ECOGRAPHY

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A dimmer shade of pale: revealing the faint signature of local assembly processes on the structure of strongly filtered plant communities

Jesús López-Angulo, Marcelino de la Cruz, David S. Pescador, Ana M. Sánchez and Adrián Escudero

J. López-Angulo (https://orcid.org/0000-0003-3539-2545) ✉ (jesus.lopez.angulo@urjc.es), M. de la Cruz (https://orcid.org/0000-0002-9080-4525), D. S. Pescador (https://orcid.org/0000-0003-0395-9543), A. M. Sánchez (https://orcid.org/0000-0002-6220-3001) and A. Escudero (https://orcid.org/0000-0002-1427-5465), Depto de Biología y Geología, Física y Química Inorgánica, Univ. Rey Juan Carlos, Móstoles, Spain.

Trait-based ecology suggests that abiotic filtering is the main mechanism structuring the regional species pool in different subsets of habitat-specific species. At more local spatial scales, other ecological processes may add on giving rise to complex patterns of functional diversity (FD). Understanding how assembly processes operating on the habitat-specific species pools produce the locally observed plant assemblages is an ongoing challenge. Here, we evaluated the importance of different processes to community assembly in an alpine fellfield, assessing its effects on local plant trait FD. Using classical randomization tests and linear mixed models, we compared the observed FD with expectations from three null models that hierarchically incorporate additional assembly constraints: stochastic null models (random assembly), independence null models (each species responding individual and independently to abiotic environment), and co-occurrence null models (species responding to environmental variation and to the presence of other species). We sampled species composition in 115 quadrats across 24 locations in the central Pyrenees (Spain) that differed in soil conditions, solar radiation and elevation. Overall, the classical randomization tests were unable to find differences between the observed and expected functional patterns, suggesting that the strong abiotic filters that sort out the flora of extreme regional environments blur any signal of other local processes. However, our approach based on linear mixed models revealed the signature of different ecological processes. In the case of seed mass and leaf thickness, observed FD significantly deviated from the expectations of the stochastic model, suggesting that fine-scale abiotic filtering and facilitation can be behind these patterns. Our study highlights how the hierarchical incorporation of ecological additional constraints may shed light on the dim signal left by local assembly processes in alpine environments.

Keywords: abiotic filtering, alpine plant community, community assembly, functional trait, null model, species interaction

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Introduction

Understanding plant community assembly is an ongoing challenge in community ecology (Lortie et al. 2004, HilleRisLambers et al. 2012, Kraft et al. 2015). While a consistent theory to explain community assembly is still lacking, modern trait-based plant ecology (Grime 2006, Adler et al. 2013, Escudero and Valladares 2016, Shipley et al. 2016) has emerged during the last two decades as a powerful approach. Trait-based plant ecology suggests that biotic and abiotic environmental determinants can act as filters selecting those species with appropriate morphological or physiological traits (i.e. functional traits), that can yield good performance under a given set of environmental conditions (Keddy 1992, Cornwell and Ackerly 2009, Götzenberger et al. 2012). Accordingly, the assembly processes responsible of any realized assemblage might be inferred from functional signatures, i.e. from the dispersion patterns of functional traits in realized assemblages (Keddy 1992, Diaz et al. 1998, Dubuis et al. 2013). For example, convergence on a narrow range of trait values is expected when assembly is driven by an abiotic filter imposing very restrictive conditions (Weiher and Keddy 1995, Cornwell et al. 2006) or weaker–competitor exclusion (Chesson 2000, Grime 2006, Mayfield and Levine 2010). Conversely, trait divergence could be the result from limiting similarity imposed by competition (MacArthur and Levins 1967) although fine-scale environmental heterogeneity may also promote the coexistence of functionally different species exploiting contrasted niches (Siefert 2012).

This interpretation of functional trait patterns has resulted from the accumulation of empirical evidence mostly based on the analysis of strong environmental gradients with abrupt changes and turnovers between different habitat types and plant communities (for instance considering functional variation from forests to alpine grasslands and tundra, or from hydrophilic to xerophilous vegetation; Cornwell and Ackerly 2009, Schöb et al. 2013, Spasojevic et al. 2014, Lhotsky et al. 2016). This is due to the fact that the habitat-specific species pool (sensu Pärtel et al. 2011) is primarily determined by the large-scale environmental filters (e.g. temperature and precipitation; Woodward 1987, Diaz et al. 1998). Abiotic filtering induced by these factors strongly structures regional diversity on a variety of easily identifiable habitats and their corresponding habitat-specific species pools. However, at finer local spatial scales (e.g. for the sampling grain usually employed in community ecology), in addition to other abiotic filters, such as those related to topographic (Scherrer and Körner 2011, Graae et al. 2017, Blanco-Pastor et al. 2019) and soil conditions (Pescador et al. 2020), there is usually an increase in the relative influence of biotic interactions (Chase 2014). The fact that several local processes may operate simultaneously, sometimes pushing the trait responses in opposite directions, makes difficult to connect the signatures in the functional configuration of plant communities with their causes (Spasojevic and Suding 2012, Herben and Goldberg 2014). Thus, unravelling the assembly processes responsible

for sorting out the habitat-specific species pools into the local assemblages remains as a challenge (Shen et al. 2017).

Our main goal in this paper is assessing the relative contribution of different local processes, namely, fine-scale abiotic constraints and biotic interactions, in plant community assembly. With this in mind, we selected as a model system a high mountain fellfield community in which the integration of climate, macrorelief (Theurillat et al. 1998), limestone substrate and periglacial processes (such as cryoturbation and solifluction) determine the regional pool of species (i.e. habitat-specific species pool) (Benito 2005). This plant community extends on a very large environmental gradient where other fine-scale ecological factors, such as variations in soil depth and fertility, and changes in solar radiation and elevation, could influence the coexisting species and their abundances in the observed assemblages (Spasojevic and Suding 2012, Scherrer et al. 2019, López-Angulo et al. 2020a; Supplementary material Appendix 1 Fig. A1). At finer, local scales, community assembly could also be affected by biotic interactions, such as competition and facilitation (Anthelme et al. 2014, Michalet et al. 2016).

To determine the role played by these processes, we followed a null modelling approach with two complementary evaluations of the discrepancy between the observed and expected functional structure in each sampled assemblage: 1) a classical randomization test of trait diversity (Manly 1991, Götzenberger et al. 2016) and 2) and a linear modelling of the standard effect size (i.e. discrepancies between expected and observed values) found in each assemblage. Our null models hierarchically incorporated increasing complexity to evaluate the importance of these mechanisms in the community assembly (de Bello et al. 2012). Thus, we compared functional trait diversity of the locally observed assemblages to null distributions drawn from the expected assemblages under specific assembly processes (Karger et al. 2016, Lessard et al. 2016). Specifically, in this study we evaluated the differences between the observed functional diversity (hereafter FD) and its expectations from null assemblages generated by a) completely random assembly (stochastic model); b) random assembly constrained by the effect of abiotic factors with species tracking independently their abiotic requirements and ignoring species interactions (independent model); and c) random assembly constrained by observed species co-occurrence patterns, i.e. considering both shared responses to microenvironmental factors and species interactions (co-occurrence model).

We hypothesised that 1) if neither local abiotic filtering nor biotic interactions play a role in assembling this community in realized assemblages, the observed patterns of FD would not be different to those expected by chance; 2) if the effect of abiotic filtering caused by these small-scale abiotic environmental factors prevails in the assembly, observed FD would be smaller than FD expected from the stochastic model. Furthermore, the observed FD would not be different from the FD expected by the independence model (which account for such abiotic determinants), or the FD expected

by the co-occurrence model as long as species shared abiotic preferences. On the contrary, 3) if facilitation (that enhances less stress-tolerant species broadening the trait range in the realized assemblages) is the process that contributes more strongly to the functional pattern, we would expect that the observed FD will be higher than the simulated under the stochastic and independence models, and that it would not be different from the expectations of the co-occurrence model. 4) Under a simultaneous effect of facilitation and fine-scale abiotic filtering, we would expect that the observed FD would be smaller than the simulated by the independence model and not different from the expectations of the co-occurrence and stochastic model.

Methods

Study area

The present study was carried out in the alpine fellfields of Ordesa and Monte Perdido National Park (42°40′N, 0°03′E), which is located in the central Spanish Pyrenees (Huesca province). We sampled the patchy psicro-xerophylous pasture above the local *Pinus uncinata* Ramond *ex* DC. in Lam. & DC treeline, specifically those related to cryoturbated habitats. We avoided sampling on rocks, screes, snowbeds and waterlogged fellfields. The climate is temperate with a mild influence of the Mediterranean climate especially at lower elevations. The average annual temperature and precipitation values are 4.9°C and 1650 mm, respectively (Góriz Weather Station; 42°36′25″N, 0°01′03″E; 2200 m a.s.l.). Precipitation occurs mainly during the autumn and spring. Snow cover can last from October to May, although the duration of the snow cover varies widely according to the elevation and orientation. The surveyed vegetation mainly comprises limestone stony pasture dominated by *Festuca gautieri* subsp. *scoparia* (A. Kern. & Hack.) Kerguélen, which is accompanied by other grasses and creeping chamaephytes. These alpine fellfields are very species-rich (up to 15 species m^{-2}), with total plant cover values ranging from 10% to 40%. Low intensity livestock grazing occurs during the growing season.

Fieldwork and environmental factors

We sampled along the summer seasons of 2013 and 2014 (López-Angulo et al. 2019). We selected 24 sites along the complete elevation gradient where this plant community occurs (Benito 2005) throughout the study area (Supplementary material Appendix 1 Fig. A1; from 1650 to 2550 m a.s.l.) considering a complete range of aspects and slopes. At each site, we established a 20 × 20 m plot over an area with homogeneous and representative vegetation. In each plot, we placed five 2.4 × 2.4 m quadrats, one in each corner and a fifth at the plot centre. All plant species within each quadrat were identified and their cover visually estimated. This sample size is adequate for including the complete

variability of this type of plant community (Pescador et al. 2015). The elevation and aspect were recorded using a GPS (Garmin Colorado-300, Garmin, Olathe, USA), and the slope with the help of a clinometer (Silva Clinomaster, Silva Sweden, Sollentuna, Sweden). Aspect and slope were used to calculate the Gandullo's potential solar radiation coefficient (Gandullo 1974, López-Angulo et al. 2018). Two soil cores (5-cm-diameter × 10-cm-depth) were taken within each corner quadrat, one in an open area and the other beneath a vegetated patch. Each soil core was air dried for one month and sieved to 2 mm. We estimated eight soil variables: total organic carbon (C), total nitrogen (N), available phosphorus (P), potassium (K) and the activity of β-glucosidase and phosphatase, as well as the soil pH and electric conductivity (for details see López-Angulo et al. 2018). For each quadrat, we averaged the values of soil variables estimated in the two cores weighted by the respective cover of bare ground and vegetated area. Soil variables for the central quadrat were estimated as the average of the other four quadrats in the plot.

Plant trait measurements and functional diversity estimation

During July 2014, several plant functional traits were measured for 96 species (Supplementary material Appendix 1 Table A1), which represented 94% of the accumulated cover in our system. For each species, we measured five continuous traits related to the leaf–height–seed plant strategy (Westoby 1998), which reflect key ecological strategies for plants: the average plant vegetative height (VH), leaf dry matter content (LDMC), specific leaf area (SLA), leaf thickness (LT) and seed mass (SM). These traits were slightly correlated with each other (Supplementary material Appendix 1 Fig. A2). Ten randomly selected individuals by species were collected from the plot (20 × 20 m) and surroundings where each species was more abundant, to calculate the average trait values for each species. When ten individuals could not be found, data was completed with individuals from other plots. Seed mass was measured in at least 30 dry seeds from at least ten individuals per species. When seeds could not be collected in the field, SM was approximated by the average SM from the Royal Botanic Gardens Kew Seed Information Database (Liu et al. 2008).

Given that FD measures are sensitive to missing trait information, we excluded from the analysis five of the 120 quadrats where plant cover of the species with measured traits did not exceeded 90% of the accumulated plant cover (using a 90% relative abundance threshold; Pakeman 2014). Finally, functional trait data for 96 of the recorded species represented on average 98% cover in the quadrats. We quantified the FD using the weighted Rao quadratic entropy (RaoQ: Rao 1982, Botta-Dukát 2005) incorporating the relative cover of each species in each realized assemblage. RaoQ was computed using the R function melodic (de Bello et al. 2016a) from the matrix of pairwise Euclidean trait distances between species. Melodic computes RaoQ as:

$$RaoQ = \sum_{i=1}^{s} \sum_{j=1}^{s} d_{ij} p_i p_j$$

where S is the number of species in an assemblage, d_{ij} is the Gower distance between species i and j, and p_i and p_j are the percentage cover of species i and j, respectively.

As trait data did not encompass the whole study area for all species, we assessed whether intraspecific variation could have any effect on our results. For this, we compared the intraspecific trait variation (ITV) with the interspecific trait variation (BTV) for each trait using the coefficient of variation corrected for small sample size, i.e. $CV_b = [1 + 1/4n] \times CV$, where n is the number of samples and CV the coefficient of variation of each trait (Sokal and Rohlf 1995). Averaged ITV was lower than half of the BTV for all functional traits (SM: BTV = 1.63, ITV = 0.19; VH: BTV = 1.04, ITV = 0.34; LT: BTV = 0.41 ITV = 0.20; LDMC: BTV = 0.31 ITV = 0.13) except for SLA (SLA: BTV = 0.31, ITV = 0.19), which was removed from further analyses (Lessard et al. 2016).

Null models

To implement the null models, we first fitted the probability of occurrence of each species (i.e. estimating the probability p_{ki} of species i occurring in quadrat k) according to the constraint imposed by three null models.

1) Stochastic null model: it assumes that all quadrats are equally accessible for all species (i.e. independently of the abiotic conditions in each quadrat and the species already observed there); so, the occurrence probability was identical for any species in any quadrat.

2) Independence null model: species' occurrence probability at a quadrat depends on the response of each species to the abiotic conditions in that quadrat (i.e. elevation, solar radiation, slope and soil conditions). To estimate this probability, we fitted logistic regressions (GLMs with a binomial error distribution and a logit link function) for each species' occurrence data (i.e. presence/absence per quadrat) using as predictors the first four axes (and their quadratic terms) of a principal components analysis on 11 previously standardized environmental variables (the eight soil variables plus elevation, slope and potential solar radiation). We used a VARIMAX procedure to maximize the correlations between the PCA components and the abiotic factors considered. The four PCA components (accounting for 79% of variance; Supplementary material Appendix 1 Table A2) represented, the first axis, the variation in carbon and nitrogen stocks (37.5% of variance), the second, elevation, conductivity and potassium (17.7%), the third, slope and solar radiation (14.7%) and, finally the fourth, phosphorus (9.4%). A stepwise model-selection procedure based on Akaike's information criterion (AIC) was used to find the best predictive model for each species using the function 'stepAIC' in the package 'MASS'. We computed the fitted value for the probability p_{ki} of occurrence of each species i at each quadrat k using the function 'predict.glm' in the 'stats' package (R Core Team).

3) Co-occurrence model: species occurrences depend on the presence of other species in the assemblage and, in consequence, they are determined both by the outcome of plant–plant interactions and by their shared abiotic preferences. Thus, probabilities of species occurrence at a quadrat were estimated from the pattern of species co-occurrence in all the studied quadrats. We estimated p_{ki}, using Beals smoothing (Beals 1984, De Cáceres and Legendre 2008). Beals smoothing estimates p_{ki}, as an average of the estimated probabilities of the species i conditional on the known occurrences of each other species (De Cáceres and Legendre 2008):

$$p_{ki} = (1/S_k) \sum_{j=1}^{s} \frac{m_{ij} x_{kj}}{n_j}$$

where S_k is the number of species in quadrat k, m_{ij} is the number of joint occurrences of species i and j, n_j is the number of occurrences of species j in all the quadrats, x_{kj} is the incidence (0 or 1) of species j in quadrat k, and s is the number of different species in all the quadrats (De Cáceres and Legendre 2008). Beals smoothing was performed with the 'beals' function in the 'vegan' R package (Oksanen et al. 2010).

To simulate null assemblages, we followed two steps: First, species were assigned to quadrats based on the probabilities of occurrence previously fitted. For each quadrat, we sampled among the total species pool, the same number of species found in the observed assemblages, using the function 'sample' from the R package 'base' (R Core Team). In a second step, the observed species-cover values were randomly re-assigned to the species simulated in each quadrat. Thus, this null model framework assumes independence between the species' occurrence and abundance patterns.

Observed versus expected functional diversity

To compute the expected FD, we simulated 999 null assemblages for each quadrat (2.4 × 2.4 m) and for each of the tree null models considered. For each trait, quadrat and null model, we assessed the discrepancies between the observed and the expected FD (RaoQ) by estimating the standardized effect size (SES sensu Gotelli and McCabe 2002)

$$SES = (RaoQ_{obs} - mean(RaoQ_{sim})) / (sd(RaoQ_{sim}))$$

where $RaoQ_{obs}$ is the observed FD, $mean(RaoQ_{sim})$ is the expected FD (i.e. the mean FD in the 999 simulated assemblages) and $sd(RaoQ_{sim})$ the standard deviation of these simulated values. In addition, for each trait, quadrat and null model, we determined the percentile rank of the observed FD among the null distribution of simulated FD values.

Significance testing

We followed two approaches to evaluate the significance of the deviations of the null models. Our first approach consisted

Table 1. Classical randomization tests. Number of quadrats (out of a total of 115) in which observed FD was significantly smaller (convergence) or larger (divergence) than the expected values under the stochastic, independence and co-occurrence null models for each of the four considered traits.

	Stochastic		Independence		Co-occurrence	
	Convergence	Divergence	Convergence	Divergence	Convergence	Divergence
Seed mass	4	0	3	0	3	1
Leaf thickness	4	1	4	2	1	1
Vegetative height	0	0	5	0	4	1
LDMC	1	1	3	1	3	3

on a classical randomization test (Manly 1991, Ulrich and Gotelli 2010): for each trait, we considered the observed FD in each quadrat significantly different from the null distributions defined for that quadrat at a significance level of 0.05 when its percentile rank was smaller or larger than the 2.5th or 97.5th percentiles of the null distribution, respectively. Smaller and larger percentile ranks indicated respectively that FD was smaller and larger than expected FD according to the null model. For our second approach, we implemented a procedure to simultaneously test the null hypotheses of our null models: for each trait, we fitted a linear mixed model (Pinheiro and Bates 2000) to the SES values obtained in the three null models, using null model type as a fixed factor and plot and quadrat as random factors. Fitted null model group coefficients were considered significantly different from zero when their 95%-confidence intervals do not overlap zero (greater than zero: functional divergence; less than zero: functional convergence). When the fitted coefficient for null model type resulted statistically significant, we performed post hoc tests to assess pair wise differences between the null models. Linear mixed models were fitted with function 'lmer' in the package 'lme4' (Pinheiro and Bates 2000). Post hoc tests were performed with function 'emmeans' in package emmeans (Lenth 2018).

Results

In addition to *Festuca gautieri* subsp. *scoparia*, which had a mean cover of 4.47% per quadrat, the most abundant species were other graminoids such as *Koeleria vallesiana* (Honck.) Gaudin (4.57% of mean cover) and *Helictotrichon sedenense* (DC.) Holub (1.96% of mean cover). The most frequent species were *Koeleria vallesiana* (77.4%), *Festuca gautieri* (71.3%) and *Helictotrichon sedenense* (57.4%), together with some creeping chamaephytes such as *Thymus gr. serpyllum* L. (92.2%) and *Galium pyrenaicum* Gouan (68.7%). Only these five species occurred in more than a half of quadrats (Supplementary material Appendix 1 Table A1), whereas more than a half of the recorded species occurred in less than a 10% of the quadrats suggesting a high species turnover across assemblages. Furthermore, our data set showed significant variation in species composition strongly affected by our composite abiotic variables (C and N stocks: PCA 1; elevation: PCA 2; and solar radiation: PCA 3; redundancy analysis results in Supplementary material Appendix 1 Table A2).

The species composition of the simulated assemblages varied depending on the null model used (Supplementary material Appendix 1 Fig. A3). Except for the stochastic null model, species frequencies in the simulated assemblages was close to the observed, with only a few, very abundant species and many rare ones (Supplementary material Appendix 1 Fig. A4). Overall, observed FD for each of the analysed traits (vegetative height, seed mass, LDMC and leaf thickness) in each quadrat was not significantly different than expected for any of the three null models. Specifically, the percentile rank of the observed FD in 110 of the 115 observed assemblages was between the 2.5th and 97.5th percentiles of the null distribution which suggests they were compatible with the expectations of the different assembly simulation scenarios (Table 1).

The linear mixed models revealed that the observed FD of seed mass, leaf thickness and vegetative height was significantly different than expected by some of the null models. More specifically, for seed mass, the observed assemblages had significantly less FD than the stochastic null model simulated assemblages (i.e. negative SES values, Fig. 1a). On the contrary, for leaf thickness, the observed assemblages had significantly more FD than the stochastic null model simulated assemblages (i.e. positive SES values, Fig. 1b). For both traits, the SES of the stochastic null models were significantly different (and more deviant) than the SES of the independence and co-occurrence null models (Fig. 1a–b). In the case of vegetative height, the observed assemblages had less FD than the expected by the three null models (i.e. significantly negative SES, Fig. 1c). This result indicated that the locally observed assemblages tended to be less diverse in vegetative height compared to the expected under our three different scenarios (Table 2). In the case of LDMC, we did not find differences between the observed FD and the FD expected from any of the three null models since SES values were not significantly different from zero (Fig. 1d).

Discussion

One of the key assumptions of the filtering hypothesis (Diamond 1975, Keddy 1992) is that the functional structure of plant communities results from the constraints imposed by abiotic and biotic processes (Lavorel and Garnier 2002, HilleRisLambers et al. 2012). The persistent challenge of disentangling the role of these ecological
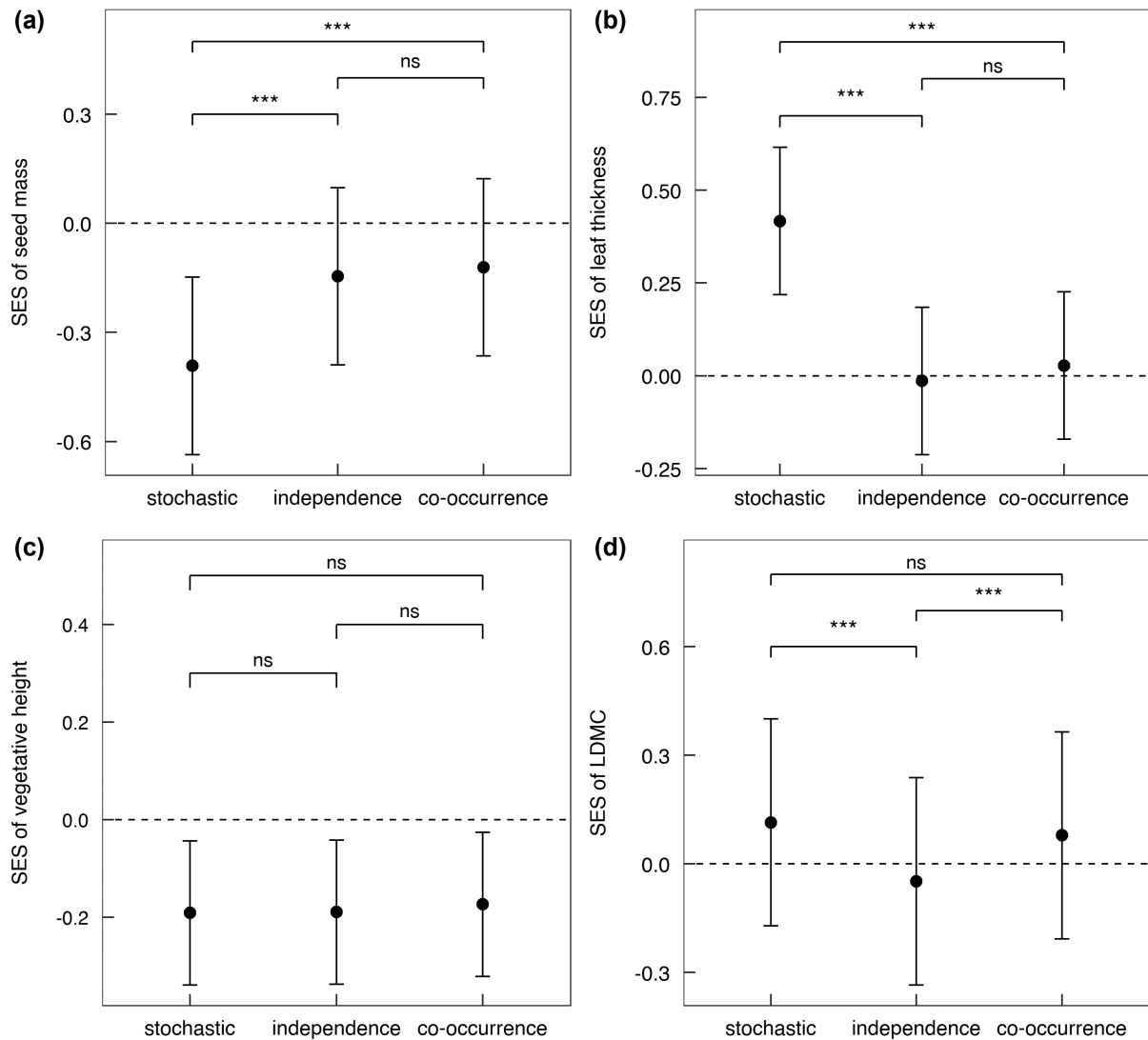
Figure 1. Mean SES values of FD fitted by the linear mixed models for the stochastic, independence and co-occurrence null models. Quadrat and plot were included as random factors in the model. Panels show the fitted mean SES values for (a) vegetative height, (b) seed mass, (c) LDMC and (d) leaf thickness. Error bars represent confidence intervals. Asterisk symbols indicate significant differences (p < 0.05) according to post-hoc Tukey tests (*** p < 0.001; ** p < 0.01; * p < 0.05; and ns, not significant).

mechanisms in structuring plant communities has been relatively successful at relatively large spatial and/or environmental scales (Götzenberger et al. 2012, HilleRisLambers et al. 2012). However, the picture is more imprecise when examining community assembly at very large spatial scales (Münkemüller et al. 2020) or, on the contrary, when the focus is set on the local communities of a unique type of vegetation (Götzenberger et al. 2012). Our study shows that by using a hierarchical combination of increasingly complex null models, it is possible to unravel the faint signal of processes affecting local community assembly after the sieving action of the strong primary abiotic filters that sort out the regional species pool (Keddy 1992, Pärtel et al. 2011). Although our results do not discard the relevance of stochastic sorting at this ecological scale, they offer support for both fine-scale

abiotic filtering and abiotic interactions as drivers of community assembly in this rich alpine plant community.

Stochastic processes shape the functional patterns across assemblages

Overall, we found that FD did not differ among observed and simulated assemblages. The observed FD was compatible with those expected for random assembly but also for the deterministic ecological processes simulated with the independence and co-occurrence models. The lack of significant departure from null models has been widely reported (see a synthesis in Götzenberger et al. 2012). It is well-known that null models which constrain species frequencies and quadrat richness, such as our independence and

Table 2. Summary of the results of the likelihood-ratio tests assessing the difference of fit among the tree null models for the linear mixed model (LMM) fitted to the standardized effect sizes (SES) of each model and trait.

LMM	F	p-value
Seed mass	56.4153	< 2e-16
Leaf thickness	275.7918	< 2e-16
Vegetative height	0.1823	0.83349
LDMC	44.8874	< 2e-16

co-occurrence null models, tend to be conservative, failing to reject the false null hypothesis more often than it should be (i.e. large type II error) a phenomenon that has been named 'Narcissus effect' (Colwell and Winkler 1984, Gotelli 2000, Chalmandrier et al. 2013, Perronne et al. 2017, Ulrich et al. 2017). On the contrary, null models that avoid restraining richness or, as our stochastic null model, species frequencies, tend to be much liberal (what has been called the 'Jack Homer effect'; Wilson 1995). Curiously, neither the conservative nor the liberal randomization tests detected significant departures from the null models in our case.

Some authors have argued that the lack of significant departure from the null distributions is more frequent when the randomized species pool include species from a unique type of vegetation (de Bello et al. 2012, Götzenberger et al. 2012, 2016). For example, in forest habitats, the functional signature of ecological processes was detected more often when the species pool included non-forest species (Götzenberger et al. 2012). Although we studied a long elevation gradient (almost 1000 m), the habitat-specific species pool available for these fellfields is, probably, the result of an intense filtering of a very diverse regional species pool produced by the integration of macrorelief, low temperature, limestone substrate and periglacial processes (Theurillat et al. 1998, Benito 2005). These environmental factors selected a set of functionally similar species, well-adapted to thrive under these particular environmental conditions. Thus, most of the species entering these assemblages usually exhibit low stature and possess similar vegetative functional traits, with a prevalence of thick leaves and low SLA as an adaptation to wind, coldness and low nutrient conditions (Körner 2003, Choler 2005, Takahashi and Tanaka 2016).

Therefore, irrespective of the null model employed, the functional patterns generated in the simulated assemblages were functionally similar and organized around a very reduced range of functional trait values (Cadotte et al. 2011), even with the high taxonomic variability found within the entire community. In any case, species composition was markedly different among sites (i.e. high levels of turnover, Supplementary material Appendix 1 Table A3) suggesting that species differed in other environmental preferences or niche requirements, beyond the primary abiotic filters previously mentioned. One possible reason is that alternative ecophysiological traits, others than the employed in this study, could be mediating the response of the community to fine-scale environmental filters (Kraft et al. 2015,

Magaña-Ugarte et al. 2019). For example, freezing resistance (Sierra-Almeida et al. 2009, Pescador et al. 2016) or efficiency in belowground resource acquisition (Körner et al. 1991) are critical traits for alpine plants rarely addressed in community ecology. The consideration of such traits could probably lead to significant differences between the observed FD and their null expectations and so, different ecological strategies related to environmental variations along the abiotic gradients would emerge. Another explanation would be related to the possible existence of a relevant intra-specific trait variation. For example, Blanco-Pastor et al. (2019) in a study of orophilous species in Sierra Nevada found significant correlation both between genetic diversity of the four species studied and between genetic diversity and topographic complexity. In the same way, intraspecific trait variability may be responding to the biotic and abiotic constraints considered in our null models but, our analyses, standing on the average trait values for each species are unable to detect that response.

Ecological assembly processes leave identifiable signals in trait diversity

In contrast to simple randomization tests, the linear mixed model analysis of null model deviations revealed the effects of different assembly processes on the diversity of functional traits. The larger and significant differences among the SES of the stochastic and deterministic null models for seed mass and leaf thickness suggest a certain role for niche-based assembly in this Pyrenean fellfield. The smaller diversity of observed seed mass, in comparison to the expectations of the stochastic model, and its similarity to the expectations of the independence model, support our first hypothesis. These results suggest that co-occurring species in this alpine community are more functionally similar than expected by chance due to small-scale abiotic filtering. Some studies of grassland communities have found that species appeared to be filtered according to their seed mass (Franzén 2004, Schamp et al. 2011), although the opposite pattern in seed mass has also been reported as the result of the divergence of successful regeneration strategies (Viard-Crétat et al. 2011). Our results suggest that the abiotic filtering can be related to some of the abiotic variables considered in the independence model. Furthermore, these results indicate a joint response of the species to the abiotic filtering which would be reflected in a pattern of species co-occurrence. Seed mass is strongly related to establishment and colonization (Pakeman et al. 2008, Pérez-Harguindeguy et al. 2013). The peculiar abiotic conditions of these alpine fellfields (i.e. shallow soils, cryoturbated, resource-poor and buried under rock debris) could be exerting a filter on safe-site acquisition which in turn could profoundly affect the community structure (Chambers et al. 1991, Azcárate et al. 2002). Thus, this fellfield could be only colonized by species of similar dispersal and establishment ability which would be mediated by seed mass (Tackenberg and Stöcklin 2008).

The high deviation of the observed leaf thickness FD from the expectations if the stochastic null model may result from the

influence of limiting similarity that prevents coexisting species from being too similar (MacArthur and Levins 1967, Stubbs and Wilson 2004). Facilitation usually dominates the plant to plant interaction networks in alpine systems (Pescador et al. 2014, Danet et al. 2018, Losapio et al. 2018, Navarro-Cano et al. 2019), and plays a critical role in the assembly of alpine communities (Callaway et al. 2002, Anthelme et al. 2014). Its effect usually is reflected in the diversity of traits related to resource exploitation (Schöb et al. 2012). Even if competition became more important due to the collapse of facilitative interactions (Michalet et al. 2006, Maestre et al. 2009), plant communities would tend to be functionally diverse which would reflect the prevalence of niche differentiation (Kraft et al. 2008). Nevertheless, the fact that this pattern fades away after controlling the effect of the abiotic factors casts doubts on the idea that biotic interactions are necessarily responsible of this functional pattern. An alternative explanation would be that the divergence in leaf thickness represents the effect of fine-scale spatial heterogeneity which could promote coexistence of functionally different species exploiting contrasted niches (Siefert 2012, Scherrer et al. 2019).

One of the most striking results of our study was the coincidence in the discrepancies between the observed and the expected FD of vegetative height for the three models. This significantly lower diversity remained even after accounting for the effects of topographic (i.e. elevation, slope) and soil variables in the independence model. Some authors have interpreted the convergence in plant height as a result of cold- and resource-mediated abiotic processes (Pellissier et al. 2010, Bernard-Verdier et al. 2012, de Bello et al. 2012, Spasojevic and Suding 2012), but none of the environmental variables considered in our independence model seem to account for this convergence. In addition, this alpine community had also lower trait diversity than expected by co-occurrence processes, indicating a minor role of weaker–competitor exclusion or competitiveness among functionally similar species (Chesson 2000, Pescador et al. 2019, Scherrer et al. 2019). In any case, other factors not accounted for in the independence model could be also involved in this result. For example, wind exposure could be behind the functional convergence pattern exhibited in some high-mountain communities (Wilson 1959, Spasojevic and Suding 2012, Takahashi and Tanaka 2016). Although elevation could be a proxy for wind exposure (Choler et al. 2001, Tackenberg and Stöcklin 2008), sometimes this relationship does not occur (Körner 2007). For instance, in low elevations experiencing a long snow-free period, wind can be particularly damaging for plant species precisely due to this lack of snow-cover protection (Choler 2005, Bruun et al. 2006). Convergence in plant height could also be due to the effect of grazing. These fellfields are extensively grazed by a semi free-ranging livestock (Aldezabal et al. 1999) which may selectively filter species based on the height of plant species (Díaz et al. 2001, Deléglise et al. 2011, Dainese et al. 2015).

Overall, we found no differences between SES generated by the independence and co-occurrence models. This result is in line with Ronk et al. (2016) which using similar modelling approaches, species co-occurrence (i.e. beals smoothing) and species distribution (SDM) models, provided similar local species assemblages (dark diversity sensu Pärtel et al. 2013) across Europe. However, several studies have found substantial differences in the species assemblages simulated by these two approaches (de Bello et al. 2016b, Karger et al. 2016). The similar SES for the independence and co-occurrence models suggest that the effect of biotic interactions and responses to abiotic variables are indistinguishable at the local scale of our community quadrats, agreeing with the delimited vegetation units found in this alpine fellfield (i.e. phytosociological associations: Aldezabal et al. 1999, Benito 2005, Ninot et al. 2007).

In summary, our results showed that the diversity of plant functional traits within rich, local plant communities (i.e. with similar taxonomic composition and physiognomy) can be explained by the same assembly mechanisms which have been considered at larger environmental scales and involving very different vegetation types. Some authors have suggested that niche processes would not prevail at such fine spatial scales (Chase 2014). However, we found that for several functional traits, the observed functional diversity was different from the expected under chance while similar to the expected from the implicit consideration of fine-scale abiotic variations and plant to plant interactions. The opposite patterns of leaf thickness and seed mass diversity, also supported the idea that several trait-based processes are simultaneously driving community assembly at this ecological scale (Weiher et al. 1998). Classic randomization tests, even based on the simplest null models (i.e. random), and with liberal constraints (i.e. equiprobable species frequency) were unable to detect significant functional structures in our community. Our proposed approach, consisting in fitting linear mixed models to standardized effect sizes of different, hierarchically complex null models, allowed to reveal the effects of deterministic assembly processes responsible of shaping the locally observed assemblages from a habitat-specific species pool.

Data availability statement

All data and R code used in the analyses are available on the Dryad digital repository (https://doi.org/10.5061/dryad.qrfj6q5d7) (López-Angulo et al. 2020b).

(equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – original draft (equal). **Marcelino de la Cruz**: Conceptualization (equal); Formal analysis (equal); Supervision (equal); Writing – review and editing (equal). **David Pescador**: Data curation (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Ana Sánchez**: Data curation (equal); Methodology (equal); Writing – review and editing (equal). **Adrián Escudero**: Conceptualization (lead); Funding acquisition (lead); Investigation (equal); Methodology (lead); Project administration (lead); Supervision (lead); Writing – review and editing (equal).

Conflicts of interest – The authors declare no conflicts of interest.

Permit – Permission to sample in our study area was given by the Ordesa-Monte Perdido National Park.

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