One to rule them all? Assessing the performance of Forest Europe’s biodiversity indicators against multitaxonomic data

Impact statement

Biodiversity indicators used to assess the state of Europe’s forests perform unequally; a combination of indicators is more informative

Keywords

Sustainable forest management; taxonomic indicators; multi-taxa diversity; forest structure

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Abstract

Most broad-scale forest biodiversity indicators are based on data from national forest inventories and are used to assess the state of biodiversity through several regional initiatives and reporting. Although valuable, these indicators are essentially indirect and evaluate habitat quantity and quality rather than biodiversity *per se*. Besides, most of these indicators are applicable at regional or national scales, while their use at a more local level is difficult. Therefore, their link to biodiversity may be weak, which decreases their usefulness for decision-making.

For several decades, Forest Europe indicators assessed the state of European forests, in particular its biodiversity. However, no extensive study has been conducted to date to assess the performance of these indicators against multitaxonomic data. We hypothesized that – as implied by the reporting process – no single biodiversity indicator from Forest Europe can represent overall forest biodiversity, but that several – eventually combined – indicators would reflect habitat quality for at least some taxa in a comprehensive way. We tested the set of indicators proposed by Forest Europe against the species richness of six taxonomic and functional groups (tracheophytes, epixylic and epiphytic bryophytes, birds, saproxylic beetles, saproxylic non-lichenized fungi and epixylic and epiphytic lichenized fungi) across several hundreds of plots over Europe. We showed that, while some indicators perform relatively well across groups (e.g. deadwood volume), no single indicator represented all biodiversity at once, and that a combination of several indicators performed better. Surprisingly, some indicators showed weak links with the biodiversity of the six taxonomic and functional groups.

Forest Europe indicators were chosen for their availability and ease of understanding for most people. However, our analyses showed that there are still gaps in the monitoring framework, and that surveying certain taxa along with stand structure is necessary to support policymaking and tackle forest biodiversity loss at the large scale.

Keywords

Sustainable forest management; taxonomic indicators; multi-taxa diversity; forest structure

Introduction

Monitoring biodiversity in the face of global change is a challenge in many ecosystems across the world (IPBES 2019; Lindenmayer & Likens 2010). Despite large-scale initiatives such as GEOBON (Group on Earth Observation Biodiversity Observation Network 2008) and collaborative networks (Burrascano et al. 2023), no standard biodiversity monitoring scheme has been agreed in Europe or elsewhere. Long-term biodiversity monitoring hence currently relies on a limited number of initiatives that are used to assess the impact of climate change (e.g.Jiguet et al. 2012), habitat loss (Betts et al. 2017) or pollution (Rigal et al. 2023). Initiatives combining monitoring of biodiversity, types of pressure and ecosystem-level variables remain quite rare, or may concern only single pressure vs. single taxon assessment (e.g. Proença et al. 2017; Weber et al. 2004). However, different taxonomic and functional groups likely respond differently to a given pressure, which challenges prioritization of policy initiatives and tools (Pereira & David Cooper 2006).

Forest ecosystems are no exception to the rule, despite the large use of National Forest Inventory data to indirectly assess the state and evolution of biodiversity (Chirici et al. 2012; Heym et al. 2021; Reise et al. 2019). Originally designed to assess wood stock and production, National Forest Inventories provide nationwide data on forest ecosystems that allow, notably, to assess criteria and indicators of sustainable forest management and ecosystem services (Simons et al. 2021). At the European level, data from National Forest Inventories have been aggregated and published every five years for more than three decades (Forest Europe 2020) and provide a set of indicators to inform sustainable forest management.

In this process, the Sustainable Forest Management Criterion 4 is dedicated to the "*Maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems*". Composed of ten indicators, this criterion aims at helping decision makers to assess biodiversity-friendly sustainable forest management at the national and European scales. However, most of the indicators are indirect (structural) proxies of the forest ecosystem state (e.g. deadwood or forest fragmentation), whose link with biodiversity often lacks strong scientific evidence (Gao et al. 2015; Paillet et al. 2018; Storch et al. 2023; Zeller et al. 2022). Indeed, only two indicators involve other species than trees (namely 4.8 Threatened forest species, 4.10 Common forest bird species, Table 1) and to date, despite a large corpus of individual studies and few syntheses (Zeller et al. 2023), no global and systematic assessment of the correlations between multi-taxonomic biodiversity and Forest Europe indicators has been attempted.

In this context, our aim was to provide an *ex post* validation of these indicators and propose improvements to the reporting process. For this, we: i) assessed the link between indicators and several - multi-taxonomic (i.e. taxonomic and functional groups) - *indicanda*; ii) identified the indicators that performed best and universally - i.e. for all groups; iii) defined, if possible, the most effective combination of indicators for forest biodiversity.

To address these aims, we first tested Forest Europe's biodiversity indicators against each taxonomic and functional group. Second, we used a model selection approach to search for the best indicators in terms of taxonomic and functional group. Third, we tested the effect of a combination of indicators by searching for the best and most parsimonious combination of biodiversity indicators. We used a multi-taxonomic database (Burrascano et al. 2023; Trentanovi et al. 2023) combining species inventories and forest structure to analyze the correlations between Forest Europe's biodiversity indicators with the biodiversity of six groups (tracheophytes, epixylic and epiphytic bryophytes, birds, saproxylic beetles, saproxylic non-lichenized fungi and epixylic and epiphytic lichenized fungi).

Materials and Methods

Database

We used the database gathered within the framework of the COST action "BOTTOMS-UP" (CA18207 – Biodiversity Of Temperate forest Taxa Orienting Management Sustainability by Unifying Perspectives). In a nutshell, this database comprises biodiversity samplings along with forest plot descriptions (Burrascano et al. 2023). It merges 34 different datasets from 12 European countries and more than 3500 sampling units. From this database, we extracted the six most represented taxonomic and functional groups, namely tracheophytes, epixylic and epiphytic bryophytes (hereafter bryophytes), birds, saproxylic beetles, saproxylic non-lichenized fungi (hereafter fungi) and epixylic and epiphytic lichenized fungi (hereafter lichens).

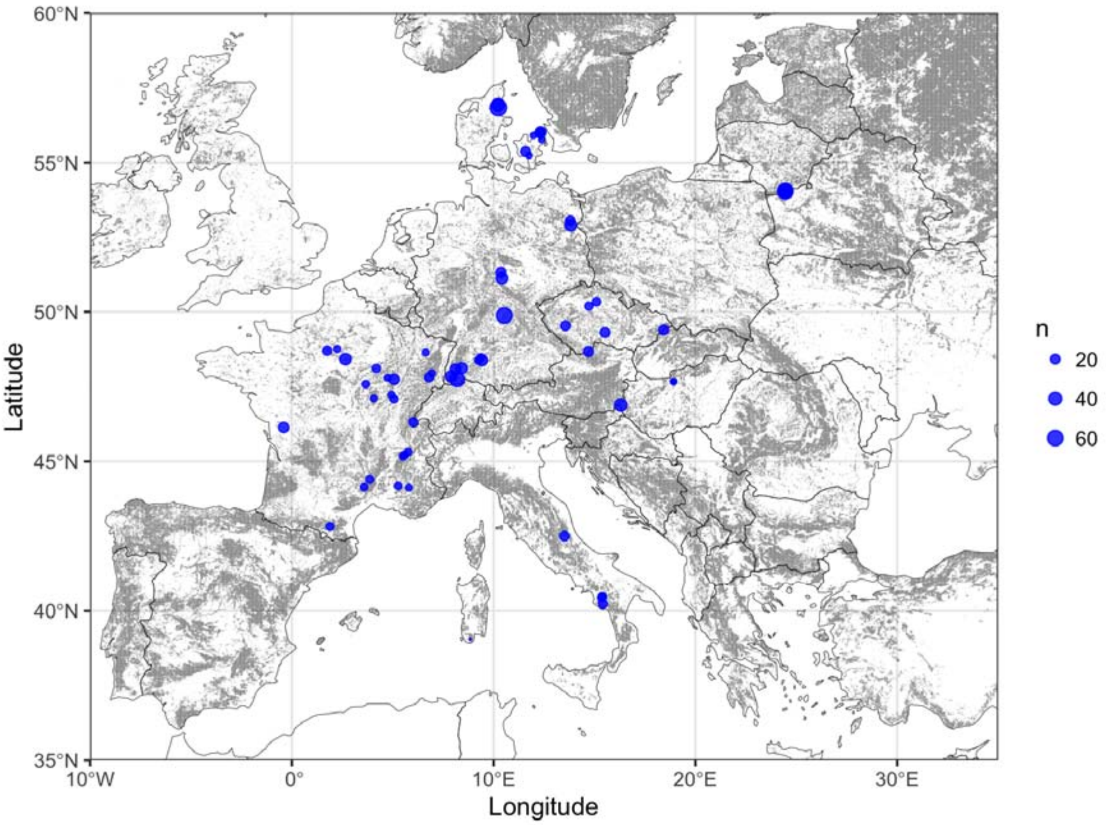

Figure 1: Spatial distribution of the sampling sites. Gray areas are covered by forests with a tree cover greater than 40% according to Kempeneers et al. (2011). The size of the dot is proportional to the number of sampling units.

While tracheophytes and birds were inventoried without any specific selection of the guilds targeted, only epiphytic and epixylic bryophytes and lichens were included (sampled on living trees and deadwood), and saproxylic fungi and beetles (dependent on deadwood substrates or on other organisms inhabiting deadwood).

Since the database is the result of the merging of different research projects, sampling designs and protocols varied across datasets (Burrascano et al. 2023; Trentanovi et al. 2023). Therefore, we standardized species richness (number of species per sampling plot) by dividing it by the asymptotic gamma richness at the site level, with site representing a homogeneous sampling area with a maximum size of a few thousand hectares. We derived site gamma diversity through plot-based rarefaction curves using the R package iNEXT (Hsieh et al. 2016). Sites with less than 6 sampling units were discarded from the final database since the estimation of the gamma richness was judged non-reliable. Exploratory analyses revealed especially large deadwood volumes linked with small plots (nugget effect). To avoid strong leveraging from these outliers (Zuur et al. 2010), we limited the maximum deadwood volume per sampling plot to 500 m3/ha, a value that corresponds to the maximal volumes observed in primeval forest of Europe (e.g. Christensen et al. 2005). The final data distribution per taxonomic and functional groups is shown in Table 1 and Figure 1.

	I4.2.Regeneration			**I4.3.Naturalness**			**Total**
Taxa	**Coppice**	**Natural**	**Planting**	**Plantation**	**Semi-natural**	**Unmanaged**	
Tracheophytes	10	734	94	94	550	194	838
Bryophytes	3	353	66	66	198	158	422
Beetles	7	408	94	94	255	160	509
Birds	10	721	94	94	537	194	825
Fungi	8	502	94	94	347	163	604
Lichens	10	332	92	92	333	9	434

Table 1: Number of plots used to fit the models distributed per taxonomic and functional groups and Regeneration origin or Naturalness following Forest Europe (2020).

Indicators' calculation

We used the State of Europe’s Forests (Forest Europe 2020) definitions to calculate the corresponding metrics for the indicators included in the Criterion 4 (Table 2). Since it was necessary to “translate” the definition into calculable values to analyze the relationship between indicator values and *indicanda* (i.e. standardized species richness), we proceeded as follows:

- indicator 4.6 *Genetic resources* was excluded since it was not possible to translate this indicator at the plot or site levels;
- indicators 4.1 *Diversity of tree species*, 4.4 *Introduced tree species* and 4.5 *Deadwood* were directly calculated from the plot measurements. Instead of introduced tree species, we considered only invasive woody species that can have a significant impact on forest biodiversity following Campagnaro et al. (2018), namely *Acer negundo*, *Ailanthus altissima, Prunus serotina*, *Quercus rubra* and *Robinia pseudoacacia* (Campagnaro et al. 2018). We limited to these species since there was no regional reference list for introduced tree species and it would have been far beyond the scope of this study to create such a list, e.g. Norway spruce (*Abies alba*) is introduced in lowland France but native in mountains where it has also been planted in some places. In addition, no reference list of invasive tree species in Europe was available in the Forest Europe (2020) report;
- indicators 4.2 *Regeneration* and 4.3 *Naturalness* were derived from declarative metadata when merging the database (Burrascano et al. 2023). In the 4.3, forests were considered ‘undisturbed by man’ when declared without intervention by the data holder (i.e. ‘abandoned’, ‘unmanaged’, ‘primeval’). Time since the last intervention was not used here since it was not homogeneously declared. ‘Semi-natural’ refers to forest plots that are under any type of forest management regime (from even-aged to uneven-aged silvicultural systems), but with natural regeneration processes of trees. ‘Plantation’ forests overlap with forest plots where regeneration derives from ‘Planting’ activities;

- indicators 4.8 *Threatened forest species* and 4.10 *Common forest bird species* were derived from biodiversity sampling and reference lists. For 4.8, we used the IUCN Red List and calculated the total number of threatened species (categories VU, EN and CR) per plot all groups together. For 4.10, we calculated the total number per plot of the 34 forest birds classified by the Pan-European Common Birds Monitoring Scheme (https://pecbms.info/trends-and-indicators/indicators/);
- indicator 4.7 *Forest fragmentation* was calculated following the protocol applied by European Commission et al. (2019) on the Corine Land Cover 2018 layer (https://efi.int/knowledge/maps/forest). The forest area density (FAD) at fixed observation scale was obtained calculating the percentage of forest pixels in a 500 ha circular buffer, centered on each plot;
- indicator 4.9 *Protected forests* was calculated based on the map of protected areas in Europe provided by the European Environment Agency (Nationally Designated areas - CDDA: https://www.eea.europa.eu/data-and-maps/data/nationally-designated-areas-national-cdda-17). We extracted the proportion of Categories Ia, Ib and II according to the IUCN in a 500ha circular buffer around each plot. We then added these three values so that the total proportion may be higher than 100.

Biodiversity indicators	**Definition (Forest Europe 2020)**	**Data source**	**Metrics**
4.1. Diversity of tree species	Area of forest and other wooded land, classified by number of tree species occurring	Plot measurements	Number of tree species per sampling unit
4.2. Regeneration	Total forest area by stand origin and area of annual forest regeneration and expansion (natural regeneration, planting, coppicing)	Metadata	3 classes: Natural regeneration Planting Coppicing
4.3. Naturalness	Area of forest and other wooded land by class of naturalness (undisturbed by man, semi-natural, plantations)	Metadata	3 classes: Unmanaged Semi-natural Plantation
4.4. Introduced tree species	Area of forest and other wooded land dominated by introduced tree species ⇨ modified to invasive ligneous species (Campagnaro et al. 2018)	Plot measurements	Number of invasive tree species per sampling unit
4.5. Deadwood	Volume of standing deadwood and of lying deadwood on forest and other wooded land	Plot measurements	Deadwood volume per ha
4.6. Genetic resources	Area managed for conservation and utilization of forest tree genetic resources (in situ and ex situ genetic conservation) and area managed for seed production	Not assessed	
4.7. Forest fragmentation (FAD)	Area of continuous forest and of patches of forest separated by non-forest lands (European Commission et al. 2019)	European Forest Institute map of forest cover	Forest area density (FAD) within 500ha around the sampling unit
4.8. Threatened forest species	Number of threatened forest species, classified according to IUCN Red List categories, in relation to total number of forest species	IUCN Red List species list	Species richness of threatened species (categories VU, EN and CR)
4.9. Protected forests	Area of forest and other wooded land protected to conserve biodiversity, landscapes and specific natural elements, according to MCPFE categories	CDDA map of protected areas	Cumulative percentage of Ia, Ib and II categories areas
4.10. Common forest bird species	Occurrence of common breeding bird species related to forest ecosystems	PECBMS	Species richness of forest birds

Table 2: Forest Europe's biodiversity indicators definitions and data sources used to calculate them in this paper.

Statistical analyses

We processed all analyses in R v.4.3.0 (R Core Team 2023). We used the standardized species richness of each taxonomic and functional group as a response variable. For each group, we fitted a single generalized linear mixed model with each indicator as an explanatory variable (9 models + the null - intercept only - model) and site as a random effect on the intercept to account for the fact that two plots from the same site were more likely to be similar than two plots from different sites. We used the beta error distribution with logit link since standardized richness was continuous, strictly positive with a maximum value below one. We scaled continuous explanatory variables to improve the convergence and to make the estimates of the models comparable. We used the glmmTMB function in the glmmTMB package (Brooks et al. 2017). We compared the magnitudes of all single effects in the models and their significance and represented this using a heatmap of the standardized effects (package ggplot2, Wickham 2016). We tested differences between estimates of categorical variables (e.g. 4.3.naturalness) using Tukey post-hoc test. To search for potential non-linear relationships between indicators and *indicanda*, we also fitted generalized additive mixed models (GAMMs) with indicators as smoothers (package mgcv, Wood 2023). We found very few differences between GLMMs and GAMMs and preferred to stick to the first (comparisons are presented in Appendix 1).

Finally, to assess the relative performance of all indicators, we first compared the Akaike Information Criterion corrected for small samples (AICc, Burnham & Anderson 2002) of all single models including a null (intercept only) model. Then, we searched for the best and most parsimonious linear combination (no interaction) of indicators that represented biodiversity based on AICc using the dredge function (package MuMIn, Barton 2023). In this process, we discarded the indicator 4.2. Regeneration since it was collinear with 4.3. Naturalness and a model containing both variables could not be fitted (see Appendix 2). When two competing models had a difference in AICc less than 2 points, we chose the most parsimonious one.

Results

Data and indicators' distribution

The most represented group in the database was tracheophytes (838 plots) followed by birds (825 plots, Table 3, see Burrascano et al. 2023 for a full description of the biodiversity dataset). All taxonomic and functional groups have been inventoried in at least 400 plots (Table 1). The distribution in the classes Regeneration (4.3.) and Naturalness (4.4.) were, however, strongly unbalanced (see also Table 1): the majority of sampling units were associated with “natural regeneration”, while “coppicing” - and “planting” to a lesser extent - were underrepresented; the majority of sampling units were within semi-natural forests, but the distribution was more balanced than for regeneration types. For quantitative indicators, the values taken were relatively balanced between groups (Table 3) and no strong collinearity was observed (see Appendix 2 for an example on tracheophytes).

Taxonomic and functional groups	**I4.1.tree.sp**	**I4.4.invasive**	**I4.5.deadwood**	**I4.7.fragmentation (FAD)**	**I4.8.threat.sp**	**I4.9.IUCN**	**I4.10.birds**
Tracheophytes	1.96(2.06) [0-11]	0.01(0.08) [0-1]	41.83(60.72) [0-444.89]	0.85(0.16) [0.13-1]	0.25(0.56) [0-3]	14.92(33.66) [0-142.4]	3.63(1.78) [1-11]
Bryophytes	1.91(1.84) [0-11]	0(0.06) [0-1]	39.15(55.86) [0-461.41]	0.84(0.18) [0.06-1]	0.2(0.5) [0-3]	27.02(43.16) [0-142.4]	4.41(2.63) [1-15]
Birds	2.49(2.18) [0-11]	0.01(0.08) [0-1]	42.03(64.56) [0-461.41]	0.85(0.16) [0.13-1]	0.29(0.6) [0-3]	15.92(34.06) [0-142,4]	4.14(2.38) [1-15]
Beetles	1.96(2.01) [0-11]	0(0.07) [0-1]	41.1(57.2) [0-444.89]	0.83(0.17) [0.08-1]	0.26(0.59) [0-5]	16.63(35.16) [0-142.4]	4.15(2.43) [1-12]
Fungi	1.47(1.95) [0-11]	0.01(0.08) [0-1]	39.73(57.98) [0-461.41]	0.82(0,.8) [0.08-1]	0.17(0.49) [0-3]	14.55(34.22) [0-100]	4.32(2.83) [1-15]
Lichens	1.93(1.85) [0-11]	0(0.06) [0-1]	39.28(56.21) [0-461.41]	0.84(0.18) [0.06-1]	0.21(0.53) [0-5]	26.65(42.93) [0-142.4]	4.43(2.62) [1-15]

Table 3: Summary table for the range of values (mean per sampling unit (sd) [min - max]) taken for each indicator distributed over the different subsets. FAD = Forest Area Density.

Correlations between indicators and indicanda

Several of the Forest Europe indicators had significant relationships with the standardized species richness of one or more of the six taxonomic and functional groups (Figure 2, see Appendix 3 for values of the estimates).

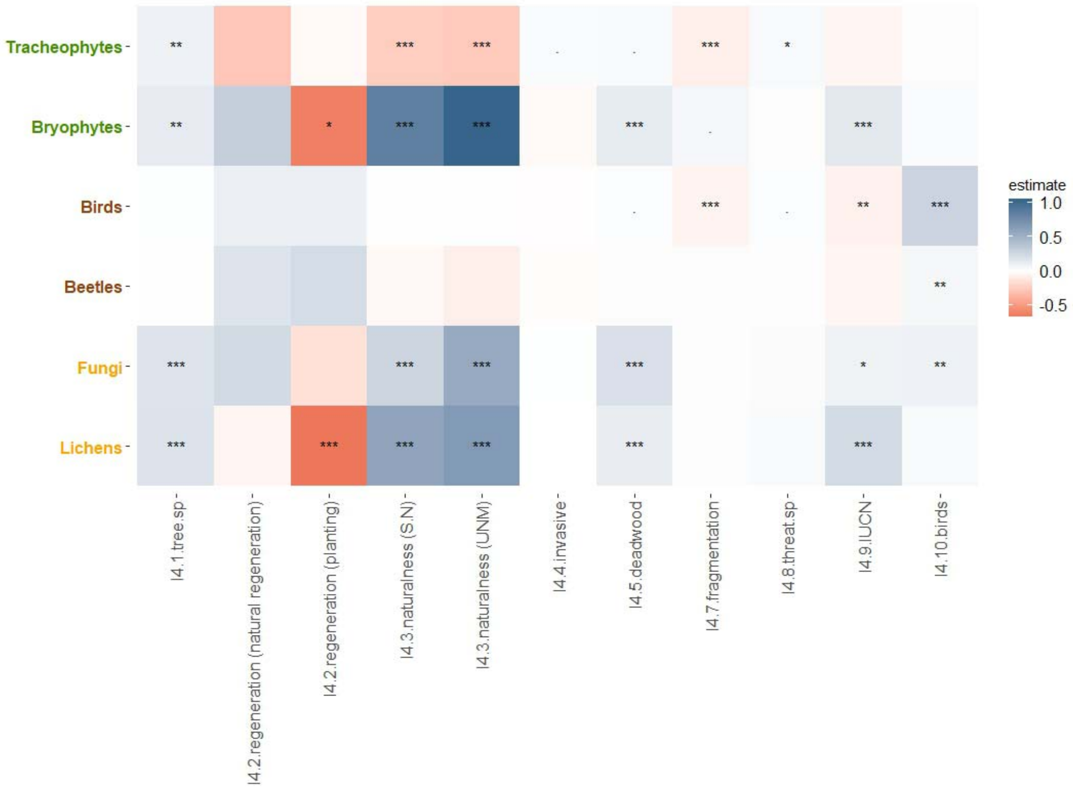

Figure 2: Heatmap representing the standardized estimates (slope) of standardized species richness obtained with generalized mixed models with Beta error distribution and logit link, using Forest Europe indicators as independent predictors. S.N = semi-natural, UNM = unmanaged. Intercept (reference) for 4.2 Regeneration is the “Coppice” class, and “Plantations” for 4.3 Naturalness (p<0.1, * p<0.05, ** p<0.01, *** p<0.001).

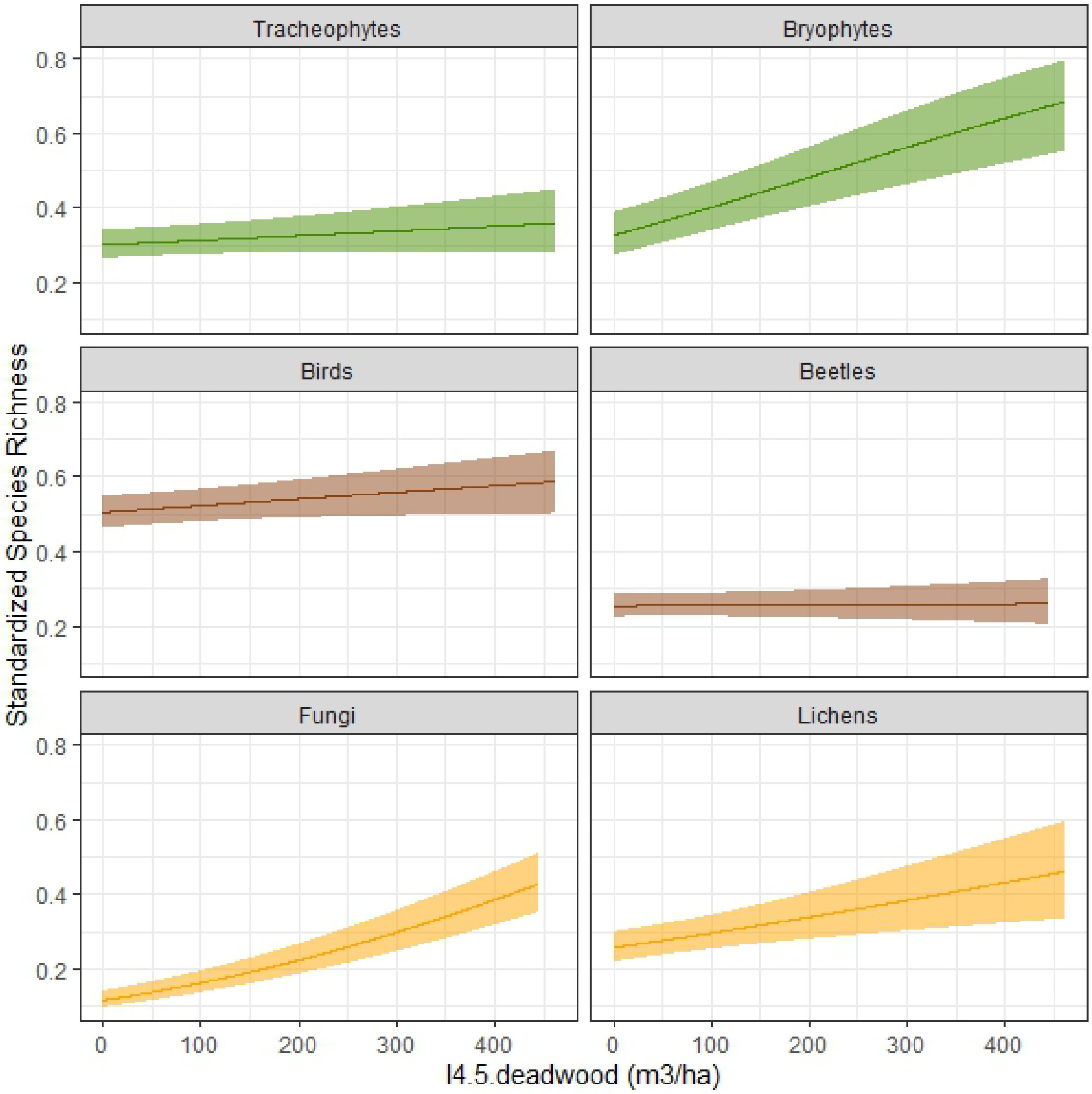

Figure 3: Relationships between standardized species richness of 6 taxonomic and functional groups and Forest Europe indicator 4.5. Total deadwood volume. Estimations are issued from generalized linear models with Beta error distribution and logit link. Plain line represents the mean estimate, ribbons the 95% confidence interval.

Deadwood (4.5, Figure 3) and Diversity of tree species (4.1) showed four positive and (marginally) significant but generally weak relationships with tracheophytes, bryophytes, fungi and lichens (Appendix 3). Other indicators showed at least three significant (or marginally significant) relationships, with varying magnitudes, i.e. Fragmentation (FAD) (4.7), Protected areas (4.9, Figure 4) and Forest Birds (4.10). Surprisingly, the proportion of protected areas around sampling plots had a negative effect on birds and no effect on tracheophytes and fungi. Regarding Naturalness (4.3, Figure 5), unmanaged forest and semi-natural forests showed higher levels of fungi, lichens and bryophytes than plantations. However, the opposite was true for tracheophytes. Threatened species (4.8) showed very few significant results (marginally positive for tracheophytes and bryophytes, positive for birds) while Invasive species (4.4) only showed a marginally significant positive relationship with tracheophytes. Plantation (4.2) showed a very strong negative relationship with lichens only, and a marginally significant negative effect on tracheophytes, while there were no differences between coppice and natural regeneration (Appendix 3).

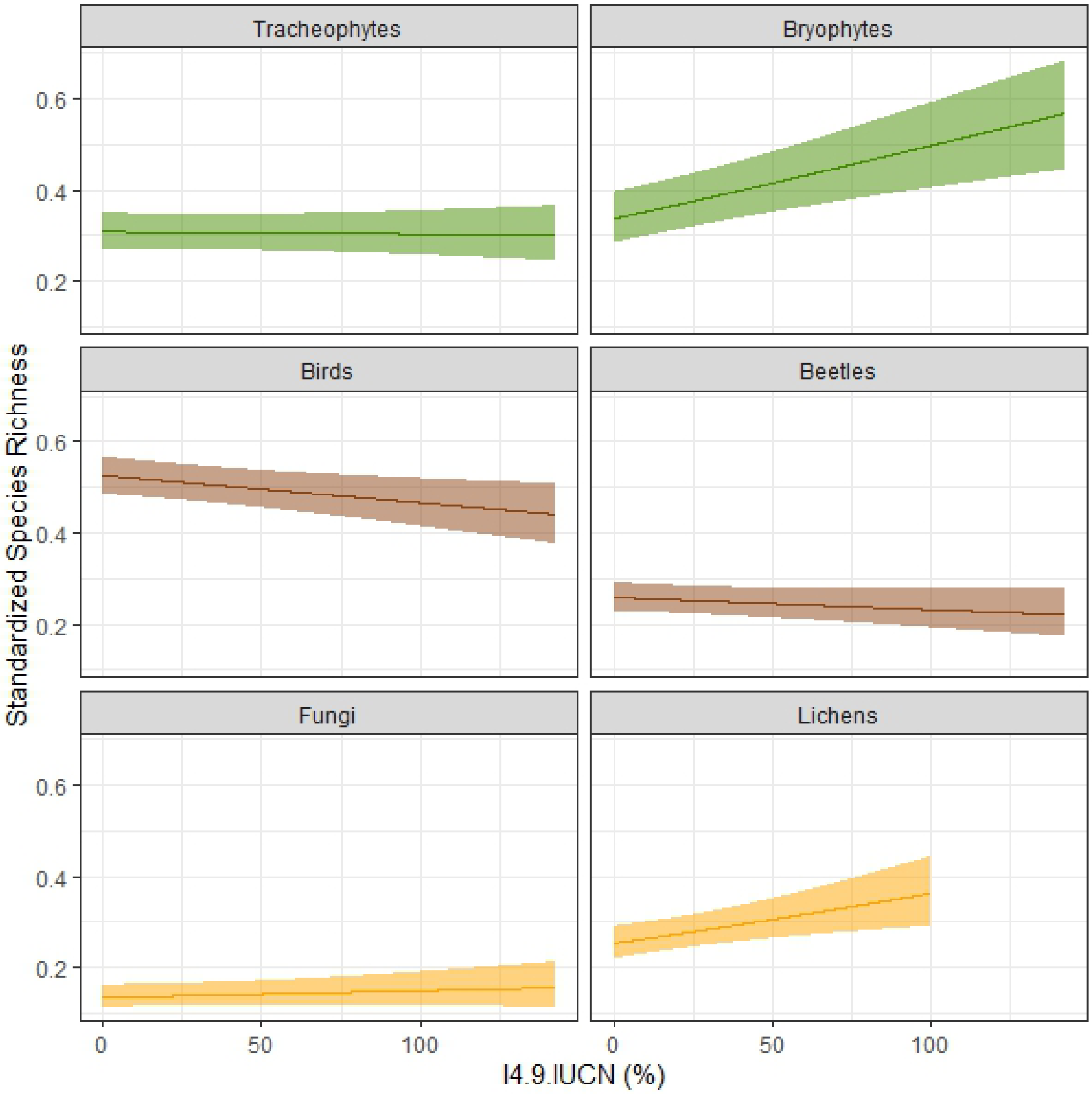

Figure 4: Relationships between standardized species richness of 6 taxonomic and functional groups and Forest Europe indicator 4.9 (Proportion of protected areas in a 500ha buffer). Estimations are issued from generalized linear models with Beta error distribution. Plain line represents the mean estimate, ribbons the 95% confidence interval.

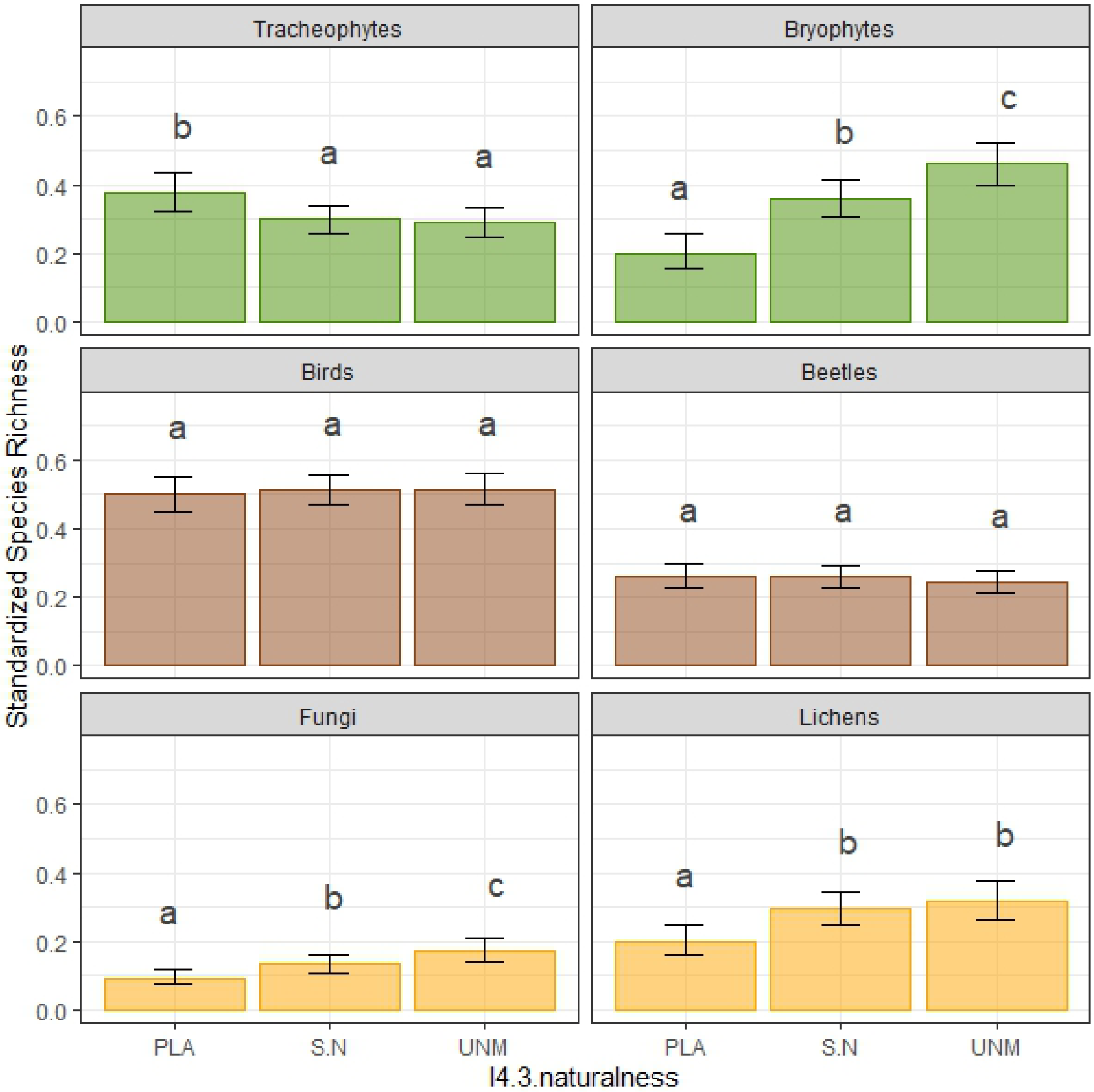

Figure 5: Relationships between standardized species richness of 6 taxonomic and functional groups and Forest Europe indicator 4.3. Naturalness: PLA = Plantations; S.N = Semi – Natural forests; UNM = Unmanaged forests. Estimations are issued from generalized linear models with Beta error distribution and logit link. Barplots represent mean estimates, error bars are the 95% confidence interval. Letters indicate significant differences per group based on Tukey post-hoc test.

Relative performance of the different indicators

Comparing the AICc (Table 4) for all single models revealed that the indicator based on forest Naturalness (4.3) best explained the scaled species richness for three out of six groups (tracheophytes, bryophytes, and lichens); Regeneration (4.2) was within 2 points of AICc for tracheophytes and lichens. For birds and beetles, the indicator based on Forest birds (4.10) was the best explanatory one, while for fungi, Deadwood (4.5) stood first. Also note that the null model was never the best one and more than 2 AICc points away from the best.

		Tracheophytes	**Bryophytes**	**Birds**	**Beetles**	**Fungi**	**Lichens**
Explanatory variables	**K**	**Delta AICc**	**Delta AICc**	**Delta AICc**	**Delta AICc**	**Delta AICc**	**Delta AICc**
Null	3	14.5	76.9	626.2	2.6	123.1	27.4
I4.1.tree.sp	4	13.3	59.9	627.1	4.2	107.1	18.4
I4.2.regeneration	5	0.5	23.5	629.5	6.0	73.3	1.6
I4.3.naturalness	5	**0.0**	**0.0**	629.7	2.7	33.9	**0.0**
I4.4.invasive	4	13.0	77.8	627.3	4.1	125.1	29.3
I4.5.deadwood	4	14.4	52.3	624.2	4.6	**0.0**	19.3
I4.7.fragmentation (FAD)	4	4.4	70.8	610.9	1.9	121.7	29.3
I4.8.threat.sp	4	12.8	75.2	623.8	4.4	124.1	28.5
I4.9.IUCN	4	16.4	64.0	622.1	2.5	124.4	21.6
I4.10.birds	4	16.3	78.7	**0.0**	**0.0**	115.4	29.4

Table 4: Differences of Akaike Information Criteria corrected for small samples (Delta AICc) for all generalized mixed models with Beta error distribution and logit link. K is the number of parameters in each model. The best model (delta AICc = 0) is in bold.

Combination of indicators

We used data dredging to find the best linear (i.e. without interaction) combination of indicators reflecting the variations in species richness of each group. Only beetles were represented by only one indicator (Forest Birds, 4.10.), all the other ones had a combination of 3 to 4 indicators in their best models (Table 5). In terms of indicators, Invasive species (4.4.) was never selected. Conversely, and as observed before, Diversity of tree species (4.1.), Naturalness (4.3.), Deadwood (4.5.) were selected four times, followed by Forest Birds (4.10, 3 times). Finally, it is interesting to note that, except for Fragmentation (FAD, 4.7.), all indicators had positive effects, and with the remarkable exception of beetles, all multivariate models performed better than single ones (in terms of AICc, they had at least 2 points less than single variable ones, Table 5).

Taxonomic and functional groups	**Tracheophytes**	**Bryophytes**	**Birds**	**Beetles**	**Fungi**	**Lichens**
Intercept	-0.47	-1.28	0.11	-1.03	-2.14	-1.34
I4.1.tree.sp	0.11	0.17			0.12	0.12
I4.3.naturalness	+	+			+	+
I4.4.invasive						
I4.5.deadwood	0.06	0.09			0.17	0.07
I4.7.fragmentation (FAD)	-0.072		-0.07			
I4.8.threat.sp			0.05			
I4.9.IUCN						
I4.10.birds			0.65	0.05	0.08	
Df	8	7	6	4	8	7
AICc	-1246.18	-384.61	-1678.81	-1123.87	-1743.14	-547.79
Delta AICc	0.61	1.42	0.19	0.96	1.23	1.69
AICc (best single variable models)	-1226.72	-375.82	-1648.93	-1123.87	-1671.48	-541.632

Table 5: Scaled estimates of the models selected by data dredging combining all indicators from Forest Europe (without interaction). Estimates are issued from generalized linear mixed models with Beta error distribution and logit link. "+" indicates the presence of the factor in the model. The best model was the most parsimonious (lowest degrees of freedom - df) with the lowest Akaike Information Criterion corrected for small samples (AICc). "delta" indicates the AICc difference with the best model. logLik = logarithm of the likelihood.

Discussion

We analyzed the links between Forest Europe's biodiversity indicators and the biodiversity of six taxonomic and functional groups on a unique multi taxonomic dataset covering most forest types in Europe (Burrascano et al. 2023). We showed that these indicators perform unequally: while some correctly describe the biodiversity of several groups, no one acted as a universal indicator, questioning their strength to predict biodiversity in European forests. In contrast, our results reinforced the approach based on multiple complementary indicators of the same *indicandum*. This also raises the question of contextualization of these indicators, to better assess state and trends of biodiversity across Europe, and opens perspectives for improvement.

Performance of current forest biodiversity indicators

While evidence on the link between some indicators and the biodiversity they are supposed to indicate remains incomplete (Gao et al. 2015; Penone et al. 2019; Zeller et al. 2023), our results highlighted several habitat-species relationships and habitat preferences of different groups.

We first observed strong effects of Regeneration origin (4.2) and Naturalness (4.3) on the biodiversity of the six groups. The biodiversity of bryophytes and fungi was higher in unmanaged forests compared to semi natural forests, and, including lichens, higher than in plantation forests (Figure 5). On the contrary, plantations had a marginal positive effect on tracheophytes compared to semi natural and unmanaged forests, and naturalness had no effects on birds and beetles. The negative effects of plantations, and the positive effects of management abandonment or primeval forests have been thoroughly documented (e.g. Chaudhary et al. 2016; Paillet et al. 2010). However, our results should be nuanced by the fact that the distribution of the data in the different categories of regeneration and naturalness were strongly unbalanced, with only few plots located in coppice-managed forests and a vast majority in semi-natural forests (Table 1). That said, unmanaged forests had a generally positively influence on biodiversity in our dataset, especially for deadwood dependent species (epixylic bryophytes and lichens), while plantations had detrimental effects on several other groups. Indeed, habitat provision and continuity are higher in semi-natural forests, not to speak of unmanaged forests, which allow the persistence of dispersal limited species (e.g. Boch et al. 2013; Boch et al. 2021). The positive response of tracheophytes in plantations may seem surprising, but probably reflects a higher share of disturbance tolerant herbs in more disturbed sites, as shown in several individual studies (Boch et al. 2013). In addition, the semi-natural category encompasses a wide range of management types (Trentanovi et al. 2023), and unmanaged forests in our dataset have mostly been recently abandoned, which may cause a decrease in the biodiversity of tracheophytes during the first decades after abandonment (e.g. Paillet et al. 2010).

Deadwood volume, followed by diversity of tree species, were two indicators that often correlated with scaled species richness, both in univariate and multivariate analyses. Deadwood and diversity of tree species have complementary roles for biodiversity (Storch et al. 2023). Deadwood provides a substrate and a resource for numerous species that depend on it for part of their life cycle (Lassauce et al. 2011; Müller et al. 2019; Müller et al. 2015; Parajuli & Markwith 2023), but also for facultative species (Graf et al. 2022). Indeed, the richness of bryophytes, fungi and lichens, and to a lesser extent birds, correlated positively to deadwood volume in our analyses. Surprisingly however, saproxylic beetles richness did not correlate significantly to deadwood volume despite a weak positive effect. It is likely that, for this group in particular, deadwood does not act as a universal indicator that could be transposed in all situations (see also Zeller et al. 2023). For example, Lassauce et al. (2011) showed that the correlation between richness of saproxylic beetles and deadwood volume was higher in boreal than in temperate forests, a result that was however not confirmed by Parajuli and Markwith (2023). Müller et al. (2015) showed compensation effects between deadwood and temperature, supporting that the influence of deadwood on saproxylic beetle richness declines with increasing temperature, both in geographical space, but also locally in relation to canopy openness (e.g. Koch Widerberg et al. 2012). It is also possible that the observed deadwood volumes (mean 40 m^3/ha, Table 3) lead to relatively poor beetle communities. However, in most cases, the mean deadwood values in our dataset were above the average deadwood volume per European country (which was 11.5m3/ha on average, but varied from 2.3 to 28m3/ha between countries, Forest Europe 2020). Consequently, while the positive role of deadwood for biodiversity remains unchallenged, its use as an indicator should probably be refined by a better integration of the context (macroclimate, microclimate, position on the deadwood volume gradient) in the relation. It is also true that deadwood quality (e.g. including size and decay stage Vítková et al. 2018) is as much relevant as its quantity. Some saproxylic beetle species (e.g. the red-listed species *Rosalia alpina*, Campanaro et al. 2017) develop in large logs, snags and standing dead trees within canopy gaps. In most of the sampling units we analyzed, deadwood was represented by relatively small fragments (mostly around 15-20 cm diameter) likely deriving from thinning processes occurring in closed forests (Burrascano et al. 2023). Further, many rare taxa depend on the occurrence of tree-related microhabitats (Larrieu et al. 2018), such as the protected umbrella species *Osmoderma eremita,* which larvae develop in large cavities in living trees (Dubois et al. 2009). Since several tree-related microhabitats are very scarce in managed forests (Paillet et al. 2017), and not readily quantified as part of the deadwood pool (Müller et al. 2014), their role is not currently taken into consideration.

Diversity of tree species also showed positive correlation with the biodiversity of several taxonomic and functional groups (bryophytes, fungi, lichens and more marginally tracheophytes). Different tree species provide different habitat conditions for epiphytic and saproxylic species living in forests (e.g. Boch et al. 2021; Cavard et al. 2011; Leidinger et al. 2021). These conditions encompass direct biotic interactions, different chemical properties of the bark and wood, decomposition rates as well as differential light interception (Gosselin et al. 2017; Zeller et al. 2023). This in turn provides niche heterogeneity for several species and thus enhances biodiversity and confirms the role of diversity of tree species as a biodiversity indicator.

Among the other indicators, forest fragmentation showed negative effects on tracheophytes and birds, and a positive effect on bryophytes, and marginally on beetles and fungi. It should be noted that since it is based on forest area density (European Commission et al. 2019), it represents forest cover rather than its discontinuity and configuration, but has the advantage of being calculable and homogeneous across Europe. Besides, the landscapes surrounding our sampling units presented a high forest cover (77% on average, in a 500 ha buffer, Table 1). Thus, the observed correlations reflect that forest area density could have been beneficial for forest interior species that are sensitive to edge effects (bryophytes or lichens), but detrimental to non-forest, open habitat or light demanding species, such as tracheophytes and open-habitat birds (but see Bełcik et al. 2020, who show an increase before a plateau in taxonomic diversity with increasing forest area in agricultural landscapes). The inferences on the effect of fragmentation on biodiversity, based on the Single Large vs Several Small principle (Diamond 1975), support that large continuous habitat should have a greater effect on biodiversity conservation, compared to several small ones. However, recent multitaxa studies proved the disproportionately high value of small patches, harboring richer assemblages, even when focusing only on protected species (Riva & Fahrig 2022). Besides, it has been highlighted that biodiversity conservation in human-modified forest landscapes is better achieved maintaining at least 40% of forest cover, rather than focusing on fragmentation and configuration (Arroyo-Rodríguez et al. 2020). Hence, the role of fragmentation, as it is currently estimated, should be probably be reconsidered to take into account both the amount of forest cover and the value of the patches.

Contrary to the previous indicators, threatened species and birds are based on direct biodiversity sampling (other than trees). These indicators directly describe the evolution of a small part of the biodiversity, but generally correlate poorly to the richness of other taxa and most of the results observed are linked to the fact that these indicators represent subsets of larger groups (evidently forest birds vs. birds). However, despite several pieces of evidence showing that congruence between taxa is generally small, especially in forests (Burrascano et al. 2018; Westgate et al. 2017), forest birds positively correlated to beetles and fungi. Probably these groups respond to the same favorable habitat conditions, but this was not reflected in the multivariate analyses.

The proportion of IUCN-protected areas around the plots positively influenced the richness of bryophytes and lichens, highlighting the positive effects of protection for these groups, but surprisingly had a negative effect on birds (see Honkanen et al. 2010).

Finally, invasive tree species did not show any correlation with biodiversity, apart from a marginal positive effect on tracheophytes supporting high local tracheophyte diversity to be often an indicator of disturbance. Despite the negative effects of invasive species introduction on native flora, fauna and mycota, this effect is rather limited in our dataset since it contains very few invasive species in total (maximum one tree species per plot) reflecting that no projects targeted the effects of plantations rich in, or dominated by, introduced tree species on biodiversity. This limited gradient probably does not allow to show significant effects on biodiversity. In addition, an indicator on introduced species rather than invasive ones – as it is defined in Forest Europe’s indicators – may perform better.

Limitations of Forest Europe indicators to predict biodiversity patterns and implications for improvements

Our study is one of the first to test Forest Europe indicators against multitaxonomic data at the European level. During the model selection process, the best single variable models were more often involving naturalness (tracheophytes, bryophytes and lichens) followed by forest birds (birds and beetles) and deadwood (fungi). However, the multivariate models did perform better than single ones (except for beetles), and often the best ones combined several indicators to reflect variations of the *indicandum*. Only beetles were best indicated by forest birds, but with a low magnitude, and birds by three combined indicators (including forest birds and threatened species). The magnitude of the effects in the multivariate models were comparable to those of single variable models (Appendix 3) which confirmed that indicators were not collinear.

We studied only total richness as a response variable, and evidently, the results may be different for other, more specialized groups, or other metrics of biodiversity (abundance, occurrence of individual species, functional diversity). Such approach remains to be tested (see e.g. Lelli et al. 2019) but was beyond the scope of the present study. In addition, some of the references we used were probably incomplete regarding some groups: e.g. almost no lichens are included in the list we used for red-listed species, but the proportion of threatened species at the national levels may be high.

We limited our approach to the strict definition of the indicators as used in Forest Europe, but higher performance could probably be reached by at least two improvements. First, adding context to the indicators could probably reveal that they need to be adapted locally (Chiarucci et al. 2012; Honkanen et al. 2010). Examples of context could be: elevation (mountain vs. lowlands), biome (Mediterranean, temperate, boreal) and European forest types. Second, most of the metrics we used are abundance metrics (apart from tree species richness) that quantify habitat available for species. However, indicators based on diversity of resources (following the heterogeneity-diversity theory, Tews et al. 2004) could perform better, e.g. in the case of deadwood and saproxylic beetles (Bouget et al. 2013), or tree-related microhabitats and birds and bats (Paillet et al. 2018). It would then be interesting to assess the performance of other indicator metrics vs. the current ones in assessing forest biodiversity.

Conclusions: towards new indicators definitions and better reporting

Many forest biodiversity indicators are proxies based on pre-existing data mostly issued from National Forest Inventories (Tomppo et al. 2010). Despite recent progresses based on international initiatives (namely the Essential Biodiversity Variables, GEOBON, IPBES), monitoring the state and trends of forest biodiversity solely based on proxies is not satisfactory: while proxies are generally easier to measure than species themselves, they are prone to demographic effects such as extinction debts or colonization credits. In other words, the presence of a given habitat - such as deadwood - does not guarantee the presence of the species that depend on it (e.g. Paillet et al. 2018). In addition, the response of biodiversity to a given indicator depends on the taxonomic or functional group studied (Zeller et al. 2022), so no indicator may represent biodiversity overall. This was confirmed by our analyses. We showed that, while some indicators performed correctly for several taxonomic and functional groups in terms of significance and magnitude, we did not highlight a predominant role of one indicator over the others.

Stevenson et al. (2021) claimed that indicators were often implemented without clear considerations of their purposes and utility in terms of decision-making. We argue that, while combinations of current Forest Europe indicators are useful to delineate general trends in biodiversity, taking into account context and analyzing the performance of other - more diversity-driven - metrics would help better reporting on biodiversity (e.g. Alterio et al. 2023; Paillet et al. 2018). Such improvements would also be beneficial to the use of indicators beyond general trends to include evaluating management and policy actions, decisions, or set biodiversity targets (Stevenson et al. 2021). For example, we showed that larger negative effects on biodiversity were observed in planted forests. This poses key challenges for making the 3 billion trees planting promoted by the European Forest Strategy for 2030 a beneficial action for biodiversity in forests (Sills et al. 2020), if high growing rate plantations such as introduced Douglas fir (*Pseudotsuga menziesii*) or eucalyptus (*Eucalyptus* spp.) are promoted against semi-natural forests. Conversely, promoting old-growth and unmanaged forests, as well as restoration of monocultures and conversions towards semi-natural forests, could have a positive effect on biodiversity. It is crucial to assess and balance these potential effects with the use of current data available and biodiversity indicators before taking actions or to modulate actions in favor of biodiversity against detrimental ones.

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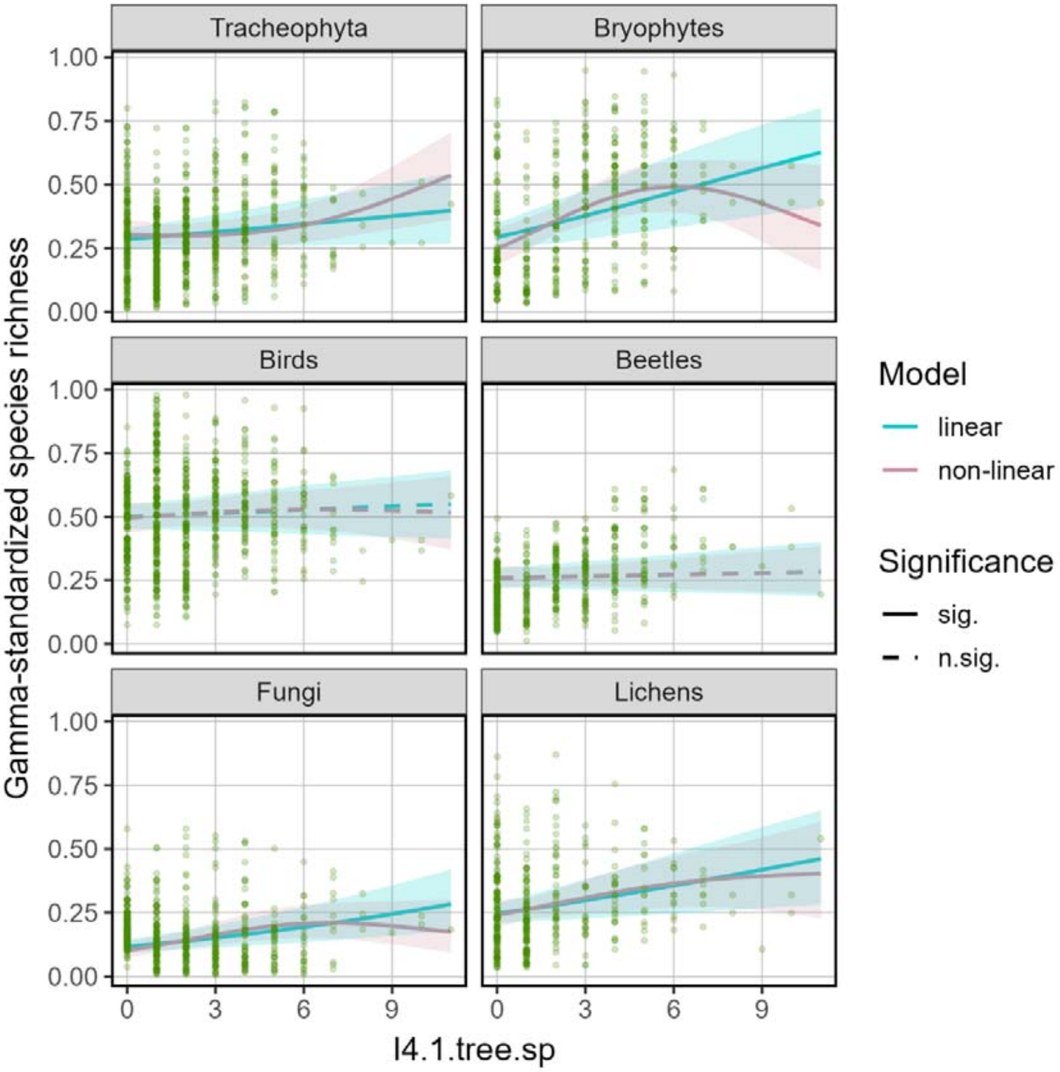
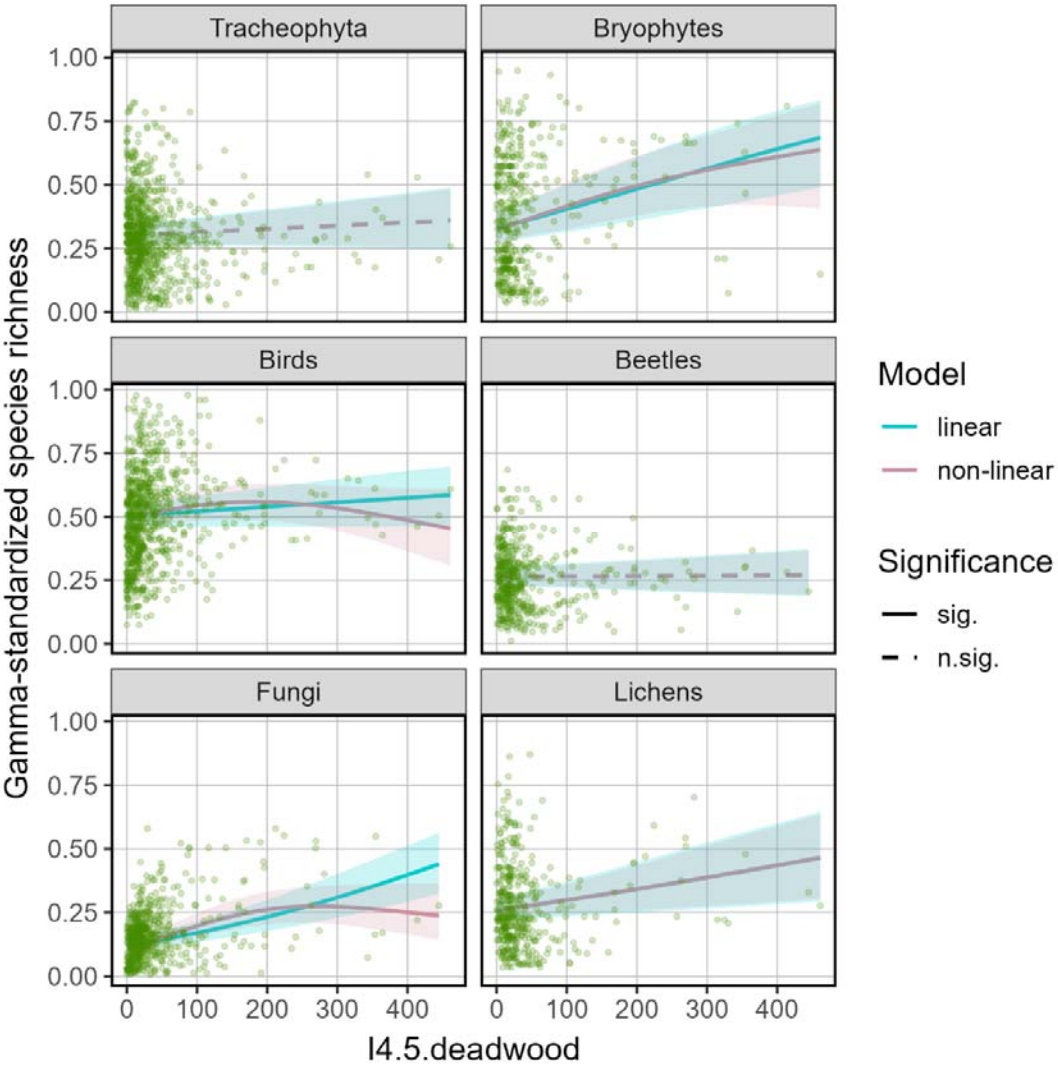
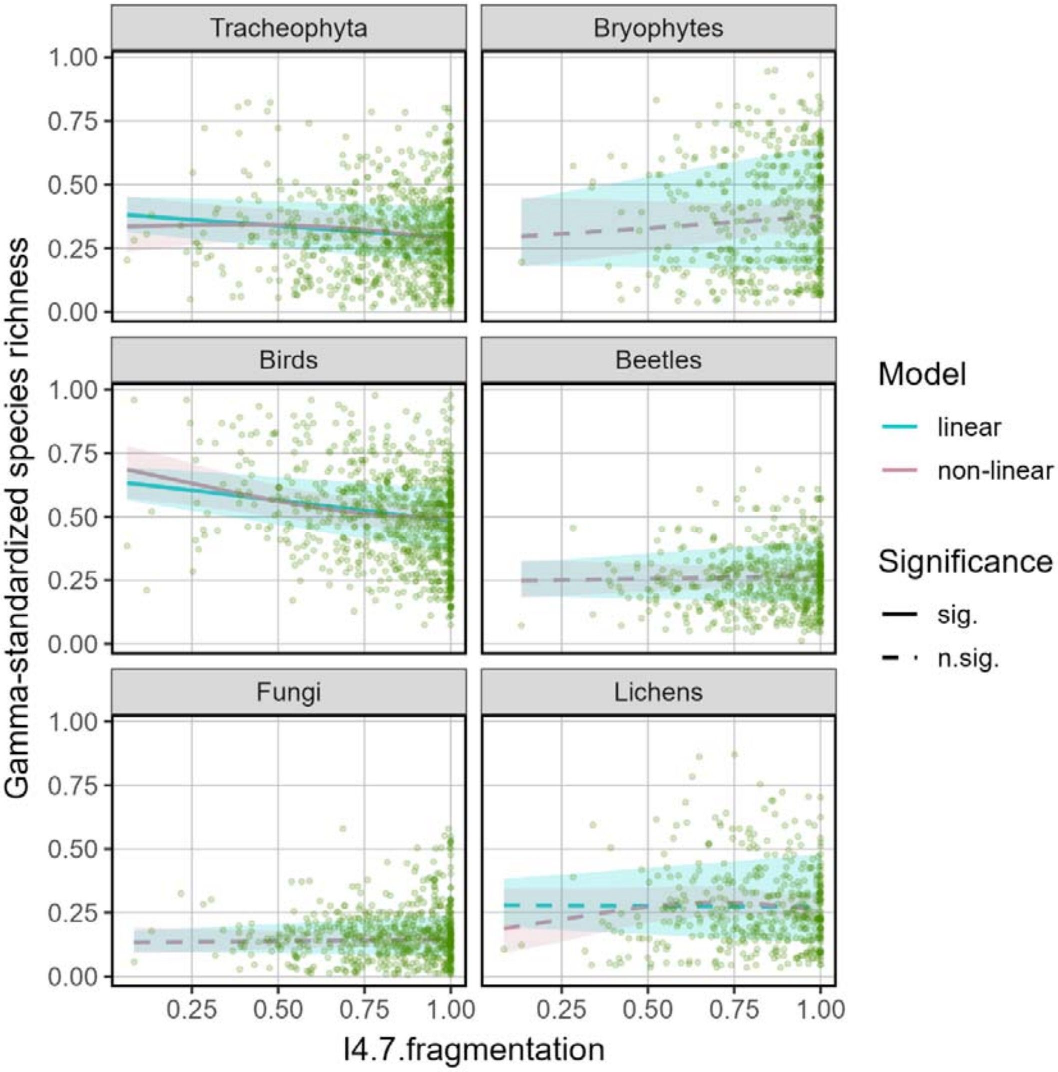
Appendices

Appendix 1: Comparison of linear (GLMMs) vs non-linear (GAMMs) models analyses between standardized species richness and several Forest Europe's biodiversity indicators.



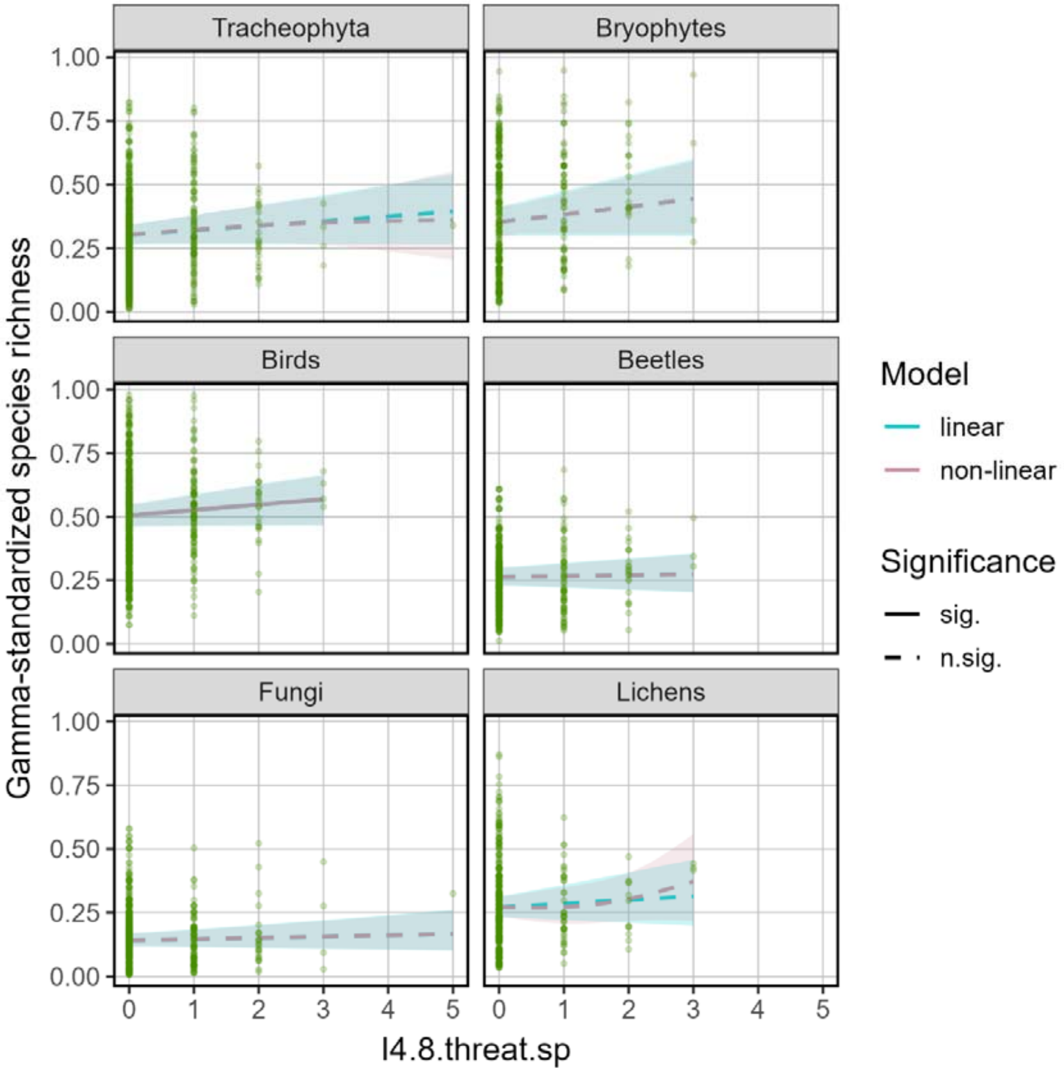

Tracheophyta
Bryophytes
Birds
Beetles
Fungi
Lichens
Gamma-standardized species richness
1.00
0.75
0.50
0.25
0.00
0
100
200
300
400
I4.5.deadwood
Model
linear
non-linear
Significance
sig.
n.sig.



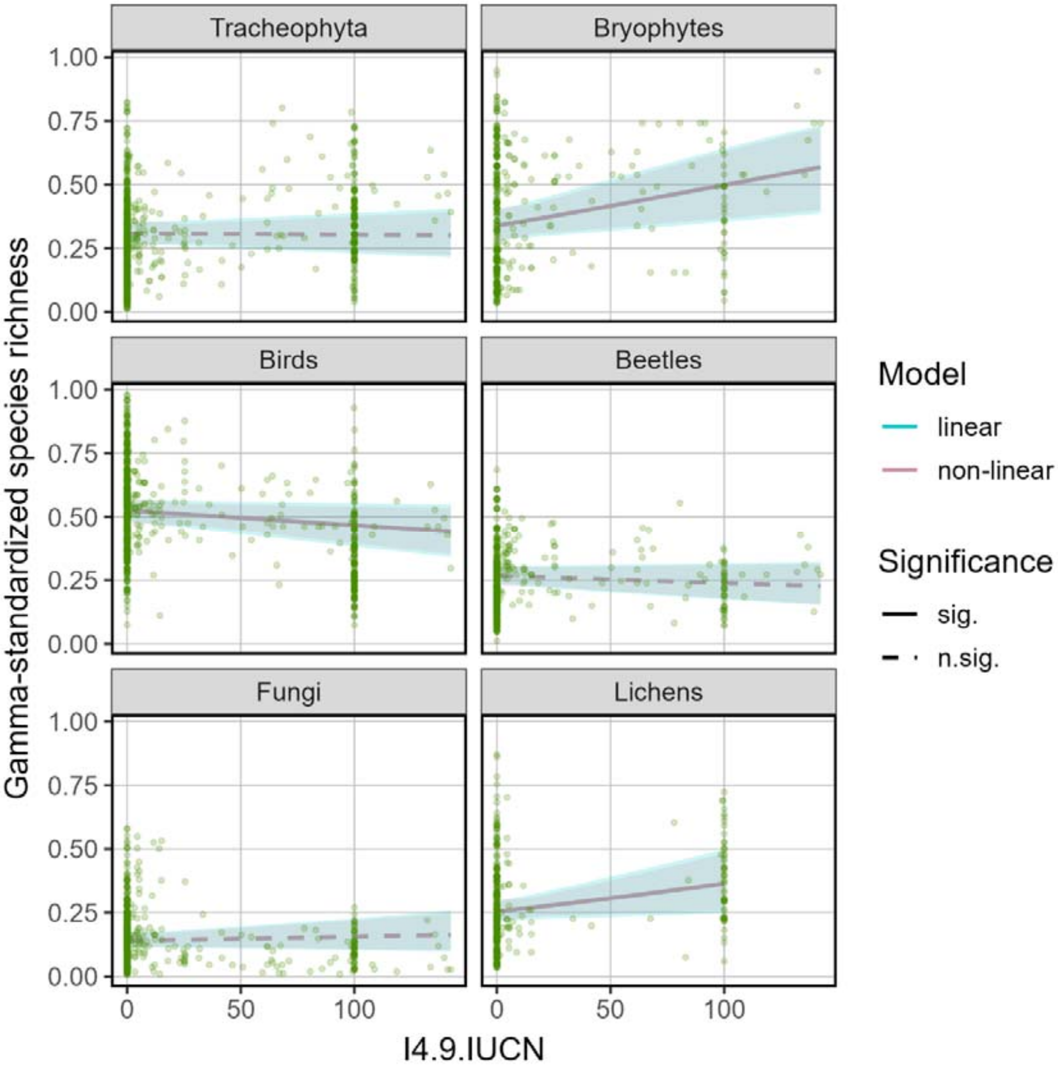
Tracheophyta
Bryophytes
Birds
Beetles
Fungi
Lichens
Gamma-standardized species richness
1.00
0.75
0.50
0.25
0.00
0.25
0.50
0.75
1.00
I4.7.fragmentation
Model
linear
non-linear
Significance
sig.
n.sig.

764

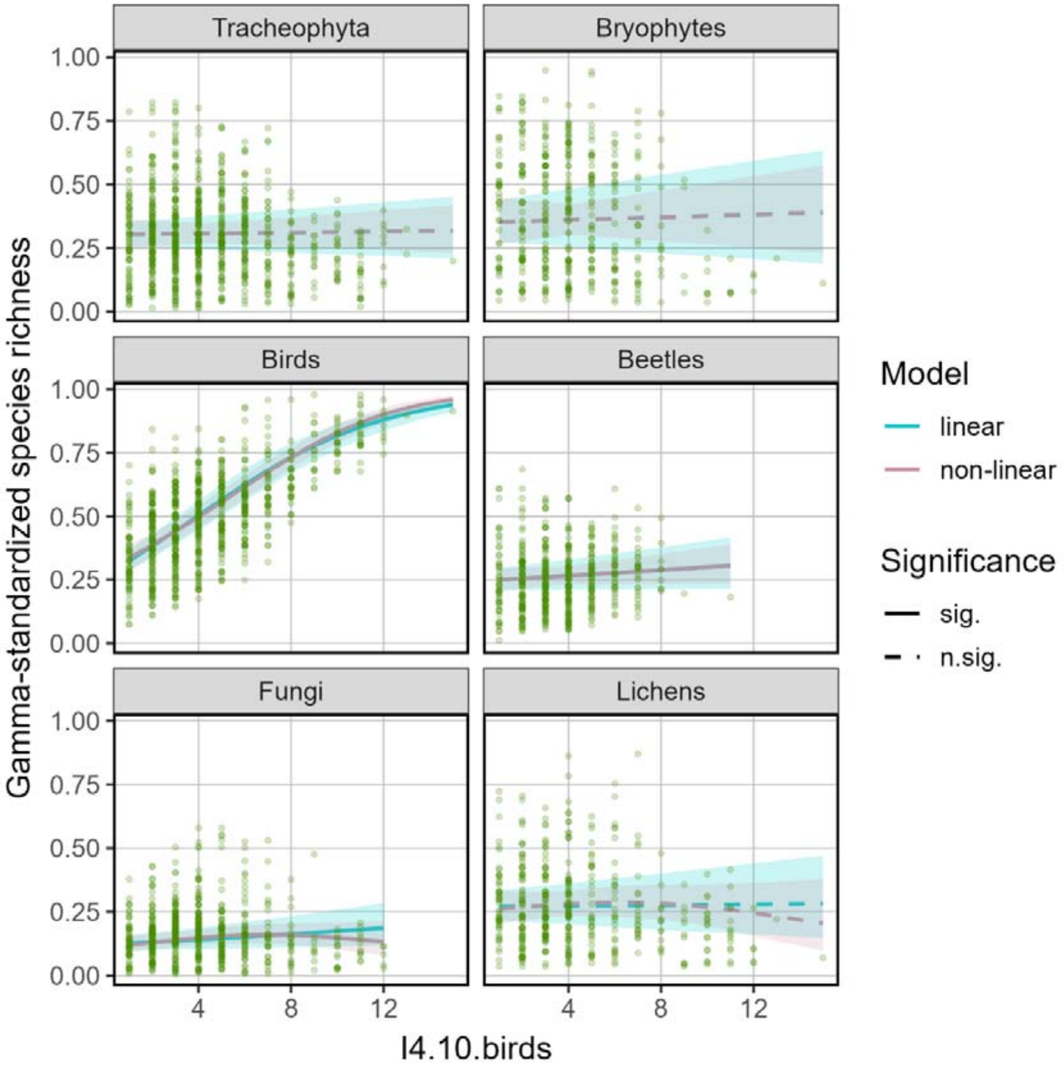
765



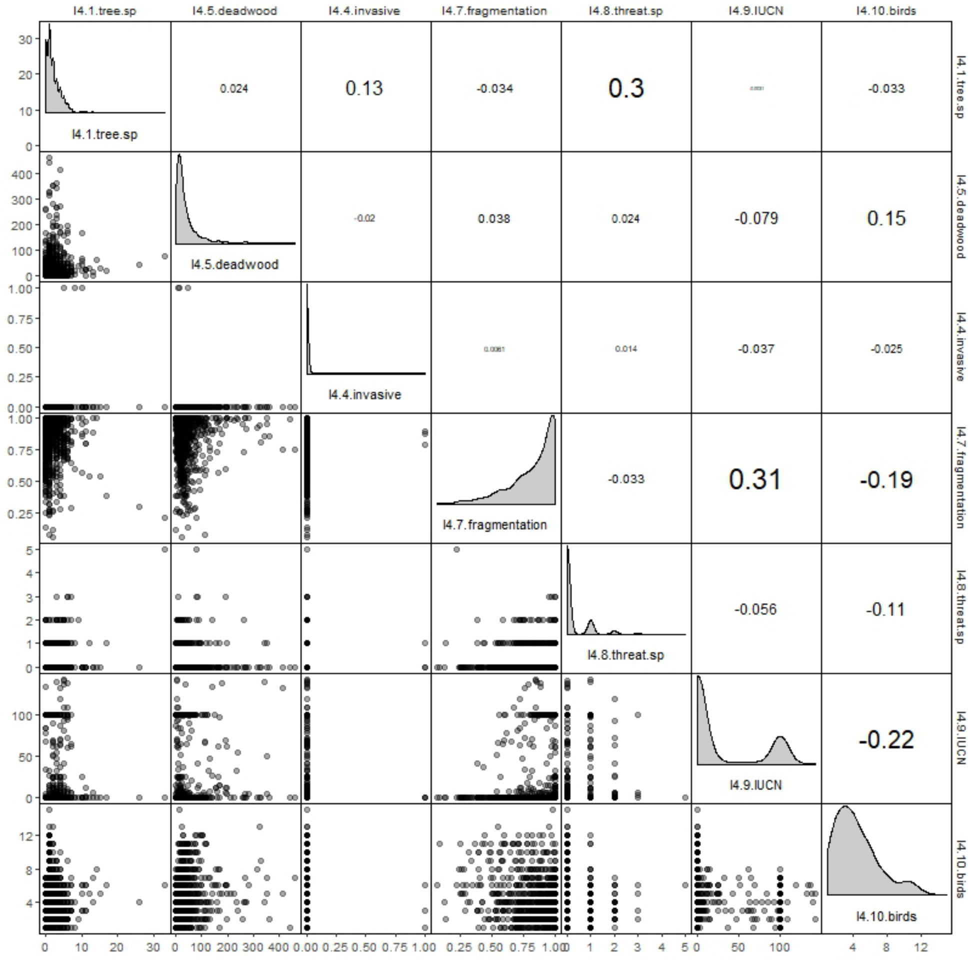
Tracheophyta
Bryophytes
Birds
Beetles
Fungi
Lichens
1.00
0.75
0.50
0.25
0.00
0
1
2
3
4
5
Gamma-standardized species richness
I4.8.threat.sp
Model
linear
non-linear
Significance
sig.
n.sig.


Tracheophyta
Bryophytes
Birds
Beetles
Fungi
Lichens
Gamma-standardized species richness
0.00
0.25
0.50
0.75
1.00
0
50
100
I4.9.IUCN
Model
linear
non-linear
Significance
sig.
n.sig.

767


Tracheophyta
Bryophytes
Birds
Beetles
Fungi
Lichens
Gamma-standardized species richness
1.00
0.75
0.50
0.25
0.00
4
8
12
I4.10.birds
Model
linear
non-linear
Significance
sig.
n.sig.

Appendix 2: Correlation between indicators of Forest Europe from the tracheophytes dataset. Figures on the right are Pearson correlation coefficients, biplots on the left and histograms on the diagonal represent the distribution of the data. Regeneration (4.2) and Naturalness (4.3) are categorical variables not represented here.



Appendix 3: Standardized richness estimates table for all single generalized mixed models with beta error distribution and logit link. Intercept for I4.2.Regeneration is “Coppice”, and for I4.3.Naturalness “Plantation” (PLA). S.N = semi-natural forest, UNM = Unmanaged forests. se = standard error of the mean, pl = critical probability, (*) p<0.1, * p<0.05, ** p<0.01, *** p<0.001.

Group	**variable**	**estimate**	**se**	**p**	
Tracheophytes	I4.1.tree.sp	0.0648	0.0359	0.0712	(*)
	I4.2.regeneration(natural regeneration)	0.1431	0.2606	0.5828	
	I4.2.regeneration(planting)	0.5186	0.2754	0.0597	(*)
	I4.3.naturalnessUNM	-0.3878	0.0889	<0.001	***
	I4.3.naturalnessS.N	-0.2073	0.1429	0.147	
	I4.4.invasive	0.0376	0.0193	0.0508	(*)
	I4.5.deadwood	0.0318	0.0219	0.1463	
	I4.7.fragmentation	-0.0898	0.0256	<0.001	***
	I4.8.threat.sp	0.0428	0.0221	0.0522	(*)
	I4.9.IUCN	-0.0087	0.0416	0.8344	
	I4.10.birds	0.0122	0.0326	0.707	
Bryophytes	I4.1.tree.sp	0.2828	0.0633	<0.001	***
	I4.2.regeneration(natural regeneration)	0.4156	0.4546	0.3606	
	I4.2.regeneration(planting)	-0.5511	0.4716	0.2426	
	I4.3.naturalnessUNM	0.8606	0.128	<0.001	***
	I4.3.naturalnessS.N	1.5727	0.1745	<0.001	***
	I4.4.invasive	-0.0409	0.0388	0.2917	
	I4.5.deadwood	0.2097	0.04	<0.001	***
	I4.7.fragmentation	0.1384	0.0486	0.0044	**
	I4.8.threat.sp	0.0776	0.0402	0.0539	(*)
	I4.9.IUCN	0.2268	0.0585	<0.001	***
	I4.10.birds	0.0235	0.0571	0.6806	
Birds	I4.1.tree.sp	0.0341	0.0323	0.2916	
	I4.2.regeneration(natural regeneration)	0.0996	0.2114	0.6375	
	I4.2.regeneration(planting)	0.0452	0.2249	0.8407	

Group	variable	estimate	se	p	
	I4.3.naturalnessUNM	0.0388	0.0785	0.6207	
	I4.3.naturalnessS.N	0.2011	0.1259	0.1104	
	I4.4.invasive	-0.0177	0.0186	0.3417	
	I4.5.deadwood	0.0402	0.0203	0.0469	*
	I4.7.fragmentation	-0.1018	0.0243	<0.001	***
	I4.8.threat.sp	0.043	0.0205	0.0365	*
	I4.9.IUCN	-0.1031	0.041	0.012	*
	I4.10.birds	0.6521	0.0218	<0.001	***
Beetles	I4.1.tree.sp	0.0242	0.034	0.4762	
	I4.2.regeneration(natural regeneration)	0.1411	0.2247	0.53	
	I4.2.regeneration(planting)	0.1782	0.233	0.4444	
	I4.3.naturalnessUNM	-0.0338	0.0638	0.5965	
	I4.3.naturalnessS.N	-0.0749	0.109	0.4917	
	I4.4.invasive	-0.0135	0.0175	0.441	
	I4.5.deadwood	0.0045	0.0204	0.8238	
	I4.7.fragmentation	0.0435	0.0263	0.0983	(*)
	I4.8.threat.sp	0.0096	0.0196	0.6255	
	I4.9.IUCN	-0.0526	0.0357	0.1409	
	I4.10.birds	0.05	0.023	0.0297	*
Fungi	I4.1.tree.sp	0.1476	0.0343	<0.001	***
	I4.2.regeneration(natural regeneration)	0.1607	0.2444	0.5109	
	I4.2.regeneration(planting)	-0.3632	0.2542	0.1531	
	I4.3.naturalnessUNM	0.5017	0.0691	<0.001	***
	I4.3.naturalnessS.N	0.9083	0.1434	<0.001	***
	I4.4.invasive	0.0035	0.0189	0.8526	
	I4.5.deadwood	0.2228	0.0181	<0.001	***
	I4.7.fragmentation	0.054	0.0292	0.0644	(*)
	I4.8.threat.sp	0.0226	0.022	0.3039	
	I4.9.IUCN	0.0422	0.0466	0.366	
	I4.10.birds	0.1021	0.0324	0.0016	**
Lichens	I4.1.tree.sp	0.1714	0.0507	<0.001	***

Group	**variable**	**estimate**	**se**	**p**	
	I4.2.regeneration(natural regeneration)	0.0169	0.258	0.9479	
	I4.2.regeneration(planting)	-0.5447	0.2736	0.0465	*
	I4.3.naturalnessUNM	0.5513	0.1028	<0.001	***
	I4.3.naturalnessS.N	0.7687	0.2439	0.0016	**
	I4.4.invasive	0.0092	0.0313	0.7691	
	I4.5.deadwood	0.1139	0.0343	<0.001	***
	I4.7.fragmentation	0.0137	0.0442	0.7564	
	I4.8.threat.sp	0.0339	0.0348	0.329	
	I4.9.IUCN	0.1778	0.061	0.0036	**
	I4.10.birds	0.0067	0.0559	0.904	