Elevation differentially shapes functional diversity patterns in understorey forest communities when considering intraspecific and interspecific trait variability

Elevation differentially shapes functional diversity patterns in understory forest communities when considering intraspecific and interspecific trait variability

Running title: Elevation and Intraspecific trait variability

Arianna Ferrara1,*, Alessandro Bricca2, Davide Alberti3, Francesco Maria Sabatini1,4,#, Alessandro Chiarucci1#

1 BIOME Lab, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum - University of Bologna, Via Irnerio 42, 40126 Bologna, Italy (ORCID: AF: 0000-0002-8178-3910; FMS: 0000-0002-7202-7697; AC: 0000-0003-1160-235X)

2 Faculty of Agricultural, Environmental and Food Sciences, Free University of Bozen-Bolzano, Bolzano, Italy (0000-0003-0202-6776)

3 Parco Nazionale Foreste Casentinesi, Monte Falterona e Campigna, Arezzo, Italy

4Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Suchdol, Czech Republic

# These authors contributed equally to this work and share senior authorship

*Correspondence: arianna.ferrara4@unibo.it

Abstract

Questions: What is the relative importance of inter- and intraspecific trait variation and their covariation in the herb-layer of European temperate beech forests, and how do they vary with elevation? Is there evidence of interspecific trait convergence at higher elevations, as postulated by the habitat filtering hypothesis, and is this convergence enhanced or counteracted by intraspecific variation?

Location: National Park “Foreste Casentinesi, Monte Falterona and Campigna”, Italy.

Methods: We measured four functional traits – plant height, specific leaf area (SLA), leaf dry matter content (LDMC), and leaf area – across 775 individuals from 60 herb-layer species in 28 forest plots (10x10 m) spanning an 800 m elevation gradient. For each trait in each plot, we computed community weighted means (CWMs) and the standardized effect size of functional diversity (SES-FD), and decomposed total trait variation into its interspecific and intraspecific components, and their covariation. Linear regression models assessed the impact of elevation on these three components of functional variation. Lastly, we investigated whether higher elevation communities exhibited lower SES-FD, indicating functional convergence that could hint to a stronger habitat filtering.

Results: Interspecific trait variation was more important than the intraspecific counterpart both for CWMs and SES-FD. Only CWMs calculated for plant height and LDMC showed a significant relationship with elevation. Low-elevation communities featured taller, more conservative species, while shorter, faster-growing species were more common at higher elevations. SES-FD remained consistently negative for species turnover and total variation, suggesting stable functional convergence across the gradient.

Conclusions: Our findings suggest that inter- and intraspecific trait variability can be decoupled along an elevation gradient, stressing the importance of individually considering each component of trait variation when studying community composition. Elevation significantly influenced various components of plant community trait variation, with habitat filtering playing a substantial role in selecting plants with specific traits across elevations.

Keywords

Functional diversity, herb-layer, intraspecific trait variability, leaf dry matter content, plant height, specific leaf area, temperate forests, trait convergence

Introduction

Environmental conditions, ecological processes, and natural communities covary along elevation gradients (Körner, 2007; Körner, 2016). Towards higher elevations, temperature decreases, and precipitation normally increases, with strong repercussions on the distribution of plant species (Körner, 2007; Sundqvist et al., 2011; Bricca et al., 2022). This distribution is the result of selective climatic pressures on plant fitness, and plants might use diverse ecological strategies to cope with changing environmental conditions (Pérez-Harguindeguy et al., 2016). This phenomenon extends to forest ecosystems, not just at the tree level but also when considering the herb-layer. While accounting for less

than 1% of the total forest biomass, the herb-layer, defined as the layer of vascular species up to 1 m in height, represents around 90% of plant biodiversity in temperate forests (Gilliam, 2014). The herb-layer has a disproportionate importance on different aspects of forest functioning, including energy and nutrient cycles (Gilliam, 2014), being responsible for up to 4% of forest net primary productivity and around 20% of total litter production (Muller, 2003; Gilliam, 2014). Yet, the distribution of herb-layer species along elevation gradients has received considerably less attention compared to trees.

Both the distribution of herb-layer species and their role in forest functioning are mediated by functional traits (*sensu* Violle et al., 2007; Bricca et al., 2023). Traits vary both across species and among individuals of the same species (Funk et al., 2017; Midolo et al., 2019; Westerband et al., 2021). This means that the total trait variation of a community can be decomposed into three main components: species turnover (e.g. species identity or covers change but not their trait value); intraspecific trait variation (e.g. species traits change but not their cover or identity); and their covariation. Covariation can be either positive or negative, depending on whether turnover and intraspecific trait variation go in the same (reinforcing the community response) or opposite direction (compensating the community response) along an environmental gradient (Lepš et al., 2011). How the relative importance of these different components varies across traits, species, and habitats, however, is still largely unexplored.

The component of trait variation which depends on species turnover generally exceeds that arising from intraspecific trait variability (Kichenin et al., 2013; Pescador et al., 2015; Luo et al., 2016; Burton et al., 2017). Exceptions exist, however. For instance, intraspecific trait variation accounts for up to 70% of total variation for Nitrogen-related traits in Alpine plant communities, while it ranges from 25 to 40% for leaf-related traits (Henn et al., 2018). Various abiotic factors, including temperature and moisture, might explain this pattern by selecting for specific characteristics within and among species. Quantifying the role of intraspecific trait variation compared to turnover across different traits might provide insights into which traits are undergoing the highest selective pressure in the ecosystem and how species adapt to diverse environmental conditions (Dunne et al., 2003; Anderson and Gezon, 2015; Moran and Ormond, 2015).

All three components of functional trait variation are likely to change with elevation in the herb-layer of temperate forests. The influence of elevation on species turnover is relatively well understood. Species with smaller stature, thicker leaves, and slower growth rates tend to be more frequent at higher elevations, since stress-tolerant species are more likely to thrive in harsh, high-elevation environments (Kichenin et al., 2013; Pescador et al., 2015; Di Biase et al., 2021; Ratier Backes et al., 2023). Most

studies, however, focus on alpine ecosystems, mountain grasslands or forest trees, while the herb-layer of forest ecosystems remains less studied (but see Auger and Shipley, 2013). Similarly, less attention has been given to the relationship between elevation and intraspecific trait variation (but see Umaña and Swenson, 2019). Plant species which exhibit greater intraspecific trait variation, either for having higher genetic variability or higher phenotypic plasticity, might be better equipped at passing different environmental filters and might be more effective at coping with a wider range of environmental conditions, such as those encountered at different elevations (de Bello et al., 2021). Investigating how different components of functional trait variation change with elevation across traits might provide a deeper understanding of how the environment shapes the assembly of herb-layer communities in temperate forests.

When exploring trait variation of ecological communities, both the variability of trait distribution among organisms and the average trait value of a community require consideration (de Bello et al., 2021). Functional diversity quantifies the value, range, and relative abundance of functional traits of co-existing species (Díaz and Cabido, 2001; Tilman, 2001), and can shed light on mechanisms regulating species coexistence, i.e., their assembly rules (Götzenberger et al., 2012). According to the habitat filtering hypothesis, environmental conditions select for those species having specific traits or adaptations to survive and thrive in a particular habitat (Keddy, 1992). The habitat filtering hypothesis postulates that the harsher the environmental conditions, the narrower the range of trait values, as only species with specialized traits can survive and reproduce under extreme conditions (de Bello et al., 2021). This implies that the stronger habitat filtering at higher elevations compared to lowlands (Tardella et al., 2022) will result in plant communities being more functionally similar than expected at random, a phenomenon defined as functional convergence (Read et al., 2014). Yet, an increase in functional convergence along an environmental gradient is normally explained solely at the interspecific level, i.e., referring to species turnover alone. When considering total trait variation, however, there might be situations where intraspecific trait either reinforces or compensates interspecific trait convergence. In the first case, plant communities are characterized by functionally similar species, each composed by relatively homogeneous individuals. In the second case, intraspecific trait variation might counteract species turnover convergence, for instance, when a community is composed by functionally similar species with high intraspecific variation, or by functionally dissimilar species each with low intraspecific variation. Whether convergence is enhanced or counteracted by intraspecific variation along an elevation gradient, however, is still incompletely understood, which hinders our

comprehension of the general assembly rules and of the impacts of environmental pressures on herb-layer diversity (Lepš et al., 2011; Bricca et al., 2022).

Using four widely studied functional traits describing independent dimensions of plant strategies, namely plant height and leaf area mirroring the plant size dimension, and specific leaf area (SLA) and leaf dry matter content (LDMC) representing the leaf economics dimension (Diaz et al., 2016), we tackle two questions:

i) What is the relative importance of inter- and intraspecific trait variation and their covariation in the herb-layer of European temperate beech forests, and how do they vary with elevation?

ii) Is there evidence of interspecific trait convergence at higher elevations, as postulated by the habitat filtering hypothesis, and is this convergence enhanced or counteracted by intraspecific variation?

Methods

Study area

The study area is in the National Park "Foreste Casentinesi, Monte Falterona and Campigna" (43°51'35.3"N; 11°45'32.2"E), situated in the northern Apennines between the Emilia-Romagna and Tuscany region, center Italy (Figure 1). The park extends over 368,43 km^2, and its elevation ranges between 400 and 1657 m a.s.l.. The park belongs to the temperate bioclimatic region (Pesaresi et al., 2017). Based on climatic data for the period of 1991-2014, the mean annual temperature is 10°C, with a mean annual precipitation of 1338 mm (Antolini et al., 2017). The national park is characterized by three main geological formations: siliceous sandstone on the Tuscan side, solid limestone in the southeast massifs, and sandstone-marly flysch formations on the Romagna side (Merla and Bortolotti, 1969).

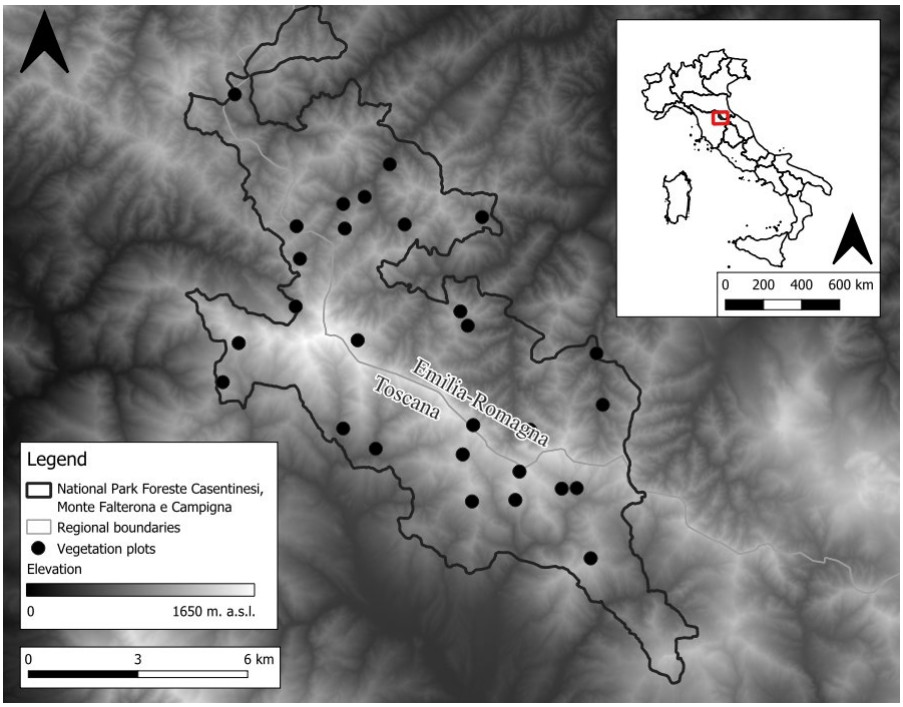

Figure 1 – Distribution of vegetation plots within the National Park "Foreste Casentinesi, Monte Falterona e Campigna"

Land cover is mainly forests, with European beech (*Fagus sylvatica* L.) forest as the dominant forest type, and current management practices are characterized by very low intensity thinning interventions, which aim towards the restoration of natural forest conditions (Bresciani et al., 2008). Forest stands dominated by *Abies alba* Mill. also occur locally, bearing the historical imprint of the religious order of 'Camaldolesi' who started managing the forest in the middle-age. The park also includes the strictly protected forest reserve 'Sasso Fratino', an old-growth forest which has been recently included in the UNESCO world heritage list. The northern side of the park was historically dominated by croplands and pastures. The socio-economic changes in the mid-20th century first, and the onset of legal protection (1993) later, have led to the gradual abandonment of marginal agricultural land, and to a drastic reduction in forest harvesting, coupled with a strong expansion of *Quercus pubescens* L., *Q. cerris* L. and *Ostrya carpinifolia* Scop. forests (Haller and Bender, 2018). The plant communities of the national park have been quite intensively studied from 1934 onwards (Lelli et al., 2018), and vegetation resurvey analysis show that forests are now quite mature (Lelli et al., 2021)

Data collection

We retrieved unpublished vegetation data, which were sampled across the National Park following a probabilistic approach in 2018, when the Park area was divided into a regular grid of 1 km x 1 km cells, and one random point was extracted within each cell. The 87 points falling into forested areas were

sampled through 10 x 10 m vegetation plots. Species were categorized into three layers based on height: herb (less than 1.3 m), shrub (1.3 to 3 m), and tree (greater than 3 m). Plant cover was visually estimated using an ordinal cover class scale with class limits 0.5%, 1%, 5%, 10% and thereafter every 10% up to 100% of the projected ground cover within the plot. Species nomenclature followed Conti, Abbate, Alessandrini, and Blasi (2005).

We stratified these original 87 plots based on both the elevation gradient and the dominant tree species. Specifically, we divided the elevation gradient into 7 belts, aiming to encompass approximately 100 m of elevation in each belt to ensure comprehensive coverage of the elevational variation. For each belt, we randomly selected two plots in pure *F. sylvatica* forests, and two in beech forest sites where *F. sylvatica* was dominant but associated also with other deciduous trees (e.g. *O. carpinifolia* and/or *Q. pubescens*), resulting in a total of 28 plots. After relocating these plots in the field, we measured the functional traits of five individuals for each of the herb-layer species that cumulatively covered at least 80% of the total cover of the plot, excluding tree saplings, shrubs and ferns from the original species list. In total, we sampled 775 individuals belonging to 60 different species. The measured functional traits described the two primary dimensions of plant strategies, as outlined by Diaz et al., (2016): plant size dimension (plant height and leaf area) and the leaf economic spectrum (SLA and LDMC). All traits were measured on fully grown individuals following the standardized protocol described in Pérez-Harguindeguy et al. (2016). For each plot, we also measured the following environmental variables: elevation (m), aspect (azimuth, degrees, converting from the 0-360 compass scale to a 0-180 linear scale; Warren, 2008), slope (vertical degrees), the total cover of each forest layer (%), moss cover (%), rocks and stones cover (%), litter and deadwood cover (%). Soil depth was measured by hammering a graduated metal rod into the soil until hitting the bedrock or alternatively down to a depth of 1 meter. Finally canopy closure was measured using hemispherical photographs through the smartphone app GLAMA (Tichý, 2015). A list of all environmental variables measured in each plot is in Appendix 1.

Calculation of functional indices

After log10 transforming each trait to increase normality (Májeková et al., 2016), we calculated separately for each trait two complementary indices at community level: community weighted mean (Garnier et al., 2004) and functional diversity with Rao's Quadratic Entropy (Ricotta and Moretti, 2011).

Community Weighted Mean (CWM) quantify the mean trait value in a species assemblage, weighted by the species abundances. It was calculated as:

193 $$CWM = \sum_{i=1}^{S} x_i p_i$$

194 where S is the number of species, p_i the relative cover and x_i the trait value for the species *i*.

195 Rao's Quadratic Entropy is an index widely used to quantify the functional diversity (FD) of a
196 community, as it expresses the expected dissimilarity between two random individuals of a given
197 assemblage:

198 $$FD = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S-1} d_{ij} p_i p_j$$

199 Where d_{ij} is the dissimilarity between species *i* and *j*, p_i and p_j their relative cover. Between-species
200 dissimilarity (d_{ij}) was calculated with Gower distance, which for quantitative traits reduces to a range-
201 normalized Manhattan distance. It ranges from 0 (when two species have equal trait value) to 1 (when
202 two species are at the opposite endpoints; Pavoine et al., 2009; Legendre and Legendre, 2012).

203 Finally, to find evidence of functional convergence, and make inference about the underlying
204 community assembly processes, we calculated the Standard Effect Size (SES) of functional diversity (de
205 Bello, 2010) as:

206 $$SES - FD_{\square} = \frac{FD_{obs} - mean\ FD_{exp}}{sd(FD_{exp})}$$

207 where FD_{obs} is the functional diversity observed in a community and FD_{exp} is the expected functional
208 diversity of the same community, calculated after randomly shuffling traits across species, and keeping
209 species composition constant in 999 permutations. This randomization technique aligns with the T1
210 methodology introduced by Götzenberger et al. (2016). We took values of $SES_{FD} < 0$ as evidence of
211 functional convergence (Botta-Dukát and Czúcz, 2016).

212 *Importance of different trait variation components along the elevational gradient*

213 We first computed an exploratory Non-metric Multidimensional Scaling (NMDS) to visually inspect
214 how species composition varied along the elevation gradient (Appendix 2). To quantify the relative
215 contribution of turnover and intraspecific trait variation for CWM and FD indices, we used the approach
216 proposed by Lepš et al., (2011). This approach decomposes the total community functional variation
217 into its different components: intraspecific variation, species turnover and their covariation. It does so

by calculating a functional index (CWM or SES-FD in our case) for a given trait twice: 1) a “fixed-index” using species-level traits, i.e., holding traits constant as the species mean, thus incorporating only turnover, and 2) a “specific-index” based on an individual by trait matrix, therefore incorporating both turnover and intraspecific trait variation. The difference between the “specific-index” and the “fixed-index” returns the “intraspecific-index", which incorporates only intraspecific trait variation. In this way, we could decompose the total trait variation into its species turnover and intraspecific components for each of our two indices (CWM and SES-FD) based on each of our four traits.

To test whether these three components covary with elevation, we fitted a set of linear regression models, with elevation as main predictor. In a first set of 12 (four traits x three components) models, we used CWM of individual traits as response variable. To control for confounding effects not directly related to elevation, we incorporated soil depth (as a proxy for water and nutrient availability), canopy closure (as a proxy for light availability), and forest type (two classes: pure beech, and mixed deciduous) as covariates. These three covariates were selected after checking for collinearity across all environmental variables (Appendix 3). Specifically, we calculated Pearson’s r correlation among all pairwise combinations of variables, and progressively dropped variables until no pair of highly correlated ($r \geq 0.5$) variables remained. We visually checked the assumptions of the linear regression models (Zuur et al., 2010). Following the regressions, we extracted the model sum of squares (SS) to calculate the covariation between the turnover and intraspecific trait variation components AS: $SS_{cov} = SS_{specific} - SS_{fixed} - SS_{ITV}$ (for detail see Lepš et al. 2011).

Contribution of intraspecific variation to trait convergence along the elevation gradient

To check whether communities at higher elevation had lower than expected functional diversity compared to communities at lower elevations, indicative of stronger habitat filtering, we fit a second set of 12 models. We fitted separate models for each individual trait and functional component using SES-FD as response variable and the same predictors as above. We interpreted the slope of the regression coefficient for elevation as an indication of increasing/decreasing convergence. Finally, we performed a two tailed t-test to check whether each of the three components of variation was significantly greater or smaller than 0 on average. In this way we were able to assess more precisely whether the traits exhibited a pattern of convergence (SES-FD < 0) or divergence (SES-FD > 0) across the entire elevation gradient.

All analyses were carried out using the software R version 4.3.3 (R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org). NMDS was carried out through the metaMDS

function (vegan package; Oksanen et al., 2022), FD was calculated using the *RaoRel* function (cati package; Taudiere and Violle, 2015), while CWM with the *cwm* function (weimea package; Zelený, 2018). Linear regression models were run with the *lm* function (stats package; R Core Team, 2024) and the decomposition of the functional components with the *traitflex.anova* function (cati package). The t-tests were run using the *t.test* function (stats package). Plots were made using the *ggplot* function (ggplot2 package; Wickham, 2016).

Results

Importance of different trait variation components along the elevation gradient

The decomposition of total functional community variation into their main components returned similar results for the two indices (CWM and SES-FD). The range of total explained variation across all models, indices and traits (R^2) spanned from 3% to 47%. Across all traits, most of the variation derived from turnover, the only exception being for traits related to the plant size dimension, namely the CWM calculated for leaf area and SES-FD calculated for plant height, for which we observed higher intraspecific than interspecific variability (Figure 2). Specifically, for $CWM_{Leaf\ area}$ turnover explained 1% of variation while intraspecific trait variation 2%, with a positive covariation of 3%. For $SES\text{-}FD_{Plant\ height}$, turnover explained 0.3% of variation, while intraspecific trait variation 1%, with a negative covariation of 1%. Positive covariation strongly increased total variation of traits related to plant size, namely $CWM_{Plant\ height}$ and $CWM_{Leaf\ area}$. Covariation was also positive for $SES\text{-}FD_{Leaf\ area}$ and $SES\text{-}FD_{LDMC}$, although with smaller magnitudes compared to CWM.

As elevation increased, the CWM decreased significantly for species turnover and total variation for plant height. For LDMC, the decrease in CWM was observed only for species turnover (Figure 3). $CWM_{Leaf\ area}$ and CWM_{SLA} showed no significant relationship with elevation (Appendix 4; Appendix 5).

Finally, the covariates included in the analysis generally did not contribute significantly to overall variations in CWM and SES-FD, with few exceptions. Canopy closure and soil depth significantly contributed to the variation of the CWMs calculated on leaf area and plant height. In the case of leaf area these contributions were significant mainly for intraspecific variation (8% for canopy closure and 3% for soil depth; Appendix 5) whereas for plant height only for species turnover (7% for soil depth; Appendix 5). For SES-FD, forest type contributed significantly to the variation of species turnover for both SLA and LDMC (34% and 13% respectively; Appendix 6).

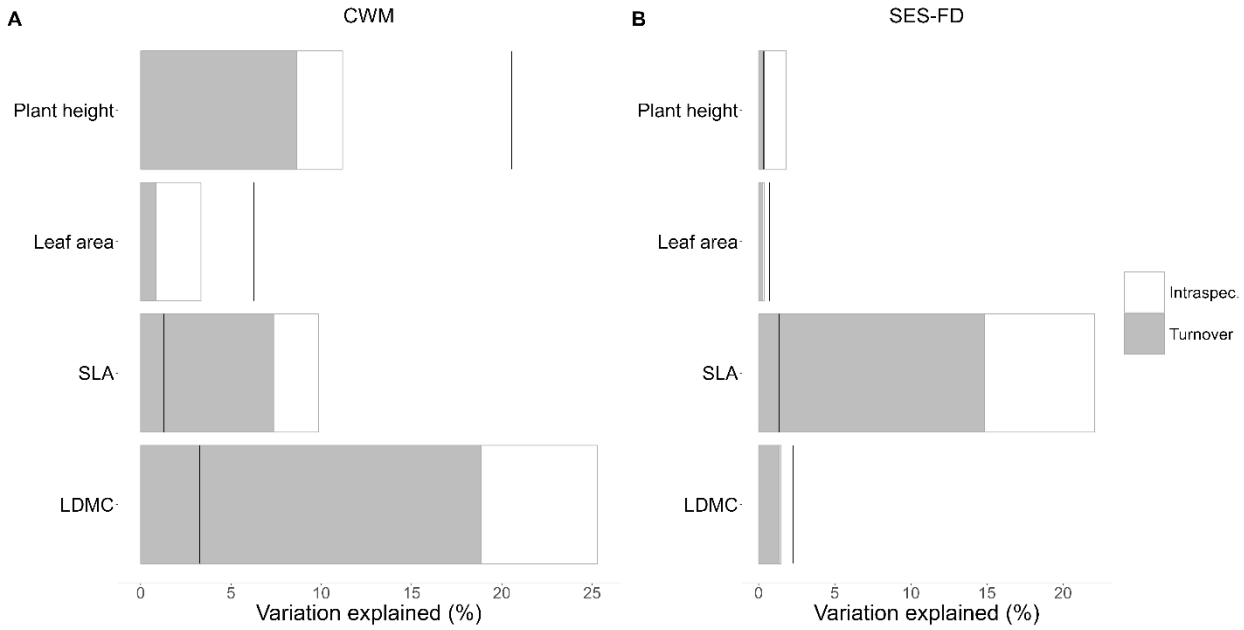

Figure 2 - Decomposition of total variation by a linear model including elevation, canopy closure, soil depth and forest type, across functional traits and indices. A) decomposition of the Community weighted means (CWMs); B) decomposition of the standard effect size of functional diversity (SES-FD). Grey area represents the variation explained by turnover, the white area the variation explained by interspecific trait variability (ITV). The black line represents the total variation explained. The space between the right end of the bar and the black line corresponds to the effect of covariation: if the black line is beyond the right end of the bar, covariation is positive; if it crosses the bar, covariation is negative.

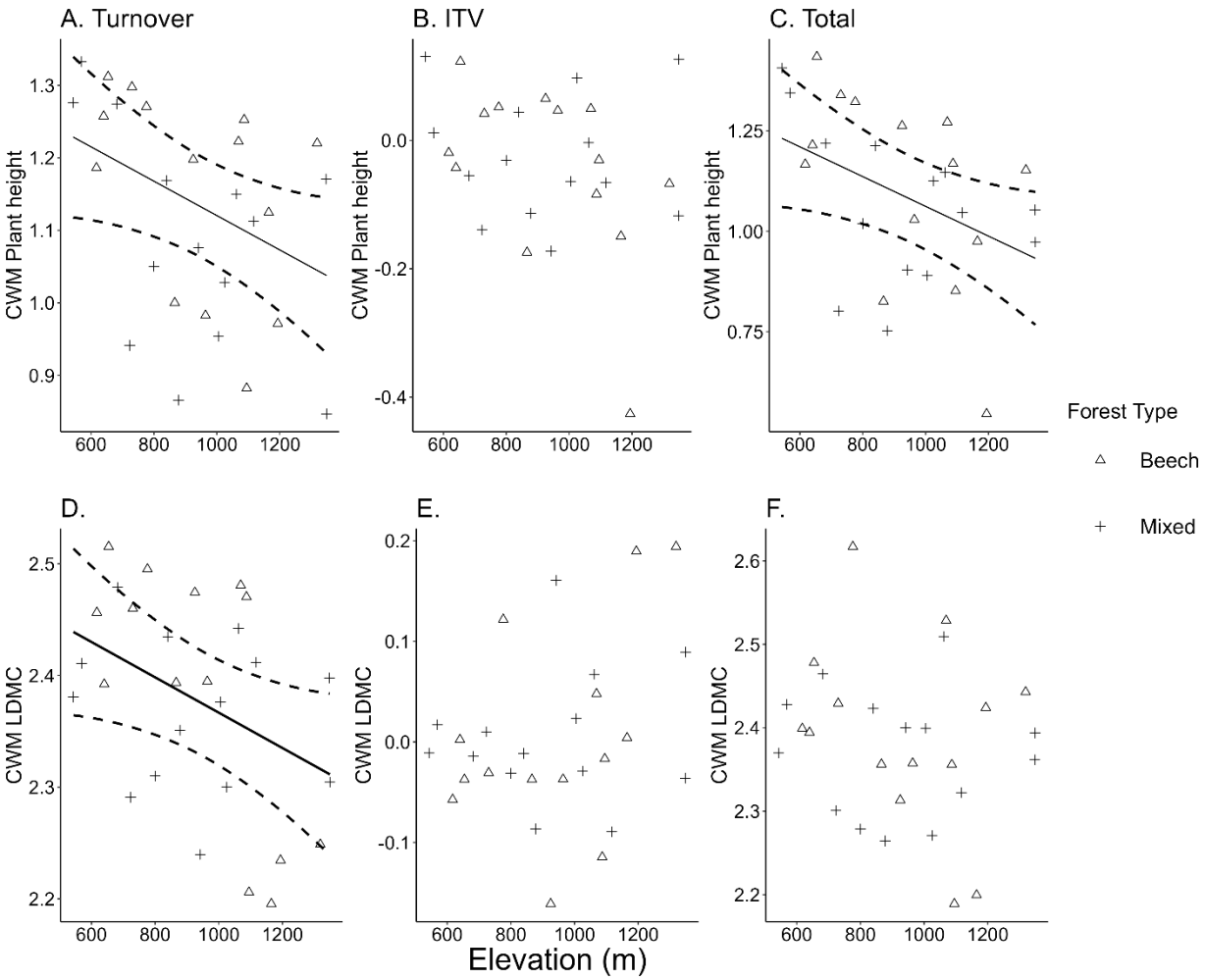

Figure 3 – Community weighted means (CWMs) regression for plant height (top row: A,B,C) and leaf dry matter content (LDMC – bottom: D,E,F) for: turnover (i.e., fixed traits: A,D), intraspecific trait variation (ITV: B,E) and total variation (i.e., specific traits: C,F). Triangles represents plots in pure beech forests, plus (+) symbols represent plots where *Fagus sylvatica* was associated with other deciduous trees (e.g. *Ostrya carpinifolia* and/or *Quercus pubescens*). The graph shows the model fit (smooth line), together with the standard error (dashed line) of significant models.

Contribution of intraspecific variation to trait convergence along the elevational gradient

We did not observe any significant relationship between SES-FD and elevation, in any of the three components of variation, for any of the traits. The functional diversity of the species turnover component, however, was mainly characterized by plot values lower than those expected by chance, returning a SES-FD significantly lower than zero for all traits but leaf area ($p < 0.01$ in all three cases), indicating a pattern of convergence (Figure 4; Appendix 6; Appendix 7; Appendix 8). Intraspecific trait variation never deviated from a random distribution, the only exception being plant height for which it was consistently greater than zero (SES-FD>0) indicating a pattern of divergence.

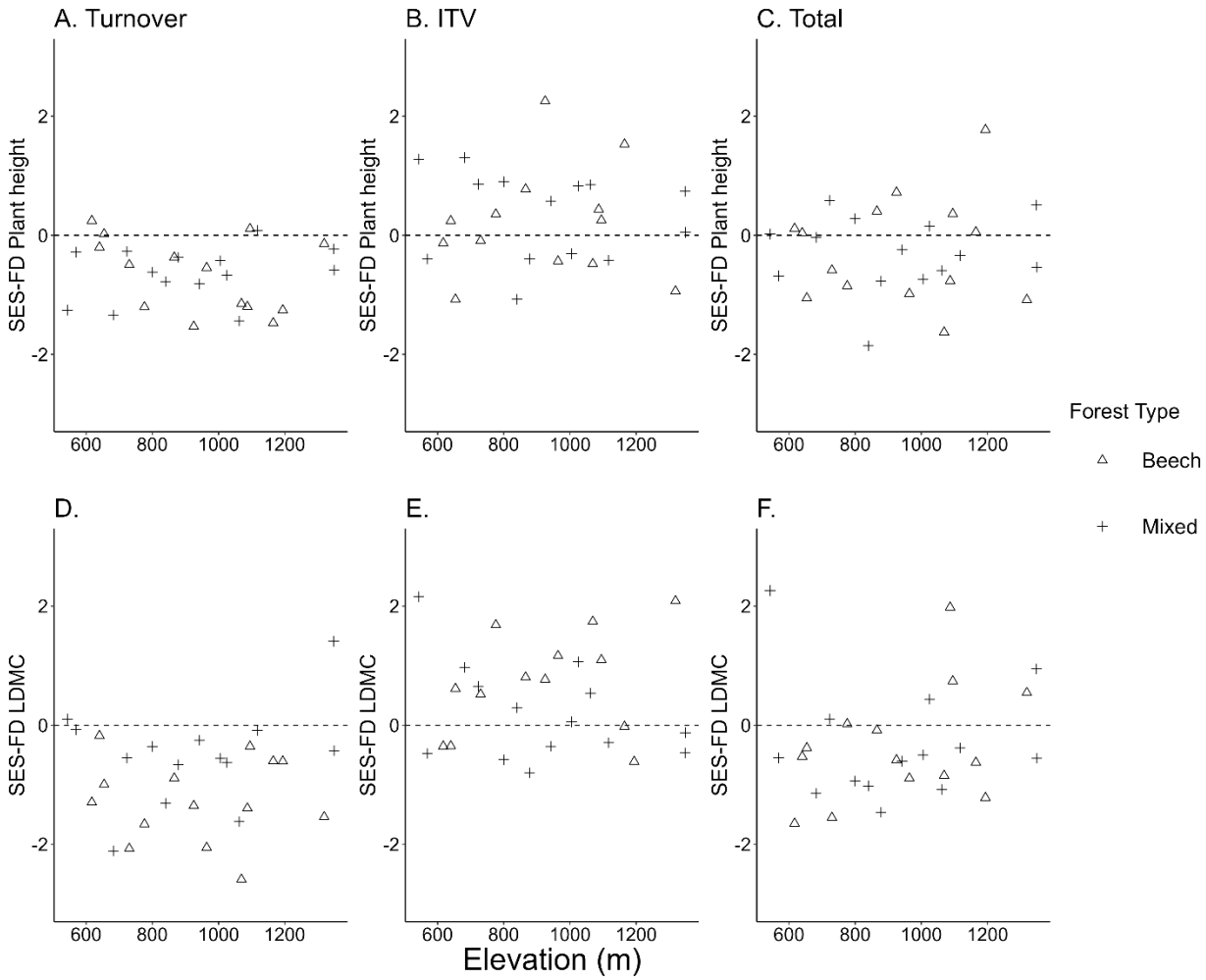

Figure 4 – Standard effect size of functional diversity (SES-FD) regression for plant height (top row: A,B,C) and leaf dry matter content (LDMC – bottom row: D,E,F) for: turnover (fixed traits: A,D); intraspecific trait variability (ITV: B,E); total variation (specific traits: C,F); Triangles represents plots in pure beech forests, plus (+) symbols represent plots where *Fagus sylvatica* was associated with other deciduous trees (e.g. *Ostrya carpinifolia* and/or *Quercus pubescens*). The horizontal dashed black line serves as a reference point denoting zero.

Discussion

In this study, we explored how elevation influences the functional variation of the herb-layer of European beech forests across a protected landscape. We used a trait-based approach to disentangle the three components of total community functional variation, i.e., species turnover, intraspecific trait variation, and their covariation (Lepš et al., 2011). With few exceptions, species turnover was consistently the main component of total functional variation across all the traits and indices we considered, even if the explained variation was generally very low. Specifically, we observed that at higher elevations herb layer assemblages have smaller plant size (lower plant height), displaying faster growing strategies (lower LDMC). No effect of elevation was detected on functional diversity variation,

although the communities were either converging or randomly assembled, depending on the trait and the functional component taken into consideration. In other words, herb-layer assemblages were composed by species more similar than expected by chance from the point of view of acquisition strategy and size, irrespective of elevation.

Species turnover drives the decrease in trait variation with elevation

By decomposing the total functional variation of the herb-layer, a similar pattern was observed for both CWM and SES-FD. The explained variation was generally low in both cases, likely attributable to the homogeneous characteristics of the study area and the dominance of species with similar trait values within the communities. Notably, trait variation was found to be driven mainly by species turnover across most of the traits we considered, implying that changes in species composition play a crucial role in shaping community functional variation and that functional traits tend to vary more between species than among individuals of the same species, which is in line with previous research (Garnier et al., 2001; Jung et al., 2010; Kichenin et al., 2013; Burton et al., 2017). Nevertheless, we did find exceptions. Specifically, the $CWM_{Leaf\ area}$ and $SES\text{-}FD_{Plant\ height}$ displayed greater intraspecific variability, which at least for leaf area contradicts the broader pattern observed by Siefert et al., 2015. In general, traits which exhibit higher intraspecific trait variation refer to the plant economic spectrum, such as SLA and LDMC, and to whole plant traits (i.e., plant height), probably because these traits tend to have a greater plastic response to local conditions such as light availability and/or other environmental factors (Meziane and Shipley, 1999; Rozendaal et al., 2006; Blondeel et al., 2020; Chelli et al., 2021, 2024). We interpret the high intraspecific trait variability observed for leaf area as the result of the intricate interplay of climatic, microclimatic, and allometric factors, shaping leaf characteristics (Diaz et al., 2016), also given its significant correlation with canopy closure (Appendix 5).

As elevation increased, total trait variation generally decreased, although this pattern was only significant for the species turnover component of plant height and LDMC. The lack of a significant effect of elevation on intraspecific trait variation partially contrasts with the general response found in a recent meta-analysis across different mountain ranges worldwide (Midolo et al., 2019). While this might be due to the relatively short elevation gradient considered in our work, it is noteworthy that we did observe a negative covariation between turnover and intraspecific variation for CWM_{LDMC}. This indicates that the increase in the contribution of fast-growing species at higher elevations is coupled with an increase of slow-growing individuals within species. We also observed a negative covariation between turnover and intraspecific trait variability for CWM_{SLA} along the elevation gradient, with an increasing

trend for species turnover coupled with a decreasing one for intraspecific trait variation. In line with Kichenin et al., (2013), the decreasing trend of SLA among individuals could be attributed to possible increases in light quantity and evapotranspiration as elevation increases, leading to species which are lower in stature, with thicker leaves and slower-growing rates. However, this pattern is counteracted by species turnover, which increases with elevation, suggesting that the decrease in temperature associated to higher elevations may favour species with thinner leaves and faster-growing rates. Given the considerable ambiguity that persists regarding the intricate compensating effect of plant communities to environmental factors, however, further research is needed to explain the ecological meaning of this negative covariation (Lepš et al., 2011; Campetella et al., 2019).

Convergence is widespread in herb-layer communities but does not vary with elevation

We did not observe any significant effect of elevation on functional convergence based on SES-FD, which was surprising both given the theoretical expectations stemming from the habitat filtering hypothesis (Keddy, 1992), and previous findings on leaf (Read et al.,2014) and seed traits (Rosbakh et al., 2022). Yet, we did find that convergence was the norm in herb layer communities across our entire elevation gradient, at least when considering the species turnover component. In other words, the herb layer was composed by species more functionally similar than expected by chance, suggesting that habitat filtering processes are at play (Pillar et al., 2020), and that the magnitude of these processes is constant across the entire elevation gradient we considered. We attribute this effect to the constant and intense shade exerted by the dense canopy cover of beech forests. Forest stands with high canopy closure cover are generally characterized by species having similar adaptations to face shade conditions (Cubino et al., 2021). Previous studies have highlighted the important effect of canopy closure, as the primary habitat filter in forest herb-layer assemblages, especially when considering leaf traits (Burton et al., 2017) and the species turnover component (Chelli et al., 2019; Vanneste et al., 2019; Maes et al., 2020). The correlation between leaf characteristics and canopy density arises from the trade-off between the high structural investment (high LDMC, low SLA) per unit area in well-lit conditions versus maximizing light absorption and leaf lifespan (low LDMC, low SLA) in shaded environments (Burton et al., 2017). Our results suggest that it is light condition, rather than elevation-related climatic conditions, to drive leaf trait variation in herb layer communities of European beech forests. In contrast, intraspecific variation did not differ significantly from the random expectation, suggesting the lack of deterministic processes.

While the impact of elevation on SES-FD was not statistically significant, it is crucial to note that forest type had a significant effect on functional diversity, specifically for the turnover component of SLA and LDMC. Due to the consistency of *F. sylvatica* dominance in the tree layer composition across the entire gradient, implying similarity in abiotic conditions, the observed variations in functional diversity for SLA and LDMC could suggest influences that go beyond the tree layer composition. These variations could potentially be attributed to systematic changes in soil conditions and topography along the elevation gradient, that our study design and selection of covariates could only partially account for. We cannot exclude that other factors play a role, however, such as land-use history and current forest management practices which have had and continue to have effects primarily on the amount of light reaching the herb layer.

Although our study sheds light on several important aspects of plant functional variation across an elevation gradient within a major forest ecosystem, there are a few limitations that should be taken into consideration. We focused on the primary axes of functional specialization, neglecting the belowground axes (Carmona et al., 2021). Plants in harsher environments, such as those found at higher elevations, may also change their root-to-shoot investment patterns to complete their life cycle faster, leading to a different pattern for belowground functional traits (Larcher, 2003). Another possible limitation was that the overlap in species along the gradient was minimal, making it difficult to distinguish the effect of species turnover and intraspecific variability (Lepš et al., 2011). Even if the two forest types were similar from an ecological point of view, differences in species composition could be due to the past and current management practices that characterize the study area, introducing variability and influencing the observed patterns of species composition, and functional diversity (Dieler et al., 2017).

Conclusion

In our study, we explored the impact of elevation on trait selection in temperate forest herb-layer communities. By dissecting the functional variation within these communities, we identified species turnover as the primary driver of variation, except for plant height and leaf area, where the intraspecific component accounted for most of the total variation. Notably, as elevation increased, we observed a significant reduction in average community-level plant height and leaf dry matter content. This trend was evident when considering species turnover and total trait variation. Furthermore, our investigation of functional diversity revealed that these communities exhibited either a convergent or random assembly pattern at species turnover level, and that this pattern did not vary with elevation. These findings shed light on how environmental factors, such as elevation and canopy closure, influence trait

selection within temperate forest herb-layer communities. They underscore the need for better accounting for intraspecific variation as an important driver of functional plant response to climate change.

Author Contribution

A.F. conceived the research idea, collected data, performed statistical analyses, and led the writing; A.B. and F.M.S. contributed in the writing and editing of the original draft; D.A. and A.C. contributed in reviewing and editing the final manuscript; A.C. and F.M.S. equally supervised the entire project; all authors discussed the results and commented on the manuscript.

Data availability statement

Data can be accessed and downloaded from Zenodo though the following doi: 10.5281/zenodo.10599617; R scripts used can be accessed and reproduced from Github through the following link: https://github.com/AriannaFerrara/Elevation-and-Intraspecific-trait-variability.git

Acknowledgements

A.F. acknowledges the support of the National Park “Foreste Casentinesi, Monte Falterona e Campigna” in the PhD project ‘Conservation of natural vegetation dynamics within the National Park of Casentinesi Forests’. The Arma dei Carabinieri - C.U.F.A. - Reparto Biodiversità di Pratovecchio Arezzo (Comandante Magg. Paola Ciampelli), are acknowledged for their valuable logistical assistance and data contributions. F.M.S. acknowledges the support of the Italian Ministry of University and Research, under the Maria Rita Levi Montalcini program (2019). Additionally, Chiara Lelli, Alessandra Ronco and Qubo are acknowledged for their important contribution in the vegetation data provision and subsequent trait data collection. Finally, heartfelt gratitude is extended to Giacomo Cangelmi for his steadfast support throughout the project and beyond.

References

Anderson, J. T., Gezon, Z. J. (2015) Plasticity in functional traits in the context of climate change: a case study of the subalpine forb *Boechera stricta* (Brassicaceae). Global Change Biology, 21, 1689-1703. https://doi.org/10.1111/gcb.12770

Antolini, G., Pavan, V., Tomozeiu, R., Marletto, V. (2017) Atlante climatico dell'Emilia-Romagna 1961-2015. Arpae E-R. https://www.arpae.it.

Auger, S., Shipley, B. (2013) Inter-specific and intra-specific trait variation along short environmental gradients in an old-growth temperate forest. *Journal of Vegetation Science*, 24, 419–428. https://doi.org/10.1111/j.1654-1103.2012.01473.x

Blondeel, H., Perring, M.P., De Lombaerde, E., Depauw, L., Landuyt, D., Govaert, S. et al. (2020) Individualistic responses of forest herb traits to environmental change. *Plant Biology*, 22, 601-614. https://doi.org/10.1111/plb.13103

Botta-Dukát, Z., Czúcz, B. (2016) Testing the ability of functional diversity indices to detect trait convergence and divergence using individual-based simulation. *Methods in Ecology and Evolution*, 7, 114–126. https://doi.org/10.1111/2041-210X.12450

Bresciani, A., Borchi, S., Chiccioli, P., Fantoni, I., Nicoloso, S. (2008) Il piano di gestione del complesso regionale Foreste Casentinesi (AR): la selvicoltura quale strumento di realizzazione delle finalità del Parco nazionale. *III Congresso Nazionale di Selvicoltura*, 109–115.

Bricca, A., Musciano, M.D., Ferrara, A., Theurillat, J.-P., Cutini, M. (2022) Community assembly along climatic gradient: Contrasting pattern between- and within- species. *Perspective in Plant Ecology, Evolution and Systematics*, 56, 125675. https://doi.org/10.1016/j.ppees.2022.125675

Bricca, A., Bonari, G., Padullés Cubino, J., Cutini, M. (2023) Effect of forest structure and management on the functional diversity and composition of understorey plant communities. *Applied Vegetation Science*, 26, 12710. https://doi.org/10.1111/avsc.12710

Burton, J.I., Perakis, S.S., McKenzie, S.C., Lawrence, C.E., Puettmann, K.J. (2017) Intraspecific variability and reaction norms of forest understorey plant species traits. *Functional Ecology*, 31, 1881-1893. https://doi.org/10.1111/1365-2435.12898

Campetella, G., Chelli, S., Wellstein, C., Farris, E., Calvia, G., Simonetti, E. et al. (2019) Contrasting patterns in leaf traits of Mediterranean shrub communities along an elevation gradient: Measurements matter. *Plant Ecology*, 220, 765-776. https://doi.org/10.1007/s11258-019-00951-y

Carmona, C.P., Bueno, C.G., Toussaint, A., Träger, S., Díaz, S., Moora, M. et al. (2021) Fine-root traits in the global spectrum of plant form and function. *Nature*, 597, 683-687. https://doi.org/10.1038/s41586-021-03871-y

Chelli, S., Simonetti, E., Campetella, G., Chiarucci, A., Cervellini, M., Tardella, F.M. et al. (2019) Plant diversity changes in a nature reserve: a probabilistic sampling method for quantitative assessments. *Nature Conservation,* 34, 145–161. https://doi.org/10.3897/natureconservation.34.30043

Chelli, S., Ottaviani, G., Simonetti, E., Campetella, G., Wellstein, C., Bartha, S. et al. (2021) Intraspecific variability of specific leaf area fosters the persistence of understorey specialists across a light availability gradient. *Plant biology*, 23, 212-216. https://doi.org/10.1111/plb.13199

Chelli, S., Bricca, A., Tsakalos, J.L., Andreetta, A., Bonari, G., Campetella, G. et al. (2024) Multiple drivers of functional diversity in temperate forest understories: Climate, soil, and forest structure effects. *Science of the Total Environment*, 916, 170258. https://doi.org/10.1016/j.scitotenv.2024.170258

Conti, F., Abbate, G., Alessandrini, A., Blasi, C. (2005) An annotated checklist of the Italian vascular flora. 1-420. Palombi.

Cubino, J.P., Biurrun, I., Bonari, G., Braslavskaya, T., Font, X., Jandt, U. et al. (2021) The leaf economic and plant size spectra of European forest understory vegetation. *Ecography*, 44, 1311-1324. https://doi.org/10.1111/ecog.05598

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: Theseus and the partitioning of diversity. *Journal of Vegetation Science*, 21, 992–1000. https://doi.org/10.1111/j.1654-1103.2010.01195.x

de Bello, F., Carmona, C. P., Dias, A. T., Götzenberger, L., Moretti, M., Berg, M. P. (2021) Handbook of trait-based ecology: from theory to R tools. Cambridge University Press.

Díaz, S., Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in ecology & evolution*, 16, 646-655. https://doi.org/10.1016/S0169-5347(01)02283-2

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S. et al. (2016) The global spectrum of plant form and function. *Nature*, 529, 167–171. https://doi.org/10.1038/nature16489

Di Biase, L., Fattorini, S., Cutini, M., Bricca, A. (2021) The role of inter-and intraspecific variations in grassland plant functional traits along an elevational gradient in a Mediterranean mountain area. *Plants*, 10, 359. https://doi.org/10.3390/plants10020359

Dieler, J., Uhl, E., Biber, P., Müller, J., Rötzer, T. and Pretzsch, H. (2017) Effect of forest stand management on species composition, structural diversity, and productivity in the temperate zone of Europe. *European Journal of Forest Research*, 136, 739-766. https://doi.org/10.1007/s10342-017-1056-1

Dunne, J. A., Harte, J., Taylor, K. J. (2003) Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. *Ecological monographs*, 73, 69-86. https://doi.org/10.1890/0012-9615

Funk, J.L., Larson, J.E., Ames, G.M., Butterfield, B.J., Cavender-Bares, J., Firn, J. et al. (2017) Revisiting the H oly G rail: using plant functional traits to understand ecological processes. *Biological Reviews*, 92, 1156–1173. https://doi.org/10.1111/brv.12275

Garnier, E., Laurent, G., Bellmann, A., Debain, S., Berthelier, P., Ducout, B. et al. (2001) Consistency of species ranking based on functional leaf traits. *New Phytologist*, 152, 69–83. https://doi.org/10.1046/j.0028-646x.2001.00239.x

Garnier, E., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M. et al. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85, 2630-2637. https://doi.org/10.1890/03-0799

Gilliam, F.S. (2014) The Herbaceous Layer in Forests of Eastern North America. Oxford University Press, New York, NY.

Götzenberger, L., de Bello, F., Bråthen, K.A., Davison, J., Dubuis, A., Guisan, A. et al. (2012) Ecological assembly rules in plant communities-approaches, patterns and prospects. *Biological Reviews,* 87, 111–127. https://doi.org/10.1111/j.1469-185X.2011.00187.x

Götzenberger, L., Botta-Dukát, Z., Lepš, J., Pärtel, M., Zobel, M. and de 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, 1275-1287. https://doi.org/10.1111/jvs.12452

Haller, A., Bender, O. (2018) Among rewilding mountains: Grassland conservation and abandoned settlements in the Northern Apennines. *Landscape Research*, 43, 1068-1084. https://doi.org/10.1080/01426397.2018.1495183

Henn, J.J., Buzzard, V., Enquist, B.J., Halbritter, A.H., Klanderud, K., Maitner, B.S. et al. (2018) Intraspecific trait variation and phenotypic plasticity mediate alpine plant species response to climate change. *Frontiers in Plant Science*, 9, 1548. https://doi.org/10.3389/fpls.2018.01548

526 Jung, V., Violle, C., Mondy, C., Hoffmann, L., Muller, S. (2010) Intraspecific variability and trait-based
527 community assembly: Intraspecific variability and community assembly. *Journal of Ecology*, 98,
528 1134–1140. https://doi.org/10.1111/j.1365-2745.2010.01687.x
529 Keddy, P.A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of*
530 *Vegetation Science*, 3, 157–164. https://doi.org/10.2307/3235676
531 Kichenin, E., Wardle, D.A., Peltzer, D.A., Morse, C.W., Freschet, G.T. (2013) Contrasting effects of plant
532 inter- and intraspecific variation on community-level trait measures along an environmental
533 gradient. *Functional Ecology*, 27, 1254–1261. https://doi.org/10.1111/1365-2435.12116
534 Körner, C. (2016) Plant adaptation to cold climates. *F1000Research*, 5. https://doi.org/
535 10.12688/f1000research.9107.1
536 Körner, C. (2007) The use of 'altitude' in ecological research. *Trends in Ecology & Evolution*, 22, 569–574.
537 https://doi.org/10.1016/j.tree.2007.09.006
538 Larcher, W. (2003) Physiological plant ecology: ecophysiology and stress physiology of functional groups.
539 Springer Science & Business Media.
540 Legendre, P., Legendre, L. (2012) Numerical ecology, Third English edition. ed, Developments in
541 environmental modelling. Elsevier, Amsterdam.
542 Lelli, C., Nascimbene, J. and Chiarucci, A. (2018) Are available vegetation data suitable for assessing plant
543 diversity? A study case in the Foreste Casentinesi National Park (Italy). *Rendiconti Lincei. Scienze*
544 *Fisiche e Naturali*, 29, 355-362. https://doi.org/10.1007/s12210-018-0681-z
545 Lelli, C., Nascimbene, J., Alberti, D., Agostini, N., Zoccola, A., Piovesan, G., Chiarucci, A. (2021) Long-term
546 changes in Italian mountain forests detected by resurvey of historical vegetation data. *Journal of*
547 *Vegetation Science*, 32, e12939. https://doi.org/10.1111/jvs.12939
548 Lepš, J., de Bello, F., Šmilauer, P. and Doležal, J. (2011) Community trait response to environment:
549 disentangling species turnover vs intraspecific trait variability effects. *Ecography*, 34, 856-863.
550 https://doi.org/10.1111/j.1600-0587.2010.06904.x
551 Luo, Y.H., Liu, J., Tan, S.L., Cadotte, M.W., Wang, Y.H., Xu, K. et al. (2016) Trait-based community
552 assembly along an elevational gradient in subalpine forests: quantifying the roles of
553 environmental factors in inter-and intraspecific variability. *PLoS One*, 11, p.e0155749.
554 https://doi.org/10.1371/journal.pone.0155749
555 Maes, S.L., Perring, M.P., Depauw, L., Bernhardt-Römermann, M., Blondeel, H., Brūmelis, G. et al. (2020)
556 Plant functional trait response to environmental drivers across European temperate forest
557 understorey communities. *Plant Biology*, 22, 410–424. https://doi.org/10.1111/plb.13082
558 Májeková, M., Paal, T., Plowman, N.S., Bryndová, M., Kasari, L., Norberg, A. et al. (2016) Evaluating
559 Functional Diversity: Missing Trait Data and the Importance of Species Abundance Structure and
560 Data Transformation. *PLoS ONE*, 11, e0149270. https://doi.org/10.1371/journal.pone.0149270
561 Merla, G., Bortolotti, V. (1969) Note illustrative della Carta Geologica d'Italia alla scala 1: 100.000, Foglio
562 107 (M. Falterona). *Servizio Geologico d'Italia*, 1-52.
563 Meziane, D., Shipley, B. (1999) Interacting components of interspecific relative growth rate: constancy
564 and change under differing conditions of light and nutrient supply. *Functional Ecology*, 13, 611-
565 622. https://doi.org/10.1046/j.1365-2435.1999.00359.x
566 Midolo, G., De Frenne, P., Hölzel, N., Wellstein, C. (2019) Global patterns of intraspecific leaf trait
567 responses to elevation. *Global Change Biology*, 25, 2485–2498.
568 https://doi.org/10.1111/gcb.14646
569 Moran, E. V., Ormond, R. A. (2015) Simulating the interacting effects of intraspecific variation,
570 disturbance, and competition on climate-driven range shifts in trees. *PLoS One*, 10, e0142369.
571 https://doi.org/10.1371/journal.pone.0142369
572 Muller, R. N. (2003) Deciduous Forest Ecosystems. The herbaceous layer in forests of eastern North
573 America, 15. Oxford University Press

574 Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P. et al. (2022) vegan: Community
575 Ecology Package. R package version 2.6-4
576 Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S., Daniel, H. (2009) On the challenge of treating various
577 types of variables: application for improving the measurement of functional diversity. *Oikos*,
578 118, 391–402. https://doi.org/10.1111/j.1600-0706.2008.16668.x
579 Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. et al. (2016)
580 Corrigendum to: New handbook for standardised measurement of plant functional traits
581 worldwide. *Australian Journal of Botany*, 64, 715. https://doi.org/10.1071/BT12225_CO
582 Pesaresi, S., Biondi, E., Casavecchia, S. (2017) Bioclimates of Italy. *Journal of Maps*, 13, 955–960.
583 https://doi.org/10.1080/17445647.2017.1413017
584 Pescador, D.S., de Bello, F., Valladares, F., Escudero, A. (2015) Plant Trait Variation along an Altitudinal
585 Gradient in Mediterranean High Mountain Grasslands: Controlling the Species Turnover Effect.
586 *PLoS ONE*,10, e0118876. https://doi.org/10.1371/journal.pone.0118876
587 Pillar, V.D., Sabatini, F.M., Jandt, U., Camiz, S. and Bruelheide, H. (2021) Revealing the functional traits
588 linked to hidden environmental factors in community assembly. *Journal of Vegetation Science*,
589 32(1), p.e12976. https://doi.org/10.1111/jvs.12976
590 Ratier Backes, A., Römermann, C., Alexander, J.M., Arévalo, J.R., Keil, P., Padrón-Mederos, M.A. et al.
591 (2023) Mechanisms behind elevational plant species richness patterns revealed by a trait-based
592 approach. *Journal of Vegetation Science*, 34, p.e13171. https://doi.org/10.1111/jvs.13171
593 R Core Team (2024) R: A Language and Environment for Statistical Computing_. R Foundation for
594 Statistical Computing, Vienna, Austria. https://www.R-project.org/.
595 Read, Q.D., Moorhead, L.C., Swenson, N.G., Bailey, J.K., Sanders, N.J. (2014) Convergent effects of
596 elevation on functional leaf traits within and among species. *Functional Ecology*, 28, 37–45.
597 https://doi.org/10.1111/1365-2435.12162
598 Ricotta, C., Moretti, M. (2011) CWM and Rao's quadratic diversity: a unified framework for functional
599 ecology. *Oecologia* 167, 181–188. https://doi.org/10.1007/s00442-011-1965-5
600 Rosbakh, S., Chalmandrier, L., Phartyal, S., Poschlod, P. (2022) Inferring community assembly processes
601 from functional seed trait variation along elevation gradient. *Journal of Ecology*, 110, 2374-2387.
602 https://doi.org/10.1111/1365-2745.13955
603 Rozendaal, D.M.A., Hurtado, V.H., Poorter, L. (2006). Plasticity in leaf traits of 38 tropical tree species in
604 response to light; relationships with light demand and adult stature. Functional Ecology, 207-
605 216. https://doi.org/10.1111/j.1365-2435.2006.01105.x
606 Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A., Aarssen, L.W. et al. (2015) A
607 global meta-analysis of the relative extent of intraspecific trait variation in plant communities.
608 *Ecology Letters*, 18, 1406–1419. https://doi.org/10.1111/ele.12508
609 Sundqvist, M.K., Giesler, R., Wardle, D.A. (2011) Within- and Across-Species Responses of Plant Traits
610 and Litter Decomposition to Elevation across Contrasting Vegetation Types in Subarctic Tundra.
611 *PLoS ONE*, 6, e27056. https://doi.org/10.1371/journal.pone.0027056
612 Tardella, F.M., Bricca, A., Cutini, M., Ciaschetti, G., Frattaroli, A., Paura, B., et al. (2022) How large-scale
613 geographic factors affect the different dimensions of functional diversity. *Plant Ecology and*
614 *Evolution*, 155(1), pp.3-15. https://doi.org/ 10.5091/plecevo.84458
615 Taudiere, A., Violle, C. (2015) cati: an R package using functional traits to detect and quantify multi-level
616 community assembly processes. *Ecography*.
617 Tichý, L. (2016) Field test of canopy cover estimation by hemispherical photographs taken with a
618 smartphone. *Journal of vegetation science*, 27, 427-435. https://doi.org/10.1111/jvs.12350
619 Tilman, D. (2001) Functional Diversity, in: Encyclopedia of Biodiversity. Elsevier, pp. 109–120.
620 https://doi.org/10.1016/B0-12-226865-2/00132-2

621 Umaña, M.N., Swenson, N.G. (2019) Intraspecific variation in traits and tree growth along an elevational
622 gradient in a subtropical forest. *Oecologia*, 191, pp.153-164. https://doi.org/10.1007/s00442-
623 019-04453-6
624 Vanneste, T., Valdés, A., Verheyen, K., Perring, M.P., Bernhardt-Römermann, M., Andrieu, E. et al. (2019)
625 Functional trait variation of forest understorey plant communities across Europe. *Basic and*
626 *Applied Ecology*, 34, 1–14. https://doi.org/10.1016/j.baae.2018.09.004
627 Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E. (2007) Let the concept
628 of trait be functional! *Oikos* 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x
629 Warren, R.J., (2008) Mechanisms driving understory evergreen herb distributions across slope aspects:
630 as derived from landscape position. *Plant Ecology*, 198, 297-308.
631 https://doi.org/10.1007/s11258-008-9406-1
632 Westerband, A.C., Funk, J.L. and Barton, K.E. (2021) Intraspecific trait variation in plants: a renewed
633 focus on its role in ecological processes. *Annals of botany*, 127, 397-410.
634 https://doi.org/10.1093/aob/mcab011
635 Wickham, H. (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.
636 Zelený, D. (2018) _weimea: Weighted Mean Analysis_. R package version 0.1.4/r27
637 Zuur, A.F., Ieno, E.N., Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical
638 problems. *Methods in ecology and evolution*, 1, 3-14. https://doi.org/10.1111/j.2041-
639 210X.2009.00001.x

Supplementary Material

Appendix 1: List of measured variables with unit of measurement

Appendix 2: Non-metric Multidimensional Scaling (NMDS) depicting floristic variation along the elevation gradient

Appendix 3: Correlation matrix with all measured variables

Appendix 4: CWM regression for Leaf area and Specific leaf area (SLA)

Appendix 5: Extended results of the sum of squares for CWM's trait flex anova's relative contribution

Appendix 6: Extended result of the sum of squares for SES-FD trait flex anova's relative contribution

Appendix 7: SES-FD regression for Leaf area and Specific leaf area (SLA)

Appendix 8: SES-FD t.test results