

One taxon does not fit all: Herb-layer diversity and stand structural complexity are weak predictors of biodiversity in *Fagus sylvatica* forests



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ABSTRACT

Since adequate information on the distribution of biodiversity is hardly achievable, biodiversity indicators are necessary to support the management of ecosystems. These surrogates assume that either some habitat features, or the biodiversity patterns observed in a well-known taxon, can be used as a proxy of the diversity of one or more target taxa. Nevertheless, at least for certain taxa, the validity of this assumption has not yet been sufficiently demonstrated.

We investigated the effectiveness of both a habitat- and a taxa-based surrogate in six European beech forests in the Apennines. Particularly, we tested: (1) whether the stand structural complexity and the herb-layer species richness were good predictors of the fine-scale patterns of species richness of five groups of forest-dwelling organisms (beetles, saproxylic and epigeous fungi, birds and epiphytic lichens); and (2) the cross-taxon congruence in species complementarity and composition between herb-layer plants and the target taxa.

We used Generalized Linear Mixed Models (GLMMs), accumulation curves and Procrustes analysis to evaluate the effectiveness of these surrogates when species richness, complementarity and composition were considered, respectively.

Our results provided a limited support to the hypothesis that the herb-layer plants and the stand structural complexity were good surrogates of the target taxa. Although the richness of the herb-layer plants received a stronger support from the data than structural complexity as a predictor for the general patterns of species richness, the overall magnitude of this effect was weak and distinct taxa responded differently. For instance, for increasing levels of herb-layer richness, the richness of lichens showed a marked increase, while the richness of saproxylic fungi decreased. We also found significantly similar complementarity patterns between the herb-layer plants and beetles, as well as a significant congruence in species composition between herb-layer plants and saproxylic fungi. Finally, when different stand structural attributes were considered singularly, only the total amount of deadwood received support from the data as a predictor of the overall species richness.

At the fine scale of this study, herb-layer plants and stand structural complexity did not prove to be effective surrogates of multi-taxon biodiversity in well-preserved southern European beech forests. Rather than on weak surrogates, these results suggest that sound conservation decisions should be supported by the information provided by comprehensive multi-taxonomic assessments of forest biodiversity.

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1. Introduction

The prioritization of conservation and restoration efforts requires a thorough understanding of the spatial distribution of biodiversity although, unfortunately, this is still remarkably poor for most taxa, especially at fine spatial scales (Grussu et al., 2014; Westgate et al., 2014). Ecosystems are extremely complex, and an adequate knowledge of the whole biodiversity spectrum is hardly achievable. This has led to the development and use of proxies or surrogates to simplify, represent, and help the management of forest ecosystems (Lindenmayer et al., 2014).

A surrogate is defined as “[a measure] that readily reflects: the biotic or abiotic state of an environment; represents the impact of an environmental change on a habitat, community or ecosystem; the abundance of a particular species; or is indicative of the diversity of a subset of taxa, or of wholesale diversity, within an area” (Lindenmayer et al., 2014). Surrogates are usually divided into two broad types (1) habitat-based and (2) taxa-based surrogates (Lewandowski et al., 2010; Lindenmayer et al., 2014). Habitat-based surrogates assume that some habitats or environmental features are good proxies of the richness, composition or diversity of one or more taxa. Taxa-based surrogates, instead, assume that the biodiversity patterns observed in a given taxon (the surrogate), which is usually well known and/or easy to sample, can be generalized to one or more (target) taxa. Thus, taxa-based surrogates assume a high cross-taxon congruence that avoids the need to detect all species within a study area (Gioria et al., 2011; Westgate et al., 2014). The rationale behind the use of taxa-based surrogates has been explained by several hypotheses: for instance, the effect of one taxon diversity on another taxon’s diversity could be mediated by cross-taxon functional interactions (e.g., trophic, mutualistic, parasitic), by a similar response to the environmental conditions or through a shared biogeographic history (Toranza and Arim, 2010; Gioria et al., 2011).

In certain ecological contexts, taxon- and habitat-based surrogates could be used jointly and return complementary information on the target taxa (Lindenmayer et al., 2014). For instance, in temperate forests both vascular plants and the forest stand structural characteristics were often considered as good surrogate candidates of forest overall biodiversity. Vascular plants are a potentially effective taxon-based surrogate, since they are relatively easy to sample and their taxonomy is sufficiently well described (Santi et al., 2010; Blasi et al., 2011). On the one hand, plants represent the bulk of both ecosystems’ biomass and net primary productivity, and play a fundamental role in the trophic networks of forest ecosystems. Trophic or mutualistic interactions may account for part of the patterns of congruence between vascular plants and other forest taxa, such as insects (de Araujo, 2013) or mycorrhizal fungi. For instance, arbuscular mycorrhiza can influence the forest plant species diversity by altering the competitive balance in plant communities (Gerz et al., 2016). On the other hand, vascular plants and other taxa may respond similarly to a common disturbance history (Nordén et al., 2014) or to shared environmental conditions in the understory, e.g. forest floor humidity or light intensity. In support of these hypotheses, several works reported that richness of vascular plant species is positively correlated with that of bryophytes (Rooney and Azeria, 2015), lichens (Blasi et al., 2010), and animals such as birds (Blasi et al., 2010) and butterflies (Santi et al., 2010). Nevertheless, contrasting results were reported and thus a rigorous testing of plants as a biodiversity indicator is still needed (Lewandowski et al., 2010; Santi et al., 2010; Gao et al., 2015).

Forest structural complexity, which synthesizes the variety of structural components occurring in a stand, is also a possible candidate as a habitat-based surrogate in temperate forests. Indeed, structural complexity shows a good potential to be used as a biodiversity proxy, at least when considering those taxa that utilize

specific forest structures (McElhinny et al., 2005; Gossner et al., 2014). Linking the stand structural complexity to specific taxa provides information about the proximate causes of biodiversity change, including those related to specific silvicultural practices. For instance, the lack of a certain structure may be correlated to the absence of a particular group of organisms, as it is the case with deadwood and saproxylic beetles or fungi (Bouget et al., 2014; Gossner et al., 2014).

Whatever kind of surrogate is chosen, it is necessary to carefully assess its effectiveness (Gao et al., 2015). A growing body of literature has emerged over the last decades to evaluate surrogates and synthesize the available information (Lewandowski et al., 2010; Rodrigues and Brooks, 2007; Westgate et al., 2014). For many taxa, the assumptions behind cross-taxon congruence have not yet been sufficiently tested, nor were the identity of the factors driving the huge variation observed across systems and scales (Gao et al., 2015). These factors may result in inconsistencies that may undermine the reliability of surrogacy indicators when applied to novel contexts (Kirkman et al., 2012; Westgate et al., 2014); for instance, the degree of cross-taxon congruence may vary greatly in relation to the spatial scale of the study (Lewandowski et al., 2010; Rodrigues and Brooks, 2007).

Different surrogates can also be designed to take into account different facets of biodiversity. Early works focused either on single species (e.g. umbrella species) or on the richness of a species assemblage as a proxy of the richness of a whole taxon or community (Lewandowski et al., 2010). In this case, cross-taxon congruence was measured by analyzing the existing pairwise correlations between the values of species richness of two or more taxa sampled across many sites. Nevertheless, focusing only on the species richness fails at adequately representing the various facets of biological diversity. The use of multiple measures of community structure (e.g. richness, complementarity and composition) is hence recommended to depict a comprehensive assessment of cross-taxon congruence (Gioria et al., 2011). Complementarity, for instance, accounts for the compositional difference between sites and it is therefore often considered in conservation planning, e.g. when selecting a set of sites or actions that together could preserve the maximum number of species in a given area (Ferrier, 2002; Rodrigues and Brooks, 2007; Lewandowski et al., 2010).

In this work, we tested: (1) the effectiveness of herb-layer species richness (as a taxa-based surrogate) and of stand structural complexity (as a habitat-based surrogate) at predicting simultaneously the general patterns of species richness of five groups of forest-dwelling organisms (hereafter “target taxa”), i.e., saproxylic and epigeous fungi, beetles, birds and lichens. The effect of the forest stand structural complexity was tested both using a synthetic index and considering a set of stand structural features individually. Finally, we evaluated (2) the cross-taxon congruence in species complementarity and composition between herb-layer plants and the target taxa.

2. Methods

2.1. Study area

The data here presented were collected within the context of the restoration project LIFE+ ‘FAGUS’ (11/NAT/IT/135, www.fagus-life-project.eu), and represent the information baseline that will be used to monitor the effects of the project’s concrete conservation actions. The project focused on two habitats of European priority interest according to the EU Habitats Directive (92/43/EEC) i.e., the habitat 9210* – Apennine beech forests with *Taxus* and *Ilex*, and the habitat 9220* – Apennine beech forests with *Abies alba* and beech forests with *Abies nebrodensis*. Data were collected in six European

Table 1
Main characteristics of the study areas.

National Park	Municipality (study area)	NATURA 2000 SCI	Habitat type	Coordinates (degrees)	Altitude (m a.s.l.)	Mean Annual Precipitation (mm)	Mean Annual Temperature (°C)	Area subjected to conservation actions (ha)	Number of sampling plots
Gran Sasso NP	Pietracamela (Prati di Tivo)	SCI IT7110202 “Gran Sasso”	9210*	42.5096 N 13.5679 E	1500	1062	10.6	7.86	5
	Pietracamela (Venacquaro)	SCI IT7110202 “Gran Sasso”	9210*	42.4988 N 13.5139 E	1250	1097	10.0	17.45	7
	Crognaleto (Incodara)	SCI IT7110202 “Gran Sasso”	9220*	42.5123 N 13.4735 E	1400	1097	10.0	11.23	7
Cilento NP	Corleto Monforte	SCI IT8050033 “Monti Alburni”	9210*	40.4705 N 15.4317 E	1300	1250	10.0	20.21	3
	Ottati	SCI IT8050033 “Monti Alburni”	9210*	40.5136 N 15.3292 E	1350	718	13.6	11.82	8
	Teggiano (M. Motola)	SCI IT8050028 “Monte Motola”	9220*	40.3761 N 15.4694 E	1200	716	13.5	1.3	3

The habitat type refers to the Annex I of the EU Habitats Directive (92/43/EEC): 9210* – Apennine beech forests with *Taxus* and *Ilex*; 9220* – Apennine beech forests with *Abies alba* and beech forests with *Abies nebrodensis*.
SCI: site of community interest.

beech (*Fagus sylvatica*) forests located in the Apennines, within two Italian national parks (Table 1). Three areas are located in central Italy, within the “Gran Sasso and Monti della Laga” National Park (hereafter “Gran Sasso NP”). The remaining three study areas are located within the “Cilento, Vallo di Diano and Alburni” National Park (hereafter “Cilento NP”), in southern Italy (Fig. 1).

2.2. Sampling design

The forest structural features and multi-taxon composition were sampled through a non-aligned systematic sampling method. Based on a preliminary field survey, we first defined an area of interest for each study area, i.e. the fraction of the study area where the habitats 9210* and 9220* actually occurred. The total surface of the area of interest across the six study areas was 70 ha. A 100 × 100 m square grid was then overlapped to the area of interest, and a sampling plot was randomly located within each cell of the grid completely contained within the area of interest. For two study areas located in Cilento NP (i.e. ‘Corleto Monforte’ and ‘Ottati’), the sampling design was slightly different, in order to be coherent with the methods applied in a previous project (Blasi et al., 2010; Burrascano et al., 2011). In this case, the sampling plots were located at the nodes of a 500 × 500 m square grid. A total of 33 plots were sampled, 19 in the Gran Sasso NP and 14 in the Cilento NP. For each plot, we recorded the topographical position in terms of altitude, slope and aspect.

2.3. Forest structural complexity

We sampled the structural features of the forest plots within three concentric circular areas with a radius of 4, 13, and 20 m. We recorded the species and diameter-at-breast-height (DBH) of every standing tree (living and dead) having a DBH greater than a given threshold for each area. The diameter thresholds was 2.5 cm for the 4 m radius area, 10 cm for the 13 m radius area, and 50 cm for the 20 m radius area. We also measured the height of one out of ten sampled trees, chosen randomly. Moreover, the length and diameter of all the lying deadwood components (minimum diameter ≥ 10 cm) were recorded in the intermediate circular area (13 m radius), assessing also the decay level based on the method proposed by Hunter (1990).

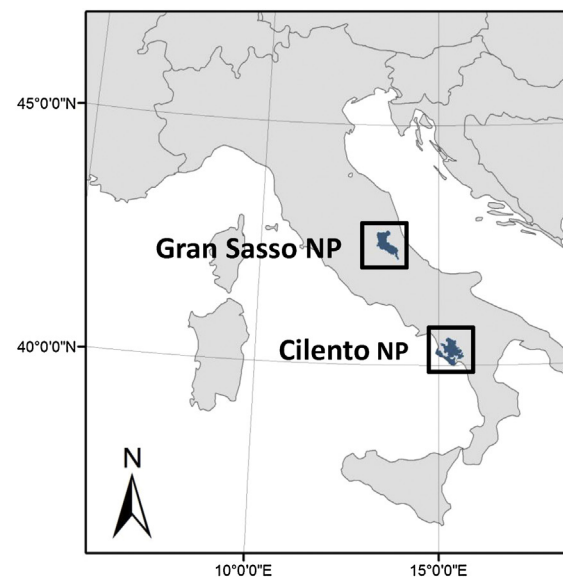
We then derived eight plot-level structural variables: (1) growing stock volume (m³/ha), (2) number of large living trees (DBH >40 cm), (3) DBH diversity (Gini-Simpson diversity index for 5-cm DBH classes), (4) tree height standard deviation, (5) coarse woody debris index (CWDI i.e. an index constructed to

score sites according to the CWD volume occurring in different decay classes, see McElhinny et al., 2006), (6) tree species richness, (7) basal area of standing deadwood (m²/ha), (8) total deadwood volume (m³/ha). These structural variables were selected among those routinely collected in plot-based forest inventories, keeping multicollinearity to a minimum, and were then used for calculating the Structural Heterogeneity Index (SHI). SHI is an index derived by Sabatini et al. (2015) which is designed to account for the main sources of structural complexity occurring in the beech forests of southern Europe, when compared to reference old-growth stands (Burrascano et al., 2013; Motta et al., 2015). In order to calculate SHI, each variable was scaled to a 0–10 range according to its overall regional variability. The eight scores were then combined into a simple additive index and transformed to percentage. SHI was calibrated against a dataset of 64 forest stands having different ages and structures, and being located across 12 forest areas in southern Italy. The calibration dataset encompasses an extent of about 137 km² with a substantial geographical overlap with the study areas here considered (Sabatini et al., 2015).

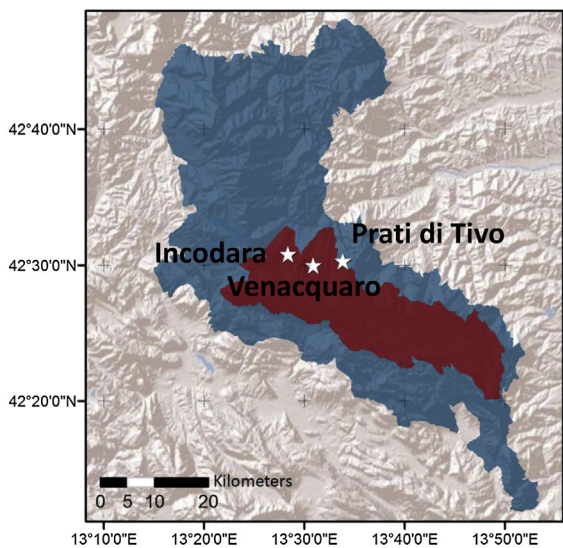
2.4. Biodiversity sampling

In 2013 we sampled the species diversity of different taxa in all the plots. For each taxon we used an *ad-hoc* protocol. The herb-layer vegetation was sampled in 20 m circular plots divided into four quadrants along the cardinal directions. We visually assigned a cover value to each species in each quadrant, 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 quadrants. Nomenclature of species follows Conti et al. (2005).

Epiphytic lichens were sampled on the three beech trees nearest to the center of each plot having a DBH equal or greater than 16 cm. Lichens were sampled using a portable 10 × 50 cm frame composed of five 10 × 10 cm quadrats; the frame was placed on the tree trunk facing the four cardinal directions, with the bottom part being at a height of 100 cm from the ground. All lichen species inside the frames were considered; at the plot level, the richness of the lichen assemblage equaled the total number of species occurring across the three sampled trees. The frequency of each species in each given plot was computed as the proportion of the 60 quadrats (10 × 10 cm) in which the species occurred. This protocol follows the European guidelines for lichen monitoring (Asta et al., 2002). Lichens nomenclature and general information on species biological traits and ecology were retrieved from Nimis and Martellos (2008).



Gran Sasso National Park



Cilento National Park

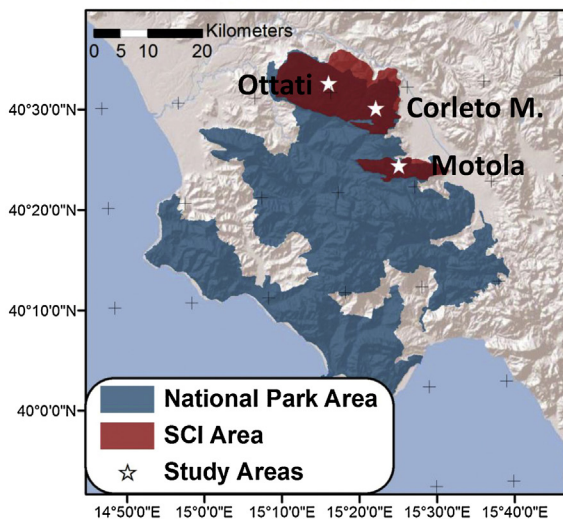


Fig. 1. Location of the national parks and of the study areas. SCI: site of community interest (*sensu* Habitats Directive; 92/43/EEC).

Fungi (both saproxylic and epigeous) were sampled in autumn 2013 in the same 13 m circular plot (530 m²) used for deadwood sampling. All the standing and downed deadwood components characterized by a mid-diameter greater than 10 cm were examined for sporocarps larger than 1 mm, and data on deadwood decay class and fungal morphogroups were also recorded. Since fungi were surveyed only once, our measure should not be considered as an inventory of the overall fungi richness, but rather as a snapshot in time. The nomenclature was based on the Dictionary of the Fungi (Kirk et al., 2008) and the CABI Bioscience Database of Fungal Names.

Forest-dwelling beetles were sampled using one window flight trap for each plot. Traps were placed at 1.5–2 m height above the ground to intercept the flight of insects; they were then trapped inside a preserving vial containing a solution of water and salt. Since this method does not exert an attraction selective with respect to saproxylic beetles, it was integrated through the use of eclectors (emergence traps). Eclectors were used for collecting saproxylic insects active in deadwood fragments on the forest floor. Depending on the availability of coarse woody debris, up to three eclector traps were set up on deadwood fragments in the first three decay classes. Traps were placed as close as possible to the plot center. Nevertheless, deadwood fragments were not available in all the sampling plots. For this reason, in order to keep the sampling effort constant through the plots in quantitative analyses, these were run only considering the beetles collected through window flight traps (~96% of the captures). The data obtained through the use of eclectors were only used to provide an integrative description of the beetle assemblages. The monitoring of saproxylic insects took place from June to September 2013. Each trap was sampled three times, once every 27–30 days. The species nomenclature follows Nieto and Alexander (2010).

Finally, breeding birds were sampled through one 10-minute count points, during which we recorded every species detected. The species nomenclature follows Brichetti and Fracasso (2015).

Each taxon was sampled by a different field team composed by one to three observers which conducted the survey in all the study areas. To ensure data quality and homogeneity a responsible in charge of supervising the fieldwork activities (S.B.) was appointed before starting sampling. We compared the sampling effort among different taxa by estimating the asymptotic richness of each assemblage using the first-order Jackknife estimator. We then calculated the ratio between the estimated asymptotic number of species and the number of species actually observed as an estimation of sampling completeness (Azzella et al., 2013; Gotelli and Colwell, 2010).

We decomposed the species diversity of each taxon into its alpha, beta and gamma components. Alpha diversity is the average number of species of a given taxon across the plots of a given study area; gamma diversity is the total number of species occurring in a study area and beta diversity was calculated with the multiplicative approach as $\beta = \gamma/\alpha$.

2.5. Using taxa- and habitat-based surrogates to predict multi-taxon species richness

To identify the response of species richness simultaneously across all the target taxa (saproxylic and epigeous fungi, beetles, birds and epiphytic lichens) to increasing levels of herb-layer species richness and stand structural complexity, we ran a set of GLMMs. The models assumed a Poisson distribution of errors and used a logarithmic link function. The response variables were the species richness values observed for each of the five target taxa across the 33 sampling plots (=165 observations). Hereafter, we refer to this as to multi-taxon species richness. We modeled the multi-taxon species richness as a function of four explanatory

variables, i.e. (1) the species richness of the herb-layer, (2) the structural heterogeneity (SHI) of a given plot, (3) habitat (categorical variable: either 9210* or 9220*) and (4) taxon (categorical variable). Since we hypothesized that each target taxon may respond differently to increasing levels of herb-layer richness, increasing structural diversity, and across different habitats, we also considered three second-order interactions, i.e. the interactions between taxon and the other three variables. Herb-layer species richness and SHI were scaled to zero mean and unit variance, in order to compare the magnitude of their effect on multi-taxon species richness. The full model was fitted with the *glmer* function in R, version 3.2.0 (R Development Core Team, 2015) within the package *lme4* (Bates et al., 2015) according to the R formula:

```
glmer(Richness~taxa * (flora richness + SHI + Habitat)
      + (1|studyarea), family = poisson)
```

We first fitted the full model and then we used the *dredge* function in R (package MuMIn version 1.12.1), to fit all the possible ($n = 35$) sub-models nested within the full model according to an Information-Theoretic (IT) approach (Burnham and Anderson, 2002). The nested models were ranked based on their AICc criterion (i.e. the small sample size correction of Akaike's Information Criteria – AIC), and the best fitting models were selected (i.e. the models within a distance of 2 AICc units from the first ranking model). After testing the selected models for overdispersion, these were used to calculate the weighted average (and relative 95% confidence interval) of parameter estimates through multi-model inference and model averaging (Burnham and Anderson, 2002). Parameters were estimated using the natural average method (Burnham and Anderson, 2002; Grueber et al., 2011).

In this way, we ranked several models and provided a quantitative measure of the relative support provided by the data to each competing hypothesis. When two or more models achieved similarly high levels of support, we used model averaging to provide a robust estimation of regression parameters. In comparison to more traditional approaches (e.g. stepwise methods), the IT approach has the advantage to account for model uncertainty (Burnham and Anderson, 2002; Grueber et al., 2011). In this way, we tested: (1) which of the two surrogates (i.e., herb-layer species richness or SHI) received more support from the data as predictors of multi-taxon species richness and (2) whether they acted in a complementary or redundant way.

Finally, we tested whether either the species richness of the target taxa or the residuals of our GLMM models showed a consistently lower spatial autocorrelation in those study areas where the sampling plots were located further apart (i.e., 'Corleto' and 'Ottati'). We calculated the Moran's I statistic for each taxon separately and found no systematic lower autocorrelation (results not shown).

2.6. Modeling the response of multi-taxon species richness to forest structural attributes

Besides testing the effect of SHI on multi-taxon species richness, we also used GLMMs to explore the effect of individual structural variables, in order to obtain insights on which structural parameters have a higher predictive power on the patterns of multi-taxon species richness. We fitted nine GLMMs, models 1–8 included each one of the structural attributes used for calculating the SHI, model 9 was a null model. All the models also included the co-variables 'taxon' and 'habitat'. Models 1–8 also included the interaction terms between taxon and (1) the target structural variable and (2) habitat. Finally, we ranked these nine models as described above to understand which individual structural variable best predicted the

multi-taxon species richness, verifying if any of these performed better than the null-model.

2.7. Congruence in complementarity patterns between the herb-layer and other taxa

Species complementarity between a surrogate and a target taxa measures whether the two taxa cumulate species at the same rate as the number of plots increases. Ferrier (2002) derived an index of species complementarity (Species Accumulation Index – SAI) based on accumulation curves. SAI first calculates an optimal curve (O-curve), i.e. an accumulation curve which plots the proportion of species of a target taxon represented when the plots are selected in the order that maximizes the rate of accumulation of target species. Then it calculates a surrogate curve (S-curve), i.e. an accumulation curve reporting the average percentage of target species represented when selecting plots with the order that maximizes the species richness of the surrogate taxon (in this case the herb-layer plants). Finally, these curves are compared to a mean random curve (R-curve), which is the mean of 999 individual accumulation curves that plot the cumulative number of species of a target taxon when plots are selected in a random order without reference to the surrogate data. SAI is calculated as:

$$SAI = \frac{S - R}{O - R}$$

where S = the area under the surrogate curve, R = the area under the mean random curve, and O = the area under the optimum curve. The index ranges between -1 and 1 . It is equal to 1 for a perfect surrogate, it is 0 or less for a surrogate that performs no better than a random selection of plots. We used bootstrapping to calculate the confidence limits as described in Ferrier (2002). The R script for calculating and plotting SAI and its confidence intervals is provided in the Supplementary material – Appendix 1.

2.8. Species composition of target taxa vs. herb layer plants and forest structural attributes

Based on species composition data, we created an ordination diagram for each taxon using nonmetric multidimensional scaling (NMDS). We ran NMDS using Hellinger dissimilarities for those taxa for which we had abundance data (i.e. herb-layer vegetation, epiphytic lichens and beetles), and Jaccard dissimilarity for taxa for which only presence-absence data were used (i.e. birds, saproxylic and epigeous fungi). In each case, we run 500 NMDS ordinations with random starting configuration to find the most stable solution (i.e., lowest stress value). To help the interpretation of the ordination plots we superimposed those structural and environmental variables significantly related to the ordination axes according to the *envfit* routine of the *vegan* package (Oksanen et al., 2013). Significance was tested using permutation tests ($n = 999$). Given the nested structure of our dataset (i.e. each study area encompassed more than one sampling plot), the permutation of plots was constrained at the study area level using the argument *strata* in the functions *envfit*. Since plots within a given study area are expected to be more similar to each other than two plots randomly chosen over the whole dataset, this permutation strategy returned a conservative estimation of the significance of the results. Explanatory variables included SHI, the eight structural variables described above, stand basal area and density, and altitude.

Finally, we made a NMDS ordination (same procedure as above) based on the eight structural variables used for calculating SHI. The eight structural variables were scaled to zero mean and unit variance and then used to build a Euclidean dissimilarity matrix.

The paired congruence between the NMDS ordinations based on the species composition of different taxa and (1) the species

Table 2

Alpha-, beta- and gamma-diversity observed for each taxon in the 33 sampling plots, asymptotic number of species (estimated gamma) and its ratio with the number of species actually observed. The standard deviation of alpha diversity is reported in parenthesis.

	Alpha	Beta	Observed Gamma	Estimated Gamma (Jackknife 1)	Observed/expected (%)
Plants (herb-layer)	35.5 (16.6)	6	179	231.4	77.4
Beetles	15 (6.3)	8.7	130	193.0	67.3
Fungi (saproxylic)	8.8 (4.0)	10	88	131.6	66.9
Fungi (epigeous)	5.6 (2.8)	11.5	65	96.0	67.7
Birds	6.8 (1.6)	6.9	47	62.5	75.2
Lichens	16.3 (5.9)	3.6	58	64.8	89.5

composition of herb-layer plants and (2) stand structural variables was assessed using Procrustes rotation on NMDS ordination (Legendre and Legendre, 1998). The significance of the fit of the ordination configurations was estimated using permutation-based ($n = 999$) *protest* analysis (function *protest* in the R package *vegan*). *Protest* verifies whether two data sets exhibit greater congruence than would be expected at random, by testing whether the Procrustes statistic m^2 (which represents a goodness-of-fit statistic of orthogonal Procrustes analysis) is smaller than expected by chance. Again, we used the argument *strata* to account for the nested structure of the dataset.

3. Results

3.1. Species diversity of the considered taxa

The herb-layer was the most species rich taxon among those considered in this study, both at the alpha and gamma level (Table 2). The plant species most commonly encountered in the herb-layer were *Rubus hirtus* and *Viola reichenbachiana*. *Lactuca muralis* and *Auremonia agrimonoides* were very common in habitat 9210* while *Daphne laureola* and *Geranium robertianum* were the most frequent species in the herb-layer of habitat 9220*.

Lichens had a relatively high alpha diversity when compared to the other taxa, but a low beta and gamma diversity, indicating that this taxon had a low between-plot variation. The most frequently recorded lichen species were *Lecidella elaeochroma*, the commonest epiphytic lichen of Italy, and two species of the *Lecanora* genus, i.e. *L. allophana* and *L. intumescens*, the latter usually found on smooth bark, with optimum in humid beech forests (Nimis and Martellos, 2008). Interestingly, we found *Anaptychia crinalis* (study area Incodara), a particularly rare and vulnerable species (Nascimbene et al., 2013) which is confined to humid beech forests (Nimis and Martellos, 2008). We also found fertile thalli of *Lobaria pulmonaria* (Corleto Monforte and Ottati), a lichen typically associated to stands with a long ecological continuity that is considered a good indicator of the occurrence of other rare and sensitive lichen species (Brunialti et al., 2010; Nascimbene et al., 2010).

Fungi had in general, the highest beta diversity among the six considered taxa. The species most frequently found in the study areas were *Mycena pura*, *Hebeloma sinapizans* and *Marasmius wynneae* among the epigeous species, and *Bisporella citrina*, *Xylaria hypoxylon* and *Polyporus melanopus* among the saproxylic species. We also found the species *Ossicaulis lignatilis* (Incodara), which is among the 21 indicator species suggested for assessing the conservation value of beech forests in Europe (Christensen et al., 2004), and the species *Fomes fomentarius* (Corleto and Ottati), which is frequently encountered in unmanaged beech forests and constitutes a habitat resource for several *Lepidoptera* and *Coleoptera* species (Müller et al., 2007).

The beetle species most frequently encountered were *Mesodasytes plumbeus*, *Athous haemorrhoidalis*, *Nothodes parvulus*, *Stenurella melanura* and *Agriotes infuscatus*. Noteworthy, we found two specimen of *Mordellochroa milleri* (study areas Ottati and Venacquaro) which is classified as critically endangered in the

Italian red list of saproxylic beetles (Audisio et al., 2014). Out of the 130 beetle species encountered, we found a high proportion of singletons (57), i.e. species for which we found only one individual. Approximately 80% of the species were saproxylic, i.e., species that depend on deadwood, during at least a part of their life cycle.

The most common bird species found were *Periparus ater*, *Fringilla coelebs*, and *Erithacus rubecula*. In some study areas, we also detected some priority species according to Annex 1 of the Birds Directive (2009/147/EC), i.e. the collared flycatcher (*Ficedula albicollis* found in Ottati, Corleto, Incodara and Venacquaro), the European honey buzzard (*Pernis apivorus* in Incodara), the white-backed woodpecker (*Dendrocopos leucotos* in Incodara) and the black woodpecker (*Dryocopus martius* in Ottati).

The completeness of the sampling (Table 2) was overall satisfying and comparable among five out of six taxa (66–77%), with the exception of lichens for which the sampling completeness was much higher (89.5%).

3.2. Forest structural heterogeneity

The SHI index ranged widely across the forest plots and study areas: it was comprised between 26.8% for a plot in the study area Ottati and 83.4% for a plot in Incodara (Table S1). The study areas located in Cilento NP had lower SHI averages than those located in Gran Sasso NP. In the former, mean SHI ranged between 39.2% and 51.4%, while in the latter they ranged between 55.5% and 66%.

3.3. Performance of taxa- and habitat-based surrogates at predicting the species richness of target taxa

The best-fitting GLMM model, i.e. the model returning the lowest AICc, included as explanatory variables the species richness of the herb-layer, taxon and their interaction (Table 3). The only other model receiving some support from the data (i.e. having a $\Delta AICc < 2$) had the same structure of the best-fitting model but also included SHI as explanatory variable. Interestingly, the models including SHI but not the herb-layer species richness received almost no support from the empirical data, and were thus not included in the list of the best-fitting models.

The magnitude of the overall effect of herb-layer species richness on the other taxa was relatively small (Fig. S1, Table S2). The interaction between 'taxon' and herb-layer species richness was always included as an explanatory variable among the two best-fitting models, indicating that different taxa responded differently to increasing levels of herb-layer diversity (Fig. 2). On the one hand, we did not see a strong relationship between the species richness of the herb-layer when compared to the richness of beetles, epigeous fungi and birds. On the other hand, we observed a clear relationship between the species richness of the herb-layer and the richness of saproxylic fungi and lichens. Plots with higher herb-layer species richness were poorer in saproxylic fungi (Table S2), but contained more species of lichens (Fig. 2, Fig. S1). After back-transformation, our models returned that for an increase of 10 species in the herb-layer (from 30 to 40 species), the expected change in richness was ca. −1.2 units for saproxylic fungi and +1.1 units for lichens.

Table 3

List of the best-fitting GLMMs models (i.e. the models encompassing 95% of the Akaike weights), modeling the response of multi-taxon species richness to (1) herb-layer species richness, and (2) forest stand structural complexity across five target taxa. Multi-taxon species richness is here defined as the species richness values observed for each of the five target taxa (saproxylic and epigeous fungi, beetles, birds and lichens) across the 33 sampling plot (=165 observations). Each model accounts for different study areas ($n = 6$) as a random effect (intercept), assumes a Poisson error structure and uses a logarithm link function. For each model (row headings) we reported: (1) either the estimated regression coefficient (for quantitative variables) or a check mark '✓' (for nominal variables and interactions) indicating when a particular term (column heading) was included in the model, (2) the degrees of freedom (df), (3) the log-likelihood, (4) AICc, (5) Δ AICc and (6) the Akaike weight. The models were ranked by AICc. Δ AICc represents the distance in AICc units from the best fitting model.

	Intercept	Plant richness	SHI	Taxon	Plant richness: taxon	df	logLik	AICc	Delta	Weight
mod.26	2.742	0.0275		✓	✓	11	−437.6	899.0	0	0.669
mod.30	2.742	0.0247	0.036	✓	✓	12	−437.1	900.4	1.41	0.331

Table 4

Ranking of the 8 GLMMs models each including an individual structural variables used as predictor of multi-taxon species richness, and a null model, i.e. a model including only the covariables but not the stand structural variables as explanatory. Each model accounts for different study areas as a random effect, assumes a Poisson error structure and uses a logarithm link function. For each model (row headings) we reported: (1) the estimated regression slope estimated for the target structural variable (β), (2) the degrees of freedom (df), (3) the log-likelihood, (4) AICc, (5) Δ AICc and (6) the Akaike weight. The models were ranked by AICc.

Model	β	df	logLik	AICc	Δ AICc	Weight
Total deadwood volume	0.100	13	−439.4	907.2	0.0	0.648
Null model	–	7	−447.5	909.8	2.6	0.178
Tree sp. Richness	0.081	13	−441.4	911.3	4.1	0.084
Growing Stock	−0.017	13	−442.6	913.6	6.4	0.026
GINI	−0.062	13	−442.6	913.7	6.5	0.025
LLT (dbh > 40 cm)	−0.013	13	−443.1	914.6	7.3	0.017
Height (sd)	−0.025	13	−443.1	914.6	7.4	0.016
CWDI	0.090	13	−444.5	917.4	10.2	0.004
Standing deadwood (BA)	−0.027	13	−445.3	919	11.8	0.002

Overall, SHI had a very weak effect on multi-taxon species richness. For an increase in 10 units of SHI (from 30 to 40%), the richness of the target taxa was expected to increase of ca. 0.3 units; this result was constant across taxa, since the interaction between 'taxon' and SHI was never included among the best-fitting models. Similarly, the hypothesis that the richness of the target taxa responded differently to increasing levels of herb-layer species richness across the two habitats here considered received no support from the data.

3.4. Response of multi-taxon species richness to forest individual structural attributes

Out of the eight structural variables we tested, only the total deadwood volume performed better than a null model at

predicting multi-taxon species richness (Table 4). The null model was the second best-fitting model (Δ AICc = 2.6). The other structural variables instead, did not receive support from the data as predictors of multi-taxon species richness.

Although being positively related to the multi-taxon species richness, the total deadwood had a relevant predictive effect only for the species richness of certain taxa (Fig. 3). For instance in the habitat 9210*, the model predicted that, for an increase in the amounts of deadwood from 30 to 40 m³/ha, the richness of beetles and saproxylic fungi is expected to increase by 1.4 and 2.2 species respectively while the richness of lichens is expected to decrease by 0.7 species (Table S3). For habitat 9220*, the results were qualitatively similar, although all the regression coefficients were slightly lower. The response of the species richness of other taxa to deadwood availability was very weak.

3.5. Congruence in complementarity patterns between herb-layer and other taxa

The analysis of SAI patterns showed only a limited congruence in species accumulation between the herb-layer vegetation and the target taxa (Fig. 4). In particular, plants were a good surrogate only for beetles (SAI = 0.19, $p < 0.05$), while when considering other target taxa SAI was not significantly different from zero.

3.6. The surrogacy of herb-layer vegetation and stand structure for the species composition of target taxa

The two-dimensional NMDS returned a sufficient to good representation of species diversity of the considered taxa: the stress values were comprised between 0.134 for plants and 0.206 for beetles (Fig. S2). We observed that different structural features correlated with the ordination axes of different taxa. In particular, the species richness of the tree layer correlated with the axis 2 for both the beetles and epigeous fungi. Growing stock was significantly correlated with the species composition of plants and epigeous fungi. The species composition of saproxylic fungi was significantly correlated both with the GINI-Simpson index (an

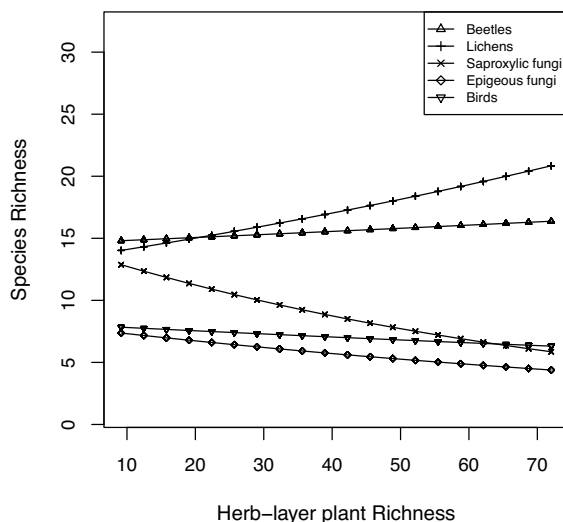


Fig. 2. The model-averaged response of the species richness of the five target taxa to increasing levels of herb-layer plant richness as predicted by the best-fitting GLMMs models. The study area was treated as a random effect (random intercept). Models were compared and averaged in an Information-Theoretic context. The models assumed a Poisson distribution of errors and used a logarithmic link function.

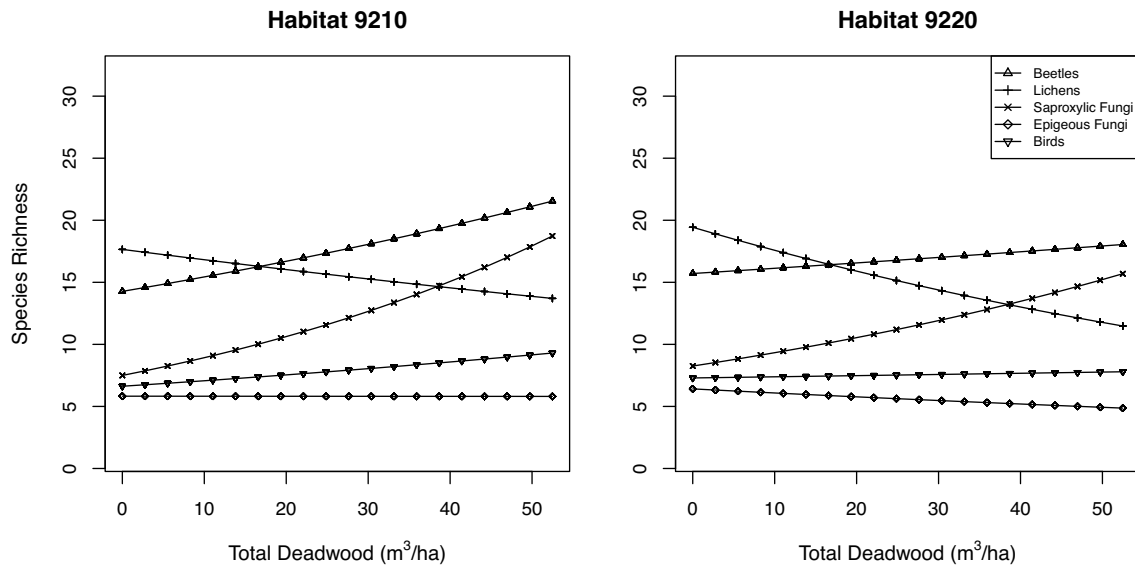


Fig. 3. Response of the species richness of the five target taxa to increasing levels of total deadwood across the two habitats here considered (either 9210* or 9220*). The relationship was modeled through GLMMs which assumed a Poisson distribution of errors and used a logarithmic link function. Study area was treated as a random effect (random intercept).

indicator of the uneven-aged structure of a stand) and with the volume of standing deadwood. Finally, altitude correlated significantly with the NMDS axes of three taxa, i.e. plants, beetles and lichens (Fig. S2).

The Procrustes rotation (Table 5) showed that the correlations observed between the herb-layer and the target taxa were relatively high (0.319–0.777) and greater than those observed between

the forest structure and the target taxa (0.180–0.401). Nevertheless, most of these correlations were not statistically significant, possibly because of the nested nature of the dataset. Only the saproxylic fungi had a statistically significant community congruence with herb-layer plants. None of the considered taxa showed a significant concordance with the NMDS ordination based on the structural variables.

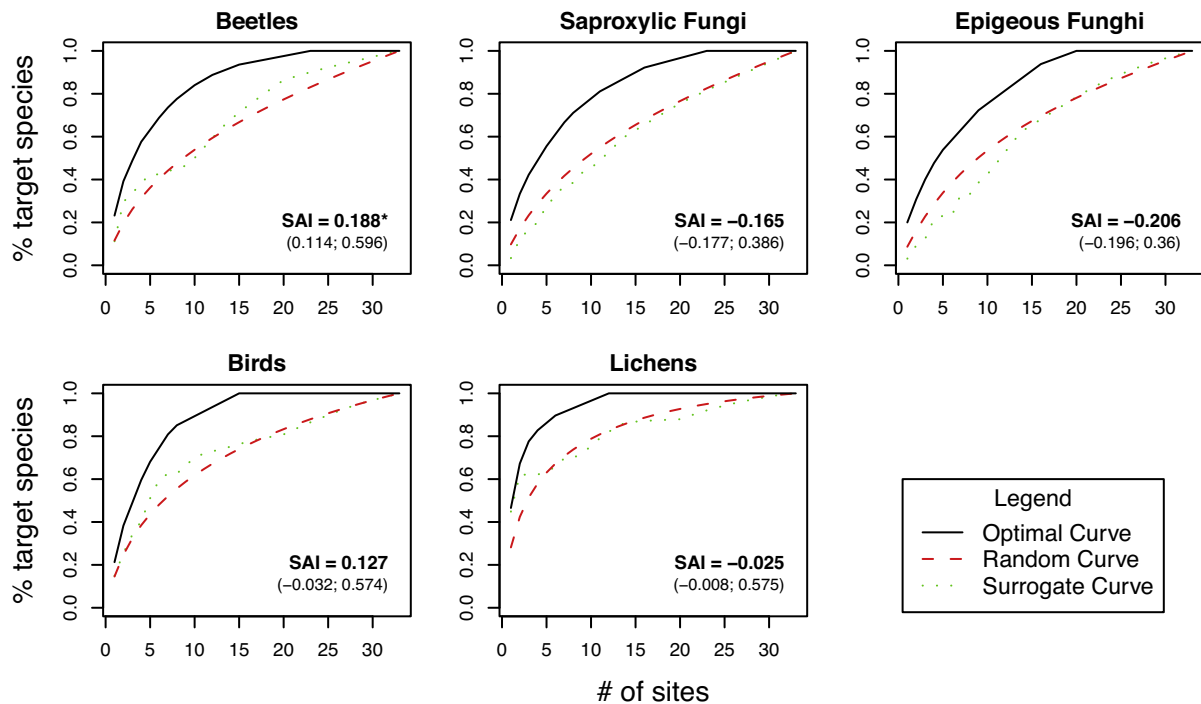


Fig. 4. Between-taxa complementarity as assessed using Species Accumulation Index (SAI). Species complementarity was assessed by comparing: a surrogate curve, indicating the average percentage of target species represented when selecting plots with the order that maximizes the species richness of the surrogate taxon (in this case herb-layer); a random curve, indicating the average percentage of target species represented when plots are selected randomly over 999 replications; an optimum curve which maximizes the number of target species represented. SAI (bold) and the relative confidence intervals (in parenthesis) are reported for each curve (the asterisk represents a significant value at $p < 0.05$).

Table 5

Congruence between the multivariate ordinations based on either (1) the herb-layer species composition or (2) the stand structural attributes and the ordinations based on the community composition of different taxa, as returned by Procrustes analysis. m_{12}^2 is the sum of the squared distances between corresponding points of the two ordinations.

	Herb-layer plants			Forest Structure		
	m_{12}^2	Correlation	p-value	m_{12}^2	Correlation	p-value
Beetles	0.396	0.777	0.188	0.840	0.401	0.280
Lichens	0.751	0.499	0.616	0.890	0.332	0.597
Fungi (saproxylic)	0.898	0.319	0.034*	0.982	0.135	0.950
Fungi (epigeous)	0.79	0.458	0.247	0.968	0.180	0.601
Birds	0.744	0.506	0.123	0.936	0.252	0.964

* Significant results at $p < 0.05$.

4. Discussion

4.1. Limited cross-taxon congruence between herb-layer plants and other taxa

Our data provided a limited support to the hypothesis that the herb-layer plants or the forest structural complexity can be used as surrogates of the overall multi-taxon species richness of a site, at least in the investigated study areas. Across the three facets of biodiversity here considered (i.e. species richness, complementarity and composition), we observed only a few significant congruent patterns between these two surrogates and the target taxa. These results are in line with a recent review over the strength of biodiversity indicators, which found only a weak evidence that vascular plants may be effective surrogates in European forests (Gao et al., 2015).

Nevertheless, when considering species richness, the herb-layer plants performed better than stand structural complexity at predicting multi-taxon species richness, and was consistently selected as the best predictor even if the overall magnitude of this relationship was weak. The weak positive relationship between herb-layer plants and the multi-taxon species richness was partially driven by the effect of two specific taxa, namely lichens and beetles (Fig. 2). In the case of lichens, another study performed in the beech forests of the Apennines (Blasi et al., 2010) found a similar congruence that may on the similar light requirements shared by these two taxa. Although we did not directly measure the canopy openness in the sampled plots, we infer that those plots where the canopy is relatively open, i.e. where more sunlight reaches the forest-floor, are more likely to host a higher density and diversity of both understory vegetation (Sabatini et al., 2014b) and epiphytic lichens (Aragon et al., 2010).

Also the congruent patterns of species complementarity between plants and beetles may be partially explained by the occurrence of gaps in the forest canopy. Gaps are usually characterized by an increased abundance of flower- and fruit- bearing plants (e.g. *Rubus* spp.), which may represent a key resource for many saproxylic beetles (Bouget et al., 2014). Indeed, the beetle species we captured more frequently have a saproxylic behavior during their larval stage, while the adults are often found on flowering plants in both the tree- and herb-layer. A typical example is *Stenurella melanura* (Cerambycidae), which feeds on decaying wood during its larval stage, while as an adult it relies on the pollen of herb-layer species, such as *Digitalis purpurea*, *Rubus fruticosus* and several Asteraceae and Apiaceae species (Sama, 2002).

The relationship between plants and saproxylic fungi was instead complex. These taxa showed similar patterns of species composition (as shown through the Procrustes analysis). Nevertheless, when the species richness was considered, we observed that higher levels of herb-layer species richness were associated to species-poor saproxylic fungi communities and vice versa. A possible explanation for this decoupled trend of cross-taxon congruence between species composition and richness may rely on

the role of European beech in these ecosystems. Firstly, beech is a shade-tolerant species which forms very dense canopies. Under a dense beech cover, the light levels at the forest-floor are usually very low. Consequently, the herb-layer is usually poor of plant species since only those species specialized to very low light levels are able to thrive (Burrascano et al., 2011; Mölder et al., 2008; Sabatini et al., 2014a). Secondly, a dense forest canopy may increase the humidity at the forest floor and this may have a favorable effect on the diversity of saproxylic fungi. Finally, in beech forests, the highest number of saproxylic fungi species is usually associated to beech deadwood in intermediate decay classes (Müller et al., 2007; Brunet et al., 2010; Persiani et al., 2015; Granito et al., 2015). Beech lacks typical heartwood and is similar to some species of softwoods, especially those with a high moisture content in the trunk (Penninckx et al., 2001). Beech wood is also characterized by the homogeneous distribution of syringyl lignin throughout the xylem and is highly susceptible to a great range of wood decaying fungi which can colonize and readily degrade it (Schwarze, 2007). For these reasons, we hypothesize that, to a certain extent, the negative relationship between herb-layer and saproxylic fungi species richness may be mediated by the contrasting correlation that these two taxa may have in relation to the dominance of European beech. Similarly, the congruence in species composition may be interpreted by hypothesizing similar patterns of occurrence of those shade-tolerant herb-layer plants that are more typically found in beech forests and of the species assemblages of saproxylic fungi that are strictly related to beech.

4.2. Forest structural heterogeneity is not an effective predictor of the biological diversity of the target taxa

The structural heterogeneity of a forest stand has often been assumed as a good predictor of its contribution to overall biodiversity (McElhinny et al., 2005; Gossner et al., 2014). This assumption has been insufficiently tested in literature and different studies reported contrasting results (Gossner et al., 2014; Gao et al., 2015). In the present study, we tested whether an index of structural complexity (SHI) explicitly designed to account for the main sources of structural complexity occurring in the beech forests of southern Europe could be used for predicting the multi-taxon species richness of a stand. SHI performed worse than the herb-layer and we only found a moderate evidence that SHI may be used to complement the information provided by the herb-layer. In fact, even if we found that for increasing levels of SHI the species richness of the target taxa is expected to increase, the magnitude of this effect was extremely weak. Noticeably, we did not find a differential response of different target taxa to increasing levels of SHI.

When considered individually, most of the structural variables were not good surrogates of the overall biodiversity either. The only exception was deadwood volume. For increasing levels of deadwood amounts, the richness of beetles and saproxylic fungi was predicted to increase. Furthermore, the composition of saproxylic

fungi assemblages was significantly related to the amount of standing deadwood in a plot (Fig. S2), suggesting that, besides the total amount of deadwood, the quality of the deadwood (e.g. standing vs. lying, as well as the decay stage, see Section 4.1) may also have an important role in determining the composition of saproxylic fungi assemblages (Persiani et al., 2010). Indeed, to maintain rich saproxylic beetle assemblages in beech forests, both lying and standing deadwood of varying dimensions are necessary (Brunet et al., 2010). In general, deadwood volume and its diversification among various components are key variables for predicting the richness of beetles and saproxylic fungi (Christensen et al., 2004; Brunet et al., 2010), also in European forest ecosystems (Gao et al., 2015).

Surprisingly, we did not find any relationships between multi-taxon species richness and other structural variables that are usually acknowledged as potential biodiversity indicators. For instance, our data did not support the hypothesis that the richness of the tree layer could be used to predict the richness of other taxa, although the tree layer was often reported as a good indicator of forest biodiversity (Barbier et al., 2009), and despite the richness of the tree- and herb-layers were found to be significantly correlated to each other in several European beech forests (Abbate et al., 2015; Burrascano et al., 2011; Sabatini et al., 2014a). Similarly, the density of large living trees did not perform better than a null model at predicting neither the multi-taxon species richness in general nor the richness of forest-dwelling birds and epiphytic lichens, although these taxa are often associated to key structural features that are usually associated to large living trees, e.g. tree cavities for birds (Brunet et al., 2010; Brunialti et al., 2010). Possibly, this is because the forest stands that we sampled are still exploited for timber production, although extensively; therefore, even if trees with a DBH greater than 40 cm occur, this does not implicitly indicate the occurrence of key structural features, nor of the species that are likely to take advantage of them. Indeed, the conventional management of beech stands usually actively removes hollow- and fungus-bearing trees, since these have a low economic value. For this reason, in managed stands or recently managed forests, the density of large living trees is an imperfect indicator of the occurrence of these important structures, as it was found in a previous study, where the species richness of saproxylic beetles was strictly related to the actual density of relevant microhabitats, but not to the density of large trees (Bouget et al., 2014). As regards to lichens, most of the species that are related to unmanaged forest stands have a dispersal potential limited to short distances. For these species, the long-term continuity and spatial distribution of large living tree remnants, which serve as a source of propagules after harvesting, may be much more important at explaining their presence than the current density of large living trees (Hazell and Gustafsson, 1999).

Based on our results, each taxon responded to a particular set of structural variables. Therefore, the choice of a structural feature to be used as a habitat-based surrogate should be driven by the knowledge of the habitat requirements of the target taxa. Nevertheless, other confounding factors may arise and weaken the effectiveness of a surrogate. Past stand disturbance history, environmental covariates, as well as thresholds or nonlinearity in the response of target taxa may all contribute at weakening the surrogate-target relationships, especially when sampling size is relatively small, and when fine-scale patterns are considered (Lombardi et al., 2015).

4.3. Factors potentially affecting surrogacy: power and scale

The low magnitude of the cross-taxon congruence between plants and other individual taxa, as well as the little predictive power of the habitat-based surrogates we used, represents a new piece of evidence that surrogates are a useful tool only when they

are properly designed and carefully tested. Some recent meta-analyses reported that cross-taxon congruence varies enormously, even for the same pairs of taxa, among studies encompassing different spatial scales or biogeographic contexts (Rodrigues and Brooks, 2007; Lewandowski et al., 2010; Westgate et al., 2014). Understanding the robustness of a given surrogate is probably the most compelling challenge for the proximate future. Some general trends are emerging in the literature: for instance a higher cross-taxon congruence is expected when a broader spatial extent is considered (Lewandowski et al., 2010; Westgate et al., 2014). When the spatial scale is broad, a higher environmental variability is usually sampled, and thus the diversity patterns of different taxa are more likely to co-vary, also in relation to the common biogeographical and evolutionary history shared by these taxa (Gioria et al., 2011; Rooney and Azeria, 2015). In addition, the sampling effort as well as the size of the regional species pools may have a relevant effect on the strength of the relationship between two taxa, since larger species pools may provide greater biological resolution to detect changes in environmental condition (Rooney and Azeria, 2015).

In this study, we considered a nested dataset with limited number of sampling plots (33), which were relatively similar in terms of overstory composition, altitudinal range and bioclimate. Although the spatial domain was relatively broad (the farthest plots were about 300 km apart), the dataset was designed not to encompass any major environmental gradients. Indeed, we limited our analysis to relatively well-preserved, low intensity managed beech forests, and we only explored the cross-taxon congruence therein at a fine spatial scale (small grain). In this context, we cannot exclude that sampling stands along a broader environmental gradient, would result in stronger pattern of cross-taxon congruence. Indeed, when considering stands characterized by different conservation status, management regimes or disturbance history, a higher cross-taxon congruence is likely to occur than when considering relatively similar stands as in our case.

Similarly, a higher number of sampling plots may also improve the results. Nevertheless, a small dataset is the rule rather than the exception when research aims at informing forest management for biodiversity conservation, or monitoring restoration projects, since high-quality biological data collection is very expensive and time-consuming. To be useful, a surrogate should have a power sufficient for detecting the variation of a target taxa even when the sampling size is small (Lindenmayer et al., 2014). If a strong cross-taxon congruence cannot be assumed, like in our case, it appears justified to undertake the effort of performing an extensive assessment of multi-taxonomical diversity to limit the likelihood of taking poor conservation decisions based on the use of weak or ineffective surrogates (Gao et al., 2015).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2016.04.012>. These data include Google maps of the most important areas described in this article.

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