Community assembly processes along a sub-Mediterranean elevation gradient: analyzing the interdependence of trait community weighted mean and functional diversity

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Abstract Community-weighted mean (CWM) and functional diversity (FD) describe the two aspects of plant communities' functional structure. While they have been often used separately to infer assembly processes, their covariation can actually provide useful insights into the prevalence of a particular assembly process over the other. We propose a framework where positive or negative covariation of these indices can be related to different assembly processes along an environmental gradient. We tested this framework in grassland communities along elevation gradient in Central Apennines by collecting species cover and traits of the most abundant species and calculating the effect size CWM and FD. We performed major axis regression for each effect size of CWM-FD relationship for different belts along the elevation gradient. The observation that Plant Height showed a positive CWM-FD relationship only under more stressful conditions indicates that there may be a tendency towards habitat filtering. Seed Mass showing positive covariation in each belt may indicate the presence of both habitat filtering and limiting similarity acting with different intensity depending on the environmental stress level. Negative covariation

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between CWM-Plant Height and Seed Mass-FD under less stress suggests biotic filter, while positive covariation between CWM-Plant Height and both Seed Mass and SLA FD under stressful conditions suggests the presence of habitat filtering. Ultimately, the relationship of CWM and FD may provide information on how different communities assemble along an environmental gradient. Moreover, combining the information of CWM with the FD and environmental stress level might help to identify the processes behind the same functional pattern.

Introduction

Elevation gradients are a natural laboratory for studying vegetation changes along environmental gradients (Schöb et al. 2013; Körner 2016) because of the rapid changes that can be observed in a relatively short distance and their impact on important biological processes (Michalet et al. 2014; Rosbakh et al. 2015; Körner 2016). In Mediterranean mountains, elevation gradients are quite complex as both temperature and precipitation increase along opposite directions, leading to a bell-shaped stress gradient (Mitrakos 1980; Linares and Tíscar 2010; Theurillat et al. 2011) that affects species assembly (Michalet et al. 2014). At lower elevation, summer water limitation selects only functionally similar species exhibiting aridity-adapted strategies (Pescador et al. 2015). Similarly, in the upper mountain sections, lower temperatures select only those functionally similar species with cold-adapted features (Dainese et al. 2012; de Bello et al. 2013). At intermediate elevations, abiotic conditions should be more benign (lower drought and higher temperatures) and biotic drivers such as competition may take the lead in defining species assemblages (Cornwell and Ackerly 2009). Identifying the processes that drive the assembly of plant communities along these environmental gradients is not always straightforward, but it is crucial for understanding the drivers of vegetation turnover in light of imminent global change (Sala et al. 2000). Over the years, researchers have identified several

mechanisms regulating species coexistence; the combination of these mechanisms and the community patterns that identify them are called assembly rules (Götzenberger et al. 2012). Indeed, researchers identify assembly processes on the basis of species patterns that can be observed. In particular, the study of functional patterns has proven useful for understanding such processes (Lavorel and Garnier 2002; Conti et al. 2017), shedding light on how species and communities respond to biotic and abiotic factors (Mason et al. 2011; Gross et al. 2013; Wellstein et al. 2014; Tardella et al. 2017; Scolastri et al. 2017).

Functional diversity (FD) quantify how dissimilar the coexisting species are within a community, and thus it is widely used to detect assembly rules (Botta-Dukát 2005; Laliberté and Legendre 2010). There has been a recent increase in the number of studies that implement FD together with complex null models in which the observed value is compared with randomly generated expected community values (de Bello 2012; Botta-Dukát 2018). Consensus has been reached on the use of standardized effect size of functional diversity (SES-FD) to quantify the magnitude of assembly processes (de Bello 2012; Botta-Dukát 2018). According to Gotelli and McCabe (2002), SES is calculated as $(I_{obs} - I_{sim})/\sigma_{sim}$, where I_{obs} is the observed value of the FD, I_{sim} is the mean of the expected FD and σ is the expected FD standard deviation. Positive SES values (> 0) indicate higher observed values than expected ("functional divergence"), while negative values indicate lower observed values than expected ("functional convergence") and values close to zero means random assembly pattern (de Bello 2012). Nevertheless, inferring processes from FD patterns is not so straightforward, as different processes can lead to the same functional pattern. Indeed, functional convergence may arise not only when abiotic factors filter only those species with a viable trait combination (habitat filtering; Keddy 1992; Cornwell and Ackerly 2009), but also when highly competitive species filter out weaker competitors (weaker competitor exclusion; Mayfield and Levine 2010; Lepš 2014). On the other hand, functional divergence may arise not only when negative biotic interactions constrain the niche overlap between coexisting species (limiting similarity; MacArthur and Levins 1967), but also when theoretically, nurse plants-created microsites were exploited by "facilitated species" bearing different sets of traits

(facilitation; Bertness and Callaway 1994; Valiente-Banuet and Verdú 2013; McIntire and Fajardo 2014; Navarro-Cano et al. 2016).

In addition to FD, the functional structure of a biological community is also described by community-weighted mean (CWM; Ricotta and Moretti 2011). CWM reflects the dominant trait value and is often used to quantify shifts in such values along different environmental conditions (Garnier et al. 2004; Chelli et al. 2019). CWM and FD are most often analysed in parallel (Dainese et al. 2012; de Bello et al. 2013; Gross et al. 2013; Nunes et al. 2017) even though it is widely recognized that they are mathematically related to one another (Ricotta and Moretti 2011). Indeed, when CWM approaches upper and lower bounds of the trait range, FD will necessarily decrease because only species with similar trait values (high or low, respectively) will be present, leading to a hump-shaped relationship (Dias et al. 2013). To our knowledge, their interdependence and the potential of this pairing for biological interpretation, have been largely unexplored (but see Vojtkó et al. 2017). In the present study, we propose a framework based on the interdependence of these two metrics that could help shed light on the most widely investigated assembly rules. In particular, we suggest that a framework combining null model-based approach, environmental conditions and CWM values may help to disentangle the processes behind the same FD pattern (convergence/divergence). We apply this framework to grassland communities along an elevation gradient as a surrogate of stress gradient, using traits regarding the Leaf-Height-Seed scheme (Westoby 1998). According to the literature, lower values of CWMs for Plant Height, SLA and Seed Mass are common in communities subjected to environmental stress such as frost (de Bello et al. 2013; Gross et al., 2013) or drought (Nunes et al. 2017).

We discerned alternative scenarios of CWM-FD relationships based on their SES values, pointing to different processes, according to the environmental condition and the biological meaning of the three traits analysed (Fig. 1):

1. *Positive covariation* would entail the shift from abiotic filtering to limiting similarity. In fact, under stress conditions we expect abiotic filters to filter the species that are able to survive in the community, thus leading to negative values of
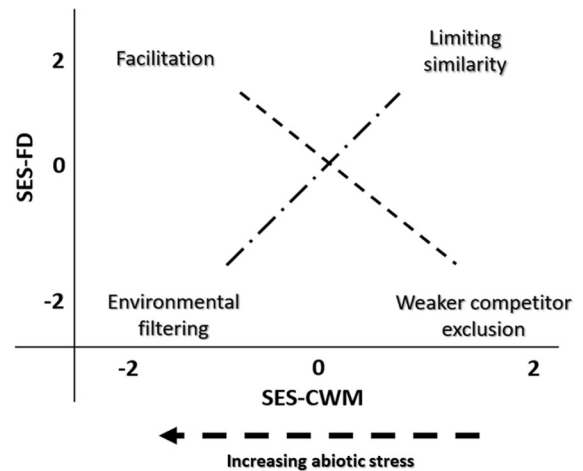

Fig. 1 Conceptual scheme summarizing the four hypothetical scenarios of SES-CWM and SES-FD pattern combinations for traits referred to the LHS scheme along a gradient of environmental intensity. Positive covariation, that is, variation of SES-CWM and SES-FD in the same direction, suggests a change in assembly rules from habitat filtering processes to limiting similarity with decreasing of stress. Negative covariation, that is, opposite variation of SES-CWM and SES-FD, suggested assembly rules from facilitation to weaker competitor exclusion with decreasing of environmental stress

SES for both FD and CWM. On the contrary, the presence of positive values of SES-FD and SES-CWM points to limiting similarity, which should be more dominant under less stressful environmental conditions (e.g. Dainese et al. 2012; de Bello et al. 2013; Gross et al. 2013; Nunes et al. 2017; Fig. 1).

2. *Negative covariation* would entail the shift from facilitation to weaker competitor exclusion. Negative values of SES-FD and positive values of SES-CWM would indicate the prevalence of hierarchical competition leading to weaker competitor exclusion, which we expect to find under less stressful environmental conditions (e.g. Mayfield and Levine 2010). In contrast, positive values of SES-FD and negative values of SES-CWM might indicate the prevalence of facilitation processes that are expected to be more often found under more stressful environmental conditions (Valiente-Banuet and Verdú 2013; Fig. 1).

This framework can also be applied between metrics based on different traits. In this case, we considered as an example the covariation between Plant Height CWM (SES-CWM$_H$) and SES-FD of the other

measured traits. Plant Height is involved in the response to resource availability and tolerance/avoidance of drought and frost (Nunes et al. 2017; Körner 2016), as it relates to competitive ability (Lepš 2014), and is a fundamental functional trait of plants (Westoby 1998). The trade-off between Plant Height and other traits has been previously investigated at the species level (see de Bello et al. 2012), but the relationship that Plant Height may have with the diversity of other traits at the community level has yet to be explored. As previous works found that leaf cover has both positive and negative effects on seed diversity, according to the climatic conditions (see Janeček and Lepš 2005), we also investigated the covariation between Plant Height and the diversity of SLA and Seed Mass. We expected that *positive* covariation between SES-CWM$_H$ and SES-FD of SLA or Seed Mass would indicate the prevalence of symmetrical competitive processes, ultimately driving the niche partitioning in resource use or reproductive strategies (positive SES-FD$_{SLA}$ or FD$_{SM}$, respectively) of coexisting species as competition for light becomes more intense under more benign environments; a *negative* covariation between SES-CWM$_H$ and SES-FD of SLA or Seed Mass would entail the prevalence of hierarchical competition (biotic filter or weaker competitor exclusion) as taller plants in the communities might act as a selective pressure, only allowing the coexistence of species with certain resource use and/or reproductive strategies. We focused only on stress avoidance to consider also the disturbance effect, since theoretical predictions about how disturbance regimes may affect assembly rules vary between studies, depending on the type, on the intensity and on the frequency of the disturbance regime, and also on the fact that disturbance is expected to affect species coexistence differently across biomes (Laliberté et al. 2013).

In consideration of the above, this research sought to determine the dominant assembly processes in plant communities along a sub-Mediterranean elevation gradient by analysing the relationship between SES-CWM and SES-FD metrics. In detail, our aims were to determine (i) the relationship between SES-CWMs and SES-FD can be used to discern assembly processes; (ii) there are changes in this relationship along an elevation gradient, *that is* , the dominant assembly process shifts along the gradient; (iii) there are changes in covariation between SES-CWM$_H$ and

SES-FD$_{SLA}$ or SES-FD$_{SM}$ along the elevation gradient.

Methods

Study area

We studied the vegetation along an elevation gradient on Monte Velino (2486 m a.s.l.), which is located in the Central Apennines (Abruzzo Region) in Italy. The massif is entirely composed of limestone (Cosentino et al. 2010). In terms of climate, the Velino massif is found in the Mediterranean region, and its bioclimate is sub-Mediterranean with a short summer drought period at low elevations and winter frost stress at higher elevations. Climate data were gathered from weather stations located in the area along the elevation gradient at regular intervals of 250 m (Table 1). We collected daily and monthly measurements of both temperature and precipitation, starting in May 2006. During the summer season (June–August), the mean temperature is around 17 °C at 1450 m a.s.l. and 8 °C at 2200 m, while the mean precipitation is around 212 mm and 213 mm, respectively. During the winter season (December-February), the mean temperature is around 10 °C at 1450 m a.s.l. and − 5 °C at 2200 m (Theurillat et al. 2011; Theurillat et al. unpubl.). The southern side of the Velino Massif has been logged for millennia, and the peak activity in the mid-19th century almost completely deforested the areas above 1200 m.a.s.l. For centuries, shepherds have grazed their livestock at the base of the mountain (below 1200 m. a.s.l.), but this activity has declined sharply beginning in the 1950s. Thus, secondary ungrazed dry grasslands with *Bromus erectus*, *Carex humilis*, *Globularia meridionalis* and *Sesleria juncifolia* dominate up to approximately 2000 m a.s.l. Above this elevation, the vegetation is mainly dominated by primary grassland including alpine elements such as *Silene acaulis* and *Potentilla crantzii* (Petriccione 1993). The summit of the study area belongs to the "Apennine high ecosystems" macrosites of the Long-Term Ecological Research (LTER) monitoring systems, where climatic and vegetation studies are carried out regularly (Malavasi et al. 2018; Rogora et al. 2018; Petriccione and Bricca 2019).

Table 1 Climatic characterization of the study area (Theurillat et al., unpublished data)

Termopluviometric station	1	2	3	4
Altitude (m a.s.l.)	1450	1700	1950	2200
T summer air (°C)	17.04	14.92	13.56	9.82
T winter air (°C)	1.0	− 0.99	− 1.37	− 4.76
MAT	8.64	6.52	5.50	2.06
Summer days (%)	33	23	13	2.5
Frost day (%)	71	80	88	98
P summer (mm)	212.84	204.64	218.04	211.96
PET summer (mm)	312.30	300.30	278.85	260.45
Aridity Index (P/PET)	0.68	0.68	0.78	0.81

T summer = mean values of temperature during summer season (June, July and August); P summer = sum of precipitations for summer season (June, July and August); PET summer = sum of potential evapotranspirations for summer season (June, July and August); P/PET = aridity index during the summer season (June, July and August); T winter = mean values of temperature during the winter season (December to February); MAT = mean annual temperature; summer days (%) = relative frequency of number of days in which the Tmax is > 25 °C during summer season; Frost days (%) = relative frequency of number of days in which the Tmin is < 0 °C during winter season (for indices see Oliver 2008)

Sampling of vegetation and functional traits

From May to August 2016, we revisited a selection of 84 plots (2 × 2 m) initially established in 2006 following a random stratified design, with a minimum distance of 200 m from each other to avoid pseudoreplication (for details see Theurillat et al. 2011). To minimize interplot environmental heterogeneity along the elevation gradient, in 2016, we only revisited plots that met four conditions. They had to be on open calcareous grassland with absence of domestic grazing, and in the same successional stage, that is, without shrubland species such as *Juniperus oxycedrus* and/or *Arctostaphylos uva-ursi*. Also, they had to be located in areas with a southwest aspect (227° ± 43°) and with the same slope values (33° ± 4°). This resulted in 45 plots positioned along the elevation gradient from 1325 m a.sl. to 2375 m a.s.l (Online Resources 1). For each plot, species presence was recorded, and species cover was visually estimated using the Braun-Blanquet method. Prior to analysis, these records were transformed to percentage values as follows: +: 0.1%, 1a: 2.5%, 1b: 5%, 2a: 10%, 2b: 20%, 3a: 31.25%, 3b: 43.75% 4a: 56.25%, 4b: 68.75%, 5a: 81.25% and 5b: 93.75%.

Since it is not practical to sample trait values for all species present in all plots, trait-based studies focus on the local species that are the most abundant in terms of plot cover (reaching 80%; see Pakeman and Quested 2007) or in terms of the whole dataset, that is, species pool cover (reaching 80%; see Májeková et al. 2016). In areas where there is a low turnover of dominant species along ecological gradients, it is possible to set trait sampling thresholds using the whole species pool (Swenson et al. 2011). Even though we observed low values of beta diversity (2.99 expressed as beta = gamma/mean alpha and calculated both on the regional scale and with Jost correction as recommended by de Bello et al. (2010)), we decided to use a more detailed trait sampling method by using different species pools along the gradient. We divided the elevation gradients into 4 belts of almost 250 m. The first section (1325–1575 m a.s.l.) had 9 plots; the second (1575–1825 m a.s.l.) 10; the third (1825–2075 m a.s.l.) 11; and the last section (2075–2375 m a.s.l.) 15. Then, we pooled together the cover values of each species of all the plots in each elevation belt and selected all those species whose relative cumulative cover reached 80% of the total vegetation cover in each elevation belt. The resulting sampled species accounted for 80% of the cover of almost all plots (Online Resource 1). For each species we measured the traits used in Westoby's leaf-height-seed (LHS) strategy scheme (Westoby 1998). For Plant Height (cm) and for SLA (mm^2/mg) at least 10 individuals were measured, and for Seed Mass (mg), we collected at least 2 seeds per individual from no fewer than 3 individuals. All the individuals were

gathered at the centre of each elevation belt, where the topographic factors of the plots were the same, and they were measured according to an internationally recognized standardized trait measuring protocol (Pérez-Harguindeguy et al. 2013). In total, we identified 26 species, 14 of which were dominant in more than one belt of the elevation gradient. This resulted in 52 mean trait values partitioned into 12 values for the first section, 11 for the second section, 12 for the third section and 17 for the last section (see Online Resource 2).

Data analysis

We used elevation as a proxy of the climatic gradient caused by changes in temperature and precipitation. In this sense, for the statistical analysis we divided all the elevation gradient into three belts with the same number of plots (n = 15), starting with the plot at the lowest elevation: the lowest belt was found to be characterized by higher aridity and lower frost intensity, the highest belt was characterized by lower aridity but higher frost intensity and the middle belt did not have conditions of particular climatic stress (see climatic features in Table 1).

Then, using species cover at plot level and trait values collected at the mid-point of each elevation belt (see Sampling of vegetation and functional traits), we computed for each plot the community-weighted mean (CWM; Garnier et al. 2004) and, as a measure of functional diversity, the functional dispersion (FD; Laliberté and Legendre 2010). CWM corresponds to the average trait value in a community weighted by the relative abundance of the species carrying each value (Garnier et al. 2004). FD quantifies the degree of functional dissimilarity within the community and is calculated as the weighted mean distance, in multidimensional trait space, of individual species from the weighted centroid of all species, where weights correspond to species relative abundances (Laliberté and Legendre 2010). The reliability of the trait sampling was checked (Online Resource 3) with the reduced FD function in the "traitor" package provided in Májeková et al. (2016). The CWM and FDis indices were computed with the dbFD function in the R package, "FD" version 1.0 (Laliberté et al. 2014).

To analyse whether CWM and FDis of each trait for each plot were different from random expectation, we applied "between-plot randomization" (sensu Botta-

Dukát and Czúcz 2016), creating a null model by reshuffling 999 times the trait values among the species in the whole dataset containing all of the local communities. This algorithm assumes a null model so that any species can occur in any local community with any abundance (and thus the dispersal effect is kept); therefore, it is suitable for detecting processes leading to functional convergence or functional divergence, with the advantage of having lower Type I error rates (Botta-Dukát and Czúcz 2016). Since the null distributions for SLA and Seed Mass did not follow normal distribution, we used probit-transformed p values as effect sizes (ES; Botta-Dukát 2018) because using standardized effect size (SES; Gotelli and McCabe 2002) would cause misleading results (Botta-Dukát 2018). However, as was the case for SES, the positive values for ES (> 0) were attributed to higher than expected observed values, in contrast to negative values (< 0), which meant lower than expected observed values (Botta-Dukát 2018).

As we did not expect a causal relationship between two indices, and because we were interested in assessing changes in the covariation between FD and CWM, for the same trait and between traits, we fitted major axis regressions (MA; Legendre and Legendre 2012) for each belt separately using (S)ES-CWM and (S)ES-FDis. Line fitting within individual sets with 95% slope confidence intervals was calculated with the lmodel2 package for the R software (R Development Core Team, Vienna, Austria). This particular regression method or model takes into account the fact that the two variables in the regression equation are random, that is, they are not controlled by the researcher, by minimizing the sums of squares of the perpendicular distance between each point and the regression line (Legendre and Legendre 2012). In addition, the spatial autocorrelation was excluded by using Moran's I autocorrelation coefficient indices (see Online Resource 4).

Results

In general, we found a linear decreasing trend along the elevation gradient for the total cover (from 76 to 50%) and species richness (from 28 to 19). Also, we found a slight unimodal trend for species Plant Height, SLA and Seed Mass trait values (Table 2).

Table 2 Mean values, with standard deviation in brackets, of the biological characteristics of the three elevation belts into which we grouped all the elevation gradients

	1	2	3
Total cover	76.4 (25.3)	61.9 (23.4)	50.3 (28.5)
Species richness	28.1 (6.5)	21.6 (6.5)	18.9 (5.4)
Plant Height (cm)	16.0 (10.8)	17.7 (10.1)	9.8 (7.5)
Specific leaf area (mm^2/mg)	11.1 (3.1)	11.4 (5.6)	10.0 (3.2)
Seed Mass (mg)	2.7 (2.5)	2.9 (2.5)	1.3 (1.2)

Cover and species data refer to plot level, while traits data (Plant Height, Specific Leaf Area and Seed Mass) refer to species, unweighted by species cover

In detail, for SES Plant Height we found a significant covariation only for the higher belt (Table 3), with a positive trend between FDis and CWM (slope coefficient 1.44; p value < 0.001). For ES-SLA, we found no significant covariation, neither positive nor negative, for each of the considered belts. Finally, for ES Seed Mass, we found a significant relationship between FD and CWM with the same trend of positive covariation, for each of the three belts (first belt slope coefficient 0.636, p-value < 0.05; second belt slope coefficient 1.086, p-value < 0.01; third belt slope coefficient 1.119, p-value < 0.001). Slope coefficients for each of the models considered are reported in Table 3, while Fig. 3 reports the significant covariation between indices of the same trait.

The results of the analyses to investigate the covariation between traits, that is between SES-CWM_H and ES FD_{SLA} and FD_{SM}, are reported in Table 3. We found a significant positive covariation between CWM_H and FD_{SLA} only for the third belt (slope coefficient 2.8; p-value < 0.05), while for FD_{SM}, we found one negative covariation for the second belt (slope coefficient -0.05; p-value < 0.01) and one positive covariation for the third belt (slope coefficient 2.73; p-value < 0.01).

Discussion

CWM and FD indicate the mean and the dispersion of a trait, and describe two aspects of the functional dimensions of a plant community. Even though their interdependence has been demonstrated mathematically (Ricotta and Moretti 2011), they convey different

Table 3 Slope coefficient and adjusted-R^2 values of each of the major axis regression models between (S)ES of community-weighted-mean (CWM) and functional diversity (FD) for Plant Height (SES-H), effect size specific leaf area (ES-SLA) and effect size Seed Mass (ES-SM)

Metric	Elevation belt	Slope Coefficient	R^2 (%)
FD_H-CWM_H	1	0.19	3
	2	-0.81	5
	3	**1.44*****	64
FD_{SLA}-CWM_{SLA}	1	-6.01	6
	2	0.347	3
	3	-1.125	1
FD_{SM}-CWM_{SM}	1	**0.636***	38
	2	**1.086****	51
	3	**1.119*****	65
FD_{SM}-CWM_H	1	0.193	1
	2	$-$**0.512****	46
	3	**2.739***	30
FD_{SLA}-CWM_H	1	-0.234	6
	2	0.325	20
	3	**2.805***	32

In bold the significant slope estimates

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

and complementary information. To the best of our knowledge, only a few studies have attempted to analyse the degree of their interdependence (Nunes et al. 2017; Vojtkó et al. 2017) and incorporated both indices in a united model (Dias et al. 2013); to date, there is still a lack of evidence based on biological information to explain this interdependence.

Patterns in plant height (H)

The effect of aridity on Plant Height is a well-known pattern (Gross et al. 2013; Nunes et al. 2017). However, contrary to our expectation, we did not find any significant trend in the first belt, where aridity was expected to be higher (Fig. 2a), nor did we find it in the second belt under less stressful climatic conditions. In contrast, in the higher elevations, we found that communities were constrained into a lower variety of Plant Height values (low SES-FD) and at the same time had a relatively low value of SES-CWM (Fig. 2a). This seems to suggest that habitat filtering may be especially important in communities at these elevations. These findings are in line with previous works stating that abiotic factors will be more dominant in the structuring of communities in areas under more stressful environmental conditions (Weiher and Keddy 1995; Mason et al. 2011; Lhotsky et al. 2016). In grassland communities at higher elevations characterized by low temperature, small size is certainly the most prominent adaptation of plants

(Theurillat et al. 2011; Dainese et al. 2012; de Bello et al. 2013): by reducing their stature, plants are able to benefit from the soil heat accumulated during the day (Körner 2016). Furthermore, short plants tend to be more protected from desiccation by snow cover (Grime 2006).

Patterns in specific leaf area (SLA)

While many studies have indicated that Plant Height appears to be linked to assembly mechanisms along the climatic variables of the elevation gradient, there is no clear evidence of any such link between SLA and these assembly mechanisms along the gradient, perhaps due to the lack of a clear relationship between this leaf trait and the elevation gradient (Dainese et al. 2012; de Bello et al. 2013; Pescador et al. 2015). Therefore, more studies are required to better understand the covariation of CWM and FD along a stress gradient. Indeed, to date, there is no general consensus on the variation of SLA in relation to aridity or lower temperature. Aridity has been suggested to act as an

Fig. 2 Point type represent the plot for each elevation section (circle for lowest elevation section; triangle for middle elevation section; square for highest elevation section). Arrow type represent the significant co-variation (dot and dashed lines for lowest elevation section; dashed lines for middle elevation section; continuous lines for highest elevation section)
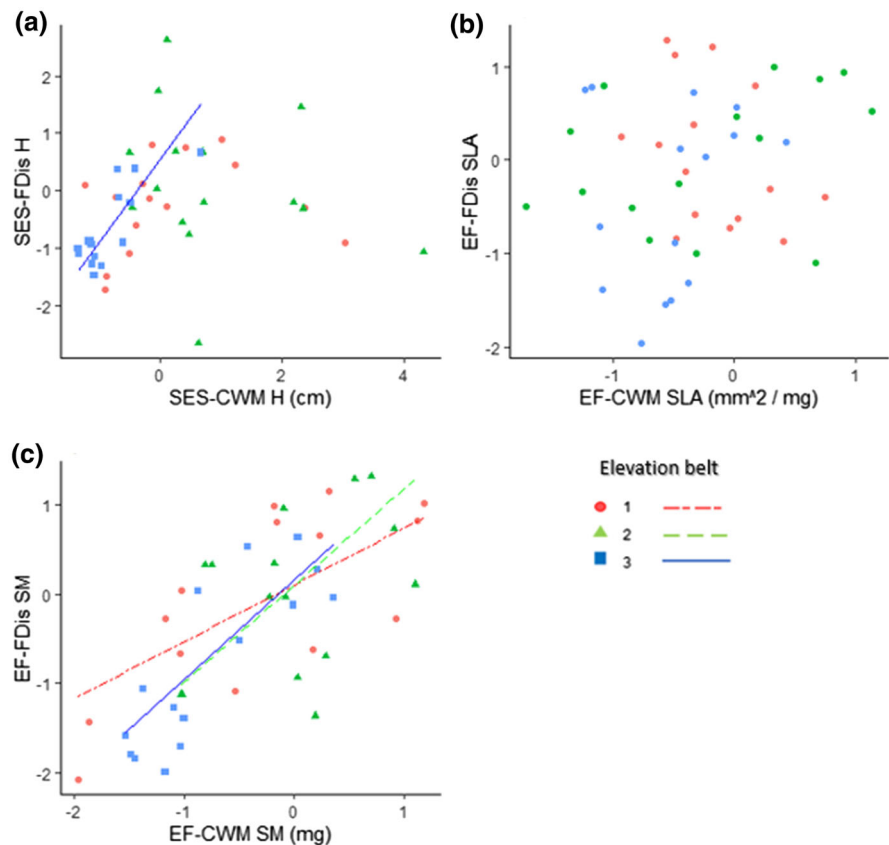
Fig. 3 Point type represent the plot for each elevation section (circle for lowest elevation section; triangle for middle elevation section; square for highest elevation section). Arrow type represent the significant co-variation (dot and dashed lines for lowest elevation section; dashed lines for middle elevation section; continuous lines for highest elevation section)
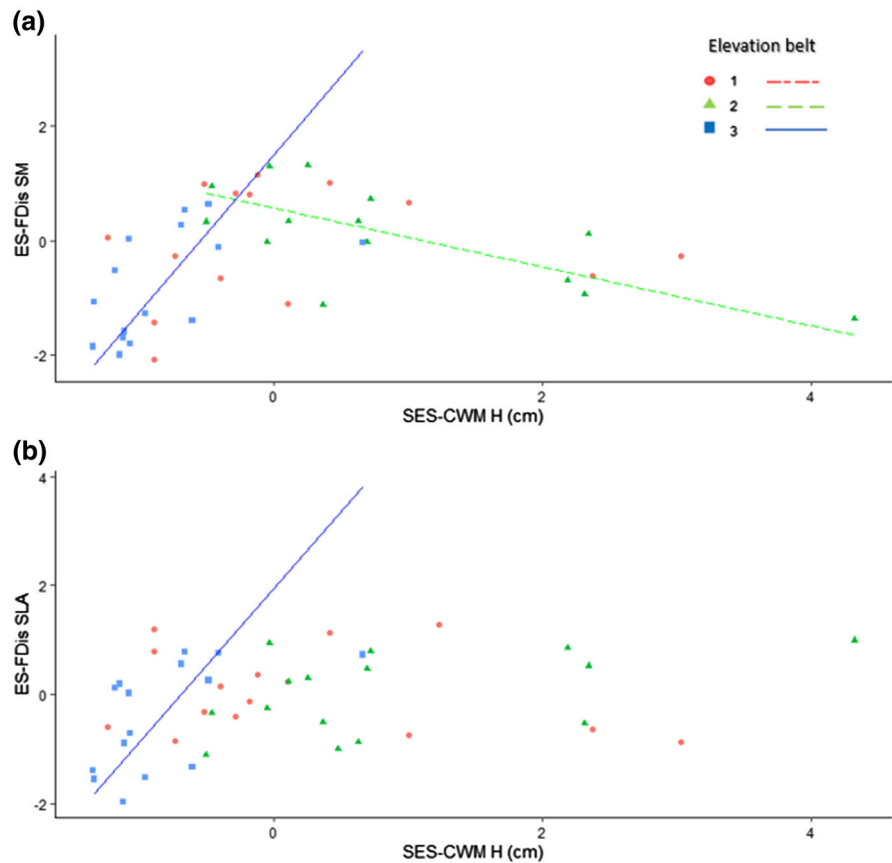
abiotic filter, promoting a decrease of functional diversity (Nunes et al. 2017) and a decrease of SLA values (Garnier et al. 2019). However, the opposite trend has been observed, with an increase of aridity correlated with an increase of both CWM and FD (Gross et al. 2013). In the case of lower temperature, harsh environmental conditions on mountain summits were reported to promote stress-tolerant species that invest more carbon on a per-leaf basis (Körner 2016), resulting in a community with a functional convergence pattern towards lower SLA values (de Bello et al. 2013; Rosbakh et al. 2015). Nevertheless, also in this case, other studies have found a contrasting pattern, such as the absence of such a relationship (Dainese et al. 2012) or a positive trend with the community showing a functional divergence pattern towards higher SLA values (Pescador et al. 2015).

Moreover, although SLA is sometimes considered to be positively correlated with relative growth rate and competitive ability (Westoby 1998; Pérez-Harguindeguy et al. 2013), previous studies have linked

this trait to competitive responses, that is, the ability to avoid being suppressed by other individuals, rather than competitive effects, that is, the ability to suppress other individuals (Goldberg and Landa 1991; Conti et al. 2018). Species competitive responses will be context dependent, and therefore, whether the SLA of communities is shaped by competitive processes will depend on how the single species in the community respond to the specific environmental conditions and to the specific biotic interaction, making it difficult to find a clear pattern along elevation gradient.

Patterns in Seed Mass (SM)

The positive covariation between ES-CWM and ES-FDis suggest the presence of different processes for each belt acting with different intensity. In the lowest belt, we detected different assembly rules, ranging from habitat filtering to limiting similarity, on the basis of the positive covariation of ES values for both indices, ranging from negative to positive (Fig. 2c).

These findings seem in line with the absence of a clear effect of aridity on Seed Mass patterns (Nunes et al. 2017), and with the suggestion that alternative strategies to cope with aridity may coexist between communities under the same climatic condition.

A similar pattern was also found for the middle belt. However, in this case, we found a gradient of limiting similarity processes and absence of habitat filtering, since only one plot shows negative ES values for both indices (Fig. 2c). This highlighted a tendency towards communities with species bearing larger seeds (positive ES-CWM) and divergent strategies (positive ES-FDis). These results seem in line with the stress gradient hypothesis (Bertness and Callaway 1994), since under more benign environmental conditions, negative competitive interactions may be the main drivers of assembly processes (Weiher and Keddy 1995). However, the presence of multiple strategies (higher ES FD) related to Seed Mass in the lowest and middle belts may also suggest that there is a temporal partitioning of the plant regeneration niches. The coexistence of multiple 'regeneration niches' (Moles and Westoby 2006) might be a general structuring pattern in plant communities with high levels of competition, as previously suggested by Bernard-Verdier et al. (2012).

In contrast to the lowest and middle belts, in the highest belt we found a strong tendency towards only habitat filtering, as highlighted by the positive covariation of ES between CWM and FDis, with mostly negative values of the metrics. The decline of Seed Mass with increasing elevation is a common pattern that has been explained as an environmental response to lower temperatures and to the shorter growing season (Grime 2006; Dainese et al. 2012; de Bello et al. 2013). Indeed, these may act as abiotic filters, reducing the seed growth (Körner 2003) and decreasing the available time for seed development (Baker 1972).

Between-traits relationship

The negative covariation between Plant Height and Seed Mass found for the middle belt may suggest the tendency towards hierarchical competition processes (biotic filtering effect), as the increase of Plant Height and decrease of seed diversity seem to suggest (Fig. 3a). Under the canopy light may become a limiting factor that promotes a stressful

microenvironment in which only a few Seed Mass strategies are selected. On the contrary, the decrease of Plant Height (decreasing hierarchical competition for light) and increase of Seed Mass diversity probably are connected to the decrease of stressful microenvironmental conditions. Therefore, developing seedlings may start to compete among each other (as mentioned above in Patterns in Seed Mass), thus increasing the number of strategies.

Increases in abiotic constraints dramatically changed the covariation between Plant Height and Seed Mass diversity, also affecting the resource exploitation strategy (SLA). The positive covariation found in the highest belt for Plant Height and both Seed Mass and SLA diversity seems to highlight the effect of habitat filtering, since the diversity of both traits decrease with the decrease of mean Plant Height. In contrast, their parallel increase with Plant Height seems to suggest the existence of symmetrical competitive processes. However, it is possible that the environmental conditions of these alpine communities are so stressful that only a few ecological niches are currently available, and thus the decrease of stress intensity leads to an increase in the number of ecological niches, thus possibly increasing the diversity.

Conclusions

Our analysis reveals that the relationship between these two metrics may provide information on the assembly processes shaping plant communities. We pointed out that different traits are affected by different assembly processes, and that the covariation of CWMs and FD may offer a solution for identifying the processes behind the same FD pattern (convergence/divergence). However, this has been made possible by combining the trait information with the environmental context, that is, the stress level. Indeed, the strength of one process or another depends on the particular stress intensity, so habitat filtering is stronger at higher elevations, where there are more stressful conditions, and limiting similarity is stronger in the intermediate belt, where the conditions are less stressful.

However, we must introduce a word of caution. First, though the elevation gradient was about 1 km long, it did not have a marked gradient of climatic aridity (from 0.60 to 0.80; see Table 1). Instead, there

was a highly intense aridity along the entire elevation gradient. This is in contrast to a marked temperature gradient (from 17.04 to 9.82 for summer temperature and from 8.64 to 2.06 for mean annual temperature), since the higher plant communities are clearly distinctive. Second, we did not consider our approach here as *ultima ratio*, since other mechanisms like microenvironmental heterogeneity or interactions with organisms of other trophic levels such as herbivores and mycorrhizae may also potentially influence the trait values and consequently the assembly processes. Third, it is essential to consider the ecological meaning of each trait used in order to reach a better biological interpretation of the covariation of the indices. Indeed, while FD values are more straightforward (divergence or convergence), this is not true for the CWM index. For example, high values of CWMs for SLA mean high resource acquisition, namely, fast-growing species. In contrast, high values of CWM for LDMC mean high resource conservation, namely, slow-growing species, and thus, such a framework could not be applied to LDMC. In this sense, with this study, we want to provide a framework to disentangle some of the popular assembly processes for trait-based community assembly studies, providing an example with the most widely used traits in the LHS scheme (Westoby 1998).

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