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RESEARCH ARTICLE

Integrating experimental and observational approaches facilitates scaling species interactions to biodiversity patterns

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Abstract

1. To investigate how niche and fitness differences determine the outcome of species interactions and shape local biodiversity patterns, research has typically focused on either simplified experimental systems that test specific mechanisms or observational studies where processes are inferred from functional trait or phylogenetic patterns. While each approach has yielded valuable insights, both have drawbacks, and few studies have integrated these approaches to connect mechanistic processes with observed biodiversity patterns.
2. To this end, we paired a 3-year neighbour removal experiment involving 22 species pairs with spatial point pattern analyses conducted in 8 spatially explicit 2 m × 2 m plots arrayed across a stress-resource gradient in the alpine tundra of Colorado. By employing this dual approach of experiment and observational study, we can test the role of trait dissimilarity (limiting similarity) and trait hierarchies (traits that differ from a competitive optima) as mechanisms shaping plant performance and then map these mechanisms directly onto species co-occurrence patterns in surrounding communities.
3. In the neighbour removal experiment, we found that species interactions were largely determined by hierarchical competition based on plant size. These same traits were also most important for predicting patterns of pairwise spatial associations across community types in the observational study, but also highlighted how composite trait metrics like principal component axes can obscure the role of individual traits in mediating species interactions. Moreover, the spatial point pattern analysis also identified community specific context dependence missing from the experimental approach. Specifically, in the more resource rich community, hierarchical differences in plant height and dissimilarity in leaf area had the largest effects on pairwise spatial association patterns, while in the more resource poor communities we found the reverse, with dissimilarity in height and hierarchical differences in leaf area having the largest effects.
4. By coupling process-based experiments and pattern-based observational approaches, we were able to experimentally test coexistence mechanisms, demonstrate how these mechanisms manifest as functional trait patterns in the surrounding natural community and highlight context dependent responses

based on local abiotic conditions. Taken together, our results suggest that future research should prioritize process-to-pattern mapping by coupling mechanistic experiments with observational studies.

KEYWORDS
alpine, functional traits, neighbour removal, Niwot Ridge LTER, spatial associations

1 | INTRODUCTION

A fundamental goal of ecology is understanding how species interactions shape local patterns of biodiversity (Chesson, 2000; MacArthur & Levins, 1967; Mittelbach & McGill, 2019). In recent decades, modern coexistence theory has helped resolve how relationships among species determine the outcome of interactions through a balance of niche and fitness differences (Chesson, 2000; HilleRisLambers et al., 2012). Niche differences reflect discrepancies in the strength of interspecific versus intraspecific competition such that when intraspecific competition is stronger than interspecific competition, species at low abundance gain a demographic advantage, which promotes stable multi-species coexistence (Chesson, 2000). Fitness differences, on the other hand, capture differences in absolute competitive ability, where one species maintains an advantage over its competitors regardless of its relative abundance, leading to competitive exclusion when fitness differences are large and coexistence when fitness differences are small (Chesson, 2000). Decades of experiments examining paired species interactions have refined our understanding of niche and fitness differences and the best methods for quantifying these mechanisms (Kraft et al., 2014; Pérez-Ramos et al., 2019; Spaak et al., 2023). However, challenges remain for scaling up these experiments to observed patterns of biodiversity in nature. While experiments are an invaluable tool for isolating and testing mechanisms, they necessarily use highly simplified designs (e.g. often only two species interacting at a time) and understandably involve a limited number of species from the species pool (Adler et al., 2013; Kraft et al., 2014; Pérez-Ramos et al., 2019). These limitations make it difficult to translate the results of experiments to highly complex natural communities which may be composed of hundreds of species and have even led some to argue that experimental approaches are so contingent and localized as to be useless for forming broader generalizations about species coexistence (Lawton, 1999; Simberloff, 2004).

A contrasting approach for investigating coexistence mechanisms is the use of observational studies, where the outcome of coexistence mechanisms in natural communities are inferred through the interpretation of functional trait patterns (Spasojevic & Suding, 2012; Yin et al., 2021). Traits are thought to provide effective proxies for coexistence mechanisms because they are linked to fitness and mediate how species interact with each other and their abiotic environment (Adler et al., 2013; McGill et al., 2006; Spaak et al., 2023). For example, niche differences may be represented via trait dissimilarity, where species with more similar traits are expected to compete more strongly due to greater niche overlap (MacArthur & Levins, 1967; Stubbs & Wilson, 2004). Subsequently, if niche differences are the primary mechanism determining the outcome of species interactions in an ecological community, patterns of trait overdispersion may be observed as species with similar traits segregating to avoid strong competition (He & Biswas, 2019; Weiher & Keddy, 1995). In contrast, fitness differences are often represented via a trait hierarchy where species possessing dominant trait values maintain a competitive advantage over species with subordinate trait values (Carmona et al., 2019; Funk & Wolf, 2016; Kraft et al., 2014; Kunstler et al., 2016). This results in the intensity of competition increasing as trait similarity decreases and may result in patterns of trait clustering (underdispersion) at the community level as species possessing similar traits coexist due to no one being able to establish a competitive advantage (Kunstler et al., 2012; Mayfield & Levine, 2010; Yin et al., 2021). While numerous studies have leveraged trait patterns to explore the supposed action of coexistence mechanisms in nature (He & Biswas, 2019; Kunstler et al., 2012, 2016; Spasojevic & Suding, 2012), these studies have been widely criticized for their ensconced assumptions, some of which have limited support (Gerhold et al., 2015; Münkemüller et al., 2020). One notable problem is that identical trait patterns can result from multiple distinct processes. For example, environmental filtering, where harsh abiotic conditions limit community membership to a subset of the regional species pool, can also produce patterns of trait clustering indistinguishable from those generated via trait hierarchies (Mayfield & Levine, 2010; Spasojevic & Suding, 2012). Thus, while observational approaches examine natural communities in their full complexity, they cannot definitively attribute patterns to specific coexistence mechanisms (but see Suding et al., 2003; Gross et al., 2009).

Increasingly, integration of process-focused experiments and pattern-focused observational studies has been advanced as a way to mitigate the weaknesses and highlight the strengths of each of these approaches (Gerhold et al., 2015; Münkemüller et al., 2020). Critically, functional traits provide an avenue for linking experimental and observational approaches since trait dissimilarities and trait hierarchies (acting as proxies for niche and fitness differences, respectively) can be used to simultaneously evaluate changes in species demography/performance and species co-occurrence patterns and can be applied across species (McGill, 2010). Thus, explicit process-to-pattern mapping in a specific community can be achieved via a two-step process where: (1) researchers select a subset of species from the community of interest and conduct an experiment which assesses species demography/performance as a function of relevant trait similarity and trait hierarchy metrics; and then (2)

researchers conduct an observational study of trait patterns to determine whether those same trait metrics are correlated with species co-occurrence patterns in natural communities. Employing both experiments and observational studies within a single system ensures that specific mechanisms are rigorously tested and that these mechanisms provide relevant insights into the assembly of natural communities. Despite recognition of the need for this type of integrative approach (Gerhold et al., 2015; Münkemüller et al., 2020), studies which use both experiments and observational studies to explore coexistence mechanisms are rarely conducted.

Here we examined how trait dissimilarity, trait hierarchies and abiotic gradients shape diversity patterns in alpine tundra plant communities by coupling an in-situ neighbour removal experiment with spatial point pattern analyses of eight 4 m^2 plots arrayed along a stress-resource gradient. By employing the dual approach of experiment and observational study, we can first test the role of trait dissimilarity and trait hierarchies as mechanisms shaping plant performance and then map these mechanisms directly onto species co-occurrence patterns in the surrounding community. Specifically, we ask three questions: (1) How do trait similarities or hierarchies impact species performance in our experiment, and which traits best capture these mechanisms? (2) Do these same trait mechanisms predict pairwise spatial association patterns in natural communities? (3) Do the trait mechanisms which predict pairwise spatial association patterns differ across alpine community types?

2 | METHODS

2.1 | Study site

This study was conducted in alpine tundra at the Niwot Ridge Long Term Ecological Research site (40.03′ N, 105.35′ W) in the Front Range of the Colorado Rocky Mountains, approximately 40 km West of Boulder, CO, USA. Research permit was granted by the U.S. Forest Service which owns the land on which Niwot is situated. Niwot Ridge has a very short growing season (8–10 weeks, June–August) and a long winter, with an average annual temperature of −2.2°C and an average annual precipitation of 930 mm that predominantly falls as snow (~75%) (Greenland & Losleben, 2001; Litaor et al., 2008; White et al., 2023). Annual wind speeds on Niwot Ridge average 8.1 $m\,s^{-1}$ and winds typically blow from west to east (Litaor et al., 2008). Due to the high topographic relief and high wind speeds on Niwot Ridge, snow redistribution via wind is an important process for determining where snow accumulates on the landscape with cascading impacts on relative levels of soil nutrients, soil moisture and growing season length (Bowman & Seastedt, 2001; Walker et al., 2001). Some areas have low snow accumulation (dry meadow communities) or close to no snow accumulation (fellfield communities) and contain stress-tolerant species with low levels of productivity due to moisture limitation, nutrient limitation and high wind speeds (Bowman et al., 2003; Walker et al., 2001). Areas with intermediate levels of snow (moist meadow communities) are more abiotically mild and contain more resource acquisitive species with higher levels of primary productivity (Bowman et al., 2003; Walker et al., 2001).

2.2 | Trait dissimilarity, trait hierarchies and phylogenetic relatedness

For both our experiment and observational study (described below), we first quantified trait hierarchies and trait similarities (see details below) between all possible species pairs in each study using published trait data on four traits for which there is complete information in our trait database: plant height, leaf area, specific leaf area (SLA) and chlorophyll content (Spasojevic & Weber, 2022). Height is indicative of a species' competitive ability for light (Westoby, 1998). SLA and chlorophyll content are related to the leaf economics spectrum, which characterizes a species' capacity for stress tolerance versus resource acquisition (Osnas et al., 2013; Wright et al., 2004). Leaf area is indicative of a species' water/energy balance, linked with both rates of transpiration and photosynthesis (Ackerly et al., 2002; Perez-Harguindeguy et al., 2013). Trait values for each species were calculated as the mean of all individual trait measurements for that species across any community type in the Niwot Ridge trait database as we did not have community specific measurements for all species. Trait hierarchies for individual traits were quantified as directional trait differences by subtracting the trait value of one species from its companion's trait value, producing a metric which contains information on both the direction and magnitude of trait difference between both species. Trait dissimilarities were quantified by calculating the absolute value of directional trait values (i.e. Euclidean distance) and thus only reflect the magnitude, not the direction, of trait difference between species.

To reduce the number of trait predictors needed for subsequent statistical modelling, we also conducted a principal component analysis (PCA) of the four individual traits using the 'prcomp' function from the 'stats' package. We retained the first two principal components (PC) from this analysis for use which explained 49.5% and 25.1% of the trait variance, respectively (Supporting Information S1A). Height and leaf area loaded primarily onto PC1 which thus generally describes a species overall plant size, while SLA loaded onto PC2 (Supporting Information S1B,C). PC scores were multiplied by negative 1 to make them more intuitive (i.e. larger values of PC1 indicate larger plants). We calculated trait hierarchies and dissimilarities for these PCs in the same manner described above for individual traits, with trait hierarchies capturing the direction and magnitude of PC trait difference between species while dissimilarities exclusively reflect the magnitude of trait difference.

In addition to calculating individual and PC trait hierarchies and dissimilarities, we also calculated phylogenetic relatedness among all species pairs. Phylogenetic relatedness is often used as a substitute for trait similarity, as closely related species are thought to possess similar traits due to phylogenetic niche conservatism (Cavender-Bares et al., 2009; Webb et al., 2002). To calculate phylogenetic relatedness, we first built a phylogeny for all 143 species contained in

the Niwot Ridge trait database (Spasojevic & Weber, 2022) using the mega-phylogeny developed by Jin and Qian (2019) as a backbone. We subset this mega-phylogeny using the 'phylo.maker' function from the 'V.PhyloMaker' package (Jin & Qian, 2019) and resolved any remaining genus level polytomies using the 'multi2di' package in the 'ape' package (Paradis et al., 2004). Importantly, resolving polytomies in this way does not affect branch lengths (Paradis et al., 2004). Finally, we estimated phylogenetic relatedness among all species pairs as cophenetic distance using 'cophenetic.phylo' function in the 'ape' R package (Paradis et al., 2004).

To determine whether phylogenetic relatedness was correlated with functional similarity for any of our four traits, we examined patterns of phylogenetic signal for each trait by calculating Pagel's lambda (Pagel, 1999) using the 'phyloSignal' in the function 'phylosignal' package in R (Keck et al., 2016). Pagel's lambda ranges from 0 to 1, with 0 indicating no phylogenetic signal and values close to 1 indicating traits evolution under Brownian motion model (Pagel, 1999; see details in Supporting Information S2). We calculated Pagel's lambda at four levels: (1) across the entire Niwot trait database; (2) for species used in our neighbour removal experiment; (3) across all communities in our point pattern analysis; (4) within each community type (fellfield, dry meadow, moist meadow) in our point pattern analysis (Supporting Information S2).

2.3 | Experimental study—Neighbour removal

To examine how trait dissimilarities and trait hierarchies affect plant performance (Question 1), we established a neighbour removal experiment involving a series of 'interaction arenas' located at the interface between dry- and moist meadow tundra on Niwot Ridge and monitored changes in the biomass in the same focal individuals across 3 years (2018–2020) by collecting non-destructive traits correlated to biomass in the first 2 years and biomass in the third year (data availble at Spasojevic and Huxley (2026)). Interaction arenas were installed in 2018 and constructed using ~10 cm (4 in.) diameter PVC collars hammered approximately 10 cm into the ground (up to the soil surface) to isolate two naturally growing individuals of different species from their surrounding biotic environment, placing them into direct interaction. The 10 cm diameter arena was large enough to contain two interacting alpine plants, which are relatively small and deep enough to isolate the root interaction zone from the surrounding below-ground community (Ashton et al., 2008). If individuals other than the two focal individuals were present within the interaction arenas, we removed their above-ground biomass using scissors upon installation and then maintained this removal for the duration of experiment. Many, but not all, alpine species are clonal and reproduce vegetatively through the growth of rhizomes (Korner, 2003), so to maintain consistency across species, only single clonal ramets were considered as focal individuals. All species pairs included in the experiment were composed of one individual of *Artemisia scopulorum* (ARTSCO hereafter; Asteraceae) and another individual from one of 22 species (see Supporting Information S3A). Each of the 22 species pairings had 15 co-located interaction arenas (330 total arenas): 5 replicates containing an ARTSCO individual and an individual from one of the paired species, 5 replicates containing ARTSCO growing alone, and 5 replicates containing the paired species growing alone for a total of 440 individuals across all interaction arenas (see Supporting Information S3B). ARTSCO was included in all species pairs to act as a control for the strength of competition (Funk & Wolf, 2016), as it is one of the few species which grows abundantly across the tundra (Walker et al., 1993). No individuals of *Potentilla diversifolia* (Rosaceae) survived the 3 years of the experiment and this species was dropped, resulting in 21 different species (Supporting Information S3A).

For all individuals, we tracked changes in biomass over the 3-year duration of the experiment. In these long-lived, perennial alpine plant species, which rarely sexually reproduce, changes in biomass can serve as an effective proxy for performance and ultimately fitness (Sultan, 2001). However, because measuring above-ground biomass requires the destructive harvest of individuals, for the first 2 years (2018–2019) of the study we collected allometric measurements on all focal individuals which we used to estimate biomass (see details in Supporting Information S3B; data availble at Spasojevic and Huxley (2026)).

Next, we quantified how interactions between focal individuals affected changes in biomass by calculating relative interaction index scores (RII), which capture how individuals of each species performed when grown in paired versus isolated arenas. For individuals which survived the full 3 years of the experiment's duration (all species except *P. diversifolia*; Total = 276/440, 62.7%; ARTSCO = 130/220, 59.1%; non-ARTSCO = 146/220, 66.4%) we calculated biomass change by subtracting biomass at the end of experiment (Year 3, 2020) from biomass at the beginning of the experiment (Year 1, 2018). Measured biomass was used for 2020 values, while allometric estimates of biomass were used for 2018 values. Because many individuals lost biomass over the course of the experiment (long-lived perennials grew back smaller without dying), we added a constant of 1 to all values to ensure all biomass change values were positive while retaining their position relative to each other. We then calculated RII scores using the following equation $\mathrm{RII} = \frac{(P - A_{\mathrm{mean}})}{(P + A_{\mathrm{mean}})}$ where (P) stands for the biomass change value of an individual grown in a paired arena (i.e. interacting with an individual of another species) and (A_{mean}) stands for the mean biomass change of all individuals of that same species grown isolated arenas (i.e. not interacting with an individual of another species) (Armas et al., 2004; Carmona et al., 2019). RII is centred at 0 and symmetrically bounded with a minimum of −1 and maximum of 1, with negative RII values indicating that biomass mass changes were more negative in paired arenas than in isolated arenas (i.e. competition), and positive values indicating that biomass changes were more positive in paired arenas than in isolated arenas (i.e. facilitation) (Armas et al., 2004; Carmona et al., 2019).

Finally, we examined how trait hierarchies and trait dissimilarity between species pairs affected RII using multi-model inference methods (Supporting Information S4A) following the approach

outlined in Carmona et al. (2019). To do this, we first filtered out RII values for all ARTSCO individuals, retaining only RII values for species paired with ARTSCO to investigate interaction responses (Funk & Wolf, 2016). We additionally only retained non-ARTSCO individuals which survived the full 3 years of the experiment for a total of $N = 67$. We then built a global linear mixed effects model using the 'lme4' R package with RII as the response variable, while phylogenetic relatedness, trait dissimilarities and trait hierarchies for PCs 1 (height and leaf) and 2 (SLA) traits served as fixed effects (Bates et al., 2015). Focal species identity (i.e. the non-ARTSCO species) was included as a random effect. We decided to use PCs instead of individual traits in our global model to reduce the number of fixed effects (5 vs. 9, respectively), and because trait dissimilarities and hierarchies for some individual traits (e.g. Leaf Area hierarchy and dissimilarity) were highly correlated (Supporting Information S4D). We have included a correlation matrix and variance inflation factors to assess multicollinearity among all predictors in the PC global model in Supporting Information S4B.

We used the 'dredge' function in the R package 'MuMIn' to generate all possible subsets of PC global model and rank them according to AICc score (Barton, 2020). We constrained subset models so that they could only retain either a hierarchy or dissimilarity term for each trait (e.g. if leaf area hierarchy was included, then leaf area dissimilarity was not; Carmona et al., 2019). We selected all models that had AICc scores within six points of the model with the lowest AICc score for model averaging. For model averaging, we examined both conditional and full averages of parameter coefficients. Conditional averages are calculated using only models which include the parameter of focus, while full averages are calculated using the 'zero method' which assigns values of 0 to parameter coefficients when they are missing from subset models, and thus, full averages represent more conservative estimates of parameter significance (Grueber et al., 2011). Lastly, we used the 'r.squaredGLMM' from MuMIn to obtain marginal and conditional *R*-squared values for the global model (Barton, 2020). In Supporting Information S4C–E, we have also included model outputs and collinearity checks for a global model constructed using individual trait dissimilarities and hierarchies instead of PCs.

2.4 | Observational study—Spatial point pattern analysis

To determine how the effects of species interactions manifest as spatial co-occurrence patterns at the community level (Question 2), we analysed how spatial association patterns between pairs of alpine species changed as a function of trait hierarchies and trait dissimilarities. We used spatially explicit species composition data collected by Bowman and Swatling-Holcomb (2018) for eight 2 m × 2 m plots arrayed across three community types, representing an abiotic stress-resource gradient (Question 3; two in moist meadow, three in dry meadow and three in fellfield). In each of these plots, the spatial location (*x*-*y* coordinates in centimetres) and species identity of all individuals were recorded (more detailed field methods can be found in Bowman and Swatling-Holcomb (2018); a list of species retained for analysis can be found in Supporting Information S3).

We used this spatially explicit species composition data to quantify spatial associations between all pairs of species by calculating the bivariate pair correlation function (pcf) $g_{i,j}(r)$ for a spatial window of 0–5 cm around each focal species using the programitta spatial point pattern analysis program (Wiegand, 2003). The pcf $g_{i,j}(r)$ measures the density of individuals of species *j* around focal individuals of species *i* at a given distance of *r* (Wiegand et al., 2017; Wiegand & Moloney, 2013). We chose to set $r = 0–5$ cm, as this produces a 10 cm diameter circle around individuals of the focal species, which is analogous to the size of the interaction arenas used in our neighbour removal experiment. Furthermore, we restricted our analysis of species pairs to only include those with at least 50 individuals per species per plot following the methods and rationale of Bowman and Swatling-Holcomb (2018). This resulted in 460 total species pairs, with 184 in fellfield, 216 in dry meadow and 60 in moist meadow. Reciprocal species pairs were retained for analysis (i.e. species *i* vs. species *j* and species *j* vs. species *i*) as species interactions may by asymmetric (Yin et al., 2021). We then calculated the standardized effect size for each species pair's pcf by comparing observed pcf values to 199 null model simulations. We generated null models by keeping the locations of species *i* individuals fixed while moving species *j* using the toroidal shift method, which removes the effects of species interactions by randomizing the location of species *j* with respect to species *i* while retaining the structure of species *j* individuals with respect to each other (Lotwick & Silverman, 1982). Positive pcf SES scores indicate spatial attraction between species pairs, while negative pcf SES scores indicate spatial repulsion between species pairs (Wiegand et al., 2017; Wiegand & Moloney, 2013). SES scores that have an absolute value larger than 1.96 indicate that observed pcf value is outside the 95% confidence intervals generated by the null model simulations. SES scores greater than 1.96 indicate that attraction between species is significantly different from random while SES scores lower than −1.96 indicate that repulsion between species is significantly different from random.

To determine how pairwise spatial associations changed as a function of trait dissimilarities and hierarchies, we paired the conceptual framework developed by Yin et al. (2021) with multi-model inference methods. Within Yin et al.'s (2021) conceptual framework, trait dissimilarity metrics alone (i.e. not trait hierarchies) are initially used to identify relationships between traits and pairwise spatial associations. Positive correlations between trait dissimilarity and spatial associations (i.e. spatial aggregation of species with different traits), indicate the action of *limiting similarity*, while negative correlations (i.e. spatial aggregation of species with similar traits) could indicate either the action of *trait hierarchies* or *environmental filtering*, necessitating further testing (described in the next paragraph). We implemented this approach by first constructing a global linear mixed effects model using lme4 where pcf SES values from all community types served as our response variable, while PC1 dissimilarity, PC2 dissimilarity, phylogenetic relatedness and community type

served as fixed effects (Bates et al., 2015). Additionally, interactions between trait dissimilarity/phylogenetic relatedness and community were included as fixed effects. Treatment species nested within focal species identity and plot ID were included as random effects. To determine which traits were best supported, we used the same methods described in the experimental study section to generate all possible model subsets, select the best model subsets (top 6 AICc) and calculate average model parameter coefficients. We also used the 'partR2' function from the PartR2 package to evaluate how much variance was uniquely explained by different parameters within the global model (Stoffel et al., 2021). Because interaction effects between trait metrics and community type were found to explain large amounts of variation in pairwise spatial associations in the across-community global model, we then created global models for each community type individually (moist meadow, dry meadow and fellfield). These within-community models followed the same model structure as the across-community model (except for the exclusion of the community fixed effect and interaction effects between traits and community) and we performed the same model averaging procedure described above.

To further explore how traits may shape spatial patterns, we built an additional set of models (both across and within community types) using individual trait dissimilarity metrics as fixed effects (height, leaf area, SLA and Chlorophyll Content dissimilarity) instead of PC1 and PC2. For the individual trait models, we used the same effect structure and model averaging process described above but were able to separately investigate the effects of height and leaf area (both traits load onto PC1) as well as include chlorophyll content effect which were missing in the PC model. Since these models include only dissimilarity metrics, multicollinearity between dissimilarity and hierarchy for individual traits is not a problem as it was in the neighbour removal experiment. Additionally, the relatively large sample size ($N=460$) mitigates potential issues with including two additional first order fixed effects (two PCs vs. four traits) and two additional interaction effects.

If trait parameters within our PC and individual trait community specific models had negative coefficients with 95% confidence intervals that did not overlap zero (indicating strong spatial aggregation of species with similar traits), we conducted further testing to determine whether this relationship resulted from *trait hierarchies* or *environmental filtering* following Yin et al. (2021). For trait parameters which had negative coefficients (e.g. height in moist meadow plots; Figure 2f), we conducted linear regressions to assess how pcf SES values changed as a function of trait hierarchies and trait dissimilarity for each individual species in each community where it occurred. These linear regressions show how spatial relationships between a focal species and all other pairs species change as a function of either trait hierarchy or trait dissimilarity. By comparing the magnitude of slopes for trait hierarchy versus trait dissimilarity across all species in a community, we were then able to determine whether hierarchy or dissimilarity were likely driving negative spatial associations among species at the community level. We assessed differences in the absolute values of slopes for trait hierarchy and dissimilarity linear regressions for each trait by community combination using paired *t*-tests (e.g. height hierarchy vs. height dissimilarity model for moist meadow species). If the absolute value of trait hierarchy slopes was significantly higher than trait dissimilarity slopes, we interpreted this result as evidence that trait hierarchies were driving the negative relationship between trait dissimilarity and pairwise spatial associations. Alternatively, if the difference between the absolute values of trait hierarchy and trait dissimilarity coefficients was insignificant or if trait dissimilarities were significantly larger, then we interpreted this as evidence of environmental filtering.

3 | RESULTS

3.1 | Phylogenetic signal

Across all species used in the neighbour removal experiment or the point pattern analysis observational study (both across and within community types), no traits showed significant phylogenetic signal. Across all species in the Niwot trait database, we found evidence of significant phylogenetic signal for leaf area ($p<0.01$; Supporting Information S2) and chlorophyll content ($p=0.04$; Supporting Information S2). While leaf area showed signal close to what is expected under a Brownian Motion model of trait evolution (Pagel's $\lambda=0.98$), phylogenetic signal for chlorophyll content was much weaker (Pagel's $\lambda=0.28$). No other trait exhibited a significant phylogenetic signal across the database.

3.2 | Experimental study—Neighbour removal

We found that trait dissimilarities, trait hierarchies and phylogenetic relatedness (fixed effects) explained 19.8% of the variation in RII based on the global model (RII; $R^2_c=32.1\%$). Next, using multi-model inference, we found that the PC1 hierarchy parameter had the highest sum of AICc weights (i.e. importance) across the 12 models in the top 6 AICc subset and had a 95% confidence interval which did not contain zero when examining conditional coefficient averages (i.e. coefficient averages calculated using only subset models which contain these trait parameters; Supporting Information S4A). More specifically, individuals belonging to species which were larger than ARTSCO (i.e. larger height and leaf area values) tended to gain biomass relative to their controls, while individuals belonging to smaller species tended to lose biomass (Figure 1). It is important to note that the more conservative full coefficient averages (i.e. those calculated using the 'zero method'; Grueber et al., 2011) indicated that no model parameters had confidence intervals, which did not overlap zero. However, we use conditional coefficient averages here, as the primary goal of our experiment was to identify trait mechanisms, which affect plant performance and determine if they match those observed in the observational study (Grueber et al., 2011). Results for the global model constructed using individual traits instead of PCs reinforce the results described above, despite problematic

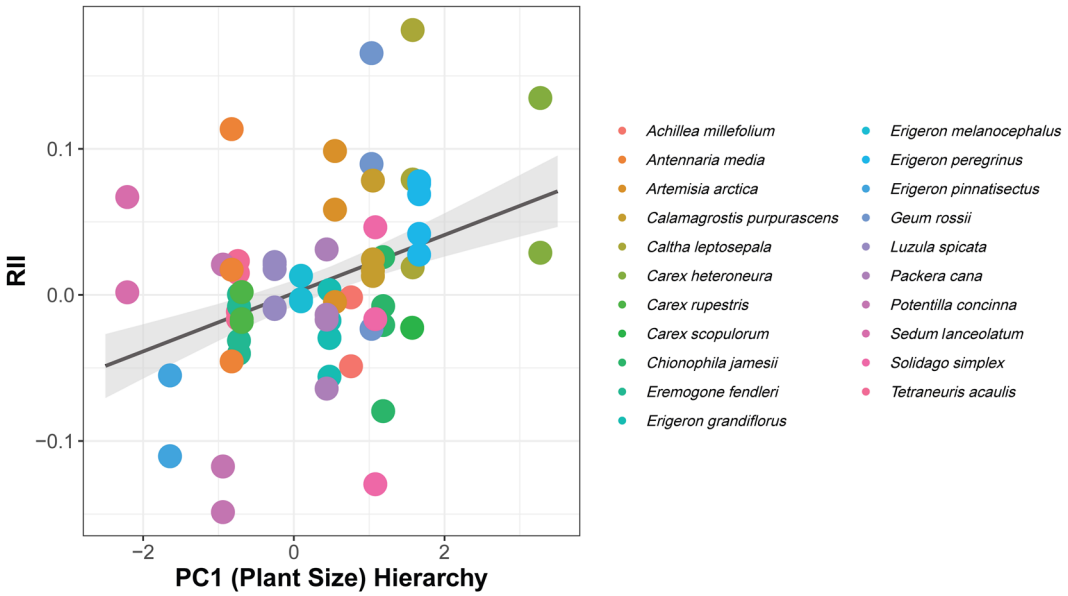

FIGURE 1 Relative interaction index (RII) as a function of principal component 1 (PC1) hierarchy. Leaf area and height load onto PC1 thus roughly summarizes overall plant size, with high positive values indicating plants that are larger than ARTSCO and negative values indicating plants that are smaller than ARTSCO. Negative RII values indicate competition, while positive RII values indicate facilitation. Colours indicate different species. The trend line is a simple linear regression ($R^2 = 0.15$) with 95% confidence intervals. The sum of the AIC weights for models including PC1 Hierarchy (i.e. Importance) in the model averaging was 0.78.

degrees of correlation between some predictor variables (i.e. leaf area hierarchy and dissimilarity; Supporting Information S4C–E).

3.3 | Observational study—Point pattern analysis

Across all alpine community types, we found that neutral pairwise spatial associations (−1.96 < pcf SES < 1.96) were the most common, comprising 81.7% of the total, while significant positive (pcf SES > 1.96) and negative associations (pcf SES < −1.96) made up 14.3% and 3.9%, respectively (Figure 2a). The proportion of significant positive associations increased with environmental stress, reaching the highest level in the abiotically harsh fellfield (20.7%), intermediate in dry meadow (11.6%) and lowest in the abiotically mild moist meadow (5%). Negative associations showed the reverse trend with the highest proportion in the moist meadow (16.7%), intermediate in the dry meadow (3.2%) and lowest in the fellfield (<0.01%).

Next, in the across-community global model, we found that PC dissimilarity, phylogenetic relatedness and community type (fixed effects) explained 19.3% of the variation in pairwise spatial associations ($R^2_c = 0.447$). More specifically, multi-model inference (using full coefficient averages) indicated first order effects for phylogenetic relatedness and community type were highly important across the two models in the top 6 AICc subset and had 95% confidence intervals which did not overlap 0 (Supporting Information S5). Interaction effects between dissimilarity metrics and community type were also highly important, with PC1 (plant size) dissimilarity and phylogenetic relatedness showing 95% confidence intervals which did not overlap 0 (Supporting Information S5). Furthermore, we found that these interaction effects explained a much larger fraction of variation in pairwise spatial associations (phylogenetic relatedness × community semi-partial $R^2 = 0.067$; PC1 dissimilarity × community semi-partial $R^2 = 0.03$; PC2 dissimilarity × community semi-partial $R^2 = 0.022$; Figure 2b; Supporting Information S6) than first order dissimilarity effects alone (all first order trait metrics had semi-partial $R^2 < 0.01$; Figure 2b). The individual trait model (constructed using trait values for leaf area, height, SLA and chlorophyll content) reinforced these results, with fixed effects explaining a greater amount of the total variation in pairwise spatial associations than the PC model ($R^2_m = 0.282$, $R^2_c = 0.443$) and once again highlighting the importance of interaction effects between dissimilarity metrics and community type (Supporting Information S5). Taken together, these results indicate that relationships between dissimilarity metrics and pairwise spatial associations differed strongly depending on community type.

Multi-model inference for the within-community models (using full coefficient averages) demonstrated how the direction and magnitude of these relationships shifted across community types. In the moist meadow PC model (global model: $R^2_m = 49.5\%$; $R^2_c = 88.7\%$; Figure 2c), we found that closely related species tended to be spatially clustered as indicated by the large negative coefficient for phylogenetic relatedness (95% confidence intervals did not overlap zero). We additionally found a slight trend towards spatial overdispersion of species with similar size (PC1) in the moist meadow. In contrast, neither trait PCs nor phylogenetic relatedness drove spatial associations in the dry meadow PC model (global model: $R^2_m = 0.055$; $R^2_c = 0.389$; Figure 2d), while PC1 (plant size) and PC2 (SLA) both drove strong spatial overdispersion (i.e. large positive coefficients with 95% confidence intervals which did not overlap zero)

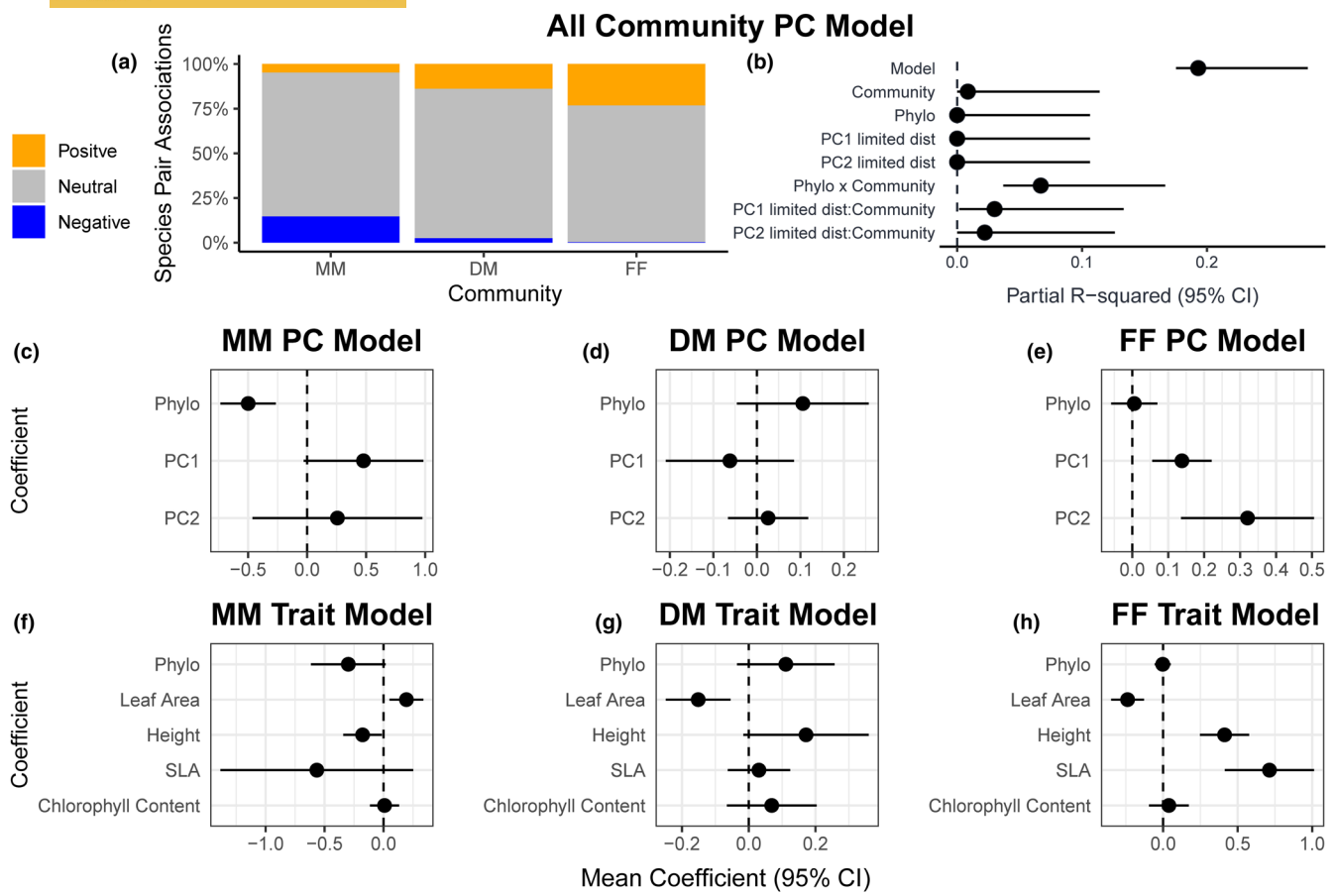

FIGURE 2 (a) Percentage of pairwise spatial associations for each community type, colours indicate association type. (b) Amount of variation uniquely explained (semi-partial R^2) by principal component (PC) model parameters in cross community model; most variation is explained by trait × community interactions. (c–e) Full coefficient averages and 95% confidence intervals (CI) for model parameters from community specific models constructed using trait principal components for moist meadow (c), dry meadow (d) and fellfield (e). (f, g, h) Full coefficient averages and 95% CIs for model parameters from community specific models constructed using individual traits moist meadow (c), dry meadow (d) and fellfield (e). Negative coefficients indicate negative slopes and positive coefficients indicate positive slopes.

in the fellfield with a negligible role for phylogenetic relatedness (global model: $R^2_m = 11.1$; $R^2_c = 0.273$; Figure 2e).

These results are further complicated by the breakdown of the individual trait models for each community. While these models supported some of the results of the PC models (e.g. few predictors of high importance in the dry meadow), the inclusion of leaf area and height as separate model predictors showed that these traits have strong and divergent effects on spatial associations despite both loading onto PC1. In the moist meadow (global model: $R^2_m = 58.2\%$; $R^2_c = 88.6\%$; Figure 2f), we found that species pairs with similar heights tended to be spatially clustered (i.e. negative coefficient; Figure 2f), while species pairs with similar leaf areas tended to be spatially overdispersed (i.e. positive coefficient; Figure 2f). Additionally, with the inclusion of individual traits rather than PCs, we found that influence of phylogenetic relatedness on spatial clustering was greatly reduced. In the dry meadow (global model: $R^2_m = 12.8\%$, $R^2_c = 39.1\%$; Figure 2d), we observed an important role for leaf area, where species pairs with similar leaf area values tended to be spatially clustered. In the fellfield (global model: $R^2_m = 21.8\%$, $R^2_c = 26.1\%$; Figure 2e), we also found spatial clustering of species pairs with respect to leaf area and spatial overdispersion for height and SLA. Overall, these results reinforce the findings of the PC models while highlighting important nuances in the impact of leaf area and height relative to PC1.

To further unpack the species interactions underlying spatial clustering (i.e. negative model coefficients), we used species specific models to investigate the three negative coefficients in the individual trait models which had 95% confidence intervals which did not overlap zero (i.e. height in moist meadow; leaf area in dry meadow; and leaf area in fellfield). Importantly, the only negative coefficient in the PC models was phylogenetic relatedness, which can only be interpreted in terms of dissimilarity, not hierarchy and thus was not assessed in this portion of our analysis. We found that the slopes of species-specific trait hierarchy models had significantly larger absolute values than species-specific trait dissimilarity models in two of three cases. Specifically, in the moist meadow, we found that the magnitude of slopes from height hierarchy models were significantly greater than slopes from height dissimilarity models (*t*-test: $p = 0.02$; Figure 3a). Similarly, in the dry meadow, slopes from leaf area hierarchy models had larger magnitudes than slopes from leaf

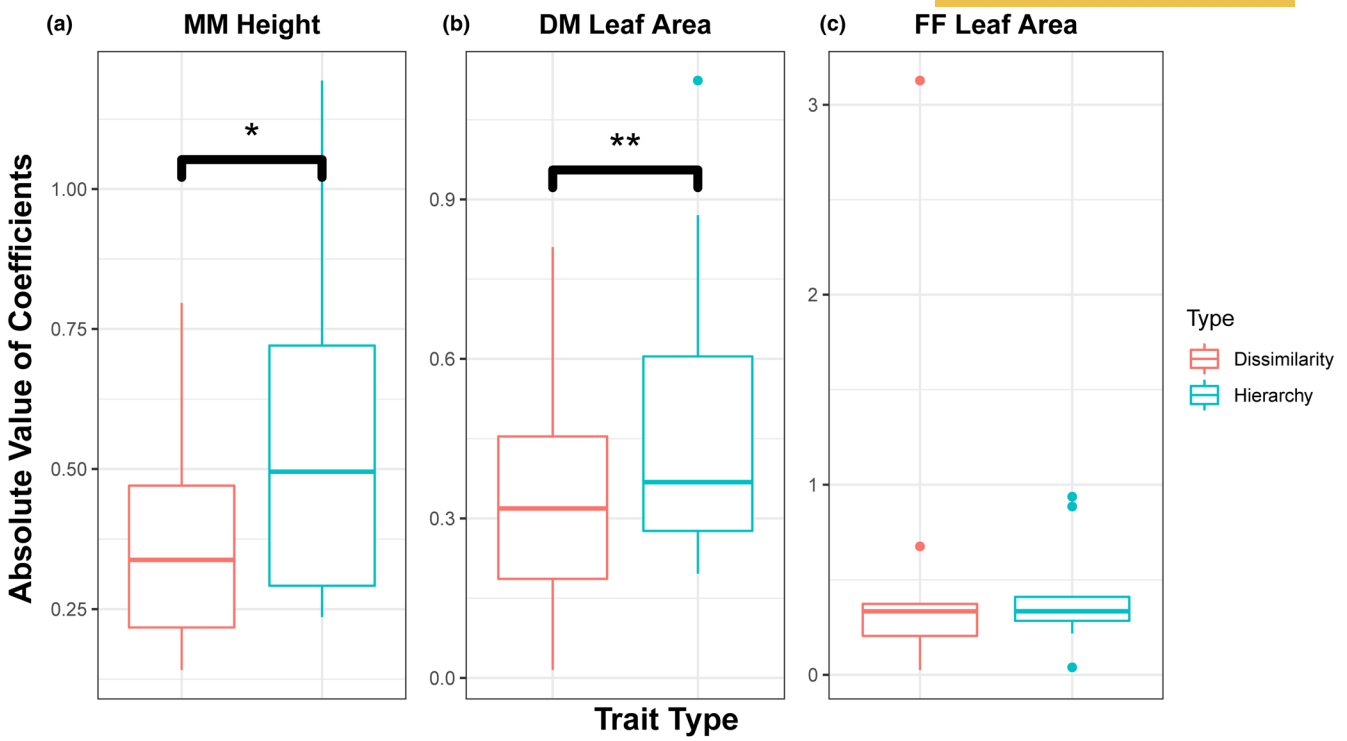

FIGURE 3 Comparisons of the absolute value of slopes for species-level hierarchy models and species-level dissimilarity models. Differences in slopes were analysed using paired *t*-tests. Only model parameters with negative coefficients and confidence intervals which do not overlap zero in community specific models are analysed. (a) Height comparison for moist meadow species ($p=0.015$). (b) Leaf area comparison for dry meadow species ($p=0.001$); (c) Leaf area comparison for fellfield species ($p=0.469$). * represents $p<0.05$, ** represents $p<0.01$.

area dissimilarity models (*t*-test: $p<0.01$; Figure 3b). Following the conceptual framework laid out in Yin et al. (2021), this suggests that height and leaf area hierarchical competition, not environmental filtering, likely drives spatial clustering of species pairs in the moist meadow and dry meadow, respectively. In the fellfield, slopes for leaf area hierarchy models were not significantly different than slopes for leaf dissimilarity models (*t*-test: $p=0.47$; Figure 3c) suggesting that environmental filtering drives spatial clustering of species with similar leaf area trait values. Slopes for all species-specific models can be found in Supporting Information S7.

4 | DISCUSSION

Process-based experiments and pattern-based observational studies have played vital roles in advancing our understanding of species interactions and biodiversity patterns, but each method has flaws, which can only be resolved through the integration of both approaches (Gerhold et al., 2015; Münkemüller et al., 2020). By coupling a neighbour removal experiment with an observational study using point pattern analysis, we were able to identify trait-based mechanisms affecting the performance of interacting species and then show how these mechanisms relate to patterns of species co-occurrence in the surrounding community. Specifically, in the neighbour removal experiment, we found that hierarchical competition based on plant size (PC1) predicted changes in biomass among interacting species. Our observational study of spatial arrangement confirmed the importance of plant size (PC1) in some community types but also highlighted how composite trait metrics like PCs can obscure the role of individual traits in mediating species interactions. For example, while the plant size composite metrics (PC1) played a strong role in driving spatial overdispersion in the fellfield PC model, the individual trait models showed that height and leaf area were important across all community types, often in contradictory ways. Height hierarchy and leaf area dissimilarity best explained associations in the more resource rich moist meadow, leaf area hierarchy best explained associations in the resource poor dry meadow and height dissimilarity and leaf area environmental filtering best explained associations in the low productivity fellfield. These changes suggest that though composite metrics are useful for summarizing broad scale trait patterns across species, they may mask how individual traits may mediate coexistence mechanisms differently depending on abiotic conditions (Pérez-Ramos et al., 2019). Below, we first independently discuss the results of the neighbour removal experiment and observational study, before integrating these two approaches to provide a more holistic understanding of species interactions and biodiversity patterns in the alpine tundra. This integration highlights how experimental and observational approaches can be used in concert to generate insights that neither method alone could provide.

4.1 | Experimental study—Neighbour removal

Our findings that hierarchical competition based on plant size (PC1) determined patterns of biomass change in our neighbour removal experiment add to a growing body of evidence demonstrating that plant size traits are often related to performance among interacting species (Alexander et al., 2015; Carmona et al., 2019; Ferenc & Sheppard, 2020). Evidence for size-based competitive hierarchies is widespread, with larger plant species exhibiting a competitive advantage over smaller plant species across a variety of ecosystems (Alexander et al., 2015; Carmona et al., 2019; Ferenc & Sheppard, 2020). Competitive hierarchies based on height are especially common, as height mediates the ability of plant species to access light, with taller plants often achieving higher levels of photosynthesis, biomass accumulation and relative fitness in comparison to shorter plants (Craine & Dybzinski, 2013; Falster & Westoby, 2003). Larger leaf area may offer a similar photosynthetic advantage, establishing a hierarchy where species with larger leaves attain competitive dominance by capturing more light and shading out smaller leafed competitors (Anten, 2005; Craine & Dybzinski, 2013).

4.2 | Observational study—Point pattern analysis

Our observational study strengthens the conclusions of previous point pattern research in alpine tundra, demonstrating that neutral, positive and negative pairwise spatial associations compose the largest, intermediate and smallest proportions of association types, respectively (Bowman & Swatling-Holcomb, 2018; Losapio et al., 2018). Our results also support a trend towards increasing positive associations and decreasing negative associations with decreasing resource availability (moist meadow < dry meadow < fellfield) which has previously been detected in systems with severe abiotic conditions like alpine tundra and deserts (Bowman & Swatling-Holcomb, 2018; López et al., 2016). Overall, this trend agrees with predictions generated under the stress gradient hypothesis and reinforces research demonstrating a role for positive species interactions in alpine tundra (Blonder et al., 2018; Butterfield et al., 2013; Callaway et al., 2002).

In keeping with the results of our neighbour removal experiment, plant size (PC1) was important in driving pairwise spatial associations in our PC models, but only in some community types and via different mechanism of species interaction. In the fellfield, and to a lesser extent moist meadow, we found spatial overdispersion with respect to plant size (PC1) indicating the action of limiting similarity rather than hierarchical competition. However, when we decomposed PC1 into the constituent traits of height and leaf area via the individual trait models, we observed a much more nuanced role for traits associated with plant size. Height and/or leaf area each showed strong correlations with pairwise spatial associations, but in opposite ways which further shifted across community types. This suggests that a composite plant size metric may obscure the opposing effects of individual traits and that these traits may act as proxies for different mechanisms depending on abiotic conditions.

In the moist meadow, the PC models detected strong spatial clustering based on phylogenetic relatedness, likely due to the presence of a *Deschampsia cespitosa* (Poaceae), a dominant grass species known to competitively exclude co-occurring species and the only monocot analysed in the moist meadow plots. Our PC models further detected mild overdispersion based on plant size; however, this relatively weak signal was explained by the contradictory trends of leaf area and height manifesting in the individual traits models. We observed strong clustering of species pairs with similar heights and also found that species-level models showed larger slopes for hierarchy rather dissimilarity. Taken together, this suggests that in more benign abiotic conditions, species engage in hierarchical competition for light with taller species excluding shorter species (Craine & Dybzinski, 2013; Falster & Westoby, 2003; Westoby, 1998). Interestingly, the signal of phylogenetic clustering was weaker in the individual trait models than the PC models, suggesting that the competitive dominance of *D. cespitosa* is at least partially attributable to its large height values (a relatively tall species in the alpine tundra). Finally, the importance of leaf area dissimilarity suggests that limiting similarity also plays a large role in structuring spatial patterns in the moist meadow, with species potentially partitioning available light through differentiation in leaf size (Anten, 2005; Craine & Dybzinski, 2013). Variation in leaf size may enable species to access light at different levels of the canopy, with larger leaves even allowing shorter species to achieve levels of photosynthesis comparable to taller species (Anten, 2005; Craine & Dybzinski, 2013).

In the intermediately abiotically stressful dry meadow, PC models showed that no dissimilarity metrics were predictive of spatial associations. This may indicate that biodiversity patterns in the dry meadow are mainly driven by neutral processes in accordance with the large fraction of neutral species pair interactions we observed in this community type (Figure 2a). However, individual trait models showed clustering of species pairs with similar leaf area coupled with large slopes for species-level models of leaf area hierarchy. This suggests the operation of hierarchical competition based on leaf area instead of height. As abiotic stress increases (i.e. higher wind speeds, lower soil nutrients, lower snow cover) and plants are no longer able to mechanically support large heights (Walker et al., 2001) species may instead compete on the basis of leaf area. However, the examination of species-level leaf area hierarchy models does not show a clear hierarchy of trait values. While species with similar, average leaf area values are clustered, we also see strong negative associations arising from two species with leaf area values on opposite ends of the dry meadow spectrum: *Kobresia myosuroides* (Cyperaceae) which has smaller leaves, and *Geum rossi* (Rosaceae) which has larger leaves, and previous research has demonstrated dominant competitive ability in both species dependent on soil resource levels (Ashton et al., 2010; Theodose & Bowman, 1997). Thus, leaf area clustering may instead be a result of two competitive dominants

producing a bidirectional competitive hierarchy, where trait values on either end of the leaf area spectrum confer a competitive advantage in dry meadow. Future research should explore if possessing trait values which differ from the community average in either direction may result in a competitive and/or demographic advantage.

Finally, in the abiotically harsh fellfield, we observed relatively congruent results with our PC and individual trait models. PC models showed overdispersion in PC1 (plant size) and PC2 (SLA), while individual trait models similarly showed overdispersion for height and SLA. Alpine cushion plants dominate in the fellfield and are known to act as nurse plants, ameliorating exposure to harsh abiotic conditions and permitting the growth of taller and/or higher SLA species (i.e. resource acquisitive species) which would not normally occur in open fellfield (Bowman & Swatling-Holcomb, 2018; Butterfield et al., 2013; Kikvidze et al., 2015). While, height and SLA overdispersion could also potentially result from limiting similarity, facilitation is more likely the driving mechanism for overdispersion due to the high proportion of positive pairwise spatial associations and near total absence of negative associations we detected in the fellfield (Figure 2a). This suggests that dissimilar species pairs are positively associated with one another, not that similar species are negatively associated (i.e. limiting similarity). Like dry meadow, fellfield also showed the clustering of species pairs with similar leaf area. However, the lack of significant difference between the slopes of leaf area hierarchy versus dissimilarity models suggests environmental filtering is driving the clustering of leaf area, not competitive hierarchy. This may be the result of micro-topographic species sorting, where large and small leafed species cluster around specific abiotic features. For example, Blonder et al. (2018) found that in a barren, fellfield-like alpine community, species were spatially clustered according to micro-topographic variation in soil characteristics, like moisture and organic matter content.

4.3 | Integration of experimental and observational approaches

Plant size (PC1: height and leaf area) was important across both facets of our study, correlated with plant performance in the neighbour removal experiment and pairwise spatial associations across community types in the observational study. This result reinforces previous research conducted in the Swiss Alps, which found that plant size (height and leaf area) differences predicted the outcome of competitive interactions between alpine species in a turf transplant experiment (Alexander et al., 2015). Furthermore, an observational study at Niwot Ridge demonstrated that functional dispersion and community weighted means for leaf area and height showed the strongest responses across an alpine stress/resource gradient out of five examined traits (Spasojevic & Suding, 2012). Importantly, our experiment was conducted at the interface between dry and moist meadow where abiotic stress decreases and competitive interactions likely increase, and we identified sized based hierarchical competition as the primary mechanism shaping plant performance. We inferred the action of those same mechanisms in the individual trait models of our observational study, with moist meadow patterns structured via height hierarchy and dry meadow patterns structured via leaf hierarchy. This parallel between the results of experimental and observational approaches suggests that: (1) trait hierarchies affect plant performance during species interactions; and (2) over ecological time, competitive hierarchies can manifest as patterns of species co-occurrence at the community scale.

Other parallels between our experiment and observational study include the lack of importance of chlorophyll content and phylogenetic relatedness, neither of which demonstrated strong relationships with plant performance or pairwise spatial associations. This result also finds agreement with Spasojevic and Suding (2012), who found weak patterns for both metrics. While phylogenetic relatedness showed minor clustering in the moist meadow, this is likely not indicative of the widespread positive association of closely related species, but instead results from strong negative associations caused by the single, dominant monocot species (*D. cespitosa*) present in the moist meadow point pattern analysis (Bowman & Swatling-Holcomb, 2018; Walker et al., 1993). Though some evidence indicates that phylogenetic relatedness may be useful as a proxy for trait similarity in some cases (Cavender-Bares et al., 2009; Webb et al., 2002), we did not detect patterns of phylogenetic signal at the level of the experiment or observational study, and only minor phylogenetic signal when all species in the Niwot trait database were considered, suggesting that phylogenetic relatedness is a poor proxy for species functional similarity in individual traits in alpine tundra.

Additionally, our integration of experimental and observational approaches suggests that though composite trait metrics are useful for summarizing broad scale trait patterns across species (Reich, 2014; Westoby et al., 2002), they may mask how individual traits may mediate coexistence mechanisms differently depending on abiotic conditions (Pérez-Ramos et al., 2019). A recent focus on trait coordination (e.g. Díaz, 2025) and the use of PC axes to explain trait syndromes (e.g. Maire et al., 2013) are often created using trait databases and such a focus may obscure local drivers of trait variation. Our findings suggest that analyses that use trait syndromes (PC axes) should also supplement these analyses with individual trait analyses, otherwise important nuance may be lost.

Lastly, our results highlight how the relationship between traits and coexistence mechanisms may change depending on abiotic conditions, as found in other studies (e.g. Mudrák et al., 2016; Pérez-Ramos et al., 2019). This is most clearly exemplified by leaf area in our individual trait models which was related to multiple mechanisms in both our experiment and observational study. Specifically, in the observational study, leaf area patterns indicated transitions from limiting similarity to hierarchical competition

to environmental filtering with increasing environmental stress. Recent research in other systems has also this highlighted potential context dependence, with Pérez-Ramos et al. (2019) finding that, under control conditions in an experimental grassland system, trait dissimilarity in water-use efficiency promoted stabilizing niche differences, while under drought conditions, a trait hierarchy formed favouring species with high water-use efficiency. While numerous studies have demonstrated relationships between traits and coexistence mechanisms (Gallego et al., 2019; Kraft et al., 2015; Yin et al., 2021), fewer have explored how those relationships may change with abiotic conditions across space and/or time and our work suggests that this should be an area of increasing focus for future research.

4.4 | Study limitations

While we believe that our study provides a mechanistic link between pattern and process by uniting experimental and observational approaches, it is important to note three limitations related to our experiment, which may affect our conclusions. First, our experiment, like all removal experiments, does not account for the effects of root legacy effects on species interactions (Dabu et al., 2024). Second, our experiment used one species (ARTSCO) to standardize the effect of competition. While this experimental design is commonplace in studies of competition (Funk & Wolf, 2016), a more robust design would involve interactions between all possible pairwise combinations of species and a larger sample size (Carmona et al., 2019; Ferenc & Sheppard, 2020). We chose to use a standardized competitor because the high relative abundance of ARTSCO made finding naturally occurring species pairs relatively easy at the moist meadow/dry meadow interface. However, because ARTSCO is on the lower end of the alpine leaf area spectrum, we inadvertently generated co-linearity between hierarchy and dissimilarity metrics for leaf area, such that species paired with ARTSCO generally have larger leaves which are also more dissimilar (Supporting Information S4). We attempted to correct this problem by conducting PCs analysis and using a plant size composite metric, which did have issues with co-linearity. However, this may have generated the knock-on problem of conflating the effects of height and leaf area, which may differ, as we demonstrated in our observational study of spatial associations.

Third, because our experiment did not extend into the fellfield, we are only able to infer a connection between observed patterns (height/SLA overdispersion and leaf area clustering) and mechanisms (facilitation and environmental filtering) for this community type, not make mechanistic links as we did with moist meadow and dry meadow. However, it is important to note that both of these inferred mechanisms are well-supported in the alpine literature (Bowman & Seastedt, 2001; Butterfield et al., 2013; Kikvidze et al., 2015; Spasojevic & Suding, 2012) and we are confident with our inference in this case.

5 | CONCLUSIONS

Overall, we found evidence that both trait hierarchies and dissimilarities for size related traits (height and leaf area) are important mechanisms governing species coexistence, reinforcing similar results from other alpine tundra sites (Alexander et al., 2015) and other ecosystems (Carmona et al., 2019; Gallego et al., 2019; Kraft et al., 2015; Yin et al., 2021). Results of our experiment and observational study largely supported one another, demonstrating how plant size traits shape plant performance during species interactions and how those interactions ultimately manifest as patterns of species co-occurrence in natural alpine communities. Our results also add to recent research suggesting that traits may relate to coexistence mechanisms differently depending on environmental context (Pérez-Ramos et al., 2019). Importantly our results also suggest that composite metrics or a focus on 'trait coordination' may mask important nuances in how individual traits operate and that traits correlated at broader scales (e.g. trait databases, regional pools) may be decoupled at local scales. Finally, this fusion of experimental and observational approaches represents a rigorous, but practical method for investigating trait-based coexistence mechanisms in systems composed of long-lived, clonally reproducing species like alpine tundra (Korner, 2003). Researchers working in other systems composed of long-lived and/or difficult to manipulate species (e.g. forests), may also benefit from adopting and modifying this integrated approach. Future research which explicitly connects experiments with observational studies is key to advancing our understanding of species coexistence, trait-based community assembly and the links between process and pattern in ecology.

AUTHOR CONTRIBUTIONS

Jared D. Huxley conceived the idea of the study with input from Marko J. Spasojevic. Jared D. Huxley collected species interaction data. Marko J. Spasojevic collected trait data. William D. Bowman collected spatial point pattern analysis data. Jared D. Huxley analysed all data. Jared D. Huxley wrote the manuscript with input from William D. Bowman and Marko J. Spasojevic.

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CONFLICT OF INTEREST STATEMENT

Spasojevic is an Associate Editor at *Functional Ecology* but had no role in the reviewing or handling of this manuscript.

DATA AVAILABILITY STATEMENT

All data are available via NWT LTER's data portal (https://nwt.lternet.edu/data-catalog). Neighbour interactions and allometry data are available at Spasojevic and Huxley (2026) and trait data are available at Spasojevic and Weber (2018).

STATEMENT ON INCLUSION

This work was conducted within the country of which all authors are citizens and was carried out entirely by the authors.

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SUPPORTING INFORMATION

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

Supporting Information S1. Principal components analysis for traits. (A) Proportion of variance; (B) Trait loadings; (C) Principal component biplot.

Supporting Information S2. Lambda (λ) values for leaf area, height, specific leaf area (SLA) and chlorophyll content (CC) for all species in the Niwot trait database, all species in the neighbour removal experiment and all species in the observational study (both across and within habitats).

Supporting Information S3. Neighbour removal experiment design. (A) Experimental design and survivorship for neighbour removal experiment. (B) Details of allometry measurements for neighbour removal experiment including methods and adjusted R^2.

Supporting Information S4. Neighbour removal experiment modelling supplemental material: (A) Neighbour removal experiment model parameters for global model constructed with trait principal components; (B) Correlation matrix and variance inflation factor scores for trait principal components model; (C) Neighbour removal experiment model parameters for global model constructed with individual traits; (D) Correlation matrix and variance inflation factor scores for individual trait model; (E) RII as a function of individual traits (Height Hierarchy, Leaf Area Hierarchy, Leaf Area Dissimilarity).

Supporting Information S5. Models examining pairwise spatial associations across community types (Full) and within community types (MM: Moist Meadow, DM: Dry Meadow, FF: Fellfield).

Supporting Information S6. Partial *R*-squared values for each model in point pattern analysis calculated with bootstrapping ($n = 100$).

Supporting Information S7. Model coefficients (i.e. slopes), standard error, *p*-values (<0.05 in bold) and adjusted R^2 values for species-level linear regressions. Coefficients of hierarchy and dissimilarity models for each species × habitat combination were compared via paired *t*-test to produce Figure 3.

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