Disentangling the processes driving plant assemblages in mountain grasslands across spatial scales and environmental gradients

Scherrer, Daniel; orcid.org/0000-0001-9983-7510; University of Lausanne, Department of Ecology and Evolution; daniel.scherrer@unil.ch, UNIL-Sorge, Lausanne

Mod, Heidi K.; orcid.org/0000-0001-7800-2688; University of Lausanne, Department of Ecology and Evolution; heidi.mod@unil.ch

Pottier, Julien; UCA, INRA, VetAgro Sup, UMR Ecosystème Prairial, 63000 Clermont-Ferrand, France; julien.pottier@inra.fr

Litsios-Dubuis, Anne; Bureau A.MAibach Sàrl & University of Lausanne, Department of Ecology and Evolution; anne.dubuis@gmail.com

Pellissier, Loïc; ETH Zürich, Department of Environmental Systems Science & University of Lausanne, & Swiss Federal Research Institute WSL, 8903 Birmensdorf, Switzerland; loic.pellissier@usys.ethz.ch

Vittoz, Pascal; orcid.org/0000-0003-4218-4517; University of Lausanne, Faculty of geosciences and environment, Institute of Earth Surface Dynamics; pascal.vittoz@unil.ch

Götzenberger, Lars; The Czech Academy of Sciences, Institute of Botany; lars.goetzenberger@gmail.com

Zobel, Martin; University of Tartu, Department of Botany; martin.zobel@ut.ee

Guisan, Antoine; University of Lausanne, Department of Ecology and Evolution & Institute of Earth Surface Dynamics; antoine.guisan@unil.ch

Abstract

1. Habitat filtering and limiting similarity are well-documented ecological assembly processes that hierarchically filter species across spatial scales, from a regional pool to local assemblages. However, information on the effects of fine-scale spatial partitioning of species, working as an additional mechanism of coexistence, on community patterns is much scarcer.
2. In this study, we quantified the importance of fine-scale spatial partitioning, relative to habitat filtering and limiting similarity in structuring grassland communities in the western Swiss Alps. To do so, 298 vegetation plots (2 m × 2 m) each with five nested subplots (20 cm × 20 cm) were used for trait-based assembly tests (i.e., comparisons with several alternative null expectations), examining the observed plot and subplot level α-diversity (indicating habitat filtering and limiting similarity) and the among-subplot β-diversity of traits (indicating fine-scale spatial partitioning). We further assessed variations in the detected signatures of these assembly processes along a set of environmental gradients.
3. We found habitat filtering was the dominating assembly process at the plot level with diminished effect at the subplot level, whereas limiting similarity prevailed at the subplot level with weaker average effect at the plot level. Plot-level limiting similarity was positively correlated with fine-scale partitioning, suggesting that the trait divergence resulted from a combination of competitive exclusion between functionally similar species and environmental micro-heterogeneities. Overall, signatures of assembly processes only marginally changed along environmental gradients, but the observed trends were more prominent at the plot than at the subplot scale.

Synthesis: Our study emphasises the importance of considering multiple assembly processes and traits simultaneously across spatial scales and environmental gradients to understand the complex drivers of plant community composition.

Keywords: community assembly, environmental gradient, habitat filtering, limiting similarity, niche differentiation, spatial partitioning, trait convergence, trait divergence

Introduction

Community assembly is assumed to work as a hierarchy of constraints with potentially varying strengths at different scales (Keddy, 1992; Zobel, 1997; Belyea & Lancaster, 1999; Lortie et al., 2004; McGill, 2010). Community dynamics and structure are therefore the outcome of a succession of filters that limit the set of potentially coexisting species from larger pools. This concept integrates many mechanisms of species coexistence (Chesson, 2000; Barot & Gignoux, 2004; Wilson, 2011). However, empirical investigations addressing actual coexistence in nature have shown little consensus over the years (Miles, Schmidt & Van der Maarel, 1988; Diaz, Cabido & Casanoves, 1998; Firth & Crowe, 2010; Mason, de Bello, Doležal & Lepš, 2011; Götzenberger et al., 2012; Concepción et al., 2017; Conti, de Bello, Lepš, Acosta & Carboni, 2017; Price et al., 2017), despite the prime importance for realistic forecasts of current and future communities (Guisan & Rahbek, 2011; D'Amen, Rahbek, Zimmermann & Guisan, 2017). More research is required to detect and disentangle the signatures of assembly processes based on assemblages observed at different scales.

When focusing on local plant communities at fine spatial scales (i.e., excluding the roles of phylogeographic and dispersal assembly filters), many studies provide evidence of habitat filtering, an assembly process that allows only the species exhibiting suitable convergent traits to coexist in particular environmental conditions (Watkins & Wilson, 2003; Firth & Crowe, 2010; Chalmandrier et al., 2017; Conti et al., 2017). Although habitat filtering is often implicitly linked to the physical constraints of the environment, the habitat is also defined by its biotic components, including competitors. Therefore, the convergence of traits at the community level may also be driven by the exclusion of weaker competitors by the stronger ones (Bengtsson, Fagerstrom & Rydin, 1994; Chesson, 2000; Mayfield & Levine, 2010; Kunstler et al., 2012). However, when plant competition is at work, the coexistence of species can be empowered by mechanisms that counteract competitive exclusion (Chesson, 2000; Barot & Gignoux, 2004; Wilson, 2011): Opposite to the trait *convergence* caused by habitat filtering, trait *divergence* results from the fact that species must differentiate to compete for different resources (corresponding to different α-niche attributes; Stubbs & Wilson, 2004; Wilson & Stubbs, 2012), usually resulting in a range of distinct traits in the community (MacArthur & Levins, 1967; Johansson & Keddy, 1991; Wilson, 2011; D'Andrea & Ostling, 2016). Such trait divergence is therefore expected to limit the trait similarity of coexisting species through α-niche differentiation (Wilson, 2011; Götzenberger et al., 2012). Simultaneous functioning of these counteracting processes (i.e., habitat filtering and limiting similarity) is assumed to be enabled by hierarchical organisation (Weiher & Keddy, 1995; Holdaway & Sparrow, 2006; Bernard-Verdier et al., 2012): abiotic constraints are expected to be more effective at coarser scales than plant interactions, whereas resource competition should mostly work at finer “neighbourhood” scales (Huston, 1999).

In addition to habitat filtering and limiting similarity, both assuming that communities are spatially homogeneous, assemblages of plant species may be driven by within community spatial partitioning (Amarasekare, 2003). Such processes account for the heterogeneous nature of communities and may be endogenous (e.g., generated by ecology of the plants themselves; Tilman, 1994; Pacala & Levin, 1997) or exogenous (e.g., generated by environmental micro-heterogeneities or disturbances; Conti et al., 2017; Price et al., 2017). Spatial partitioning is at the core of several mechanisms promoting species coexistence (Bolker, 2003; Barot & Gignoux, 2004; Adler, Fajardo, Kleinhesselink & Kraft, 2013). An example of coexistence mechanisms promoted by endogenous heterogeneity is the competition/colonisation trade-off (Levins & Culver, 1971) in which better colonisers escape competitive exclusion because they can occupy patches that are not yet occupied by the better competitors (e.g., Wildová, Wild & Herben, 2007; Moora, Opik, Zobel & Zobel, 2009). Additionally, environmental heterogeneities are well recognised to develop at a wide range of scales (Levin, 1992), including the very fine ones of the rhizosphere (Raynaud & Leadley, 2004; Scherrer, Schmid & Körner, 2011). Although they cannot be considered as a mechanism of coexistence *sensu stricto* (Wilson, 2011), such environmental heterogeneities still increase opportunities for species to co-occur.

Combined endogenous and exogenous fine-scale spatial heterogeneities are expected to segregate plant functional syndromes leading to fine-scale spatial niche partitioning (Amarasekare, 2003; Conti et al., 2017; Price et al., 2017).

Whereas the roles of different assembly processes are expected to vary in relation to spatial scale, they may also vary along environmental gradients (Mason et al., 2011; Carboni et al., 2014; Mudrák et al., 2016; Chalmandrier et al., 2017; Bowman & Swatling-Holcomb, 2018). Based on the hypotheses related to stress gradients, abiotic constraints would be expected to be decisive for co-occurrences under harsh environmental conditions, such as in cold and dry areas, whereas competition would define species assemblages in more productive habitats (Louthan, Doak & Angert, 2015). Conversely, the role of spatial partitioning should be emphasised in environments prone to patchiness in vegetation and spatial heterogeneity (Amarasekare, 2003; Stark, Lehman, Crawford, Enquist & Blonder, 2017). Variations in importance of different assembly processes along environmental gradients demonstrate that interpretations derived from one habitat cannot necessarily be generalised to communities elsewhere. Thus, quantifying the role of different assembly processes across different spatial scales and along environmental gradients is essential for better understanding community assembly (Weiher et al., 2011; Conti et al., 2017).

In this study, we aimed to disentangle the signatures of different processes defining local plant assemblies (summarised in Table 1) across spatial scales (plots of 2 m × 2 m and subplots of 20 cm × 20 cm) and environmental gradients. Our analyses were based on a nested sampling design to record the within-community heterogeneity of vegetation (Fig. 1), including information on plant functional traits combined with environmental data in abiotic habitats. We applied different null models for trait reshuffling to assess the importance of habitat filtering (interpreted from trait convergence) and limiting similarity (interpreted from trait divergence) at two different spatial scales (i.e., plot and subplot level) and spatial partitioning among subplots (i.e., interpreted from β-diversity of traits within each plot). We further assessed the variations in the investigated assembly processes along environmental gradients.

Materials and Methods

Data collection

The study area covers approximately 700 km^2 of a mountain region located in the western Swiss Alps (46°23′ N, 7°05′ E). This region is characterised by a large elevation gradient with strong variation in climatic, edaphic and land use factors. A set of 298 plots of 2 m × 2 m, each with five nested subplots of 20 cm × 20 cm, were distributed across non-forested areas within the study area from 820 to 3045 m a.s.l. according to a stratified-random sampling (using elevation, slope and aspect as strata) designed to evenly cover the range of grassland habitat conditions (Fig. 1). At the 2 m plot scale, the cover of different plant species was estimated as modified ordinal classes (Braun-Blanquet, 1964), which were then subsequently converted to percentage cover values: 0 = absent; r = 0.01 %; + = 0.2 %; 1 = 3 %; 2 = 15 %; 3 = 37.5 %; 4 = 62.5 %, 5 = 87.5 % (Pottier et al., 2013). At the 20 cm subplot level, the percentage cover of species was visually estimated in the field. All the field data were collected during the peak vegetation period between June and August 2009, starting from lower elevation sites and moving to higher elevation sites.

Plant trait information was collected from a previous study (Dubuis et al. 2013) for the 244 most frequent and locally abundant species (of 722 vascular plant species recorded in total). Four traits associated with the performance of plant species during the persistence phase of their life cycle (Westoby, Falster, Moles, Vesk & Wright, 2002; Wright et al., 2004) were measured (hereafter, growth traits): average vegetation height (VH in cm), which is associated with the ability of a plant to compete for light, and specific leaf area (SLA in mm^2 mg^{-1}), leaf dry matter content (LDMC in mg mg^{-1}) and leaf nitrogen content (LNC in % of dry leaf mass), which indicate the resource-use strategy of a species (Wilson, Thompson & Hodgson, 1999; Reich, 2014). These traits were measured for 4 to 20 individuals (generally 10) per species within the study area, evenly distributed within the bioclimatic ranges of the species as defined in Pottier et al. (2013). Trait measurements followed the basic recommendations of Cornelissen et al. (2003) and are detailed in Dubuis et al. (2013). For the details on trait data, see Supplementary material Appendix 1 Fig. A1.

For the trait-based detection of assembly processes, we discarded the plots in which trait-assigned species accounted for less than 80 % of the relative vegetation cover resulting in 269 plots for the final analyses. With the threshold of 80 %, most of the plots were retained for the analyses (e.g., a 95 % threshold would have retained only 147 plots).

The spatial variation of different assembly processes was examined against the environmental conditions of each plot. Based on preliminary analyses, elevation (m a.s.l.), growing degree-days (GDD; average of 1961-1990 with a 0 °C threshold), moisture index over the growing season (average values of 1961-1990 from June to August) and topographic position (positive values express convex topographies such as ridges, peaks, and exposed sites, whereas negative values indicate concave surfaces such as valley bottoms or lower ends of slopes) were chosen as the most influential predictors (see Supplementary material Appendix 1 Fig. A2). These variables were extracted from digital maps at a 25 m × 25 m resolution following Zimmermann and Roberts (2001).

Detecting the signatures of assembly processes

The detection of assembly processes was based on a trait-based approach and the comparison of observed patterns against patterns derived from null models. All analyses were conducted in R 3.4.1 (R Core Team, 2017; see Appendix 4 for details of the packages and functions used).

Habitat filtering and limiting similarity were tracked at both plot and subplot levels to examine scale dependency of these processes. Habitat filtering was inferred in the case of convergence of growth traits in which observed within-plot (or within-subplot) functional diversity was lower than that expected under null assembly. Correspondingly, limiting similarity was inferred in the case of divergence of growth traits in which observed within-plot (or within-subplot) functional diversity was greater than that expected under null assembly. Fine-scale spatial partitioning was inferred from spatial segregation of growth traits among subplots within each plot in which the β-component of functional diversity was greater than that under a null assembly. We measured plot and subplot functional diversity using a modified version of the α-Rao quadratic entropy index following de Bello, Lavergne, Meynard, Lepš and Thuiller (2010). This metric is based on the functional dissimilarity among species weighted by their abundance. The β-component of functional diversity within each plot was measured with the β-Rao quadratic entropy index (de Bello et al., 2010).

We considered five different representations of trait diversity: one multidimensional space considering the four growth traits simultaneously (multidimensional space combining all growth traits, CGT), and four one-dimensional spaces each consisting of one separate growth trait. All traits were log transformed and standardised (for details, see Supplementary material Appendix 1 Fig. A1).

A critical aspect of testing for assembly processes is the use of an appropriate null model that focuses only on the ecological mechanisms under study (Harvey, Colwell, Silvertown & May, 1983; Gotelli & Ulrich, 2012; Götzenberger et al., 2016). Detecting habitat filtering or limiting similarity requires testing whether the trait values of species make a difference in terms of community structuring. In this respect, we built null models in which trait values of a species were reshuffled as a unit (i.e., all traits of one species, hereafter called trait unit) among species to prevent unrealistic/unobserved combinations of traits and to preserve fundamental trade-offs between traits (Mouillot, Mason &

Wilson, 2007; Hardy, 2008). With this approach, the species abundance patterns and species richness of plots and subplots were fixed, as were the species frequencies among the plots and subplots. Therefore, this reshuffling procedure also fixed the frequency of the functional syndromes over the study area. The range of trait units considered for this reshuffling procedure differed when seeking the signature of habitat filtering or limiting similarity. Whereas the tests of habitat filtering considered the total range of trait units (i.e., based on all species recorded in the study area) at the plot level and the local range of trait units (i.e., based on all species recorded in a plot) at the subplot level, the tests of limiting similarity were based on a restricted range of trait unit values. For limiting similarity, only trait units falling into the observed range of trait values were considered, which allowed detection of limiting similarity independent of habitat filtering (Bernard-Verdier et al., 2012). For example, if the observed range of vegetation height in a plot or a subplot was 10-50 cm, only trait values of the total (for plot level analysis) or local plot range (for subplot analysis) between 10 and 50 cm were considered. Using different species pool sources for trait units, habitat filtering and limiting similarity could be detected for a given plot/subplot simultaneously.

An additional question is whether the reshuffling of trait units among species should be free or constrained allowing only the trait units of species with similar abundances (i.e., vegetation cover) to be reshuffled. To test whether reshuffling had any effect on our results, we ran three different null-models for habitat filtering, limiting similarity and fine-scale spatial partitioning: (1) model allowing trait units to be reshuffled freely independent of abundances; (2) model only allowing trait units to be reshuffled within predefined abundance classes (see Appendix 2 for more details; Hardy, 2008; Wilson & Stubbs, 2012); and (3) model constraining the reshuffling by weights according to the differences in abundance between species (i.e., reshuffling between two species with similar abundances is much more likely than between species with highly different abundances; see Appendix 3 for more details). Because the results of these three null models were similar, we only report the results for the first one here. Detailed descriptions and all results of the other two null models can be found in Appendices 2 and 3.

The null models were run 10,000 times for each test. Based on our null models, we then calculated the standard effect size (SES) of α-Rao or β-Rao for each plot and subplot as

$$SES_{Rao} = (Rao_{plot} - \mu_{Rao_{nm}})/\sigma_{Rao_{nm}}$$

where Rao_{plot} is the observed α-/β-Rao and $\mu_{Rao_{nm}}$is the mean and $\sigma_{Rao_{nm}}$is the standard deviation of α-/β-Rao of the null model simulations. With negative SES of α-Rao for the habitat filtering test, the functional diversity was lower than that expected under the null assembly (i.e., signal of habitat filtering). Conversely, positive SES of α-Rao for the limiting similarity test indicated that the functional diversity was higher than that expected under the null assembly (i.e., signal of limiting similarity). Positive SES of β-Rao for the spatial partitioning test indicated that plant traits were spatially segregated among subplots within a plot.

To test whether an overall effect of habitat filtering or limiting similarity occurred at the plot and subplot levels, and whether the effect was significantly different between these spatial scales, we used a Wilcoxon test comparing α-Rao at the plot level and the mean α-Rao at the subplot level (i.e., the mean of the five subplots nested within a plot). To test for an overall effect of fine-scale partitioning, we used a Wilcoxon test of the β-Rao among subplots.

Analysing changes in assembly processes along environmental gradients

To explore potential changes in the strength of habitat filtering and limiting similarity (at the plot and subplot levels) and spatial partitioning processes (among subplots) along environmental gradients (elevation, GDD, moisture index, topographic position), generalised linear models (GLM) for the SES (plot/subplot α-Rao, subplot β-Rao) of growth traits were fitted. Because we were not interested in building a single meaningful and accurate statistical model per assembly process but in interpreting the variation along environmental gradients, we fitted one model for each assembly process and environmental factor. Environmental factors were provided to the models as second order polynomials, and the optimal model was selected based on stepwise AIC. Because all of the strong environmental gradients in the study area were highly correlated with elevation (Pearson correlations: GDD = -0.99, moisture index = 0.88 and topographic position = 0.59; see Supplementary material Appendix 1 Fig. A2 for details), only the results for elevation as the principal stress gradient are reported in the main manuscript.

Results

The relative importance of assembly processes

The mean SES of α-Rao with total trait range reshuffling was significantly lower than zero at the plot level ($p < 0.01$, Wilcoxon test) for all growth traits except LDMC, but not at the subplot level (Fig. 2). This result indicated the predominance of habitat filtering at the coarse spatial scale of 4 m². The mean SES of α-Rao with restricted trait range reshuffling was significantly greater than zero for all growth traits (except VH at the plot level) at both spatial scales ($p < 0.01$, Wilcoxon test) but was significantly higher at the subplot level ($p < 0.01$, Wilcoxon test), indicating the predominance of limiting similarity at the fine spatial scale of 0.04 m² (Fig. 2). Trait convergence from the total range of trait values was strongest for VH and LNC, whereas trait divergence with trait reshuffling restricted to the observed range of the local plot/subplot was strongest for SLA and LDMC. Based on comparison of SES of α-Rao values with total and restricted trait range reshuffling, habitat filtering and limiting similarity at the plot level were negatively linked, indicating that these two processes acted as opposing forces (i.e., plots with strong habitat filtering showed weak limiting similarity, and plots with weak habitat filtering showed strong limiting similarity; $R^2 \approx 0.8$; Fig. 3), despite the independent null-tests. These functional patterns were not related to plot species richness (Fig. 3).

Overall, SES of β-Rao among subplots did not deviate from zero (Fig. 2). However, 3.3 to 10.3 % (depending on the studied trait) of the plots showed much greater β-Rao than that expected under null assembly, indicating that fine-scale spatial partitioning was a relevant process in our study area. Most importantly, SES β-Rao among subplots was significantly positively correlated with plot level SES α-Rao with restricted trait range reshuffling (Fig. 4), indicating strong connection of limiting similarity at the plot level with within plot (i.e., among subplots) spatial partitioning. Neither process was linked to species richness of a plot (Fig. 4).

Assembly processes along environmental gradients

Of the four growth traits (i.e., community weighted mean of the plots), only vegetative height (R^2 = 0.6) and SLA (R^2 = 0.42) varied with elevation, whereas LNC and LDMC were largely independent of elevation (R^2 < 0.15; Fig. 5). Overall, the explanatory power of environmental gradients (i.e., elevation) for SES α-Rao with total trait range reshuffling (i.e., habitat filtering; R^2 = 0.05-0.26) and with restricted trait range reshuffling (i.e., limiting similarity; R^2 = 0.02-0.17) at the plot level was weak and negligible at the subplot level (R^2<0.04; Fig. 5; for more detailed results on the other environmental gradients, see Supplementary material Appendix 1 Fig. A3). Our results for the CGT (combined growth traits) showed that habitat filtering was strongest in productive low elevation habitats; whereas limiting similarity was strongest in cold climates at high elevations. These signals were mostly driven by only two traits, with habitat filtering by SLA (R^2 = 0.26) and limiting similarity by VH (R^2 = 0.17). Nevertheless, habitat filtering for VH remained the strongest assembly process observed, although the importance was relatively constant with elevation (Fig. 5). Fine-scale spatial partitioning did not show any significant signal along environmental gradients (R^2 < 0.02; Fig. 5 and Supplementary material Appendix 1 Fig. A3).

Discussion

Variations of assembly processes with scale and traits

Our study revealed the signatures of several assembly processes across different spatial scales, with habitat filtering (interpreted from trait convergence) the dominant effect at the large scale (i.e., among plots) and limiting similarity (interpreted from trait divergence) the dominant effect at the fine scale (i.e., within a plot). Consistent with the literature (Weiher & Keddy, 1995; Holdaway & Sparrow, 2006, Götzenberger et al., 2012), we found a strong overall signal of habitat filtering for three of four growth traits (not LDMC) at the plot level and no or only a weak signal at the subplot level. In contrast to habitat filtering, limiting similarity was detected at both spatial scales with stronger effects for all growth traits at the subplot level.

At the subplot scale (0.04 m^2), limiting similarity acting at the neighbourhood scale within herbaceous plant communities was the dominant assembly process indicating species competition at fine scales (van der Maarel & Sykes, 1993; Purves & Law, 2002; Reitalu et al., 2008). However, we also detected trait divergence at the plot scale indicating that competition effects might act not only at centimetre but also at metre scales in grassland communities. Additionally, the plot level trait divergence could result from spatial partitioning processes. This interpretation was indeed supported by the positive correlation between plot level limiting similarity and spatial partitioning, which is a pattern that was also found in a recent study conducted by Conti et al. (2017). Consequently, similar to Mayfield and Levine (2010), who demonstrated that trait convergence could be due to different mechanisms, our results indicated that trait divergence could also be due to different mechanisms operating at different scales.

Despite the positive relationship between plot level trait divergence and SES of β-Rao, we detected fine-scale spatial partitioning of plant functional traits less frequently than habitat filtering and limiting similarity. Nevertheless, even if the size of our plots (4 m²) was sufficiently small to assume spatial homogeneity of the investigated environmental factors, we might still encounter either biologically generated micro-heterogeneities (e.g., very short-distance dispersal and vegetative reproduction) or fine-scale patchiness in other environmental factors (e.g., edaphic factors, spatially restricted disturbances). The observed spatial partitioning further suggests that the metacommunity concept should be accounted for at very fine scales in future studies (e.g., Kneitel & Chase, 2004; Leibold et al., 2004; Alexander et al., 2012; Laliberté, Norton, Scott & Mason, 2013). This could be accomplished, for example, by combining our approach based on β-diversity patterns and fine-scale measurements of the physical environment (Conti et al., 2017; Stark et al., 2017) with spatially explicit tests (Siefert 2012).

Additionally, our results revealed that assembly processes worked on different traits with habitat filtering mostly observed for VH and LNC and limiting similarity for SLA and LDMC. These results corroborated the observation of a strong decrease in VH with elevation: apart from the length of the growing season, fertilised lowland grasslands select tall species able to compete for light, whereas alpine/nival landscapes select strongly for small stature plants with thermic decoupling from atmospheric conditions (Körner, 2003). LNC varied across habitats depending on environmental conditions, with plants with high LNC selected for at high elevations in natural environments (Han, Fang, Reich, Ian Woodward & Wang, 2011). We also found high LNC values at low elevations, presumably related to farming-based fertilisation. By contrast, SLA and LDMC are mostly associated with the ability to compete for nutrients (Wilson et al., 1999) and therefore are expected to show trait divergence (i.e., limiting similarity).

Here, we only used four growth traits, but other traits are also expected to show strong patterns of habitat filtering (e.g., leaf form or anatomy, flower pollination, diaspore morphology; Pellissier, Fournier, Guisan & Vittoz, 2010) or limiting similarity (e.g., root depth; Cornwell & Ackerly, 2009). Indeed, recent studies concentrating on functional diversity reveal a tendency to combine traits into one functional space (e.g., in multi-traits; Cornwell, Schwilk & Ackerly, 2006; Laughlin, 2014; Carmona, de Bello, Mason & Leps, 2016). However, with this approach, or by concentrating only on one or few traits, important mechanisms depicting trait patterns to underlying assembly processes can be hidden (Mason et al., 2011; Conti et al., 2017). To discriminate between different sources of fine-scale spatial partitioning, one should consider more traits related to plant regenerative strategies and ability to pre-empt or explore space. In perennial grasslands in which regeneration is mostly vegetative, a signature of fine-scale spatial partitioning could therefore be detected by trait divergence of clonal traits/syndromes (Moora et al., 2009; Pottier & Evette, 2011; Klimešová & Herben, 2015).

Although null model approaches are widely used and tested in studies of community assembly, their outcomes, similar to any other observational method, do not imply causation. The ecological interpretation that trait convergence is driven by habitat filtering and that divergence results from competition is certainly an over-simplification (HilleRisLambers, Adler, Harpole, Levine & Mayfield, 2012). For example, competitive exclusion can also result in trait convergence, by clustering species of similar competitive ability (similar height, shade tolerance, or other competition related traits; Chesson, 2000; Mayfield & Levine, 2010; Herben & Goldberg, 2014). Although we attributed some of the changes in functional diversity to such processes, overall, the exclusion of weaker competitors was unlikely: SES values for all traits were higher at the subplot level than those at the plot level. If competitor exclusion was effective at the subplot scale, the opposite should be observed.

For community assembly studies that compare observed trait diversity patterns with randomised ones, another concern is that simultaneously acting processes may lead to random patterns, which could mask the processes that create opposing patterns (e.g., trait convergence vs. divergence) (HilleRisLambers et al., 2012; Götzenberger et al., 2016). Nonetheless, the deviation of SES value distributions from 0 to either positive or negative values can at least indicate the prevailing process acting for a given trait at a given scale. Moreover, in this study, we particularly addressed the simultaneously acting processes of habitat filtering and limiting similarity using different species pools over which trait data were randomised (Figures 3 and 4, see also de Bello et al., 2012). Although such an approach still relies on the assumption that habitat filtering and limiting similarity can be interpreted from convergence and divergence, an indication of those sites in which simultaneous processes are potentially at play is nevertheless provided.

Despite the limitations of the null model and more generally of the empirical-approach, our study supports the conclusion of Münkemuller et al. (2012) that the inference of assembly processes from diversity patterns is more relevant when based on a set of criteria rather than on a unique one. Münkemuller et al. (2012) combined α- and β-indices for taxonomic, functional and phylogenetic diversity metrics. Here, we further highlighted the importance of combining several species pool definitions and tests of assembly rules at nested scales.

Variations of assembly processes along environmental gradients

Although we found a strong influence of elevation on the mean trait values themselves (i.e., VH and SLA), the strength of the processes creating different trait dispersion patterns only varied marginally with elevation. VH showed the strongest overall signal of habitat filtering but was relatively constant across elevation ($R^2 = 0.07$). This result indicated that a strong selection for VH (trait convergence) occurred at both high and low elevations, but for opposite sizes (i.e., small at high elevation, tall at low elevation). Dominance of the best competitors for light in productive habitats is often reported (Perronne, Munoz, Borgy, Reboud & Gaba, 2017), and the advantage of short stature in the alpine/nival belt (high elevation) to allow thermic decoupling from atmospheric conditions is well documented (Körner, 2003). For SLA, the primary influence of elevation on habitat filtering was for selecting high SLA species towards lower elevations and low SLA species towards higher elevations. At low elevation, the detected pattern was most likely not a direct effect of the physical environment but an indirect effect of favourable conditions in productive habitats favouring species with quick growth and high SLAs (e.g., *Crepis biennis, Holcus lanatus*; de Bello et al., 2013). This trait convergence due to biotic interactions (i.e., competitive exclusion of weaker traits; Chesson, 2000; Mayfield & Levine, 2010) might also explain why we observed less habitat filtering at higher than at lower elevations (see also Mudrák et al., 2016). This finding further highlights the difficulty of null model approaches to distinguish trait convergence resulting from abiotic (i.e., physiological limits) and biotic (i.e., competitive exclusion) habitat filtering, because both processes might work simultaneously and on the same traits (HilleRisLambers et al., 2012).

The signal of limiting similarity was only weakly linked to elevation with the strongest effect visible on SLA and VH for which limiting similarity increased with elevation. This result is apparently contradictory to the stress-gradient hypothesis, which predicts an increase in limiting similarity in productive lowlands in which plant competition is expected to be more intense (Bertness & Callaway, 1994; He, Bertness & Altieri, 2013; Chamberlain, Bronstein & Rudgers, 2014; Chalmandrier et al., 2017). An alternative interpretation, as presented above, is that the observed patterns of trait divergence at the plot level were linked to habitat heterogeneity within plots rather than the direct effects of competition-driven limiting similarity. With increasing elevation, the plots (4 m^2) were likely to become environmentally more heterogeneous (soil depth, percentage of rock cover) leading to the coexistence of species with varying SLA and VH, such as cushion plants, succulents (on rocks) and grasses. Nevertheless, spatial partitioning did not vary significantly with any of the environmental factors tested. This suggested that fine-scale partitioning might result from a variety of mechanisms (endogenous/exogenous heterogeneity) that did not necessarily respond similarly to environmental variations, or that the analyses and underlying data could not capture the true drivers of spatial partitioning within the communities.

Our findings support the general view that topo-climatic conditions act as strong drivers of community assemblages in a mountain range, such as the one studied here, with implications for spatial modelling of plant species assemblages (Guisan & Rahbek, 2011; D'Amen et al., 2015; D'Amen et al., 2017; D'Amen et al., 2018). However, mountain grasslands are often used as grazing grounds for livestock, with intensity varying in relation to elevation. In previous studies, added fertilisation and mowing has led to observed trait convergence and divergence depending on the attribute examined and the type/intensity of treatment (Mason et al., 2011; Bloor & Pottier, 2014; Louault et al., 2017). Therefore, further investigations of assembly processes in mountain grasslands should also integrate descriptors of land management.

Conclusions

The dominating assembly process at the coarse scale across elevation was habitat filtering, particularly for VH, selecting for small plants at high and tall plants at low elevation sites. Limiting similarity was detected at plot and subplot levels, particularly for resource-acquisition traits (SLA and LDMC), but was stronger and dominating at the subplot level. Plot level trait divergence occurred particularly at high elevations, presumably indicating spatial partitioning rather than limiting similarity as the underlying mechanism. Our findings suggest that approaches studying and modelling assembly processes, such as stacked species distribution models (S-SDMs; Dubuis et al. 2011) or mechanistic models of community assembly (Shipley, Vile & Garnier 2006, Demalach, Zaady, Weiner & Kadmon 2016, Lohier, Jabot, Weigelt, Schmid, B. & Deffuant 2016), should consider the interaction of biotic and abiotic factors along environmental gradients, particularly when examining communities at fine spatial scales. Further, the detection of spatial partitioning in this study calls for high-resolution abiotic data to allow understanding and forecasting of community and biodiversity patterns at fine scales. Overall, our study highlights the importance of analysing the roles of several assembly processes simultaneously across different spatial scales and in combination with abiotic gradients to allow a deeper understanding of the complex interaction of abiotic and biotic drivers shaping natural grassland communities.

Acknowledgements

This study was initiated in the framework of the ECOCHANGE project funded by the Sixth European Framework Programme (Grant GOCE-CT-2007-036866) and of the BIOASSEMBLE project funded by the Swiss National Science Foundation (SNF Grant Nr 31003A-125145 to AG) and finalised during the SESAM'ALP project (SNF grant Nr. 31003A-1528661 to AG). IUT 20-28 and Globaalmuutuste Tippkeskus financed MZ. Computations were performed at the Vital-IT Centre for high-performance computing at the Swiss Institute of Bioinformatics (http://www.vital-it.ch).

AG and JP, with LG and MZ, conceived the initial idea. AG, ALD, LP, JP and PV led the collection of the data. JP and DS analysed the data. HM, DS and JP led the writing, with all authors contributing and helping in interpreting the results.

Data accessibility

All species, environmental and trait data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2dq836f (Guisan et al., 2018).

References

Adler, P. B., Fajardo, A., Kleinhesselink, A. R. & Kraft, N. J. B. (2013). Trait-based tests of coexistence mechanisms. Ecology Letters, 16(10), 1294-1306. doi: 10.1111/ele.12157

Alexander, H. M., Foster, B. L., Ballantyne, F., Collins, C. D., Antonovics, J. & Holt, R. D. (2012). Metapopulations and metacommunities: Combining spatial and temporal perspectives in plant ecology. Journal of Ecology, 100(1), 88-103. doi: 10.1111/j.1365-2745.2011.01917.x

Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: A synthesis. Ecology Letters, 6(12), 1109-1122. doi: 10.1046/j.1461-0248.2003.00530.x

Barot, S. & Gignoux, J. (2004). Mechanisms promoting plant coexistence: Can all the proposed processes be reconciled? Oikos, 106(1), 185-192. doi: 10.1111/j.0030-1299.2004.13038.x

Belyea, L. R. & Lancaster, J. (1999). Assembly rules within a contingent ecology. Oikos, 86(3), 402-416. doi: 10.2307/3546646

Bengtsson, J., Fagerstrom, T. & Rydin, H. (1994). Competition and coexistence in plant communities. Trends in Ecology & Evolution, 9(7), 246-50. doi: 10.1016/0169-5347(94)90289-5

Bernard-Verdier, M., Navas, M.-L., Vellend, M., Violle, C., Fayolle, A. & Garnier, E. (2012). Community assembly along a soil depth gradient: Contrasting patterns of plant trait convergence and divergence in a mediterranean rangeland. Journal of Ecology, 100(6), 1422-1433. doi: 10.1111/1365-2745.12003

Bertness, M. D. & Callaway, R. (1994). Positive interactions in communities. Trends in Ecology & Evolution, 9(5), 191-193. doi: 10.1016/0169-5347(94)90088-4

Bloor, J. M. G. & Pottier, J. (2014). (eds P. Mariotte & P. Kardol), Grazing and spatial heterogeneity: Implications for grassland structure and function. *Gransslands biodiversity and conservation in a changing world* pp. 135-162. Nova Science Publishers, Inc., New York.

Bolker, B. M. (2003). Combining endogenous and exogenous spatial variability in analytical population models. Theoretical Population Biology, 64(3), 255-270. doi: 10.1016/S0040-5809(03)00090-X

Bowman, W. D. & Swatling-Holcomb, S. (2018). The roles of stochasticity and biotic interactions in the spatial patterning of plant species in alpine communities. Journal of Vegetation Science, 29(1), 25-33. doi: 10.1111/jvs.12583

Braun-Blanquet, J. (1964). Pflanzensoziologie: Grundzüge der vegetationskunde. doi:

Carboni, M., de Bello, F., Janecek, S., Dolezal, J., Hornik, J., Leps, J., . . . Klimesova, J. (2014). Changes in trait divergence and convergence along a productivity gradient in wet meadows. Agriculture Ecosystems & Environment, 182, 96-105. doi: 10.1016/j.agee.2013.12.014

Carmona, C. P., de Bello, F., Mason, N. W. & Leps, J. (2016). Traits without borders: Integrating functional diversity across scales. Trends in Ecology & Evolution, 31(5), 382-94. doi: 10.1016/j.tree.2016.02.003

Chalmandrier, L., Münkemüller, T., Colace, M.-P., Renaud, J., Aubert, S., Carlson, B. Z., . . . Avolio, M. (2017). Spatial scale and intraspecific trait variability mediate assembly rules in alpine grasslands. Journal of Ecology, 105(1), 277-287. doi: 10.1111/1365-2745.12658

Chamberlain, S. A., Bronstein, J. L. & Rudgers, J. A. (2014). How context dependent are species interactions? Ecology Letters, 17(7), 881-890. doi: 10.1111/ele.12279

Chesson, P. (2000). Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics, 31, 343-366. doi: 10.1146/annurev.ecolsys.31.1.343

Concepción, E. D., Götzenberger, L., Nobis, M. P., Bello, F., Obrist, M. K. & Moretti, M. (2017). Contrasting trait assembly patterns in plant and bird communities along environmental and human-induced land-use gradients. Ecography, 40(6), 753-763.

Conti, L., de Bello, F., Lepš, J., Acosta, A. & Carboni, M. (2017). Environmental gradients and micro-heterogeneity shape fine scale plant community assembly on coastal dunes. Journal of Vegetation Science.

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., . . . Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany, 51(4), 335-380. doi: 10.1071/Bt02124

Cornwell, W. K., Schwilk, L. D. & Ackerly, D. D. (2006). A trait-based test for habitat filtering: Convex hull volume. Ecology, 87(6), 1465-71.

Cornwell, W. K. & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal california. Ecological Monographs, 79(1), 109-126. doi: 10.1890/07-1134.1

D'Amen, M., Dubuis, A., Fernandes, R. F., Pottier, J., Pellissier, L. & Guisan, A. (2015). Using species richness and functional traits predictions to constrain assemblage predictions from stacked species distribution models. Journal of Biogeography, 42(7), 1255-1266. doi: 10.1111/jbi.12485

D'Amen, M., Rahbek, C., Zimmermann, N. E. & Guisan, A. (2017). Spatial predictions at the community level: From current approaches to future frameworks. Biological Reviews, 92(1), 169–187. doi: 10.1111/brv.12222

D'Amen, M., Mateo, R. G., Pottier, J., Thuiller, W., Maiorano, L., Pellissier, L., . . . Swenson, N. (2018). Improving spatial predictions of taxonomic, functional and phylogenetic diversity. Journal of Ecology, 106(1), 76-86. doi: 10.1111/1365-2745.12801

D'Andrea, R. & Ostling, A. (2016). Challenges in linking trait patterns to niche differentiation. Oikos, 125(10), 1369-1385. doi: 10.1111/oik.02979 de Bello, F., Lavergne, S., Meynard, C. N., Lepš, J. & Thuiller, W. (2010). The partitioning of diversity: Showing theseus a way out of the labyrinth. Journal of Vegetation Science, 21(5), 992-1000. doi: 10.1111/j.1654-1103.2010.01195.x

de Bello, F., Price, J. N., Munkemuller, T., Liira, J., Zobel, M., Thuiller, W., . . . Partel, M. (2012). Functional species pool framework to test for biotic effects on community assembly. Ecology, 93(10), 2263-73. doi: 10.1890/11-1394.1

de Bello, F., Lavorel, S., Lavergne, S., Albert, C. H., Boulangeat, I., Mazel, F. & Thuiller, W. (2013). Hierarchical effects of environmental filters on the functional structure of plant communities: A case study in the french alps. Ecography, 36(3), 393-402. doi: 10.1111/j.1600-0587.2012.07438.x

DeMalach, N., Zaady, E., Weiner, J., Kadmon, R. & Cahill, J. (2016). Size asymmetry of resource competition and the structure of plant communities. Journal of Ecology, 104(4), 899-910. doi: 10.1111/1365-2745.12557

Diaz, S., Cabido, M. & Casanoves, F. (1998). Plant functional traits and environmental filters at a regional scale. Journal of Vegetation Science, 9(1), 113-122. doi: 10.2307/3237229

Dubuis, A., Pottier, J., Rion, V., Pellissier, L., Theurillat, J.-P. & Guisan, A. (2011). Predicting spatial patterns of plant species richness: A comparison of direct macroecological and species stacking modelling approaches. Diversity and Distributions, 17(6), 1122-1131. doi: 10.1111/j.1472-4642.2011.00792.x

Dubuis, A., Rossier, L., Pottier, J., Pellissier, L., Vittoz, P. & Guisan, A. (2013). Predicting current and future spatial community patterns of plant functional traits. Ecography, 36(11), 1158-1168. doi: 10.1111/j.1600-0587.2013.00237.x

Firth, L. B. & Crowe, T. P. (2010). Competition and habitat suitability: Small-scale segregation underpins large-scale coexistence of key species on temperate rocky shores. Oecologia, 162(1), 163-174. doi: 10.1007/s00442-009-1441-7

Gotelli, N. J. & Ulrich, W. (2012). Statistical challenges in null model analysis. Oikos, 121(2), 171-180. doi: 10.1111/j.1600-0706.2011.20301.x

Guisan, A. & Rahbek, C. (2011). Sesam - a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. Journal of Biogeography, 38(8), 1433-1444. doi: 10.1111/j.1365-2699.2011.02550.x

Guisan, A., Litsois-Dubuis, A., Pottier, J., Pellisser, L. & Vittoz, P. (2018) Data from: Disentangling the processes driving plant assemblages in mountain grasslands across spatial scales and environmental gradients. Dryad Digital Repository. doi: 10.5061/dryad.2dq836f

Götzenberger, L., de Bello, F., Bråthen, K. A., Davison, J., Dubuis, A., Guisan, A., . . . Zobel, M. (2012). Ecological assembly rules in plant communities - approaches, patterns and prospects. Biological Reviews of the Cambridge Philosophical Society, 87(1), 111-127. doi: 10.1111/j.1469-185X.2011.00187.x

Götzenberger, L., Botta-Dukát, Z., Lepš, J., Pärtel, M., Zobel, M. & Bello, F. (2016). Which randomizations detect convergence and divergence in trait-based community assembly? A test of commonly used null models. Journal of Vegetation Science, 27(6), 1275-1287.

Han, W. X., Fang, J. Y., Reich, P. B., Ian Woodward, F. & Wang, Z. H. (2011). Biogeography and variability of eleven mineral elements in plant leaves across gradients of climate, soil and plant functional type in china. Ecology Letters, 14(8), 788-796. doi: 10.1111/j.1461-0248.2011.01641.x

Hardy, O. J. (2008). Testing the spatial phylogenetic structure of local communities: Statistical performances of different null models and test statistics on a locally neutral community. Journal of Ecology, 96(5), 914-926. doi: 10.1111/j.1365-2745.2008.01421.x

Harvey, P. H., Colwell, R. K., Silvertown, J. W. & May, R. M. (1983). Null models in ecology. Annual Review of Ecology and Systematics, 14(1), 189-211. doi:10.1146/annurev.es.14.110183.001201

He, Q., Bertness, M. D. & Altieri, A. H. (2013). Global shifts towards positive species interactions with increasing environmental stress. Ecology Letters, 16(5), 695-706. doi: 10.1111/ele.12080

Herben, T. & Goldberg, D. E. (2014). Community assembly by limiting similarity vs. Competitive hierarchies: Testing the consequences of dispersion of individual traits. Journal of Ecology, 102(1), 156-166. doi: 10.1111/1365-2745.12181

HilleRisLambers, J., Adler, P. B., Harpole, W. S., Levine, J. M. & Mayfield, M. M. (2012). Rethinking community assembly through the lens of coexistence theory. Annual Review of Ecology, Evolution, and Systematics, Vol 43, 43(1), 227-248. doi: 10.1146/annurev-ecolsys-110411-160411

Holdaway, R. J. & Sparrow, A. D. (2006). Assembly rules operating along a primary riverbed–grassland successional sequence. Journal of Ecology, 94(6), 1092-1102. doi: 10.1111/j.1365-2745.2006.01170.x

Huston, M. A. (1999). Local processes and regional patterns: Appropriate scales for understanding variation in the diversity of plants and animals. Oikos, 86(3), 393-401. doi: 10.2307/3546645

Johansson, M. E. & Keddy, P. A. (1991). Intensity and asymmetry of competition between plant pairs of different degrees of similarity: An experimental study on two guilds of wetland plants. Oikos, 60(1), 27-34. doi: 10.2307/3544988

Keddy, P. A. (1992). Assembly and response rules: Two goals for predictive community ecology. Journal of Vegetation Science, 3(2), 157-164. doi: 10.2307/3235676

Klimešová, J. & Herben, T. (2015). Clonal and bud bank traits: Patterns across temperate plant communities. Journal of Vegetation Science, 26(2), 243-253. doi: 10.1111/jvs.12228

Kneitel, J. M. & Chase, J. M. (2004). Trade-offs in community ecology: Linking spatial scales and species coexistence. Ecology Letters, 7(1), 69-80. doi: 10.1046/j.1461-0248.2003.00551.x

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N. E., . . . Coomes, D. A. (2012). Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: Implications for forest community assembly. Ecology Letters, 15(8), 831-40. doi: 10.1111/j.1461-0248.2012.01803.x

Körner, C. (2003). Alpine plant life: Functional plant ecology of high mountain ecosystems. Springer Verlag.

Laliberté, E., Norton, D. A., Scott, D. & Mason, N. (2013). Contrasting effects of productivity and disturbance on plant functional diversity at local and metacommunity scales. Journal of Vegetation Science, 24(5), 834-842. doi: 10.1111/jvs.12044

Laughlin, D. C. (2014). The intrinsic dimensionality of plant traits and its relevance to community assembly. Journal of Ecology, 102(1), 186-193. doi: 10.1111/1365-2745.12187

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., . . . Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters, 7(7), 601-613. doi: 10.1111/j.1461-0248.2004.00608.x

Levin, S. A. (1992). The problem of pattern and scale in ecology: The robert h. Macarthur award lecture. Ecology, 73(6), 1943-1967. doi: 10.2307/1941447

Levins, R. & Culver, D. (1971). Regional coexistence of species and competition between rare species. Proceedings of the National Academy of Sciences of the United States of America, 68(6), 1246-1248. doi: 10.1073/pnas.68.6.1246

Lohier, T., Jabot, F., Weigelt, A., Schmid, B. & Deffuant, G. (2016). Predicting stochastic community dynamics in grasslands under the assumption of competitive symmetry. Journal of Theoretical Biology, 399, 53-61. doi: 10.1016/j.jtbi.2016.03.043

Lortie, C. J., Brooker, R. W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F. I. & Callaway, R. M. (2004). Rethinking plant community theory. Oikos, 107(2), 433-438. doi: 10.1111/j.0030-1299.2004.13250.x

Louault, F., Pottier, J., Note, P., Vile, D., Soussana, J.-F. & Carrère, P. (2017). Complex plant community responses to modifications of disturbance and nutrient availability in productive permanent grasslands. Journal of Vegetation Science, 28(3), 538-549. doi: 10.1111/jvs.12509

Louthan, A. M., Doak, D. F. & Angert, A. L. (2015). Where and when do species interactions set range limits? Trends in Ecology & Evolution, 30(12), 780-792. doi: 10.1016/j.tree.2015.09.011

MacArthur, R. & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. The American naturalist, 101(921), 377-385.

Mason, N. W. H., de Bello, F., Doležal, J. & Lepš, J. (2011). Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. Journal of Ecology, 99(3), 788-796. doi: 10.1111/j.1365-2745.2011.01801.x

Mayfield, M. M. & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters, 13(9), 1085-93. doi: 10.1111/j.1461-0248.2010.01509.x

McGill, B. J. (2010). Matters of scale. Science, 328(5978), 575-576. doi: 10.1126/science.1188528

McNickle, G. G., Lamb, E. G., Lavender, M., Cahill, J. F., Schamp, B. S., Siciliano, S. D., . . . Baltzer, J. L. (2018). Checkerboard score-area relationships reveal spatial scales of plant community structure. Oikos, 127(3), 415-426. doi: 10.1111/oik.04620

Miles, J., Schmidt, W. & Van der Maarel, E. (1988). Temporal and spatial patterns of vegetation dynamics. Springer.

Moora, M., Opik, M., Zobel, K. & Zobel, M. (2009). Understory plant diversity is related to higher variability of vegetative mobility of coexisting species. Oecologia, 159(2), 355-61. doi: 10.1007/s00442-008-1209-5

Mouillot, D., Mason, N. W. & Wilson, J. B. (2007). Is the abundance of species determined by their functional traits? A new method with a test using plant communities. Oecologia, 152(4), 729-37. doi: 10.1007/s00442-007-0688-0

Mudrák, O., Janeček, Š., Götzenberger, L., Mason, N. W. H., Horník, J., de Castro, I., . . . de Bello, F. (2016). Fine-scale coexistence patterns along a productivity gradient in wet meadows: Shifts from trait convergence to divergence. Ecography, 39(3), 338-348. doi: 10.1111/ecog.01723

Münkemüller, T., de Bello, F., Meynard, C.N., Gravel, D., Lavergne, S., Mouillot, D., Mouquet, N. & Thuiller, W. (2012). From diversity indices to community assembly processes: a test with simulated data. Ecography, 35, 468–480. doi: 10.1111/j.1600-0587.2011.07259.xPacala, S. W. & Levin, S. A. (1997). (ed^(eds D. Tilman & P. Kareiva), Biologically generated spatial pattern and the coexistence of competing species. *Spatial ecology: The role of space in population dynamics and interspecific interactions. Princeton university press, princeton, nj* pp. 204-232. Princeton, New Jersey., Princeton University Press,.

Pellissier, L., Fournier, B., Guisan, A. & Vittoz, P. (2010). Plant traits co-vary with altitude in grasslands and forests in the european alps. Plant Ecology, 211(2), 351-365. doi: 10.1007/s11258-010-9794-x

Perronne, R., Munoz, F., Borgy, B., Reboud, X. & Gaba, S. (2017). How to design trait-based analyses of community assembly mechanisms: Insights and guidelines from a literature review. Perspectives in Plant Ecology, Evolution and Systematics, 25(Supplement C), 29-44. doi: 10.1016/j.ppees.2017.01.004

Pottier, J. & Evette, A. (2011). Spatial pattern and process at the plant neighbourhood scale: Insights from communities dominated by the clonal grass elymus repens (l.) gould. Journal of Vegetation Science, 22(6), 973-982. doi: 10.1111/j.1654-1103.2011.01304.x

Pottier, J., Dubuis, A., Pellissier, L., Maiorano, L., Rossier, L., Randin, C. F., . . . Guisan, A. (2013). The accuracy of plant assemblage prediction from species distribution models varies along environmental gradients. Global Ecology and Biogeography, 22(1), 52-63. doi: 10.1111/j.1466-8238.2012.00790.x

Price, J., Tamme, R., Gazol, A., de Bello, F., Takkis, K., Uria-Diez, J., . . . Michalet, R. (2017). Within-community environmental variability drives trait variability in species-rich grasslands. Journal of Vegetation Science, 28(2), 303-312. doi: 10.1111/jvs.12487

Purves, D. & Law, R. (2002). Fine-scale spatial structure in a grassland community: Quantifying the plant’s-eye view. Journal of Ecology, 90(1), 121-129.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raynaud, X. & Leadley, P. W. (2004). Soil characteristics play a key role in modeling nutrient competition in plant communities. Ecology, 85(8), 2200-2214. doi: 10.1890/03-0817

Reich, P. B. (2014). The world-wide ‘fast–slow’ plant economics spectrum: A traits manifesto. Journal of Ecology, 102(2), 275-301. doi: 10.1111/1365-2745.12211

Reitalu, T., Prentice, H. C., Sykes, M. T., Lönn, M., Johansson, L. & Hall, K. (2008). Plant species segregation on different spatial scales in semi-natural grasslands. Journal of Vegetation Science, 19(3), 407-416. doi: 10.3170/2008-8-18381

Scherrer, D., Schmid, S. & Körner, C. (2011). Elevational species shifts in a warmer climate are overestimated when based on weather station data. International Journal of Biometeorology, 55(4), 645-54. doi: 10.1007/s00484-010-0364-7

Shipley, B., Vile, D. & Garnier E. 2006. From plant traits to plant communities: A statistical mechanistic approach to biodiversity. Science 314, 812-814.

Stark, J., Lehman, R., Crawford, L., Enquist, B. J. & Blonder, B. (2017). Does environmental heterogeneity drive functional trait variation? A test in montane and alpine meadows. Oikos, 126(11), 1650-1659. doi: 10.1111/oik.04311

Stubbs, W. J. & Wilson, J. B. (2004). Evidence for limiting similarity in a sand dune community. Journal of Ecology, 92(4), 557-567. doi: 10.1111/j.0022-0477.2004.00898.x

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. Ecology, 75(1), 2-16. doi: 10.2307/1939377

van der Maarel, E. & Sykes, M. T. (1993). Small-scale plant species turnover in a limestone grassland: The carousel model and some comments on the niche concept. Journal of Vegetation Science, 4(2), 179-188. doi: 10.2307/3236103

Watkins, A. J. & Wilson, J. B. (2003). Local texture convergence: A new approach to seeking assembly rules. Oikos, 102(3), 525-532. doi: 10.1034/j.1600-0706.2003.11630.x

Weiher, E. & Keddy, P. A. (1995). Assembly rules, null models, and trait dispersion: New questions from old patterns. Oikos, 74(1), 159-164. doi: 10.2307/3545686

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T. & Bentivenga, S. (2011). Advances, challenges and a developing synthesis of ecological community assembly theory. Philosophical Transactions of the Royal Society B: Biological Sciences, 366(1576), 2403-2413. doi: 10.1098/rstb.2011.0056

Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A. & Wright, I. J. (2002). Plant ecological strategies: Some leading dimensions of variation between species. Annual Review of Ecology and Systematics, 33(1), 125-159. doi: 10.1146/annurev.ecolsys.33.010802.150452

Wildová, R., Wild, J. & Herben, T. (2007). Fine-scale dynamics of rhizomes in a grassland community. Ecography, 30(2), 264-276. doi: 10.1111/j.0906-7590.2007.04756.x

Wilson, J. B. (2011). The twelve theories of co-existence in plant communities: The doubtful, the important and the unexplored. Journal of Vegetation Science, 22(1), 184-195. doi: 10.1111/j.1654-1103.2010.01226.x

Wilson, J. B. & Stubbs, W. J. (2012). Evidence for assembly rules: Limiting similarity within a saltmarsh. Journal of Ecology, 100(1), 210-221. doi: 10.1111/j.1365-2745.2011.01891.x

Wilson, P. J., Thompson, K. E. N. & Hodgson, J. G. (1999). Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. New Phytologist, 143(1), 155-162. doi: 10.1046/j.1469-8137.1999.00427.x

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., . . . Villar, R. (2004). The worldwide leaf economics spectrum. Nature, 428(6985), 821-827. doi: 10.1038/nature02403

Zimmermann, N. E. & Roberts, D. W. (2001). Final report of the mlp climate and biophysical mapping project. Swiss Federal Research Institute WSL/Utah State University, Birmensdorf, Switzerland/Logan, USA, 18(doi:

Zobel, M. (1997). The relative of species pools in determining plant species richness: An alternative explanation of species coexistence? Trends in Ecology & Evolution, 12(7), 266-9.

Table 1. List of the plant assembly processes that are hypothesised to drive community patterns. In this study, the coarse scale level refers to plots of 4 m^2 and the fine scale level to “subplots” each of 0.04 m^2 nested within the 4 m^2 plots (see Fig. 1). VH = vegetation height, SLA =specific leaf area, LDMC = leaf dry matter content, LNC = leaf nitrogen content, CGT = multidimensional space combining all growth traits.

Assembly hypothesis	**Short explanation of the underlying mechanisms**	**Expected pattern**	**Metric**	**Scale**	**Trait space(s) considered**
Habitat filtering	Only species sharing similar adaptation to cope with prevailing environmental conditions can co-occur.	Trait convergence	SES of α-Rao	Within plot and within subplot	No restriction of the total trait space of the study area is used. VH, SLA, LDMC, LNC and CGT
Limiting similarity	Species show limiting similarity (i.e., α-niche differentiation = differences in the traits related to the ways the species compete for a common resource) to coexist.	Trait divergence	SES of α-Rao	Within plot and within subplot	Restricted to the trait range of the plot/subplot VH, SLA, LDMC, LNC and CGT
Fine-scale spatial partitioning	Species coexist at the plot level because they segregate in space due to endogenous or exogenous spatial heterogeneity	Segregation of traits among subplots within a plot	SES of β-Rao	Among subplots of each plot	Restricted to the trait values measured for the species recorded in each plot VH, SLA, LDMC, LNC and CGT

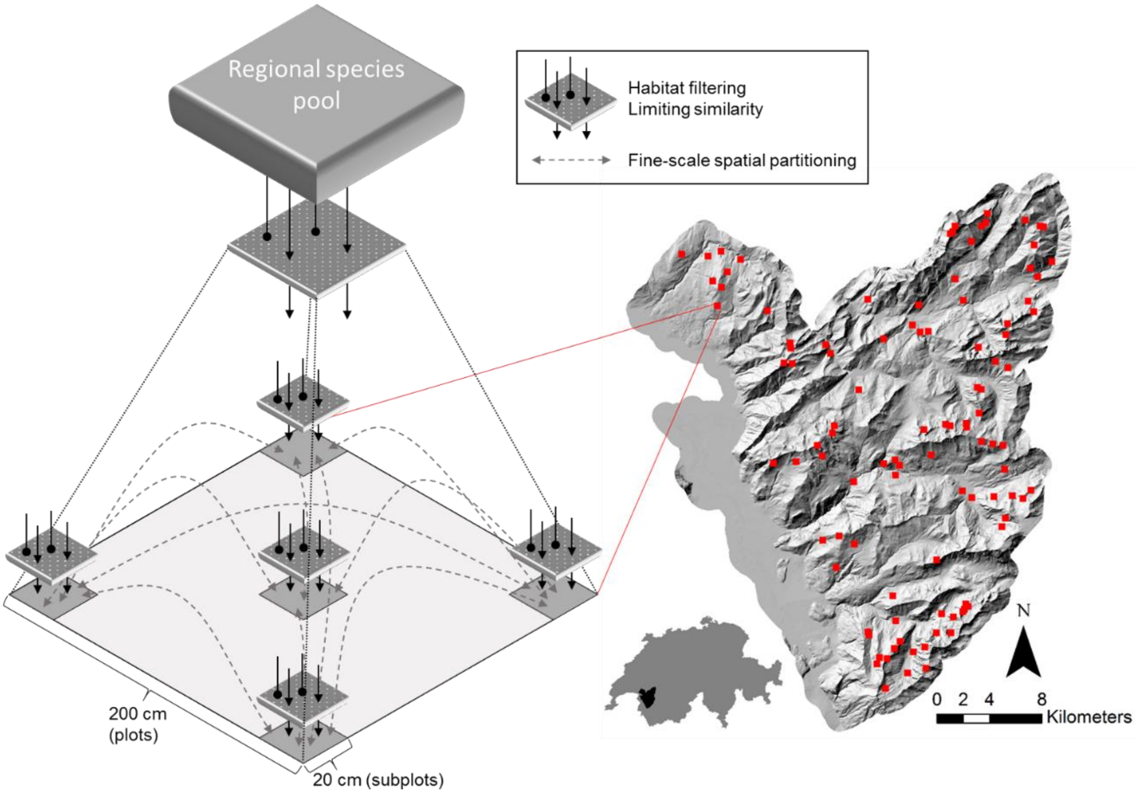

Figure 1. The general framework of the study was based on a nested sampling design to test for the signatures of different assembly processes. Habitat filtering and limiting similarity were analysed at two scales (2×2 m plots and 20×20 cm subplots) using null model approaches to compare observed trait structure with null expectations. The among subplots spatial partitioning process was analysed in each plot using a null model designed to test for spatial segregation of plant functional traits or syndromes.

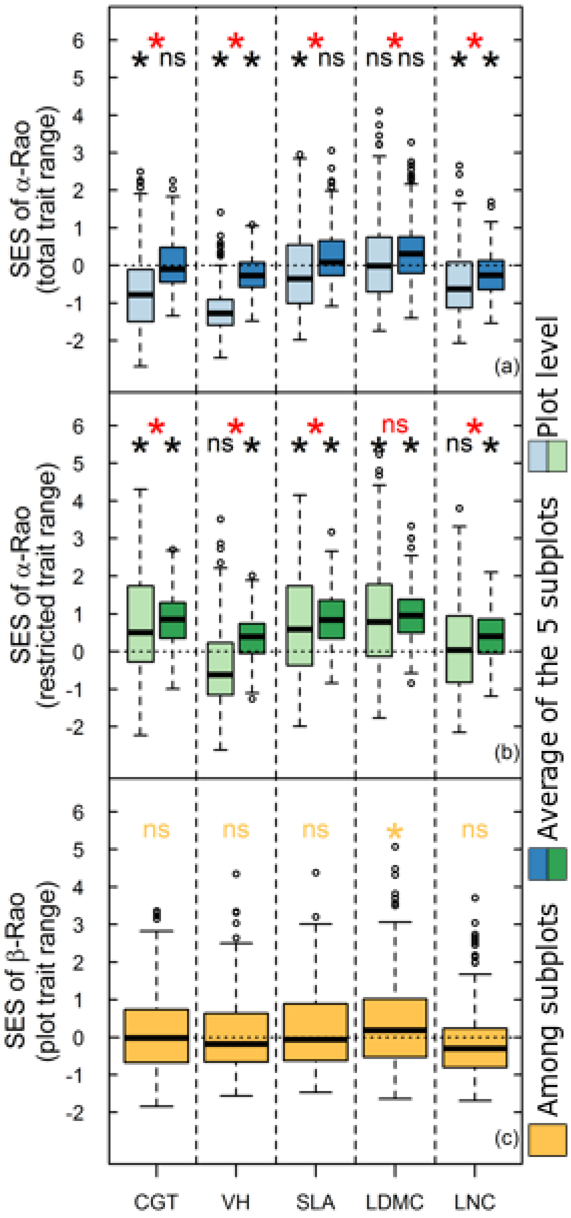

Figure 2. Distribution of SES of α-Rao at the plot level and average (of the five subplots) α-Rao at the subplot level for (a) total trait range (indicating habitat filtering) and (b) restricted trait range (indicating limiting similarity). (c) Distribution of SES of β-Rao among subplots (indicating fine-scale spatial partitioning). Black asterisks above a boxplot mark significant ($p < 0.01$) differences from zero, and red asterisks mark significant ($p < 0.01$) between plot and subplot level α-Rao. The boxes span from the 25th to the 75th percentile, and the whiskers indicate ± 2 SD. CGT= multidimensional space combining all growth traits, VH = Vegetation height, SLA = Specific leaf area, LDMC = Leaf dry matter content, LNC = Leaf nitrogen content, ns = Non significant.

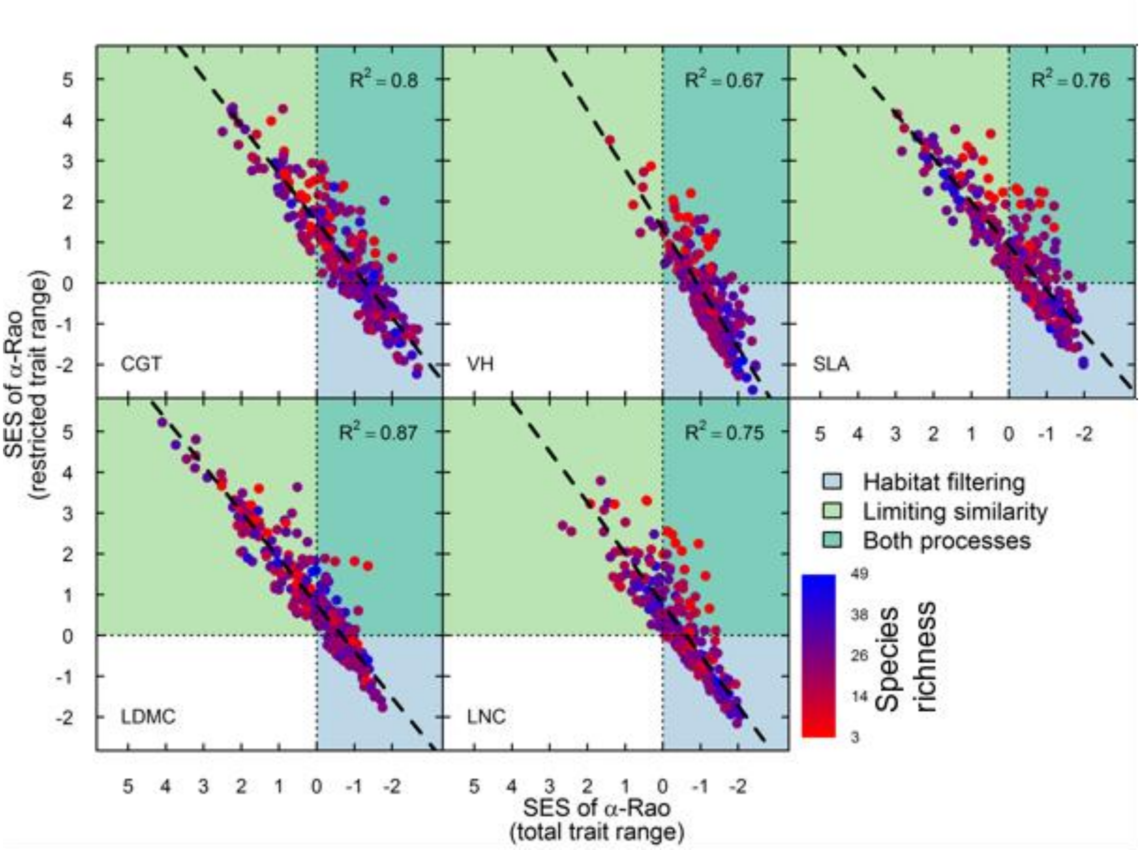

Figure 3. Correlation of strength of limiting similarity and habitat filtering measured by SES of α-Rao at the plot level. Different coloured areas indicate the dominant assembly process, and the colour gradient (red to blue) indicates the species richness of the plots. Please note that the x-axis (habitat filtering) is inversed, i.e., increasing effect to the right. See Fig. 2 for abbreviations.

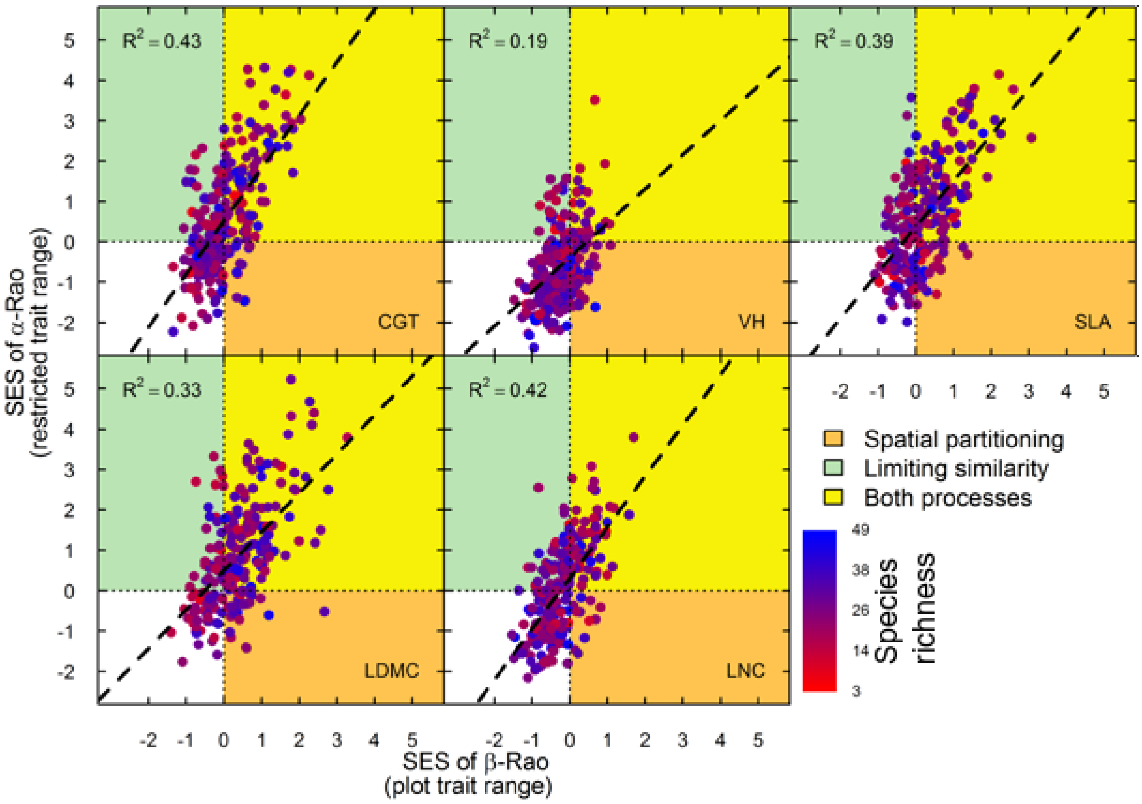

Figure 4. Correlation of strength of limiting similarity and spatial partitioning measured by SES of α-Rao at the plot level and SES of β-Rao among subplots. Different coloured areas indicate the dominant assembly process, and the colour gradient (red to blue) indicates the species richness of the plots. See Fig. 2 for abbreviations.

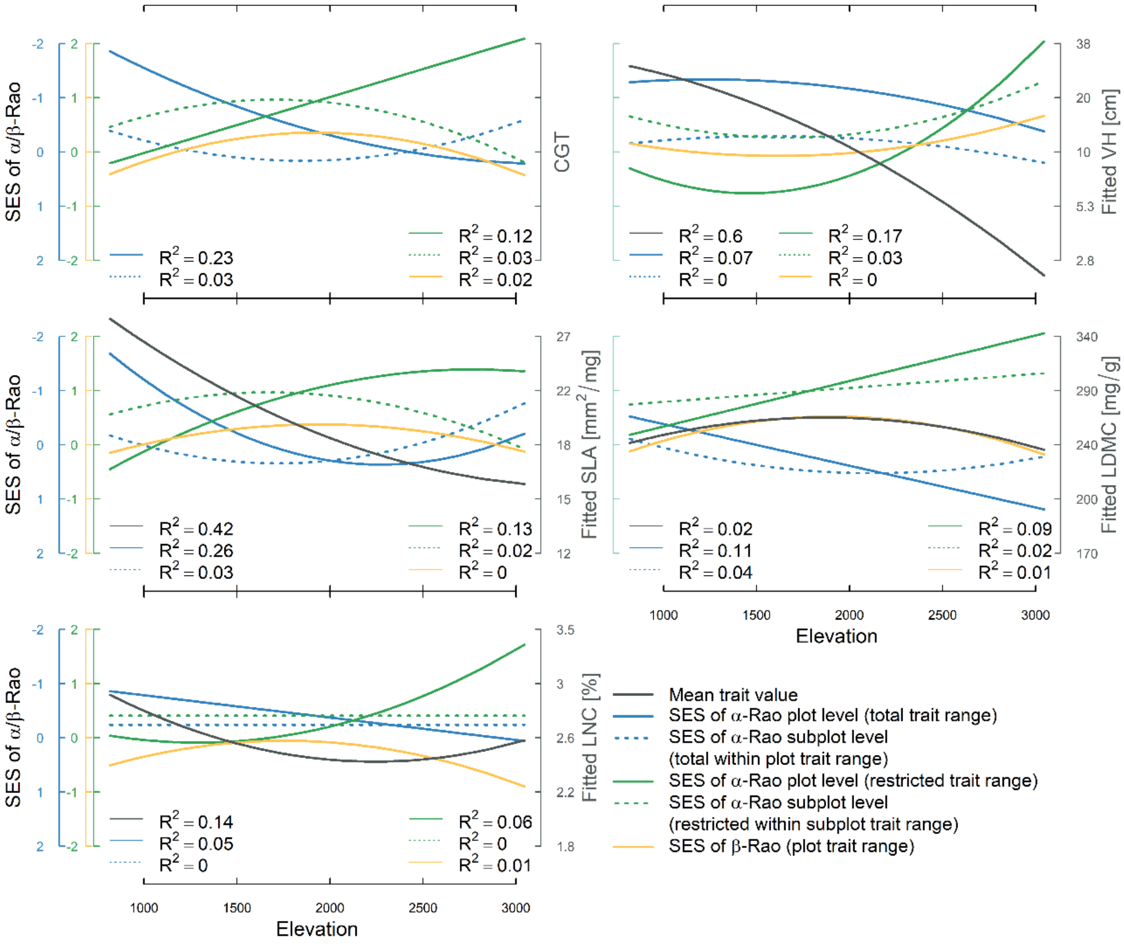

Figure 5. Generalised linear models fitted for different traits, habitat filtering, limiting similarity and spatial partitioning along the elevation gradient. Models were fitted as second-degree polynomials with stepwise AIC to select the best model. Please note that the y-axis for habitat filtering is inversed. See Fig. 2 for abbreviations.