

How large-scale geographic factors affect the different dimensions of functional diversity: evidence from the beech forest herb layer (Apennines, Italy)

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Background and aims – The research aim was to investigate the relation between large-scale geographic factors and the functional structure of the herbaceous layer of calcareous beech forests in the Apennines, managed as high forest.

Material and methods – We selected 163 plots (20 × 20 m), ranging from Central to South Italy, using a random stratified sampling design. We correlated the effect sizes of traits' community-weighted means, functional richness, evenness, divergence, dispersion, and Rao's quadratic entropy, with the main axes of variation in species composition.

Key results – The geographical range played a weak role in shaping the species composition of the herbaceous layer. However, we found evidence of functional convergence towards the northern sectors of the study area, where traits linked to resource retention strategies and vegetative spread are filtered. We did not find any evidence of convergence northwards for leaf phenology and pollination types.

Conclusion – The increase of the intensity in the environmental stress was associated with a decrease of diversity for traits related to resource conservation strategies and vegetative propagation. On the contrary, the lower cold stress intensity southwards fostered a better niche partitioning, ensuring the coexistence of species with different modalities of resource acquisition and conservation.

Keywords – Apennines; assembly rules; ecosystem functioning; *Fagus sylvatica*; functional diversity; habitat filtering; plant traits.

INTRODUCTION

The coenological and functional structures of plant communities depend on several factors acting at different

scales (Lavorel & Garnier 2002; Mayfield et al. 2010; Götzenberger et al. 2012; Laughlin & Laughlin 2013), which select the viable trait combinations (de Bello et al. 2013). Among the main components of the functional structure of

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plant communities are the community-weighted mean trait values (hereafter CWMs) and the different dimensions of functional diversity (hereafter FD). The former represents the average of trait values weighted by the relative abundance of each species and are useful to examine the shifts in single-trait values in response to environmental changes (Garnier et al. 2004; Lavorel et al. 2008; Chelli et al. 2019a). The latter are quantified by different indices (Pakeman 2011), such as functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis), and Rao's quadratic entropy (Rao's Q) (Villéger et al. 2008; Laliberté & Legendre 2010). These indices provide information on the distribution-coexistence mechanisms of species (Mouchet et al. 2010; Münkemüller et al. 2012; Bricca et al. 2021) and ecosystem functioning (Petchey et al. 2004; Mouillot et al. 2011). Specifically, FRic reflects the amount (or range) of functional space occupied by a species assemblage; FEve quantifies the regularity with which the functional space is filled by species, weighted by their abundance; FDiv expresses the degree to which abundance distribution in niche space maximizes divergence in functional characters within the community; FDis and Rao's Q estimate, in a different way, the dispersion of species in trait space, weighted by their relative abundance (Villéger et al. 2008; Laliberté & Legendre 2010).

Most of the trait-based studies used only Rao's Q as measure of FD to reveal changes along ecological/stress gradients (e.g. Botta-Dukát 2005; de Bello et al. 2006; Lepš et al. 2006; Doležal et al. 2011; Ricotta & Moretti 2011; Mason et al. 2012; Tardella & Catorci 2015; Stanisci et al. 2020; Bricca et al. 2021), whilst few of them analyzed all the components of the FD (de Bello et al. 2013; Sabatini et al. 2014; Tardella et al. 2019). As far as we know, none of them focused on how geographic-scale variations influence the different dimensions of the FD. In general, Mouchet et al. (2010) predicted that the prevalence of environmental filtering in stressed communities causes lower FD at wider geographical scales, because the selective pressure for niche differentiation between co-occurring species is less intense (Mason et al. 2013). Moreover, the trend of FD of single traits may differ depending on their adaptive meaning in a specific environmental context (Grime 2006; Tardella & Catorci 2015). However, there are several general ecological hypotheses that predict changes in the relative importance of community assembly processes along resource, disturbance, and/or stress gradients. One of them is the Stress-Dominance Hypothesis (SDH; Coyle et al. 2014, adapted from Swenson & Enquist 2007), which predicts that in a harsh environment, habitat filtering is the major driver of community composition, resulting in strong trait convergence, while in less stressful habitats limiting similarity is more important, resulting in trait divergence (Weiher & Keddy 1995).

In this study, we focused on forest ecosystems because the assessment of the variation in functional structure of plant communities along large-scale gradients has been performed mostly on grassland communities (e.g. Borgy et al. 2017), while one study focused on forest ecosystems at geographic scale, but did not assess variation in functional diversity (Chelli et al. 2019b). Specifically, we considered the herbaceous layer, as it serves a special role in maintaining

structure and function of temperate deciduous forests (Gilliam 2014), contributes to primary production, carbon storage and nutrient supply (Whigham 2004), supporting about 90% of plant species richness, and because it is sensitive to environmental and dynamic changes (Catorci et al. 2010; Campetella et al. 2011; Scolastris et al. 2014, 2017a; Bricca et al. 2020). We selected beech forests of the calcareous Apennine chain (Italy) since they are characterized by an intricate mixture of species in the understory. In the northern Apennines, there is a large number of arctic-alpine, circumboreal, and/or Euro-Siberian species, whereas the southern sectors are characterized by several endemic species and a fairly high number of amphi-Adriatic taxa. In contrast, the central Apennines lack species that could be used as differentials in relation to the other sectors (Di Pietro 2009). The macro-climate influencing these mountain forest ecosystems encompasses the Temperate and Mediterranean bioclimatic regions (Pesaresi et al. 2017) and is characterized by the alternation of a seasonal period of cold stress and one of drought stress whose intensity and duration varies across geographical and topographical gradients (Rivas-Martínez et al. 2011).

We hypothesized that in the beech forests of the calcareous Apennine chain (Italy), large-scale variability of herb species composition, due to biogeographic history and environmental heterogeneity (Di Pietro 2009), corresponds to changes in functional structure. In particular, we expected that increasing intensities of stress cause convergence of traits related to stress tolerance and avoidance strategies, in line with the SDH, and of traits linked to reproductive strategies aimed to overcome sexual recruitment problems. Cold stress indeed proved to cause a deviation from optimum temperatures for growth, leading to a syndrome of plant traits that includes very fast development, high rates of metabolism, short tissue duration, substantial below-ground storage organs (Körner 2016), as well as clonal growth organs and a self-pollination strategy to overcome sexual recruitment problems and to face unpredictable annual climatic fluctuations (Catorci et al. 2013). Drought stress, reducing soil water content (Joffre & Rambal 1993), fosters drought tolerance strategies, e.g. filtering a set of traits linked to resource retention, such as high seed mass (Baker 1972) and scleromorphic leaf anatomy (Tardella et al. 2016). Moreover, summer drought stress shortens the time available for plants to complete the vegetative cycle, therefore may foster also drought avoidance strategy, e.g. filtering a set of traits linked to resource acquisition and fast reproduction, such as spring/early summer flowering besides spring green and overwintering green leaves (Catorci et al. 2013), low plant height (Nunes et al. 2017), high Specific Leaf Area (Gross et al. 2013), and vegetative propagation by bulbils (Lee & Harmer 1980; Catorci et al. 2013).

The research questions were: i) Can variations in herb layer species composition be detected in the considered geographic range? ii) Do these variations reflect changes in the functional structure in terms of CWMs and FD? iii) Can variations in functional structure be interpreted as the response of the herb layer to large-scale changes of stress intensity?

MATERIAL AND METHODS

Study area

The study area (fig. 1) comprises the calcareous Apennine ridge (UTM coordinate system: from 33 T 313955.63 m E 4815305.47 m N to 33 S 595869.09 m E 4421909.44 m N). From a bioclimatic point of view, the thermotype is supratemperate (with a longer-lasting period of winter cold stress northwards); the ombrotype ranges from subhumid to hyperhumid/ultrahyperhumid (Pesaresi et al. 2017; Cutini et al. 2021). The territory investigated is part of two bioclimatically/biogeographically-determined sections, central and southern Apennine section (Temperate Division, Apennine Province), and southern Tyrrhenian section (Mediterranean Division, Tyrrhenian Province) (Blasi et al. 2014). In the central and southern Apennine section (including the Umbria and Marche Apennine, the Lazio and Abruzzo Apennine, and the Campania Apennine subsections), mean annual temperatures range from 6°C to 17°C; maximum temperatures of the hottest month 18.5–33.1°C, minimum temperatures of the coldest month range from -4.7°C to 4.3°C, with occurrence of frost events (Blasi et al. 2014). Annual precipitation is uneven, and ranges from 630 mm to over 2000 mm. There is a summer minimum and two maximums in autumn and winter; number of arid months 0–1 (Umbria-Marche Apennine) to 0–3 (Campania Apennine) (Blasi et al. 2014).

In the southern Tyrrhenian section (including the Lucania subsection), mean annual temperatures range from 11°C to 16°C, with maximum temperatures of the hottest month 25.2–33.2°C, minimum temperatures of the coldest month between 0.1 and 3.5°C; a frost period occurs only over 1100 m a.s.l. (Blasi et al. 2014). Annual precipitation ranges from 672 mm to 1788 mm. The pluviometric regime shows a main maximum in winter/autumn and a minimum in summer; 1–3 arid months (Blasi et al. 2014).

According to Mucina et al. (2016), the basiphytic beech forests of the study area belong to the *Fagion sylvaticae* Luquet 1926 alliance (*Geranio nodosi-Fagion* Gentile 1975) and the *Geranio striati-Fagion* alliance Gentile 1970 (*Geranio versicoloris-Fagion* Gentile 1970), while, following Willner et al. (2017), they are part of the *Fagion sylvaticae* s.l. alliance. The sampled beech forests mostly belong to the 9210* Habitat (Apennine beech forests with *Taxus* and *Ilex* EU 92/43 Directive) of the Natura 2000 Network.

Sampling design and data collection

We selected nine calcareous massifs along the Apennine chain (fig. 1). To reduce the variation due to topographic factors, we used a stratified random sampling design, considering only *Fagus sylvatica* forests growing on north-facing slopes, with angles of 15–45°, at altitudes ranging from 1,000 to 1,700 m a.s.l. We performed this selection using georeferenced distribution maps of beech forests. Moreover, we selected stands managed as high forest (information gathered from local woodcutters and the archives of the Italian Forestry Service). Using a GIS

generator of random points, we randomly selected a number of points per massif depending on the size of the massif and the extension of beech forests on each massif. We selected 190 random points and then discarded those located less than 100 m from the border of the forest patch, as well as those placed on watersheds or water drainage lines. Each point was the lower left-hand corner of a 20 × 20 m plot whose orthogonal sides are oriented northwards and eastwards. After a preliminary inspection of the sites, we excluded plots with heterogeneous aspect and/or slope angles, as well as those crossed by roads/pathways.

In total, we laid 163 plots, in which we recorded: altitude (m a.s.l.), aspect (azimuth degrees), slope (vertical degrees), and cover-abundance values of the plant species of the herbaceous layer, assigned using the Braun-Blanquet scale (Braun-Blanquet 1964). We executed relevés from mid-May to late July 2015, to observe both the spring and the summer-growing species. In surveying the herbaceous layer, we considered only “resident species” sensu Gilliam (2014), namely, species that cannot grow taller than one meter during their life, which in the studied forest ecosystems are all herbaceous. Species nomenclature followed Bartolucci et al. (2018).

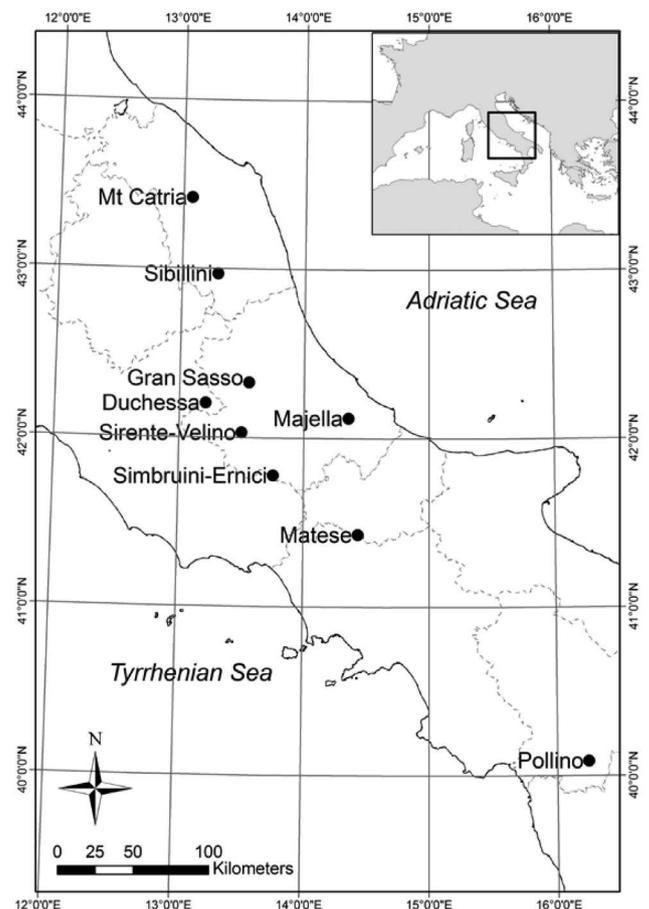


Figure 1 – The Italian Peninsula with the location of the surveyed high mountain massifs: Catria, Sibillini, Duchessa, Gran Sasso, Majella, Simbruini-Ernici, Sirente-Velino, Matese, and Pollino. Map created with QGIS v.2.14.10 (QGIS Development Team 2016).

Table 1 – List of the traits and respective states, with a brief description and a list of data sources.

Trait	Trait state	Description	Data sources
Storage organ	Rhizome	The occurrence of storage organs is usually associated with the ability of vegetative propagation and dispersal. Occurrence and type of storage organ were identified following Krumbiegel (2002) and Klimešová & de Bello (2009).	Klotz et al. (2002) and Klimešová & de Bello (2009), checked and supplemented by field observations.
	Bulb		
	Tuber		
	Tap root		
	Turio		
	Secondary storage root		
Vegetative propagation	Rhizome	Besides sexual (generative) propagation, many plant species are able to propagate and disperse asexually by vegetative propagation. Occurrence and type of vegetative propagation were identified following Krumbiegel (2002), and Klimešová & de Bello (2009).	Klotz et al. (2002) and Klimešová & de Bello (2009), checked and supplemented by field observations.
	Bulbil		
	Bulb		
	Root tuber		
	Stem tuber		
	Root/tuber splitter		
	Roots with adventitious buds		
	Root shoot		
Leaf phenology	Runner	Classification of how long a leaf persists on a plant from emergence until cast, according the categories indicated in Klotz & Kühn (2002).	Klotz et al. (2002), checked and supplemented by authors' observations.
	Turio		
	Persistent green		
	Summer green		
Pollen/spore dispersal system	Spring green	Classification of the type of pollen transfer, according the categories indicated in Klotz & Kühn (2002). The vector of spores is always wind.	Klotz et al. (2002)
	Overwintering green		
	Selfing		
	Insects		
	Wind		

To assess the differences in environmental conditions, we used as proxies the Ellenberg's Indicator Values (EIVs; Ellenberg et al. 1991), adapted to Italian flora (Pignatti 2005; Guarino et al. 2012), since EIVs proved to be useful in analyzing the drivers of vegetation change (i.e. McCollin et al. 2000; Klaus et al. 2012), especially when considered for comparison on a regional/local scale (Godefroid & Dana 2007).

To assess the trait-based response of the herbaceous layer, we selected a set of traits to encompass different plant functions (Grime 2006), namely, resource acquisition (leaf persistence and vegetative propagation; Klotz et al. 2002, Klimešová & de Bello 2009), resource retention and stress tolerance ability (storage organs; Klotz et al. 2002; Klimešová & Klimeš 2006), and reproductive strategies (type of pollen/spore dispersal and vegetative propagation; Klotz et al. 2002; Klimešová & Klimeš 2006). Indeed, in accordance with Díaz et al. (2004), Grime (2006), and Lavorel et al. (2007), plant functional dimension is a multidimensional concept which cannot be captured with a single function or trait. All traits were treated as categorical variables. A description of each trait, with a list of the respective states and data sources, is reported in table 1.

Data analysis

Preliminary analyses – We expressed species abundances in percentage values using the average cover values of Braun-

Blanquet classes: + (< 1%) – 0.5%; 1 (1–5%) – 3%; 2 (5–25%) – 15 %; 3 (25–50%) – 37.5%; 4 (50–75%) – 62.5%; 5 (75–100%) – 87.5%; rare species (r) were marked with the value of 0.1. We calculated the community unweighted mean values (CMs) of Ellenberg Indicator Values (EIVs) using presence/absence species data (Zelený & Schaffers 2012) as follows:

$$CM = \sum_{i=1}^S p_i x_i$$

where CM is the community unweighted mean value of a given EIV, S is the number of species, $p_i = 1/N$ for all N species in the plot, and x_i is the Ellenberg indicator value for species i . This index is widely used to reflect the site conditions better than the indicator values of individual species, because the occurrence of a species in a relevé may deviate from its optimum due to ecological tolerance (Kowarik & Seidling 1989). To calculate CM_{EIVs} , we used R v.3.1.1 (R Core Team 2021) and the functcomp function implemented in the R package FD v.1.0-12 (Laliberté et al. 2014).

To detect possible variations in species composition within the data set, we performed a Principal Components Analysis (PCA) on the Hellinger-transformed “relevés × herbaceous layer species (cover %)” matrix, as the Hellinger transformation is recommended for ordination of species

abundance data (Rao 1995; Legendre & Gallagher 2001). To perform PCA and Hellinger transformation, we used the `rda` and `decostand` functions in the R package `vegan` v.2.4-4 (Oksanen et al. 2017). To interpret the ecological meaning of the main axes of species variation, we calculated the regressions of altitude, slope, and CM_{EIVs} against the PC1 and PC2 object scores using the `envfit` in the R package `vegan` v.2.4-4 (Oksanen et al. 2017). To test the significance of the CM_{EIVs} , we used the modified permutation test designed by Zelený & Schaffers (2012), which uses mean randomized EIVs (i.e. calculated from species EIVs randomized among species) to remove the influence of species composition and avoid high type-I error rates (Zelený & Schaffers 2012). The modified permutation test was run in R, using the `envfit.iv` function provided by Zelený & Schaffers (2012). We calculated the correlations between PCA scores and significant variables, using the Kendall non-parametric test (the `cor.test` function in the R package `stats` v.3.1.1).

Variations of the functional structure associated with the pattern of species composition – To detect variations of functional structure, at first, we calculated for each plot and trait state the CWM value, following the equation of Garnier et al. (2004):

$$CWM_j = \sum_{i=1}^n P_{ij} T_{ij}$$

where CWM_j is the community-weighted trait state of the plot j , P_{ij} is the relative abundance of the species i in the plot j , T_{ij} is the mean trait state value of the species i in the plot j (which in this study corresponds to 1 or 0, i.e. the presence/absence of the trait state, as we treated all traits as categorical variables) and n is the number of species with the considered trait state.

Afterwards, for each plot, to capture distinct facets of FD, we calculated FRic, FEve, FDiv, FDis, and Rao's Q indices (Mason et al. 2005, 2012; Villéger et al. 2008; Laliberté & Legendre 2010; Mouchet et al. 2010) using Gower's distance (Legendre & Legendre 1998; Pavoine et al. 2009; de Bello et al. 2010). A description of the meaning of each index is shown in supplementary file 1.

Since the number of traits can affect the values of the calculated FD index (Petchey & Gaston 2002) and because different traits might respond differently to the same ecological processes (Grime 2006), analyzing the combination of multiple traits (e.g. by averaging across all traits) might not detect the pattern of functional variation (Laliberté & Legendre 2010). Therefore, to avoid such problems, we assessed FD facets of each trait separately (Garnier et al. 2004; Lepš et al. 2006; Lavorel et al. 2008; Mason et al. 2011).

Prior to calculating FD indices and CWMs, as one species may have more than one state of a trait, each trait was coded by as many binary variables as the number of potential individual states of the considered trait. For example, considering the plant trait vegetative propagation, *Orthilia secunda* had trait state value "1" for runner, root shoot, and root with adventitious buds, and "0" for the other vegetative propagation modes (supplementary file 2).

We computed these indices for each trait by processing the matrices "relevés × herbaceous layer species (cover %)" and "herbaceous layer species × trait states (presence/absence)". For species showing more than one state for the same trait, each state was weighted independently with species cover. We performed FD and CWMs calculations using the `dbFD` function implemented in the R package `FD` v.1.0-12 (Laliberté et al. 2014).

To remove the influence of confounding factors (e.g. species richness, diversity), we analysed if the FD indices and CWMs of a given trait differed from random expectation for each trait separately (Botta-Dukát & Czúcz 2016). To create the null models, we obtained 999 simulated values for each of the indices reshuffling in the whole data set the trait states among the species in the "species × trait states" matrix, keeping intact the trait states combination (between-plot randomization sensu Botta-Dukát & Czúcz 2016). We produced null distributions using the `replicate` function and the randomizations using the `taxashuffle` function in the R package `Picante` v.1.7 (Kembel et al. 2010) and checked their normality by visual inspection of frequency distribution histograms. Since the null distributions were not normal, and in this case the calculation of standardized effect size (SES; see de Bello 2012) may lead to misleading interpretations, we used probit-transformed p values as effect sizes (Botta-Dukát 2018). To calculate effect size (ES) values, we used the `Pvalue` function, provided by Botta-Dukát (2018) and the `probitlink` function, with argument `inverse = FALSE` (R package `VGAM` v.1.1-1; Yee 2021). Positive ES values (i.e. higher observed FD than expected by the null model) indicate trait divergence, while negative values (i.e. lower observed FD than expected by the null model) indicate trait convergence (Botta-Dukát & Czúcz 2016; Halassy et al. 2019).

We used Kendall's non-parametric correlation test between ES values (for each FD index of each trait, and for trait states' CWMs) and the gradient depicted by PCA axes 1 and 2 object scores to examine the variation in the intensity of abiotic filtering along an environmental gradient (Halassy et al. 2019). We ran Kendall's correlation tests using the `cor.test` function (R package `stats` v.3.1.1).

Information on species trait, observed FD and CWM indices, PCA axis score 1 and 2, and Effect Size (ES) can be found in supplementary files 2 & 3.

RESULTS

Variations in the herb layer species composition

PCA axes 1 and 2 explained 9.8% and 5.9% of the total variance of the species data set. Altitude was related to PCA axes 1 and 2 (vector scores -0.88 and 0.46 respectively; $R^2 = 0.21$; $p = 0.001$), while slope was unrelated to both PCA axes (vector scores 0.21 and -0.97; $R^2 = 0.01$; $p = 0.58$) (fig. 2). Altitude negatively correlated with PCA axis 1 scores (Kendall's tau = -0.238; $p = 7.038 \times 10^{-6}$) and positively with PCA axis 2 scores (Kendall's tau = 0.332; $p = 3.828 \times 10^{-10}$). EIVs were not significantly related to the PCA axes 1 and 2 (supplementary file 4).

The visual inspection of the PCA ordination plot (fig. 2) allowed to identify a discontinuity along the first axis, which divided plots in the southernmost part of the study area (Pollino massif) from all the others. *Asyneuma trichocalycinum* and *Cardamine enneaphyllos* were the species most strongly associated to PCA axis 1 in two opposite directions, while *Galium odoratum* was positively associated with axis 2 (fig. 2).

Variations in the herb layer functional structure

Trait states' ESs showing a positive correlation with PCA axis 1 object scores were: selfing and wind pollen/spore dispersal; rhizome as storage organ; and rhizome, bulb, and bulbil as vegetative propagation modes (table 2). Trait states whose ES values showed a negative correlation with PCA axis 1 object scores were: persistent leaf phenology, pollination by insects, secondary storage root, and runner (table 2). Several of these trait states also followed the gradient highlighted by PCA axis 2. ES values of pollination by wind, tuber, secondary storage root, and bulb were negatively related, while spring leaf phenology, pollination by insects, rhizome (with both storage and vegetative propagation functions), and runner were positively related to the axis 2 scores (table 2).

ES-FR_{ic}, ES-Rao's Q, and ES-FD_{is} values of vegetative propagation and storage organs were negatively correlated with PCA axis 1, as well as ES-FD_{iv} of vegetative propagation and ES-FE_{ve} of storage organs (table 3). In contrast, we found an increase of ES-Rao's Q and ES-FD_{is} values for pollen/spore system along PCA axis 1. ES-FD_{is} and ES-Rao's Q of pollination and ES-FE_{ve} of leaf phenology negatively correlated, while ES-FD_{iv} of leaf phenology positively correlated to PCA axis 2 scores (table 3).

DISCUSSION

Variations in herb layer species composition

The ordination of plots along the PCA axis 1 follows the biogeographical partition of the study area in the southern Tyrrhenian and central-southern Apennine sections depicted by Blasi et al. (2014). The quite low variance explained by PCA axis 1, as well as the independence of PCA axis 2 from the geographic location of plots, suggest that the considered geographical range plays a factual but weak role as driver of the recorded species differences in the herb layer. From the

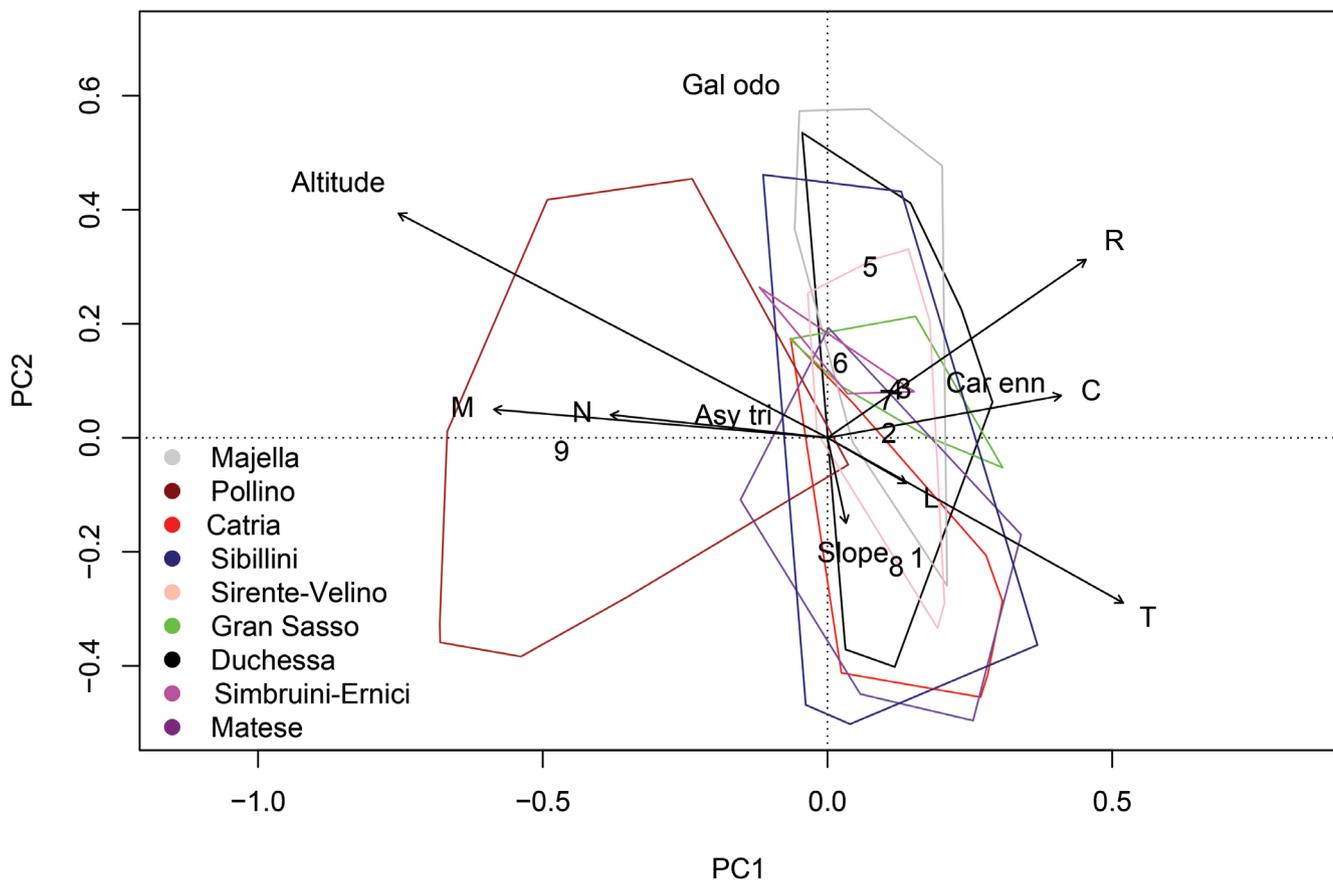


Figure 2 – Principal Components Analysis ordination graph (axes 1 and 2) performed on the species dataset. Codes of the centroids indicate massifs where relevés were carried out (1 – Catria; 2 – Sibillini; 3 – Duchessa; 4 – Gran Sasso; 5 – Majella; 6 – Simbruini-Ernici; 7 – Sirente-Velino; 8 – Matese; 9 – Pollino). Projected vectors on the ordination diagram refer to altitude, slope angle, light intensity (L), air temperature (T), continentality (C), soil moisture (M), soil reaction (R), and soil nutrients (N). Asy tri – *Asyneuma trichocalycinum*; Car enn – *Cardamine enneaphyllos*; Gal odo – *Galium odoratum*.

Table 2 – Kendall’s Tau estimates and significance levels of correlations between effect size for trait states community-weighted means and PCA axes 1 and 2 object scores. Significant results are shown in bold. ^{n.s.} $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Trait	Trait state	PCA axis	Tau estimate
Leaf phenology	Persistent green leaves	1	-0.19 ***
		2	0.02 ^{n.s.}
	Spring green leaves	1	0.11 ^{n.s.}
		2	0.17 **
	Summer green leaves	1	-0.07 ^{n.s.}
		2	-0.05 ^{n.s.}
	Overwintering green leaves	1	-0.04 ^{n.s.}
		2	-0.06 ^{n.s.}
	Leafless	1	-0.07 ^{n.s.}
		2	-0.08 ^{n.s.}
Pollen/spore dispersal system	Selfing	1	0.19 ***
		2	-0.08 ^{n.s.}
	Wind	1	0.12 *
		2	-0.13 ***
	Insects	1	-0.11 *
		2	0.20 ***
Storage organs	Tuber	1	-0.06 ^{n.s.}
		2	-0.11 *
	Rhizome	1	0.27 ***
		2	0.14 *
	Secondary storage root	1	-0.12 **
		2	-0.15 **
	Turio	1	-0.05 ^{n.s.}
		2	-0.03 ^{n.s.}
	Bulb	1	0.03 ^{n.s.}
		2	-0.06 ^{n.s.}
	Tap root	1	-0.09 ^{n.s.}
		2	-0.02 ^{n.s.}
Vegetative propagation	Rhizome	1	0.46 ***
		2	0.13 *
	Runner	1	-0.32 ***
		2	0.17 **
	Bulbil	1	0.35 ***
		2	-0.07 ^{n.s.}
	Bulb	1	0.11 *
		2	-0.11 *
	Turio	1	-0.08 ^{n.s.}
		2	-0.03 ^{n.s.}
	Root splitter	1	0.01 ^{n.s.}
		2	-0.05 ^{n.s.}
	Stem tuber	1	-0.06 ^{n.s.}
		2	-0.06 ^{n.s.}
Root tuber	1	-0.08 ^{n.s.}	
	2	-0.08 ^{n.s.}	
Root with adventitious buds	1	-0.11 ^{n.s.}	
	2	-0.06 ^{n.s.}	
Root shoot	1	0.10 ^{n.s.}	
	2	0.02 ^{n.s.}	

Table 3 – Kendall’s Tau estimates and significance levels of correlations between effect sizes, calculated for functional richness (FRic), functional dispersion (FDis), Rao’s quadratic entropy (Rao’s Q), functional divergence (FDiv), and functional evenness (FEve), and PCA axes 1 and 2 object scores. Significant results are shown in bold. ^{n.s.} p > 0.05; * p < 0.05; ** p < 0.01; *** p < 0.001.

Trait	FD index	PCA axis	Tau estimate
Pollen/spore dispersal system	FDis	1	0.12*
		2	-0.17**
	Rao’s Q	1	0.11*
		2	-0.18***
	FDiv	1	-0.07 ^{n.s.}
		2	0.09 ^{n.s.}
	FRic	1	-0.07 ^{n.s.}
		2	-0.07 ^{n.s.}
	FEve	1	-0.08 ^{n.s.}
		2	-0.04 ^{n.s.}
Leaf phenology	FDis	1	0.09 ^{n.s.}
		2	0.06 ^{n.s.}
	Rao’s Q	1	0.09 ^{n.s.}
		2	0.07 ^{n.s.}
	FDiv	1	-0.04 ^{n.s.}
		2	0.17**
	FRic	1	-0.10 ^{n.s.}
		2	-0.07^{n.s.}
	FEve	1	-0.04^{n.s.}
		2	-0.11*
Storage organs	FDis	1	-0.14**
		2	-0.10^{n.s.}
	Rao’s Q	1	-0.11*
		2	-0.08^{n.s.}
	FDiv	1	-0.09^{n.s.}
		2	0.02^{n.s.}
	FRic	1	-0.21***
		2	-0.03^{n.s.}
	FEve	1	-0.14*
		2	-0.04^{n.s.}
Vegetative propagation	FDis	1	-0.12***
		2	-0.01 ^{n.s.}
	Rao’s Q	1	-0.14***
		2	-0.08 ^{n.s.}
	FDiv	1	-0.13*
		2	0.06 ^{n.s.}
	FRic	1	-0.42***
		2	0.01 ^{n.s.}
	FEve	1	-0.04 ^{n.s.}
		2	-0.02 ^{n.s.}

floristic point of view, *Asyneuma trichocalycinum*, endemic to southern Italy, was typical of the southern Tyrrhenian section (fig. 2) (Di Pietro 2009; Bartolucci et al. 2018). Plots of the northern and central sectors of the study area (groups 1 to 8, fig. 1) shared species that are common in central Apennine beech forests, but absent from the southernmost sector of the study area (group 9, fig. 1), such as *Anemone ranunculoides*, *Cardamine enneaphyllos*, *Cardamine kitaibelii*, *Carex pilosa*, *Doronicum columnae*, *Geranium nodosum*, *Lilium martagon*, *Luzula sylvatica* subsp. *sylvatica*, *Polygonatum verticillatum*, and *Pyrola minor* (Di Pietro 2009; Bartolucci et al. 2018) (see supplementary file 2).

The not significant relation between EIVs and the PC1 and PC2 object scores, pointed out that the ecological conditions in the understory were substantially homogeneous throughout the considered geographical range. Only altitude showed a significant relation with both PCA axes 1 and 2. Our results are consistent with Di Pietro (2009), who stated that in the Apennine beech woodlands both biogeographic history and environmental factors shape the species pool and have different importance according to the geographic areas, and that biogeographical factors and altitude play a major role in southern Apennine. This observation is in line with Willner et al. (2017), who failed to find a formal classification of European basiphyllic beech forests based on either geographical or ecological criteria.

Variations in the herb layer functional structure

From a functional point of view, toward negative values of PCA axis 1 (fig. 2), i.e. the southernmost sector of our study area, corresponding to the southern Tyrrhenian section (Blasi et al. 2014), we detected the increase in abundance of species with runners (i.e. lateral shoots with long thin internodes and adventitious roots) and persistent green leaves, traits aimed to an efficient light and soil resource acquisition and space exploitation. Runners maximize the exploitation of space and soil resources, fostering the vegetative spreading (Klimeš 2008). Leaf types with a long lifespan can photosynthesize throughout the year without seasonal photosynthetic tissue regrowth (Grime 2001), maximizing photosynthetic returns where stress is not particularly severe (Chabot & Hicks 1982).

In contrast, toward positive values of PCA axis 1 (fig. 2), corresponding to the central and southern Apennine section (Blasi et al. 2014), we detected the establishment of plants equipped with rhizomes, bulbs, bulbils, and self-pollination. Rhizomes (subterranean thickened shoots with short internodes and adventitious roots), which have both vegetative propagation and storage functions, can overcome the shortage of resources (Newell & Tramer 1978) by increasing the likelihood of establishment of individuals in harsh conditions (Grime et al. 1997). Bulbs, compressed storage part of the shoot, allow for fast reproductive cycles supported by the mobilization of reserves stored in belowground organs. The unpredictable negative inter-annual climate fluctuations, typical of the sub-Mediterranean contexts, are likely the ecological filter that fosters the spread of species with bulbils (Bauert 1993). The need for a faster reproductive cycle (probably due the long-lasting winter

cold stress and the summer drought stress, which shorten the growing period of plants) may also account for the self-pollination strategy (Gugerli 1998); indeed, it is known that the decreased length of the growing season promotes self-compatibility or homogeneity (Richards 1986; Körner 2003).

These results are in accordance with the general picture of trait variation observed in several studies of functional changes along environmental gradients (Grime 1977; Lavorel & Garnier 2002; Díaz et al. 2004; Lavorel et al. 2007). Our results also allow to infer that macro-climatic conditions were harsher northwards than in the southernmost part of the calcareous Apennine ridge, due to the more intense and longer-lasting period of winter cold stress.

As regards PCA axis 2, we found trends of CWM ESs that are consistent with those of PCA axis 1, such as the adaptations to cope with cold stress at the higher elevations (rhizomes and spring green leaves), while pollination by insects and runners, were not. These outcomes seem to highlight that a complex system of interacting stressors acts in shaping the functional composition (Scolastri et al. 2017b). Altitude is related to other factors and interacts with latitude (Jump et al. 2009).

As far as functional diversity indices are concerned, we found that ES-FR_{ic}, ES-FD_{is}, and ES-Rao's Q of storage organs and vegetative propagation, and ES-FD_{iv} for the latter trait, increased toward negative values of PCA axis 1, i.e. toward the southernmost sector of the study area, in conditions of lower climatic stress intensity, fostering a better niche partitioning for the exploitation of space and soil resource niches and ensuring the coexistence of species with trait states associated with different modalities of resource acquisition, conservation and use (Tardella et al. 2019). In contrast, these functional indices decreased toward positive values of PCA axis 1, i.e. in the central and southern Apennine section of the Apennine biogeographic Province. Probably the presence of more stressful conditions positively filtered traits linked specifically to resource retention strategies and vegetative spread (in particular, rhizomes, which function also as clonal growth organ), suggesting an increase of role of environmental filtering as driver of the community's functional structure.

ESs of FD_{is} and Rao's Q regarding pollen/spore dispersal system increased toward positive values of PCA axis 1. This trend probably highlights that the differentiation of sexual reproduction strategies (see supplementary file 3) might be a suitable mechanism to cope with the shortening of the reproductive period and with the possible reduction of pollinators and density of plant populations due to stress intensification (Munoz et al. 2016).

Instead, ES-FD_{is} and ES-Rao's Q for pollen/spore transfer types decreased with the increase of PCA axis 2 scores, namely, towards higher elevations. This result is consistent with previous studies, which proved that the higher elevations cause a functional convergence, since stress intensification progressively selects strategies better adapted to facing harsher conditions (Huber et al. 2007; Körner 2007), but again this trend was not a general pattern for all traits in the study case. In fact, as far as leaf phenology is concerned, the positive correlation between FD_{iv} and PCA

axis 2 scores, indicates that in these conditions, species tend to have a more differentiated set of light acquisition strategies over time, ensuring a more efficient resource use and a better differentiation of the temporal niche (Mason et al. 2005), as suggested by the relative increase in cover of species with spring green leaves. Probably, their increase plays a role in causing the convergence of pollination types towards higher elevations, as the 95% of these species are pollinated by insects (see supplementary file 2).

Concerning the ES-FE_{ve}, our results offer experimental evidence to Mason et al. (2013) and Botta-Dukát & Czúcz (2016) observations, based on simulated data, that FE_{ve} is probably not able to detect changes in assembly processes. Also, previous studies have found little evidence for change in functional evenness in plant communities along ecological gradients (e.g. Mason et al. 2012) and that its behaviour might be difficult to support with biological interpretations (de Bello et al. 2013).

In summary, we found evidence of functional convergence toward the central and southern Apennine section (Temperate Division, Apennine Province) at least for traits related to resource conservation strategies and vegetative propagation, probably due to increase in the strength of environmental filtering (Götzenberger et al. 2016). We did not find any evidence of environmental filtering in the considered geographic range for pollen/spore dispersal and leaf phenology, the latter showing divergence toward the highest elevations. Our results also suggest that the environmental filtering on community's functional structure can depend on the trait considered (Grime 2006; Mason et al. 2011; de Bello et al. 2013), partly confirming the concept that environmental filtering in stressed communities should cause lower FD (Mouchet et al. 2010). Moreover, it is remarkable that opposite FD trends co-occur in the species pool, determining different responses from different traits. It follows that averaging FD across different traits may hide meaningful ecological patterns, resulting in a loss of information. This aspect deserves further in-depth analysis, to elucidate the mechanisms by which these opposite trends act in shaping plant communities along environmental gradients.

CONCLUSION

Our outcomes indicate that the studied geographical range, which underlies macro-climatic and biogeographic divisions and related stress variations, plays a weak but significant role in shaping the species composition and the functional structure of the studied community. However, our results are not completely in line with the Stress-Dominance Hypothesis, as only some traits responded by showing convergence (lower FD) in the conditions of higher stress, while others showed the opposite trend. Probably, the evaluated stress range could be too small (Ellenberg indicators did not show significant variations in our data set) to determine and highlight substantial and univocal variations. Thus, more in-depth research should be performed to test the Stress-Dominance Hypothesis for forest-floor species in the Mediterranean climatic context.

Our results contribute to understanding the ecological meaning of the FD indices in a real ecosystem. However, this goal is still far from being extensively achieved. We find it necessary to understand the correlation among FD indices and factors not considered in this study, such as, disturbance regimes (Scolastri et al. 2017b), patch age and size (Campetella et al. 2016; Canullo et al. 2017), and post-glacial recolonization processes (Di Pietro 2009).

SUPPLEMENTARY FILES

Supplementary file 1 – Description of Functional Diversity indices used.

<https://doi.org/10.5091/plecevo.84458.supp1>

Supplementary file 2 – A. Plot × species matrix (relevés nr. 1–10 – Mt. Catria massif; 11–40 – Sibillini; 41–69 – Duchessa; 70–74 – Gran Sasso; 75–88 – Majella; 89–92 – Simbruini-Ernici; 93–105 – Sirente-Velino; 106–131 – Matese; 132–163 – Pollino). B. Species × traits matrix.

<https://doi.org/10.5091/plecevo.84458.supp2>

Supplementary file 3 – Community-weighted means and functional diversity indices calculated for the herb layer of beech forests in 20 × 20 m plots. Massif name, hierarchical classification according to the ecoregions of Italy (Blasi et al. 2014), main topographic features, PCA object scores of axes 1 and 2 from a Principal Components Analysis performed on the “relevés-by-species” matrix are reported. FDis, functional dispersion; FDiv, functional divergence; FEve, functional evenness; FRic, functional richness; Rao’s Q, Rao’s quadratic entropy.

<https://doi.org/10.5091/plecevo.84458.supp3>

Supplementary file 4 – Scores of the community unweighted means of Ellenberg Indicator Values (CM_{EIVs}) on the first two PCA ordination axes (PC1 and PC2), R squared (R^2), and p values of the regressions of CM_{EIVs} against the PC1 and PC2 object scores.

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