCi to reflect both aspects of commonness (local relative abundance and frequency) (Avolio et al. 2019), in our case the DCi strongly correlated with species frequency but less with the mean relative abundance (Supporting information). Indicating that in our case, DCi were mainly driven by species frequency.

Were the *common* species the most important in plant spatial association networks?

Alpine and alpine warmed networks included 22 and 23 species, respectively, with 14 species shared between the two networks (Fig. 3a,c). Both networks were dominated by negative spatial associations, with only two positive associations detected overall, both in the alpine warmed network.

Species degree increased exponentially with DCi (Fig. 3b,d, $R^2 = 0.72$, $p < 0.0001$, and $R^2 = 0.54$, $p < 0.0001$, for alpine and alpine warmed treatments, respectively). In the alpine network, we observed a relative overlap between species commonness and their structural role in the network. Five of the seven *common* species were also among the *most structuring* species and were therefore classified as *keystone* species (Fig. 3b). In contrast, this overlap was much weaker in the alpine warmed network, with only two of the six *commons* being *keystone* (Fig. 3d).

Moreover, in both networks, several species with relatively low DCi still exhibited high degrees, whereas some *common* species had few links and were not among the *most structuring* species (Fig. 3b,d).

Did the association networks change under climate warming?

Changes in node composition and structure

The number of nodes (network order) increased only marginally between alpine and alpine warmed communities, from 22 to 23 nodes (Fig. 3a,c). Moreover, the identity of the nodes changed slightly after warming, with 14 nodes being shared between the two networks.

In contrast, the structuring roles of species within the networks changed substantially under warming. Five of the seven *most structuring* species in the alpine network lost this status in the alpine warmed network, leaving only two species (*Carex sempervirens* and *Plantago alpina*) among the *most structuring* species in both networks (Fig. 2b). Moreover, four of the five alpine *keystone* species lost this role under warming (Fig. 3b,d). Only *Carex sempervirens* remained *keystone* under both conditions, while *Festuca nigrescens* became *keystone* under warming. Notably, both species were also *keystone* in the subalpine treatment (Supporting information).

This reorganization was particularly pronounced for *alpine specialist* species. Five of the eight *structuring alpine specialist* species became *non-structuring* (out of graph) under warming (Fig. 2b). Additionally, two *colonizers*, *Carlina acaulis* and *Thymus pulegioides*, absent from the alpine network appeared in the alpine warmed network but occupied only peripheral positions within the network (Fig. 2b and 3d).

Changes in network connectivity

The number of spatial associations increased from 26 in the alpine network to 41 in the alpine warmed one (Fig. 3a,c), mainly due to negative associations, which accounted for 97% of all associations. Although the alpine network contained only negative associations, two positive links appeared in the alpine warmed network.

The proportion of *structuring* species increased from 33% to 41%, as the number of species in the communities declined but not the order (Fig. 3a,c). Link turnover was high: only eight links (~30% of alpine links) were shared between networks (Fig. 3a,c), indicating substantial reconfiguration of species spatial associations. Overall, while node number increased only marginally, node identity and link identity strongly changed under climate warming.

What firstly shift with warming in the communities: its composition, its commonness structure or its network?

The correspondence analysis (CA) captured the main gradient in species composition across alpine, alpine warmed, and subalpine communities along its first axis, which explained 78% of the total inertia. This axis clearly separated alpine and subalpine communities and was therefore interpreted as the alpine–subalpine community gradient. Alpine warmed communities were positioned between alpine and subalpine communities but were much closer to the alpine communities (Fig. 4a).

To evaluate whether the community shift was reflected in species commonness, we projected species DCis from all treatments onto the first CA axis (Fig. 4b). DCi projections of the alpine warmed treatment did not diverge significantly from alpine ones (weighted permutation test: $p = 0.14$; pseudo-$R^2 = 0.02$), but differed significantly from subalpine ones (weighted permutation test: $p < 0.0001$; pseudo-$R^2 = 0.28$). We also projected only *structuring* species, and the results remained qualitatively unchanged (Supporting information). These results suggest that commonness patterns in alpine warmed communities remained largely similar to those of alpine communities and have not shifted toward subalpine patterns.

Repeating the analysis for node degrees, projections of alpine warmed treatment diverged significantly from alpine ones (weighted permutation test: $p < 0.05$; pseudo-$R^2 = 0.14$; Fig. 4c), but did not differ significantly from subalpine ones (weighted permutation test: $p = 0.08$; pseudo-$R^2 = 0.10$). This indicates that the alpine warmed network shifted from the alpine toward the subalpine structure.

DISCUSSION

In this study, we investigated how a 3°C warming, an increase projected for the European Alps by the end of the century even under low-emission scenarios (Dumont et al. 2025), affects alpine plant communities. Using a combination of a whole-community transplant experiment, high-resolution vegetation mapping, and a statistical approach to infer spatial association networks, we assessed responses to warming of *common*, *network-structuring* and *keystone* species (both *common* and strongly structuring). Despite a relative stability of *common* species (80% overlap between alpine and alpine warmed treatments) and of the overall commonness structure, we found a substantial reorganization of the spatial association network: less than 30% of the *most structuring* species were shared between treatments and the number of spatial associations increased by 58%. This network reconfiguration was driven primarily by negative spatial associations, which accounted for 97% of all associations. These findings highlight that even expected climate warming under low-emission scenarios can disrupt the ecological roles of *keystone* species, reshaping alpine communities spatial organizations with potential lasting consequences for biodiversity and ecosystem resilience.

After five years of warming, community composition shifted in the expected direction but remained closer to alpine than subalpine types, consistent with findings across several transplant experiments (Bektaş et al. 2024). These lags can be explained by demographic inertia, extinction lags and lags in species establishment (Nomoto

& Alexander 2021). However, here we found that all species were not equally affected: *common* species remained relatively stable, rejecting our first hypothesis that warming alters commonness (Fig. 1). Less *common* species showed stronger responses, with *alpine specialists* declining and subalpine *colonizers* increasing, consistent with an extinction debt for *alpine specialists*, suggesting a future decline until local extinction (Dullinger et al. 2012; Rumpf et al. 2019). Similarly, strictly subalpine species may profit from a colonization credit (Rumpf et al. 2019). After five years of warming, 50% of the *subalpine specialist* species (potential *colonizers*) had not yet established in the alpine warmed communities (Fig. 2a and Supporting information), suggesting that colonization processes may lag behind the onset of favourable conditions. This is an interesting result, given that in the transplant experiment these species are not limited by dispersal lags but rather by establishment lags. Overall, our results support a growing body of literature highlighting the important time lags in the response of plant composition to climate warming and add the suggestion that these time lags are especially important for the most *common* species.

In contrast to the slow community composition response, the spatial plant-plant association network substantially reorganized under experimental climate warming (refuting our hypothesis 2, Fig. 1), with stark changes in the identity of the *most structuring* and *keystone* species (supporting hypothesis 3), and in the number of spatial associations (supporting hypothesis 4). These findings support previous studies showing that climate warming may not always affect mountain plant performance directly but rather indirectly through changes in negative and positive biotic interactions (Rysavy et al. 2016; Alexander et al. 2015). The indirect climate warming responses via plant-plant interactions would be expected to take a longer time and thus may help to explain the slowly responding changes in community composition and commonness structure. More specifically, in our experiment we found that climate warming increased the number of spatial associations by 58% (from 26 to 41) and the proportion of *structuring* species by 25%. This network reconfiguration was driven primarily by negative spatial associations, which accounted for 97% of all associations. Within the framework of the stress gradient hypothesis (Bertness & Callaway 1994), the observed increase of negative associations would be expected when abiotic stress is reduced. Because positive associations were rare in our networks, we could not robustly assess whether facilitative interactions decreased simultaneously. Given that the warming of alpine communities and the prolongation of their growing season increases their energy input, plant communities can increase their productivity over the year (Bektaş et al. 2021) and thus may experience the experimental climate warming as a reduction in stress, even though it is accompanied by reduced soil water content in summer. Moreover, *structuring* and *most structuring* species show no shift in CSR (competition–stress–ruderal) strategy distributions, and no significant shifts in trait distributions with warming (Supporting information). The only detectable functional shift was an increase in vegetative height among *most structuring* species under warming (Supporting information). Overall, our results support the idea that climate warming creates more favourable conditions that increase negative associations, as predicted by the stress-gradient hypothesis, affecting indirectly plant performance.

The stronger (and perhaps earlier) responses of the plant spatial association network to climate warming, compared to community composition support growing evidence that biotic interactions, captured here through

the proxy of spatial associations, can respond independently of species composition to environmental change. For example, Poisot et al. (2012) demonstrated that interaction networks often change independently of species composition, and Tylianakis et al. (2008) showed that interaction turnover can be decoupled from species turnover under climate change. Similarly, experimental studies on plant pairs (Verlinden et al. 2014) and recent network-based analyses (Bimler et al. 2024) found that shifts in species interactions are not consistently predicted by changes in abundance or identity. Overall, this higher responsiveness of the network in comparison to the composition emphasizes that compositional data may overlook the beginning of key structural changes in communities. In our case, examining spatial associations revealed early and critical reconfigurations of species interactions under climate warming, which may serve as early warning signals of community restructuring, extinction lags, compositional changes, and subsequent impacts on ecosystem functioning.

Beyond responses to warming, our approach addresses a key question in community ecology: which species should we focus on to understand community assembly processes? The traditional community assembly framework weighs all species by abundance, but assumes a limited number of governing processes that apply to all species. In contrast, recent work highlights that these assembly processes may differ between *common* and *non-common* species (LaPlante & Souza 2018; Arnillas & Cadotte 2019), concluding that we should look at the most *common* species. However, here we show that the most *common* species may be the most stable under changing conditions, and that early signals of community restructuring under climate warming are best captured by *keystone* species, those that are both *common* and *network's strongly structuring*. Our approach demonstrates that the importance of species in the network correlates moderately with its commonness, but considering both is essential to understand community restructuring.

Although robust, our study has certain limitations. First, our experiment spans only five years, which is insufficient to capture the full extent of long-term community restructuring. It would be very interesting to have long-term observations of such experiments to quantify the time lags involved in the different direct and indirect responses. So far the longest experiments of such type are nine years, do not include the high-resolution sampling required here and show that the composition of warmed community is far from the subalpine one (Bektaş et al. 2024). Second, we are aware that our study rely on a spatial proxy to study plant plant interaction signal, an approach known to produce spurious association (Blanchet et al. 2020). However, given the very high resolution of our sampling (pinpoint) within relatively small communities ($1m^2$) we are relatively confident on the limited effect of confounding effect such as micro environmental variations. Third, networks were generated using data collected from the same communities over three different years, which could challenge the assumption of independence required for the GASTE test, even so pinpoints were not placed at the same points in consecutive years. Moreover, the very fine spatial scale at which spatial associations are assessed, requiring individuals to be in direct contact, and the restriction of our analyse to pairwise interactions contribute to the low number of positive spatial associations detected as many facilitative patterns operate at broader neighborhood scales and across multiple species, e.g. via changed soil nutrients. Finally, the networks we built represent only sub-samples of the real spatial association networks. The method used is designed to detect consistently repeated weak and strong patterns; therefore, adding more communities to the analysis would likely reveal weaker or

less frequently repeated associations. Nonetheless, our conclusions proved robust to both the number and identity of the communities included in the analysis (Supporting information). The limited number of consistent associations may also reflect the predominance of neutral assembly processes, or simply the generally weak pairwise associations observed in ecological communities, even in much larger datasets analysed with a similar approach (Rohr et al. 2026).

Our study introduces a novel approach to investigating community reassembly by combining transplant experiments, high-resolution sampling, and recent statistical advances. By integrating information on species commonness and network structure, we found that *common* mountain plant species may exhibit substantial time lags in their responses to climate warming, yet transient community reassembly is already evident in shifting associations among the *structuring* species. Notably, if climate warming affects species more strongly through biotic interactions than through physiological constraints, this could explain the delayed responses in community composition. We conclude that focusing on *common* and *structuring keystone* species, and on changes in their interactions, is crucial for detecting emerging assembly processes under transient climate change.

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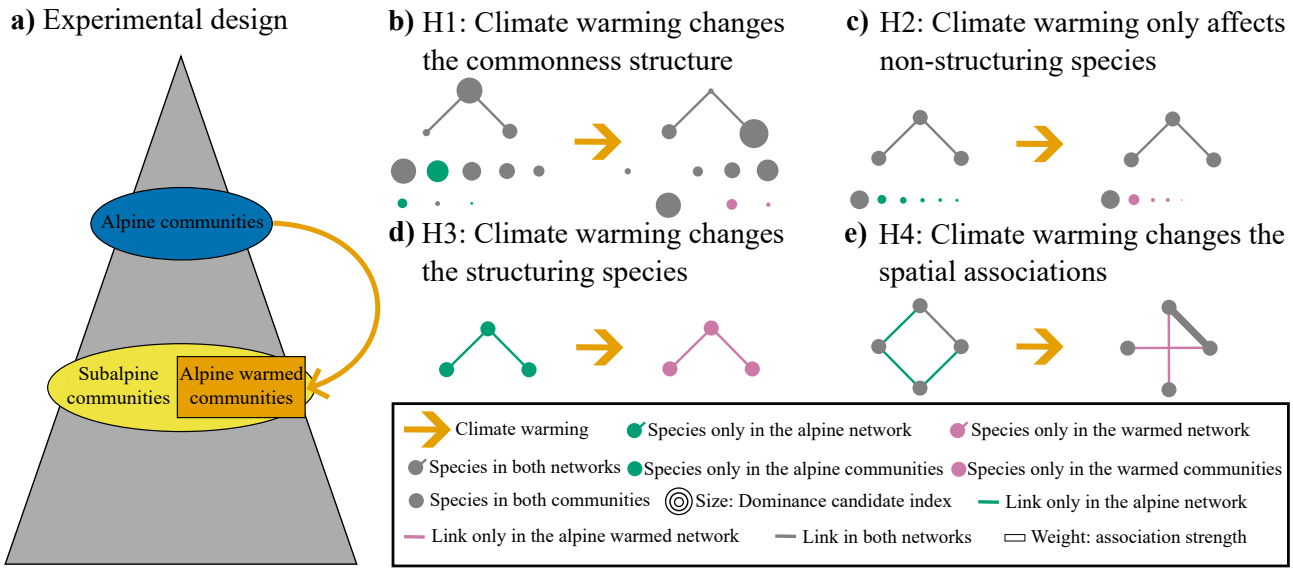


Figure 1: Conceptual representation of our experimental design and some hypotheses. **a)** Experimental design: entire alpine plant communities was transplanted 530 m downslope to a subalpine site, resulting in an experimental warming of approximately 3 °C. **b-e)** Conceptual illustrations of four tested hypotheses, showing how climate warming may affect both the structuring species in the spatial association network and the non-structuring species not represented in the network. Species or links occurring only in the alpine network and communities are shown in green, those unique to the alpine warmed network and communities in purple, and those shared by both in grey. Point size reflects species commonness and link width indicates the strength of associations.

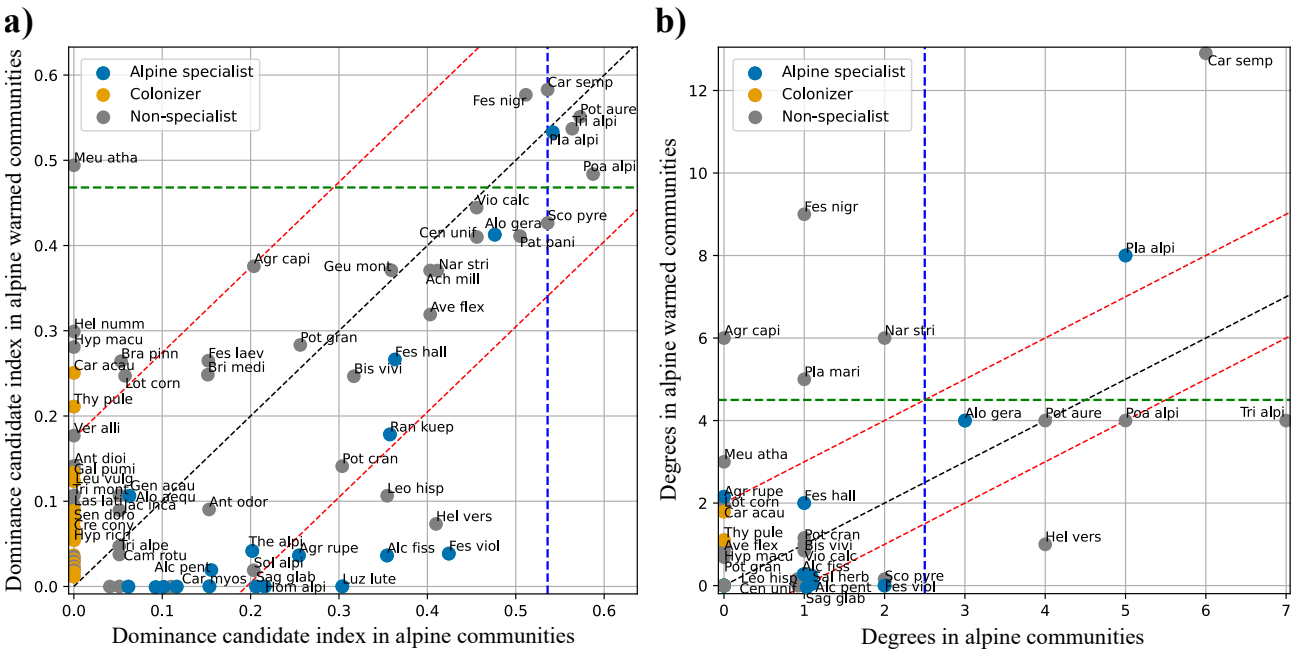


Figure 2: Commonness and degree shifts with climate warming. **a)** Evolution of the commonness structure of communities after five years of warming. **b)** Evolution of the species degrees with warming. With no effect of experimental warming, species would be close to the black dashed 1:1 line; 80% of species fall between the red dashed lines, therefore species that win or lose the more were upper or lower these lines, respectively. Green and blue dashed lines mark the top 10% most *common* **(a)** or *most structuring* **(b)** species in the alpine warmed and alpine communities, respectively. Species categories: *non-specialists* (grey; present in both background communities), *alpine specialists* (blue; present only in alpine background communities), and *colonizers* (orange; present only in alpine warmed communities). Different sets of species are shown in panels a and b because panel a includes only species recorded in a single year, whereas panel b includes species recorded across all three years. Moreover, many species appear at the (0,0) position in panel b because they were not part of the networks.

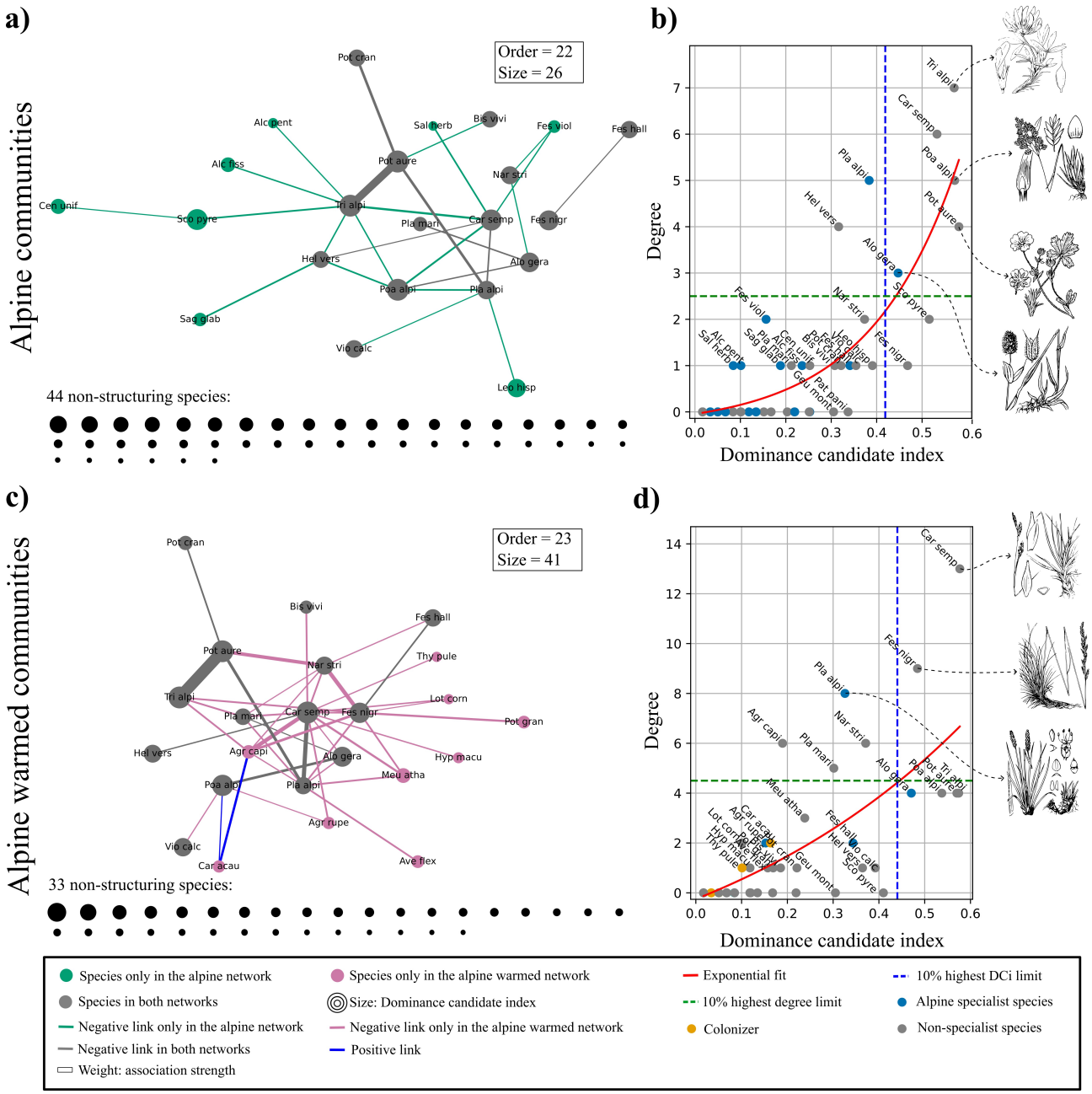


Figure 3: Spatial association networks of alpine and alpine warmed communities, and the relationship between species DCi and their degree within each network. a) Alpine spatial association network. Grey nodes and links indicate species and negative associations shared with the alpine warmed network; green nodes and links are species and negative links specific to this network. Node size reflects species DCi and link width represents association strength. **b)** Relationship between species DCis and degrees in the alpine treatment. Red line: exponential fit ($p < 0.0001$, $R^2 = 0.72$); the blue and the green dashed lines show the most *common* 10% species, and the *most structuring* 10% species, respectively. *Non-specialists* (grey dots) are species that occur in the background communities of both the alpine and subalpine communities, and *alpine specialists* (blue) occur only in the alpine communities. **c)** Alpine warmed spatial association network. Grey nodes and links are nodes and negative links shared with the alpine network; purple nodes and links are specific to the alpine warmed communities; blue links are positive links. Sizes of nodes are species DCi and weight of links are the association strength. **d)** Relationship between species DCis and degrees in the alpine warmed treatment. Red line: exponential fit ($p < 0.0001$, $R^2 = 0.54$); the blue and the green dashed lines show the most *common* 10% species, and the *most structuring* 10% species, respectively. *Non-specialists* (grey dots) are species that occur in the background communities of both the alpine and subalpine communities, *alpine specialists* (blue) occur only in the alpine communities, and *colonizers* (orange) occur only in the subalpine communities.

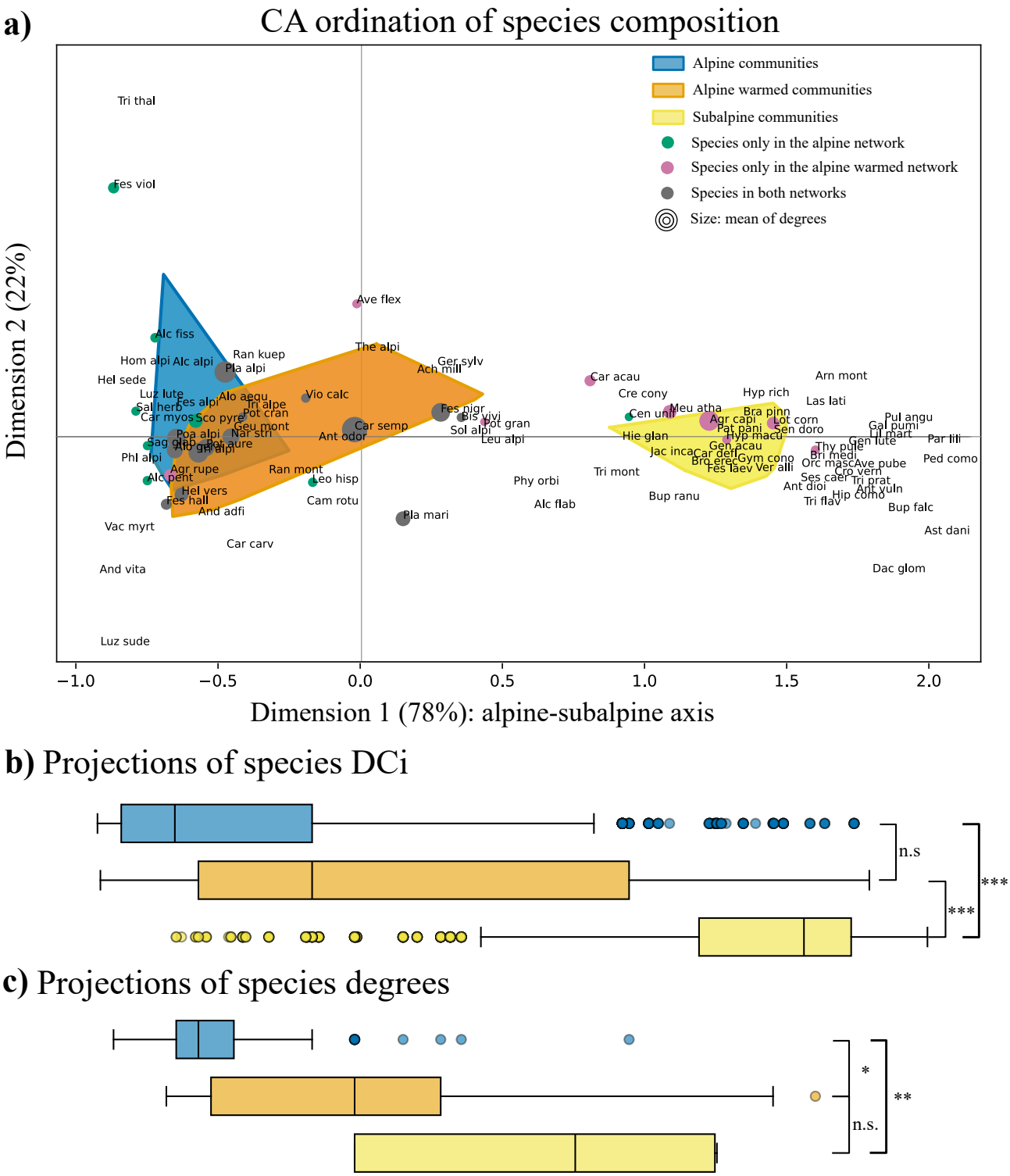


Figure 4: CA ordination of species composition, and species features positioned along the alpine–subalpine community gradient. **a)** CA ordination of species composition from all communities in the alpine, alpine warmed, and subalpine treatments. The blue polygon indicates the position of alpine communities; the orange polygon indicates the position of alpine warmed communities; and the yellow polygon indicates the position of subalpine communities. Points are coloured according to their network membership: green for species present only in the alpine network, purple for those only in the alpine warmed network, and grey for species present in both networks. Point size reflects species degree within their respective networks (for species present in both networks, we took a mean degree). **b-c)** Distribution of species projections, weighted by DCi **(b)** and by degree **(c)**, onto the first axis of the CA. The same analyses were performed using only *structuring* species, and the results remained qualitatively unchanged (Supporting information). Alpine communities in blue, alpine warmed in orange and subalpine in yellow (Significance codes: *** $p < 0.001$, ** $p < 0.01$, ** $p < 0.05$, n.s. non significant).