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It's a long way to the top: Plant species diversity in the transition from managed to old-growth forests

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Abstract

Questions: Do vascular plant species richness and beta-diversity differ between managed and structurally complex unmanaged stands? To what extent do species richness and beta-diversity relate to forest structural attributes and heterogeneity?

Location: Five national parks in central and southern Italy.

Methods: We sampled vascular plant species composition and forest structural attributes in eight unmanaged temperate mesic forest stands dominated or co-dominated by beech, and in eight comparison stands managed as high forests with similar environmental features. We compared plant species richness, composition and beta-diversity across pairs of stands (unmanaged vs managed) using GLMMs. Beta-diversity was quantified both at the scale of each pair of stands using plot-to-plot dissimilarity matrices (species turnover), and across the whole data set, considering the distance in the multivariate species space of individual plots from their centroid within the same stand (compositional heterogeneity). We modelled the relationship between species diversity (richness and beta-diversity) and forest structural heterogeneity and individual structural variables using GLMMs and multiple regression on distance matrices.

Results: Species composition differed significantly between managed and unmanaged stands, but not richness and beta-diversity. We found weak evidence that plant species richness increased with increasing levels of structural heterogeneity and canopy diversification. At the scale of individual stands, species turnover was explained by different variables in distinct stands, with variables related to deadwood quantity and quality being selected most often. We did not find support for the hypothesis that compositional heterogeneity varies as a function of forest structural characteristics at the scale of the whole data set.

Conclusions: Structurally complex unmanaged stands have a distinct herb layer species composition from that of mature stands in similar environmental conditions. Nevertheless, we did not find significantly higher levels of vascular plant species richness and beta-diversity in unmanaged stands. Beta-diversity was related to patterns of deadwood accumulation, while for species richness the evidence that it increases with increasing levels of canopy diversification was weak. These results suggest that emulating natural disturbance, and favouring deadwood accumulation and canopy diversification may benefit some, but not all, facets of plant species diversity in Apennine beech forests.

KEYWORDS
beta-diversity, deadwood, *Fagus sylvatica*, National Park, tree species richness, understorey

1 | INTRODUCTION

The increasing global demand for timber and paper products, coupled with the greater use of renewable wood energy, recently fostered a stark increase in forest products consumption worldwide (FAO 2010). So far, these trends have had a profound impact on the European forest sector that increased both the production and the import of wood products and transitioned Europe from being a net importer to a net exporter of primary wood and paper products (Forest Europe 2015; UNECE/FAO 2011). However, whereas the annual increment currently being harvested in EU-28 increased between 1990 and 2010 (from 68% to 73%), in the same period Europe gained about 11.3 million ha of forest area (Forest Europe 2015). These contrasting trends derive from a general process of land-use polarization that is being observed in Europe (Jepsen et al., 2015). On the one hand, some forests are being managed more intensively than in the past, and an increasing proportion of wood production depends on forest plantations. On the other hand, those forests located in remote, montane or protected areas are currently managed less intensively than in the past, or even abandoned (Burrascano et al., 2016).

As a consequence, the proportion of European forests in the older age classes (>80 years old) and/or having an uneven-aged structure is following a general increase, even if with strong regional differences, being more marked in Western Europe as compared to Eastern Europe (UNECE/FAO 2011). In Italy, the trend towards increasing forest age has deeper roots than in most European countries, and proceeds at least since 1950 (Vilen et al., 2012). As a forest ages, peculiar structural features develop (Bradford & Kastendick, 2010), for instance through the accumulation of high quantities of large trees and deadwood (Burrascano, Keeton, Sabatini, & Blasi, 2013). This process determines the increase in general complexity (=heterogeneity) of the forest structure; here defined loosely to include both the spatial pattern of trees, whether living or dead, as well as other commonly used attributes related to the richness and abundance of tree species (McElhinny, Gibbons, Brack, & Bauhus, 2005).

If the variety of structural components (e.g., *SD* of tree diameters) as well as other attributes (e.g., deadwood abundance, large live tree density, tree species richness) are accounted for, the structural heterogeneity of a forest can be used as a proxy for the availability of key habitats for several forest-dwelling taxa, including species of high conservation value (Lindenmayer et al., 2014; Muscolo, Bagnato, Sidari, & Mercurio, 2014), or other desirable properties, e.g., C stock (McElhinny et al., 2005; Staudhammer & LeMay, 2001). In the last decades, special attention was paid to the structure and composition of those forests that, due to specific age and structural features, were identified as old-growth, and that are characterized by both being extremely complex in structure (Franklin et al., 2002; Motta et al., 2015) and by hosting an especially high number of species of conservation concern for several taxonomic groups (see e.g., Martikainen, Siitonen, Punttila, Kaila, & Rauh, 2000; Vicol, 2016). The gradient of naturalness ranging from managed to old-growth forests is long and complex, and uncertainty still exists on how the cessation of management may affect species diversity across the intermediate levels of this gradient. According to one of the most widely accepted forest naturalness classifications, two levels are recognized between managed and old-growth forests: new and long untouched forests (Buchwald, 2005). Although these levels of naturalness are expected to display peculiar ecological features and are likely to be widely represented across European montane and protected areas, their relevance for biodiversity conservation is still uncertain. While several studies focused on the conservation value of old-growth and primeval forests (Dymytrova, Nadyeina, Hobi, & Scheidegger, 2014) or on the effects of different forest management strategies on biodiversity (Decocq et al., 2004), relatively few studies investigated species diversity in those stands whose degree of naturalness is halfway between managed and old-growth forests (Sitzia et al., 2012). A European meta-analysis on species richness in managed vs unmanaged forests found 49 studies across all taxonomic groups. The great majority of such studies investigated boreal forests and were focused on differences in the diversity of bryophytes, lichens and beetles rather than of vascular plants (Paillet et al., 2010). The response of understorey vascular plant diversity to the cessation of management remains unclear for the temperate forests on both sides of the Atlantic Ocean, since it probably depends on site-specific characteristics, type of past management and length of time since the last disturbance (Duguid & Ashton, 2013; Paillet et al., 2010).

Understorey species may account for up to 80% of plant species in forests (Gilliam, 2007), and play an important role in the functioning of forest ecosystems, e.g., influencing nutrient fluxes and trophic networks. Understanding how herb layer diversity varies across different degrees of naturalness is crucial to develop sustainable management

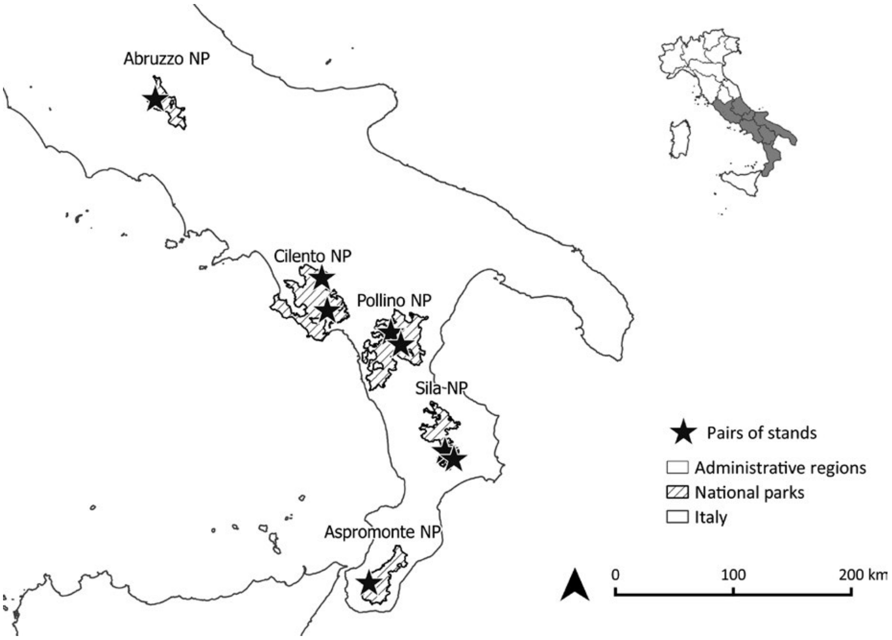

FIGURE 1 Location of the National Parks (NP) considered in this study, and the pairs of stands sampled

schemes. Furthermore, when comparing forest biodiversity, researchers should acknowledge that species richness (i.e., number of species observed in a given forest stand) is only one aspect of biodiversity, and that this is a multi-faceted concept encompassing other relevant components. Among these, species composition (i.e., relative abundance of different species) and β-diversity (i.e., extent of change in community composition; see Tuomisto, 2010) proved to be useful indicators of forest biodiversity (see Kenderes & Standovár, 2003; Standovár, Ódor, Aszalós, & Gálhidy, 2006, respectively).

In this study, we focus on temperate mesic forests across five montane national parks in central and southern Italy. We specifically investigate the differences in vascular plant species diversity by comparing unmanaged stands (newly and long untouched sites *sensu* Buchwald, 2005), and managed stands (high forests) having similar environmental conditions. Through this comparative approach that controls for site conditions, we aim to assess: (1) the differences in herb layer species richness, species composition and β-diversity between managed and unmanaged forests; (2) to what extent the species richness and compositional heterogeneity of the herb layer are controlled by structural heterogeneity, and by forest structural attributes. We hypothesize that unmanaged forests have a higher vascular plant species richness and β-diversity (Sabatini, Burrascano, Tuomisto, & Blasi, 2014) as a consequence of higher structural heterogeneity. We also hypothesized that the structural attributes of a given forest stand control herb layer plant community richness and composition (Burrascano, Lombardi, & Marchetti, 2008).

2 | METHODS

2.1 | Study area

The study area includes montane areas in central and southern Italy within five national parks (NPs), and encompasses a latitudinal range of about 600 km, from the central Apennines to the Aspromonte Massif, at the southernmost tip of the Italian peninsula (Figure 1). The five NPs here considered are (from north to south): Abruzzo, Lazio and Molise NP (hereafter Abruzzo NP), Cilento, Vallo di Diano and Alburni NP (hereafter Cilento NP), Pollino NP, Sila NP and Aspromonte NP.

Within these protected areas, we sampled eight pairs of forest stands, each pair including a managed and an unmanaged forest (see following subsection for the description of sampling design). The altitude of the sampled stands ranges from 750 m a.s.l. in the Pollino NP, to 1,840 m a.s.l. in the Abruzzo NP.

The great majority of the stands falls within the temperate climatic region, except for two pairs of stands within the Cilento NP and the Pollino NP that are within the transitional zone between the temperate and the mediterranean region (Blasi & Michetti, 2005). The sampled stands develop on lithological substrates that are mainly sedimentary and metamorphic rocks from different geologic origin (Table 1). The former characterize the stands located in the Abruzzo NP and Cilento NP, in the northern part of the study area; while metamorphic rocks characterize the stands that were sampled within Aspromonte NP, Sila NP and the Pollino NP. The complex geologic and climatic history of the study area, besides its current ecological heterogeneity, supports high levels of plant diversity, and a high density of endemic species (Peruzzi, Conti, & Bartolucci, 2014). Vast parts of the study area are included not only in national parks but also in several Natura 2000 sites (see http://www.minambiente.it/pagina/schede-e-cartografie).

2.2 | Sampling design and field methods

We collected information on the occurrence of late successional to over-mature forests that could be considered as newly or long untouched forests according to Buchwald (2005) classification of forest

TABLE 1 Site conditions (mean altitude and slope, and range of aspect values), dominant species, structural type of the sampled stands. M/UM refers to the management category (M, Managed; UM, Unmanaged). Coordinates are referred to WGS84/UTM zone 32N. All sites are high forests; the category old coppice refers to coppices that are in transition towards high forests.

Site	M/UM	Substrate	Altitude (m)	Aspect (°)	Slope (°)	Dominant Species	Structural Type
Abruzzo NP							
Vallone Ciafassa	M	Limestones	1678	360	25	*Fagus sylvatica*	Even-aged
Valle Cervara	UM	Limestones	1821	338–22	29	*Fagus sylvatica*	Uneven-aged
Cilento NP							
Monte Centaurino	M	Flysch	1146	348–50	29	*Fagus sylvatica; Quercus cerris*	Even-aged; Old coppice
Monte Centaurino	UM	Flysch	1135	320–90	29	*Fagus sylvatica; Alnus cordata*	Uneven-aged; Old coppice
Corleto Monforte	M	Limestones	1368	280–60	23	*Fagus sylvatica*	Even-aged
Corleto Monforte	UM	Limestones	1292	230–290	30	*Fagus sylvatica*	Uneven-aged; Old coppice
Pollino NP							
Bosco Magnano	M	Ophiolites	910	35–182	19	*Fagus sylvatica; Quercus cerris*	Multi-layered
Bosco Magnano	UM	Ophiolites	803	122	21	*Fagus sylvatica; Quercus cerris*	Multi-layered
Cugno Acero	M	Shales	1449	315–94	14	*Fagus sylvatica; Abies alba*	Multi-layered
Cugno Acero	UM	Shales	1485	315–95	14	*Fagus sylvatica; Abies alba*	Multi-layered
Sila NP							
Fondo Curto	M	Gneiss	1546	225–359	13	*Fagus sylvatica*	Even-aged
Fondo Curto	UM	Gneiss	1552	90–359	24	*Fagus sylvatica*	Even-aged
Monte Gariglione	M	Gneiss	1652	135–225	13	*Fagus sylvatica; Abies alba*	Even-aged
Monte Gariglione	UM	Gneiss	1712	90–225	17	*Fagus sylvatica; Abies alba*	Uneven-aged
Aspromonte NP							
Quarti	M	Gneiss	1292	236–347	21	*Fagus sylvatica*	Uneven-aged
Tre Limiti	UM	Schists	1558	100–250	38	*Fagus sylvatica; Abies alba*	Uneven-aged

naturalness. These naturalness classes include: ‘relatively intact forest (stand level) that has been essentially unmodified by human activity for the past 60–80 years (=long untouched) and ‘forest stands where forestry operations have been discontinued or never occurred since stand establishment, and which are known to have been left untouched for <60–80 years (=newly untouched).

These stands (hereafter unmanaged stands) were selected among those that, based on a preliminary survey among National Park and the State Forestry Corpse staff, displayed the following features: (1) dominated or co-dominated by European beech (*Fagus sylvatica*), (2) comply with the definition of newly or long untouched forests, and (3) show some structural features typical of the old-growth stage (see Wirth, Gleixner, & Heimann, 2009). The preliminary list was refined by maintaining only those forests that were over the rotation age typical for the area (90–100 years), and that might have experienced only minor interventions (selective cutting, light thinning) no later than 45 years ago.

For each unmanaged stand, a nearby (within 5 km) managed stand was selected. Wood harvesting is indeed allowed in the studied national parks (IUCN protected area category II) since these have among their objectives to account for the needs of local communities, including subsistence resource use (e.g., wood) in so far as these will not adversely affect the conservation objectives. To ensure that the stands could be compared, each pair of stands had similar topographic features (altitude, aspect and slope) and belonged to the same vegetation type (i.e., phytosociological association). We selected managed stands among those belonging to a mature developmental phase, and being currently managed as high forests. These included even- and uneven-aged high forests, some of which derive from old coppices. Further details on the type and severity of the last human intervention were not generally available, not even to local authorities; however, the fact that the managed stands used as comparison were in their mature developmental phase is likely to blur this kind of differences, which, however, are not dramatic across the whole study area. The average structural attributes for each stand (and relative *SD*) are reported in Appendix S1.

A total of eight pairs of stands were selected (Table 1). In each stand, we randomly located five plots, after excluding a 20-m wide buffer area running along the internal border of the stand. In the resulting 80 plots we sampled forest structural attributes and plant species composition. Standing trees were sampled in three concentric circular areas with 4, 13 and 20 m radius if their DBH was ≥2.5, 10 and 50 cm, respectively. Height measurements were made on one of every ten sampled trees; the height of the other trees was estimated using DBH–height curves. Lying deadwood was surveyed using the protocol proposed for the European ICP Forest level-II monitoring areas (Travaglini et al., 2006) in the intermediate (13 m radius) circular area used for standing trees. We measured lying deadwood components (logs, lying woody debris, stumps) with a diameter >10 cm. Measurements included DBH and length of all dead downed trees; length and diameter at half-length of all lying deadwood pieces; height and diameter at the top end of all stumps. The decay class of each deadwood component was recorded through a visual assessment of morphological wood features (presence/absence of bark and twigs; wood colour, texture and shape) according to the five-class system proposed by Hunter (1990).

Vascular plant species composition was sampled in a 20-m wide square plot concentric with the sampling unit used for the structural attributes. Each plot was divided in four subplots of 10 m × 10 m in order to ensure an accurate estimate of species cover. We visually assigned a cover value to each species in each subplot using an ordinal cover class scale with class limits 0.5%, 1%, 2%, 5%, 10%, 15%, 20% and thereafter every 10% up to 100% (each class includes its upper limit). The cover values were then averaged across the four subplots. The nomenclature of the species follows Conti, Abbate, Alessandrini, and Blasi (2005), Conti et al. (2007).

2.3 | Indices of stand structural heterogeneity and vascular plant diversity

The two categories (managed and unmanaged) were compared by means of several parameters indicating the degree of species diversity and structural heterogeneity. In order to quantify the structural heterogeneity of the overstorey in each plot, we combined a set of structural variables into a Structural Heterogeneity Index (SHI). The SHI is specifically designed for quantifying the varying sources of structural complexity in beech forests of southern Italy, taking as a reference the structural attributes of beech-dominated old-growth forests (Sabatini, Burrascano, Lombardi, Chirici, & Blasi, 2015). In order to calculate this index, eight plot-level structural variables are used: (1) growing stock volume (m^3/ha); (2) number of large living trees per hectare (DBH > 40 cm); (3) DBH diversity (Gini-Simpson diversity index—calculated as 1-Simpson concentration index described in Jost (2006) for 5-cm DBH classes); (4) tree height *SD*; (5) coarse woody debris index (CWDI); (6) tree species richness; (7) basal area of standing deadwood (m^2/ha); (8) total deadwood volume (m^3/ha). CWDI is an index that increases with the availability of deadwood across all decay classes; in particular, the CWD volume in different decay classes of a plot was compared to the reference distribution reported in the calibration data set in Sabatini et al. (2015). Each of these variables was rescaled to a 0–10 range according to its overall regional variability in the calibration data set. The eight scores were then added together and transformed to percentage to return the SHI index. For the selection of the variables included in the index, and for its calibration, we refer the reader to Sabatini et al. (2015).

Data on species composition were used to derive some indices of species diversity for the herb layer. Besides species richness, i.e., the number of plant species per plot, we quantified β-diversity using two different approaches. First, we calculated species turnover, i.e., the proportion of species composition that changes among plots, as the pair-wise Hellinger distance between each possible combination of plots, separately for each pair of stands. We used the Hellinger distance as it is commonly deemed appropriate for quantitative species data. It corresponds to a Euclidean distance between sites, where the species abundances are first divided by the site total abundance, and then square root-transformed, so that the common species contribute relatively less than rare species to the distance between sites (Legendre & Legendre, 1998). For each pair of stands, we built a plot-to-plot dissimilarity matrix, and considered its sub-diagonal elements (n = 45) as the response variable in subsequent analysis. The second approach quantified β-diversity as the distance in the multivariate species space (based on Hellinger distance) of individual plots (n = 80) from the centroid of the plots within the same stand (Anderson, Ellingsen, & McArdle, 2006). Hereafter, we refer to this concept as 'compositional heterogeneity'.

2.4 | Comparison between managed and unmanaged stands

We first tested the differences between managed and unmanaged stands in terms of SHI to verify that the unmanaged stands had a higher structural heterogeneity. Consequently, we compared the values of vascular plant species richness and compositional heterogeneity. In all cases we applied GLMMs. In the case of species richness, we assumed a negative binomial distribution and used the *log* link function (function *glmmadmb*, package *glmmADMB*; R Foundation for Statistical Computing, Vienna, Austria). In the case of compositional heterogeneity (i.e., the distance in the multivariate species space of a given plot from the stand centroid) and SHI we assumed a normal error distribution and used the *identity* link function. In all the analyses we considered the pairs of stands as a random effect. The models were checked visually for normality and homogeneity of the residuals. All analyses were run using R.

The overall difference in vascular plant species composition between unmanaged and managed stands was tested through PERMANOVA based on the Hellinger distance matrices (PERMANOVA, function *adonis*, *vegan* package). We took into account the nested sampling design by constraining the permutation within pairs of sites. Furthermore, we used the indicator species analysis (Dufrêne & Legendre, 1997) to assess the strength and statistical significance of the relationship between the abundance of individual plant species and each forest category (function *multipatt*, package *indicspecies*; De Cáceres & Legendre, 2009).

2.5 | Relationships between biodiversity indicators and forest structure and structural heterogeneity

To test the assumption that a higher structural heterogeneity (either synthesized through the SHI index, or based on individual structural attributes) corresponds to higher vascular plant species diversity, in terms of species richness, compositional heterogeneity and species turnover, we used different statistical models.

In the case of species richness and compositional heterogeneity, we used GLMMs as described in the previous paragraph, but using separately SHI and each individual structural attribute that is included in the index as explanatory variables. We fitted ten GLMMs, all including stand pair as random intercept. Nine models included either SHI or each one of the individual structural attributes on which SHI was calculated as a fixed effect. These models were compared to a null model including only the random intercept. In the case of species richness, the individual structural variables and the SHI were used after being rescaled to a 0–10 range, which is the range used for the construction of the index (see Sabatini et al., 2015). In the case of compositional heterogeneity, instead, we used as explanatory variables the absolute difference between the 0–10 values of a given structural variable in a plot and the stand median (i.e., the univariate equivalent of the multivariate dispersion from group centroids used for species composition). Finally, to understand which individual structural variable best predicted the species richness and compositional heterogeneity of vascular plants we followed an Information-Theoretic approach (Burnham & Anderson, 2002) and ranked the models according to their AICc (Akaike information criterion corrected for finite sample sizes), verifying if any of these performed better than the null model (function *model.sel*, package *MuMIn*).

We used Multiple Regression on distance Matrices (hereafter MRM; Lichstein, 2007) to assess what explanatory variables drive the variation of ground-layer species turnover, and to quantify the relative contributions of structural or environmental differences in explaining species turnover, after accounting for the spatial distribution of plots. The response variable was the matrix of plot-to-plot Hellinger distances calculated on the species composition of the herb layer. As explanatory variables, we used plot-to-plot distance matrices based on each structural and environmental variable separately. These matrices were calculated using the Euclidean distance, after standardization to *z*-scores. To account for the spatial distribution of plots, we built a matrix of log-transformed geographic distances between the centre points of the plots. Explanatory variables were organized into three sets: (1) forest structure, i.e., all the eight variables included in SHI; (2) three abiotic environmental factors, i.e., altitude, aspect and slope; and (3) plot-to-plot geographic distances. This analysis was run separately for each pair of stands since mixed effect models that manage distance matrices as response variable have not yet been developed, and thus there is no way to account for the nested nature of the data when running a single regression model on the whole data set. The important structural, environmental or spatial distance matrices for explaining species turnover were identified through forward selection. The variables that were significant ($p < .05$) after this preliminary selection were included in a full model. Successively, non-significant variables were discarded step-wise, through backward elimination. The final model was used for quantifying the total variation explained, and to identify those variables with a significant conditional effect on the prediction of species turnover. We followed standard decomposition techniques to partition the variation into 'unique' and 'shared' fractions of variance explained by the three sets of variables (Duivenvoorden, Svenning, & Wright, 2002). MRM was calculated using the R function *MRM* in the *ecodist* package (Goslee & Urban, 2007).

3 | RESULTS

3.1 | Differences between managed and unmanaged forests

Unmanaged stands returned a significantly higher SHI value when compared to managed ones (Table 2). Mean species richness and compositional heterogeneity were slightly higher in the unmanaged category when compared to managed stands (23.5 vs 22.3 for species richness, and 1.43 vs 1.21 for compositional heterogeneity), although these differences were not significant (Table 2). However, when we tested the two categories for compositional differences we found these to be highly significant (F-statistic equals 1,708 and *p*-value is .02). Only a few species were highlighted as associated to each individual category of stands (Table 3).

3.2 | Relationships between biodiversity indicators and forest structure and structural heterogeneity

When modelling species richness, two GLMMs had a lower AICc than the null model; the model including tree species richness and SHI as explanatory variable ranked as first and second, respectively (Table 4). However, both models received weak support from the data, as they had an AICc < 2 units lower than the null model. When modelling the compositional heterogeneity of the herb layer, only the model including the coarse woody debris index (CWDI) outperformed the null model, but also in this case the difference in AICc from the null model was extremely low (ΔAICc < 1; Table 5).

The relationships between forest structure and herb layer species turnover, as modelled through MRM, differed greatly among pairs of stands both in terms of total variation explained and in the explanatory variables retained in the final models (Figure 2). When considering each structural variable individually, the variables that were most often included were those related to lying deadwood, i.e., the total deadwood volume and the coarse woody debris index (CWDI). Other structural variables that were significantly related to species turnover in at least one pair of stands were: number of large living trees (in two pairs of stands), tree species richness, the DBH Gini-Simpson diversity index and growing stock. The geographic distance among plots had a significant marginal effect in five out of the eight pairs of plots (Figure 2).

The fraction of total variation explained by the final MRM models (i.e., after backward elimination of redundant variables) ranged between 0% and 80% (median 32.8%; see Figure 3). The structural variables accounted, on average, for the largest part of the variation explained (median 17.3%), followed by the spatial distance among plots (median 9%). The environmental variables (topography) explained a significant fraction of variation only in two stands, although in one case (Aspromonte) topography accounted for almost the totality of the share of the variation explained.

TABLE 2 Results of the GLMMs for the index of structural heterogeneity (SHI), species richness and compositional heterogeneity

Variable	Estimate	*SE*	*df*	statistic	*p*-value
SHI					
(Intercept)	53.926	3.934	8	13.71	<.001***
Management	8.399	1.978	71	4.25	<.001***
Species richness					
(Intercept)	2.994	0.157	8	19.03	<.001***
Management	0.093	0.078	71	1.18	.237
Compositional heterogeneity					
(Intercept)	0.477	0.032	13	14.96	<.001***
Management	0.04	0.039	7	1.02	.34

All the models groups are defined based on the categories managed/unmanaged, and the pairs of stands are used as random effect. ***identifies highly significant variables.

TABLE 3 Species with a significant indicator value for the two categories of forest stands (managed and unmanaged)

Species	Indicator value
Managed	
Mercurialis perennis	0.489*
Doronicum orientale	0.432*
Polystichum aculeatum	0.418**
Unmanaged	
Polystichum setiferum	0.609*
Veronica chamaedrys	0.439*
Scrophularia vernalis	0.387*
Urtica dioica	0.387*

Significance levels: *.05; **.01.

4 | DISCUSSION

4.1 | Shifts in forest structural heterogeneity occur more rapidly than those in vascular plant species diversity after withdrawal of management

When left free to naturally develop beyond the usual harvesting rotation period, high forest stands accumulate attributes of structural complexity that distinguish them from mature stands under active management in comparable environmental conditions. Forest complexity is differently affected by different management systems, and is expected to increase for increasing degrees of naturalness and time since last harvesting, as was recently found for forests in France, especially in the lowlands (Paillet et al., 2015). Our results suggest that a similar pattern can be observed in montane forests dominated or co-dominated by beech.

Structural heterogeneity has direct and indirect effects on the diversification of ecological conditions for the herb layer that may explain the significantly different species composition we found between managed and unmanaged stands. Structural heterogeneity correlates with different components of plant, animal and fungal diversity (Brunialti et al., 2010; Granito, Lunghini, Maggi, & Persiani, 2015; Taboada et al., 2010), although the strength of this relationship is likely dependent on the scale of the study, the range of the heterogeneity gradient, as well as the taxon considered (de Andrade et al., 2014; Sabatini et al., 2016). A high structural heterogeneity, indeed, may concur to determine changes in the plant diversity of the herb layer by creating fine-scaled partitioning of environmental resources, as found for old-growth forests (Bartels & Chen, 2010; Sabatini, Jiménez-Alfaro, Burrascano, & Blasi, 2014). For instance, high amounts of deadwood may locally buffer forest floor temperature, given the high thermal inertia of deadwood (Christensen et al., 2005); similarly, large gaps may create microhabitats having relatively high

TABLE 4 Ranking of ten GLMMs, comparing the response of herb-layer species richness as a function either of eight forest stand structural variables, or of the Structural Heterogeneity Index (SHI) against a null model (Null)

	Estimate		*SE*						
	(Int)	Explanatory	(Int)	Explanatory	*df*	logLik	AICc	ΔAICc	*D*
Tree species richness	2.867	0.034	0.182	0.018	4	−279	567.2	0	0.860
SHI	2.831	0.040	0.200	0.026	4	−280	568.4	1.18	0.859
Null	3.045	–	0.152	–	3	−281	568.6	1.38	0.867
Height *SD*	2.827	0.031	0.233	0.026	4	−280	569.4	2.12	0.870
Coarse Woody Debris Index	2.856	0.029	0.215	0.025	4	−280	569.5	2.22	0.867
Basal area of standing deadwood	3.025	0.017	0.150	0.015	4	−280	569.5	2.22	0.882
DBH diversity	2.950	0.012	0.213	0.018	4	−281	570.4	3.19	0.871
Total deadwood volume	2.997	0.011	0.169	0.018	4	−281	570.5	3.22	0.872
Growing stock	3.162	−0.015	0.268	0.027	4	−281	570.6	3.32	0.881
Number large living trees	3.065	−0.003	0.220	0.026	4	−281	570.8	3.58	0.879

D, dispersion.

TABLE 5 Ranking of ten GLMM, comparing the response of stand compositional heterogeneity of the herb layer to the forest stand structural variables, and Structural Heterogeneity Index (SHI) against a null model (null)

	Estimate		*SE*					
	(Int)	Explanatory	(Int)	Explanatory	*df*	logLik	AICc	ΔAICc
Coarse Woody Debris Index	0.472	0.020	0.031	0.013	4	41.95	−75.40	0.00
Null	0.497	–	0.025	–	3	40.77	−75.20	0.16
Height *SD*	0.475	0.020	0.030	0.016	4	41.55	−74.60	0.80
SHI	0.481	0.003	0.029	0.002	4	41.45	−74.40	1.00
Total deadwood volume	0.478	0.012	0.030	0.011	4	41.35	−74.20	1.20
DBH Gini-Simpson Diversity index	0.486	0.007	0.030	0.010	4	41.01	−73.50	1.89
Number large living trees	0.490	0.005	0.031	0.015	4	40.83	−73.10	2.25
Tree species richness	0.499	−0.003	0.027	0.009	4	40.81	−73.10	2.28
Basal area of standing deadwood	0.496	0.001	0.026	0.006	4	40.77	−73.00	2.36
Growing stock	0.498	−0.001	0.029	0.016	4	40.77	−73.00	2.37

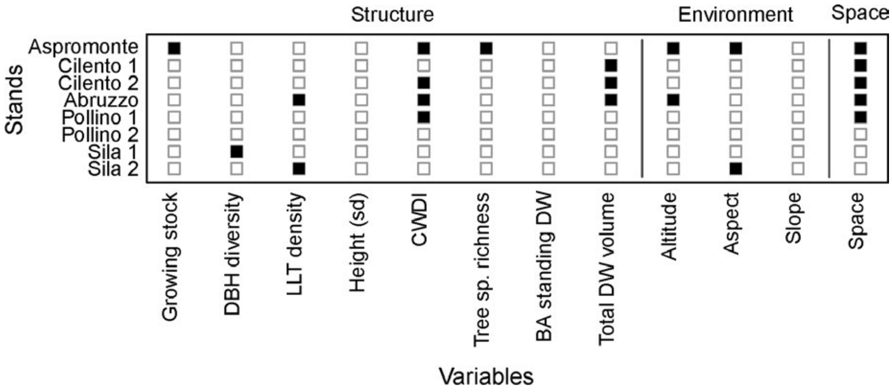

FIGURE 2 Variables that yield distance matrices with a significant ($p < .05$) marginal effect (black quadrats)

light availability coupled with high soil and air temperatures (Ritter, Dalsgaard, & Eirthorn, 2005). Consistently, the species that we identified as indicators of the unmanaged stands were characterized by ecological requirements more variable than those of the plants significantly associated to managed stands, suggesting that the ecological conditions at the forest floor of unmanaged forests were more variable than those of managed stands. Even if we did not carry out an analysis of the species richness and abundance of different ecological groups, we noticed that the species significantly associated with unmanaged stands, for instance, can be found in different types of forest vegetation (Biondi et al., 2014) and include both generalist species adapted to a wide range of temperature, soil reaction and nutrient concentration (e.g., *Urtica dioica*) and forest specialists (e.g., *Scrophularia vernalis*). In contrast, all the indicator species associated with managed forests were adapted to relatively high levels of nutrients in the soil (6–7 in the Ellenberg scale; Pignatti, Menegoni, & Pietrosanti, 2005) and were strictly associated with the thermophilous beech forests of the central Apennines (*Lathyro veneti-Fagenion*), or with the beech forest of the southern Apennines (*Geranio versicoloris-Fagion*).

Although different in terms of species composition, we did not find a significantly higher degree of species richness and compositional heterogeneity in unmanaged when compared to managed stands. In the case of species richness, our study supports the findings of a meta-analysis on North American temperate forests that found no detectable effects on species richness within the first 50 years after timber harvests (Duguid & Ashton, 2013). In the case of compositional heterogeneity, instead, our result is particularly striking given that the spatial variation of herb layer species composition is considered a particularly sensitive indicator of forest naturalness (Standovár et al., 2006). We hypothesize that an increase in species richness and compositional heterogeneity may only be detectable after a time period longer than that needed to detect changes in species composition. In this regard, it should be taken into account that several forest species, especially those that have been suggested as indicators of forest continuity (Hermy, Honnay, Firbank, Grashof-Bokdam, & Lawesson, 1999; Hermy & Verheyen, 2007), have a low colonization capacity and are affected not only by dramatic changes in land use (e.g., changes from forest to non-forest

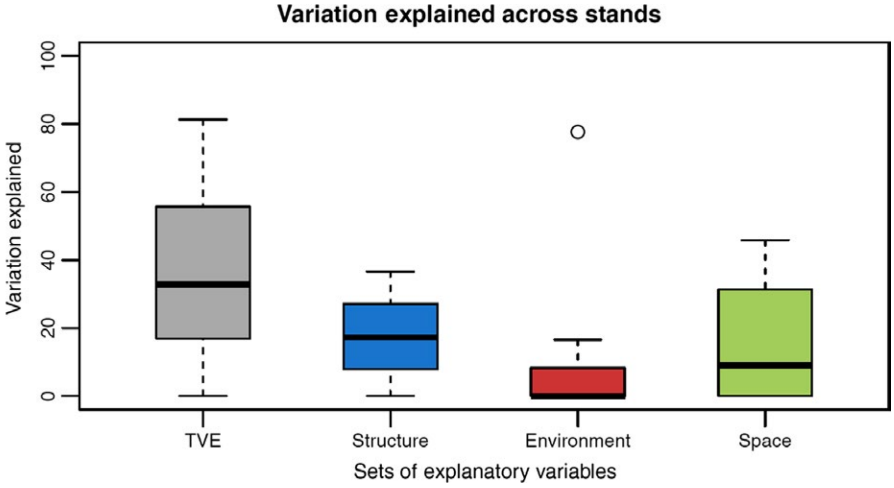

FIGURE 3 Boxplot showing the degree to which herb layer species turnover was explained by multiple regression on distance matrices (MRM) models [Colour figure can be viewed at wileyonlinelibrary.com]

and vice versa), but also by relatively severe disturbance events such as forest harvesting.

4.2 | Vascular plant species diversity is only weakly related to forest structural heterogeneity

We found weak evidence that herb layer species richness increased for increasing degrees of structural heterogeneity, as the model linking SHI to herb layer species richness was only 1.38 AICc units lower than the null model (Table 4). Therefore, the hypothesis that the complexity of forest structure has positive effects also on the richness of those organisms that may indirectly benefit from specific structural components, such as plants, received only limited support. A similar result was obtained for tree species richness. A diverse canopy creates a heterogeneous pattern of nutrients and light resources at the forest floor by determining differences in litter quantity and composition, and in the amount and quality of light that passes through the canopy (Barbier, Gosselin, & Balandier, 2008). For these reasons, canopy diversification was often demonstrated to influence vascular plant species composition (Burrascano, Sabatini, & Blasi, 2011; Burrascano et al., 2008; Sitzia et al., 2012). Even if only weakly supported by the data, the positive relationships between structural heterogeneity and canopy diversification, and the herb layer species richness suggest that resource heterogeneity rather than quantity may be the dominant control of herb layer diversity in late successional forests (Bartels & Chen, 2010).

Structural attributes together explained the highest share of the variation of species turnover within individual stands, even when accounting for the uneven number of variables included in the structural, environmental or spatial sets (data not shown). The variables having the strongest influence on plant species turnover were those related to deadwood (in five out of eight stands). At the scale of the whole data set, the only variable outperforming the null model was CWDI, but the improvement in terms of AICc was extremely modest. As a result, neither the variation in the overall structural heterogeneity (SHI), nor the individual structural variables were important predictors of compositional heterogeneity. This can be explained by the fact that the unmanaged stands we sampled were likely to have an even-aged homogeneous structure until recently, therefore they did not develop the horizontal heterogeneity typically related to the occurrence of different successional stages (Emborg, Christensen, & Helimann-Clausen, 2000), but only the scattered occurrence of some structures commonly found in old-growth forests. Indeed, while at the scale of a single stand a particular herb layer composition may directly depend on the occurrence of some specific indicators of structural heterogeneity, these relationships may not be detectable at the scale of the whole data set.

5 | CONCLUSIONS

A few decades after being withdrawn from forest management, beech-dominated and co-dominated forests had already accumulated high levels of structural heterogeneity that distinguished them from managed forests located in similar environmental conditions. This may partially explain the differences we observed in the species composition between the two categories, which likely depend on a more fine-scaled partitioning of environmental resources at the forest floor in unmanaged forests. However, in unmanaged forests the herb layer was neither more species-rich nor more variable in composition than in managed forests. Although herb layer species turnover was related to patterns of deadwood accumulation, we found limited evidence that species richness increased with increasing structural heterogeneity and canopy diversification. Therefore, where conservation goals are a priority, promoting these processes through harvesting schemes that increase the forest structural heterogeneity, e.g., by imitating gap-phase dynamics, releasing deadwood within gaps and promoting the recruitment of species other than beech, may benefit some, but not all, facets of plant species diversity in Apennine beech forests.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Appendix S1 Structural attributes of the forest stands

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