1 # One to rule them all? Assessing the performance of Forest

2 # Europe's biodiversity indicators against multitaxonomic data

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4 **Impact statement**

5 Biodiversity indicators used to assess the state of Europe's forests perform unequally; a

6 combination of indicators is more informative

7

8 **Keywords**

9 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

163   lacks strong scientific evidence (Gao et al. 2015; Paillet et al. 2018; Storch et al. 2023; Zeller

164   et al. 2022). Indeed, only two indicators involve other species than trees (namely 4.8

165   Threatened forest species, 4.10 Common forest bird species, Table 1) and to date, despite a

166   large corpus of individual studies and few syntheses (Zeller et al. 2023), no global and

167   systematic assessment of the correlations between multi-taxonomic biodiversity and Forest

168   Europe indicators has been attempted.

169   In this context, our aim was to provide an *ex post* validation of these indicators and propose

170   improvements to the reporting process. For this, we: i) assessed the link between indicators

171   and several - multi-taxonomic (i.e. taxonomic and functional groups) - *indicanda*; ii) identified

172   the indicators that performed best and universally - i.e. for all groups; iii) defined, if possible,

173   the most effective combination of indicators for forest biodiversity.

174   To address these aims, we first tested Forest Europe's biodiversity indicators against each

175   taxonomic and functional group. Second, we used a model selection approach to search for

176   the best indicators in terms of taxonomic and functional group. Third, we tested the effect of

177   a combination of indicators by searching for the best and most parsimonious combination of

178   biodiversity indicators. We used a multi-taxonomic database (Burrascano et al. 2023;

179   Trentanovi et al. 2023) combining species inventories and forest structure to analyze the

180   correlations between Forest Europe's biodiversity indicators with the biodiversity of six

181   groups (tracheophytes, epixylic and epiphytic bryophytes, birds, saproxylic beetles,

182   saproxylic non-lichenized fungi and epixylic and epiphytic lichenized fungi).

183

184   **Materials and Methods**

185   *Database*

186   We used the database gathered within the framework of the COST action "BOTTOMS-UP"

187   (CA18207 – Biodiversity Of Temperate forest Taxa Orienting Management Sustainability by

188   Unifying Perspectives). In a nutshell, this database comprises biodiversity samplings along

189   with forest plot descriptions (Burrascano et al. 2023). It merges 34 different datasets from 12

190   European countries and more than 3500 sampling units. From this database, we extracted

191 the six most represented taxonomic and functional groups, namely tracheophytes, epixylic

192 and epiphytic bryophytes (hereafter bryophytes), birds, saproxylic beetles, saproxylic non-

193 lichenized fungi (hereafter fungi) and epixylic and epiphytic lichenized fungi (hereafter

194 lichens).
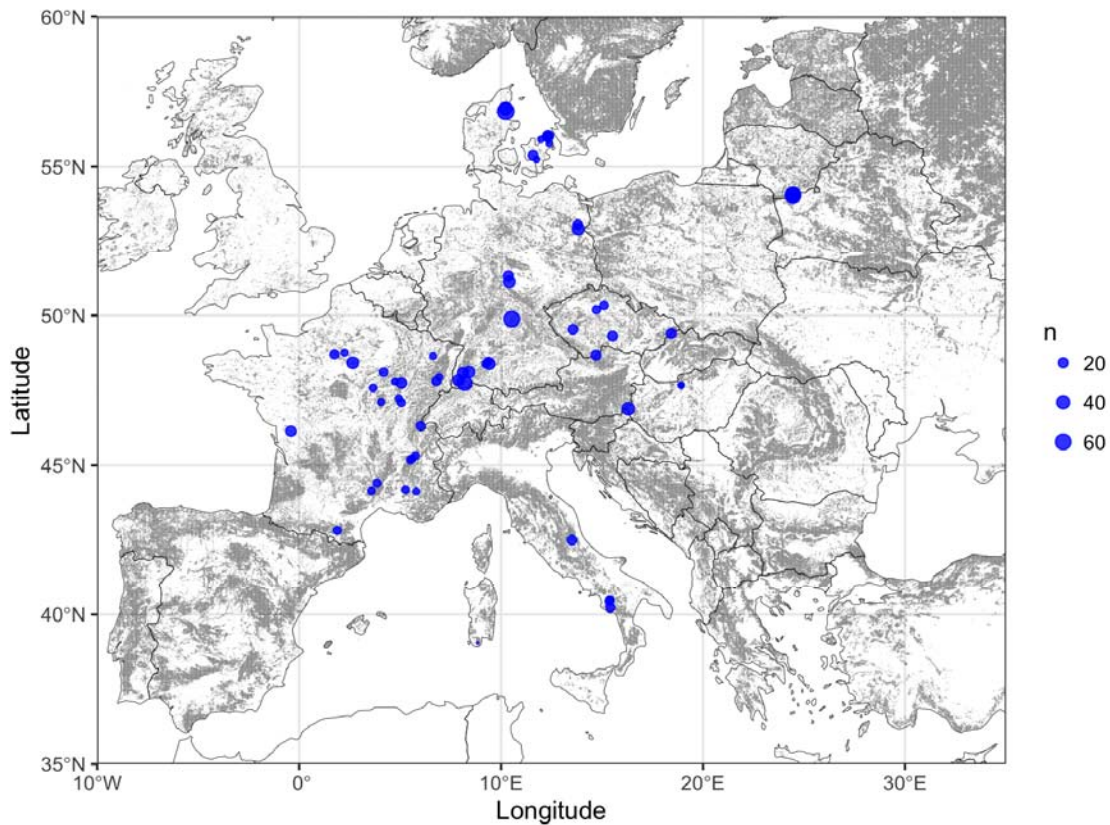
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196 Figure 1: Spatial distribution of the sampling sites. Gray areas are covered by forests with a

197 tree cover greater than 40% according to Kempeneers et al. (2011). The size of the dot is

198 proportional to the number of sampling units.

199

200 While tracheophytes and birds were inventoried without any specific selection of the guilds

201 targeted, only epiphytic and epixylic bryophytes and lichens were included (sampled on

202   living trees and deadwood), and saproxylic fungi and beetles (dependent on deadwood

203   substrates or on other organisms inhabiting deadwood).

204   Since the database is the result of the merging of different research projects, sampling

205   designs and protocols varied across datasets (Burrascano et al. 2023; Trentanovi et al.

206   2023). Therefore, we standardized species richness (number of species per sampling plot)

207   by dividing it by the asymptotic gamma richness at the site level, with site representing a

208   homogeneous sampling area with a maximum size of a few thousand hectares. We derived

209   site gamma diversity through plot-based rarefaction curves using the R package iNEXT

210   (Hsieh et al. 2016). Sites with less than 6 sampling units were discarded from the final

211   database since the estimation of the gamma richness was judged non-reliable. Exploratory

212   analyses revealed especially large deadwood volumes linked with small plots (nugget

213   effect). To avoid strong leveraging from these outliers (Zuur et al. 2010), we limited the

214   maximum deadwood volume per sampling plot to 500 m3/ha, a value that corresponds to the

215   maximal volumes observed in primeval forest of Europe (e.g. Christensen et al. 2005). The

216   final data distribution per taxonomic and functional groups is shown in Table 1 and Figure 1.

Taxa	I4.2.Regeneration			I4.3.Naturalness			Total
	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

217   Table 1: Number of plots used to fit the models distributed per taxonomic and functional

218   groups and Regeneration origin or Naturalness following Forest Europe (2020).

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220   *Indicators' calculation*

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221 We used the State of Europe's Forests (Forest Europe 2020) definitions to calculate the

222 corresponding metrics for the indicators included in the Criterion 4 (Table 2). Since it was

223 necessary to "translate" the definition into calculable values to analyze the relationship

224 between indicator values and *indicanda* (i.e. standardized species richness), we proceeded

225 as follows:

226 - indicator 4.6 *Genetic resources* was excluded since it was not possible to translate

227 this indicator at the plot or site levels;

228 - indicators 4.1 *Diversity of tree species*, 4.4 *Introduced tree species* and 4.5

229 *Deadwood* were directly calculated from the plot measurements. Instead of

230 introduced tree species, we considered only invasive woody species that can have a

231 significant impact on forest biodiversity following Campagnaro et al. (2018), namely

232 *Acer negundo*, *Ailanthus altissima, Prunus serotina*, *Quercus rubra* and *Robinia*

233 *pseudoacacia* (Campagnaro et al. 2018). We limited to these species since there

234 was no regional reference list for introduced tree species and it would have been far

235 beyond the scope of this study to create such a list, e.g. Norway spruce (*Abies alba*)

236 is introduced in lowland France but native in mountains where it has also been

237 planted in some places. In addition, no reference list of invasive tree species in

238 Europe was available in the Forest Europe (2020) report;

239 - indicators 4.2 *Regeneration* and 4.3 *Naturalness* were derived from declarative

240 metadata when merging the database (Burrascano et al. 2023). In the 4.3, forests

241 were considered 'undisturbed by man' when declared without intervention by the data

242 holder (i.e. 'abandoned', 'unmanaged', 'primeval'). Time since the last intervention

243 was not used here since it was not homogeneously declared. 'Semi-natural' refers to

244 forest plots that are under any type of forest management regime (from even-aged to

245 uneven-aged silvicultural systems), but with natural regeneration processes of trees.

246 'Plantation' forests overlap with forest plots where regeneration derives from

247 'Planting' activities;

9

248   -   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/);

254   -   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;

259   -   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.

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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

266   Table 2: Forest Europe's biodiversity indicators definitions and data sources used to

267   calculate them in this paper.

268

269   *Statistical analyses*

270   We processed all analyses in R v.4.3.0 (R Core Team 2023). We used the standardized

271   species richness of each taxonomic and functional group as a response variable. For each

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272   group, we fitted a single generalized linear mixed model with each indicator as an

273   explanatory variable (9 models + the null - intercept only - model) and site as a random

274   effect on the intercept to account for the fact that two plots from the same site were more

275   likely to be similar than two plots from different sites. We used the beta error distribution with

276   logit link since standardized richness was continuous, strictly positive with a maximum value

277   below one. We scaled continuous explanatory variables to improve the convergence and to

278   make the estimates of the models comparable. We used the glmmTMB function in the

279   glmmTMB package (Brooks et al. 2017). We compared the magnitudes of all single effects

280   in the models and their significance and represented this using a heatmap of the

281   standardized effects (package ggplot2, Wickham 2016). We tested differences between

282   estimates of categorical variables (e.g. 4.3.naturalness) using Tukey post-hoc test. To

283   search for potential non-linear relationships between indicators and *indicanda*, we also fitted

284   generalized additive mixed models (GAMMs) with indicators as smoothers (package mgcv,

285   Wood 2023). We found very few differences between GLMMs and GAMMs and preferred to

286   stick to the first (comparisons are presented in Appendix 1).

287   Finally, to assess the relative performance of all indicators, we first compared the Akaike

288   Information Criterion corrected for small samples (AICc, Burnham & Anderson 2002) of all

289   single models including a null (intercept only) model. Then, we searched for the best and

290   most parsimonious linear combination (no interaction) of indicators that represented

291   biodiversity based on AICc using the dredge function (package MuMIn, Barton 2023). In this

292   process, we discarded the indicator 4.2. Regeneration since it was collinear with 4.3.

293   Naturalness and a model containing both variables could not be fitted (see Appendix 2).

294   When two competing models had a difference in AICc less than 2 points, we chose the most

295   parsimonious one.

296

297   **Results**

298   *Data and indicators' distribution*

299   The most represented group in the database was tracheophytes (838 plots) followed by

300   birds (825 plots, Table 3, see Burrascano et al. 2023 for a full description of the biodiversity

301   dataset). All taxonomic and functional groups have been inventoried in at least 400 plots

302   (Table 1). The distribution in the classes Regeneration (4.3.) and Naturalness (4.4.) were,

303   however, strongly unbalanced (see also Table 1): the majority of sampling units were

304   associated with "natural regeneration", while "coppicing" - and "planting" to a lesser extent -

305   were underrepresented; the majority of sampling units were within semi-natural forests, but

306   the distribution was more balanced than for regeneration types. For quantitative indicators,

307   the values taken were relatively balanced between groups (Table 3) and no strong

308   collinearity was observed (see Appendix 2 for an example on tracheophytes).

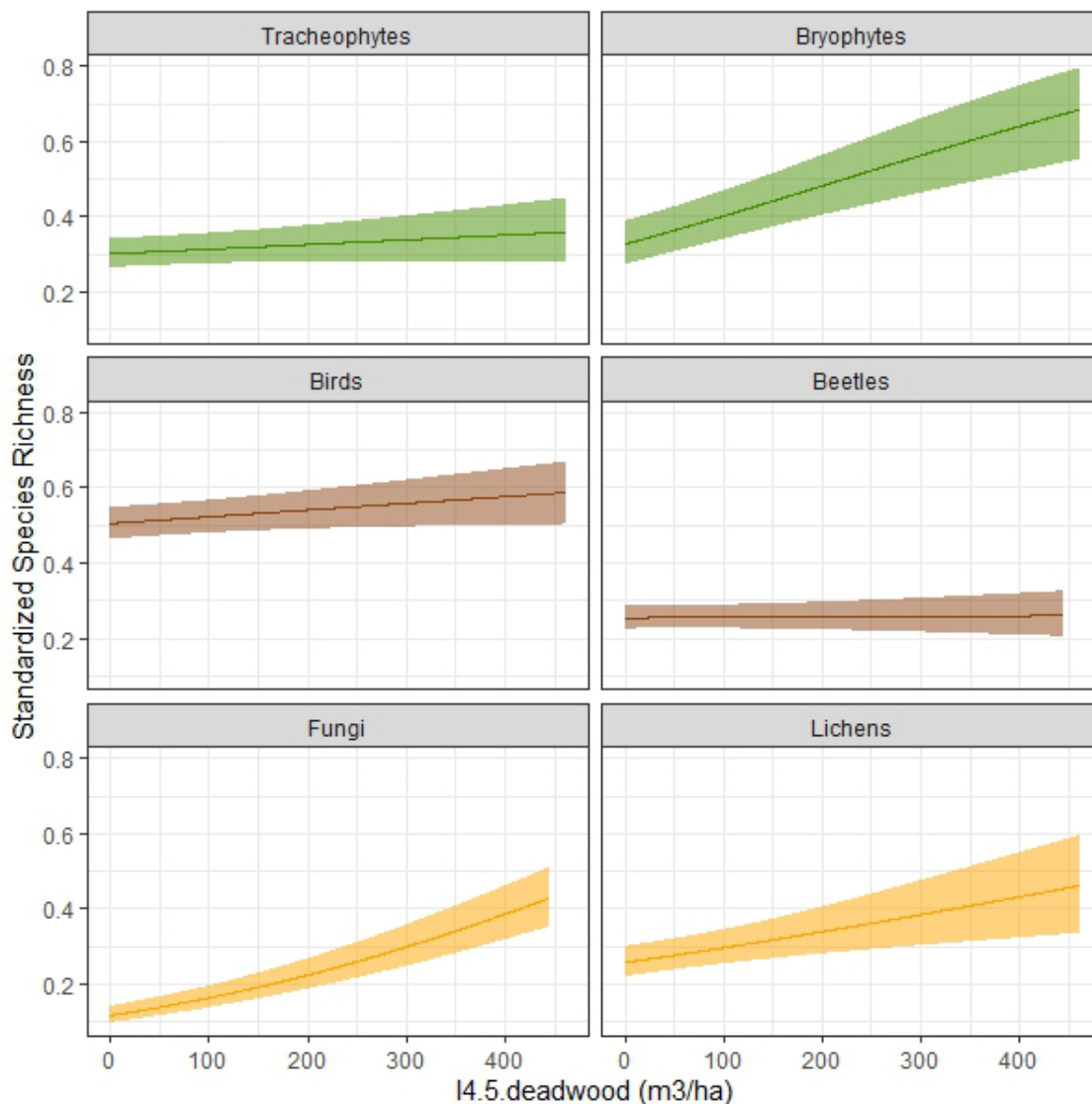| Taxonomic and functional groups	I4.1.tree.sp	I4.4.invasive	I4.5.deadwood	I4.7.fragmentation (FAD)	I4.8.threat.sp	I4.9.IUCN	I4.10.birds
Tracheophytes	1.96(2.06) [0-11]	0.01(0.08) [0-1]	41.83(60.72) [0-444.89]	0.85(0.16) [0.13-1]	0.25(0.56) [0-3]	14.92(33.66) [0-142.4]	3.63(1.78) [1-11]
Bryophytes	1.91(1.84) [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]

309   Table 3: Summary table for the range of values (mean per sampling unit (sd) [min - max])

310   taken for each indicator distributed over the different subsets. FAD = Forest Area Density.

13

311   *Correlations between indicators and indicanda*

312   Several of the Forest Europe indicators had significant relationships with the standardized

313   species richness of one or more of the six taxonomic and functional groups (Figure 2, see

314   Appendix 3 for values of the estimates).
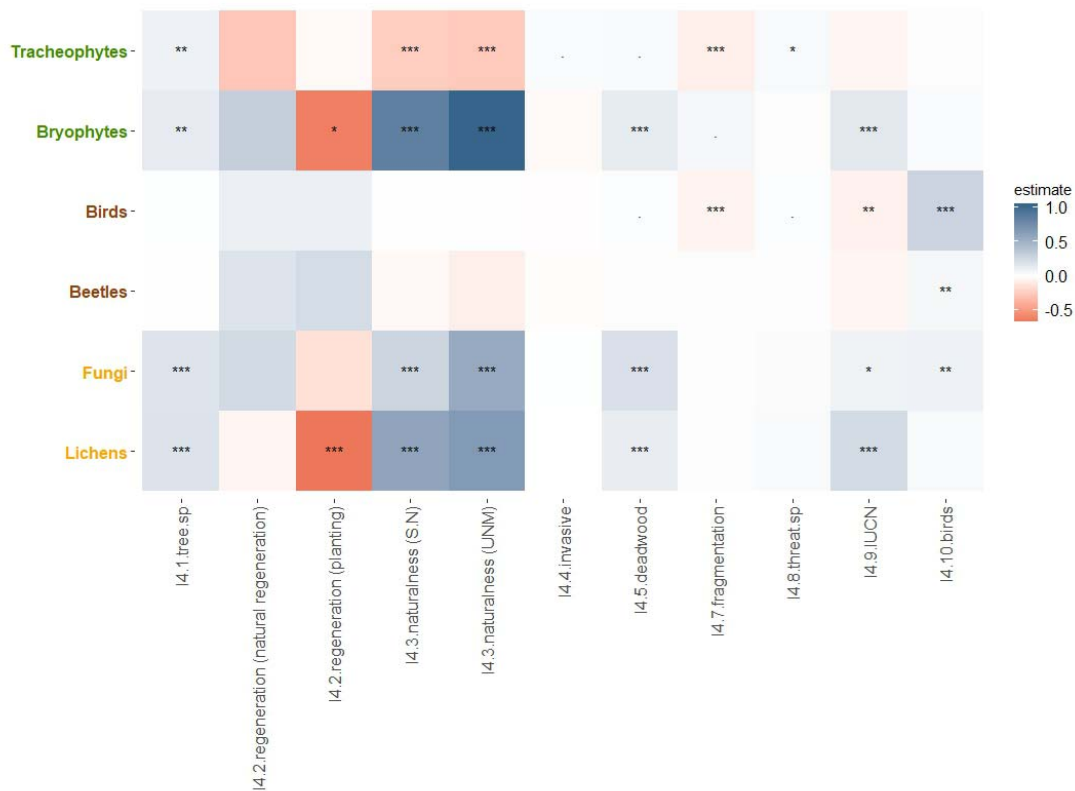
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316   Figure 2: Heatmap representing the standardized estimates (slope) of standardized species

317   richness obtained with generalized mixed models with Beta error distribution and logit link,

318   using Forest Europe indicators as independent predictors. S.N = semi-natural, UNM =

319   unmanaged. Intercept (reference) for 4.2 Regeneration is the "Coppice" class, and

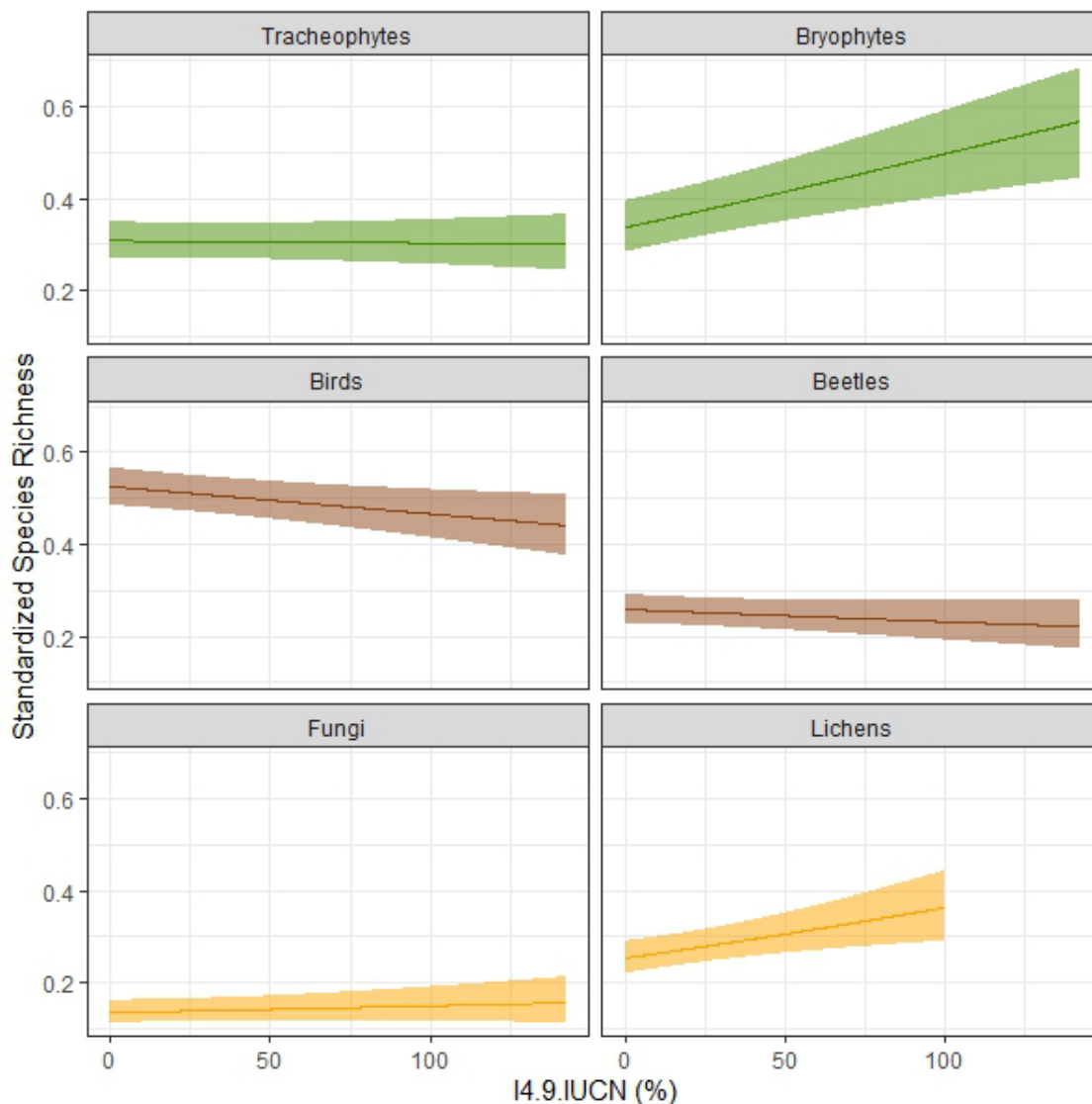320   "Plantations" for 4.3 Naturalness (p<0.1, * p<0.05, ** p<0.01, *** p<0.001).

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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.

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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),

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331   Protected areas (4.9, Figure 4) and Forest Birds (4.10). Surprisingly, the proportion of

332   protected areas around sampling plots had a negative effect on birds and no effect on

333   tracheophytes and fungi. Regarding Naturalness (4.3, Figure 5), unmanaged forest and

334   semi-natural forests showed higher levels of fungi, lichens and bryophytes than plantations.

335   However, the opposite was true for tracheophytes. Threatened species (4.8) showed very

336   few significant results (marginally positive for tracheophytes and bryophytes, positive for

337   birds) while Invasive species (4.4) only showed a marginally significant positive relationship

338   with tracheophytes. Plantation (4.2) showed a very strong negative relationship with lichens

339   only, and a marginally significant negative effect on tracheophytes, while there were no

340   differences between coppice and natural regeneration (Appendix 3).

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341

342   Figure 4: Relationships between standardized species richness of 6 taxonomic and

343   functional groups and Forest Europe indicator 4.9 (Proportion of protected areas in a 500ha

344   buffer). Estimations are issued from generalized linear models with Beta error distribution.

345   Plain line represents the mean estimate, ribbons the 95% confidence interval.

346
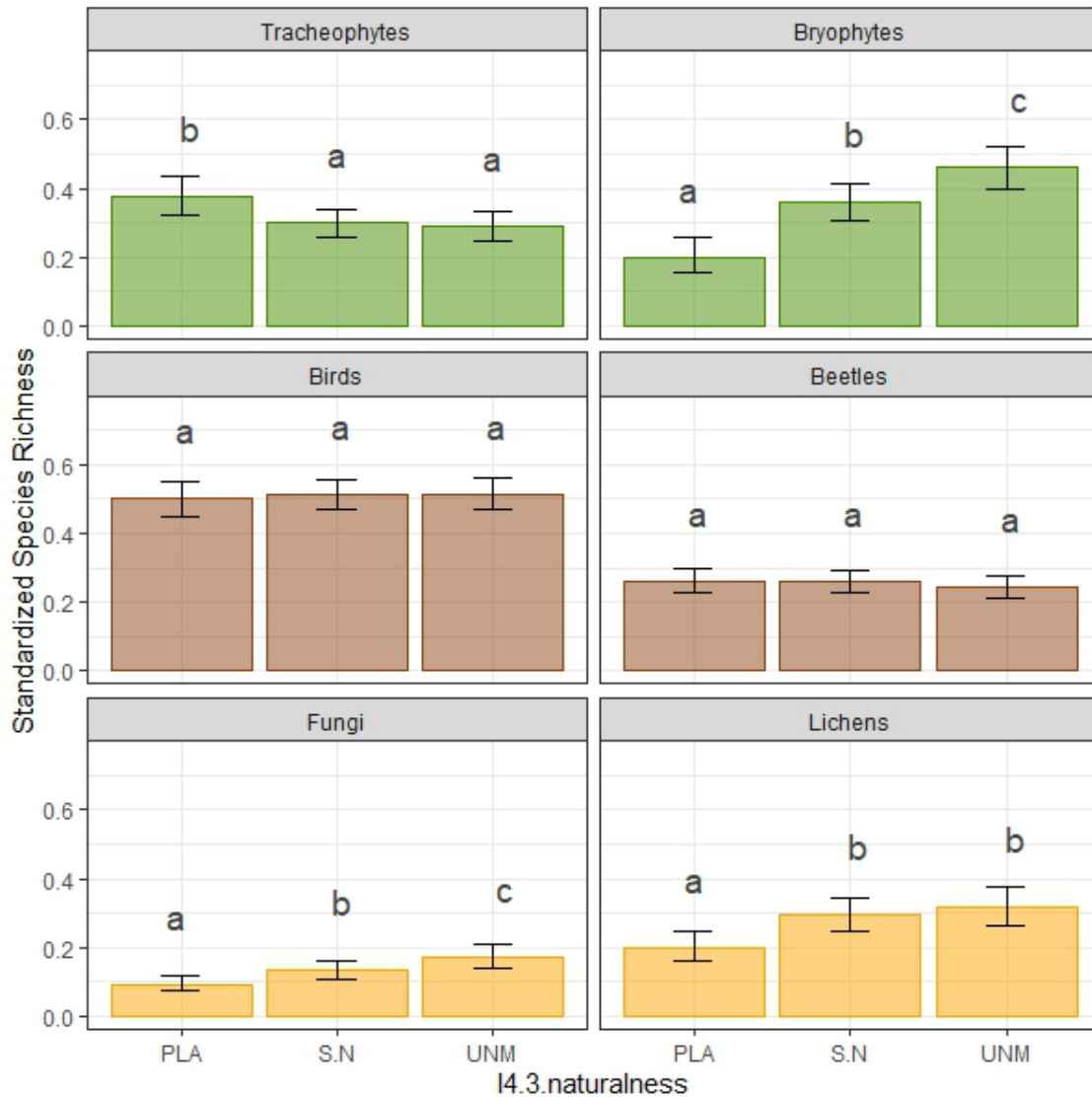
Figure 5: Relationships between standardized species richness of 6 taxonomic and functional groups and Forest Europe indicator 4.3. Naturalness: PLA = Plantations; S.N = Semi – Natural forests; UNM = Unmanaged forests. Estimations are issued from generalized linear models with Beta error distribution 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.

354 *Relative performance of the different indicators*

355 Comparing the AICc (Table 4) for all single models revealed that the indicator based on

356 forest Naturalness (4.3) best explained the scaled species richness for three out of six

357 groups (tracheophytes, bryophytes, and lichens); Regeneration (4.2) was within 2 points of

358 AICc for tracheophytes and lichens. For birds and beetles, the indicator based on Forest

359 birds (4.10) was the best explanatory one, while for fungi, Deadwood (4.5) stood first. Also

360 note that the null model was never the best one and more than 2 AICc points away from the

361 best.

Explanatory variables	K	Tracheophytes Delta AICc	Bryophytes Delta AICc	Birds Delta AICc	Beetles Delta AICc	Fungi Delta AICc	Lichens 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

362 Table 4: Differences of Akaike Information Criteria corrected for small samples (Delta AICc)

363 for all generalized mixed models with Beta error distribution and logit link. K is the number of

364 parameters in each model. The best model (delta AICc = 0) is in bold.

365

366 *Combination of indicators*

367 We used data dredging to find the best linear (i.e. without interaction) combination of

368 indicators reflecting the variations in species richness of each group. Only beetles were

369 represented by only one indicator (Forest Birds, 4.10.), all the other ones had a combination

19

370   of 3 to 4 indicators in their best models (Table 5). In terms of indicators, Invasive species

371   (4.4.) was never selected. Conversely, and as observed before, Diversity of tree species

372   (4.1.), Naturalness (4.3.), Deadwood (4.5.) were selected four times, followed by Forest

373   Birds (4.10, 3 times). Finally, it is interesting to note that, except for Fragmentation (FAD,

374   4.7.), all indicators had positive effects, and with the remarkable exception of beetles, all

375   multivariate models performed better than single ones (in terms of AICc, they had at least 2

376   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

377   Table 5: Scaled estimates of the models selected by data dredging combining all indicators

378   from Forest Europe (without interaction). Estimates are issued from generalized linear mixed

379   models with Beta error distribution and logit link. "+" indicates the presence of the factor in

380   the model. The best model was the most parsimonious (lowest degrees of freedom - df) with

381   the lowest Akaike Information Criterion corrected for small samples (AICc). "delta" indicates

382   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

411   dependent species (epixylic bryophytes and lichens), while plantations had detrimental

412   effects on several other groups. Indeed, habitat provision and continuity are higher in semi-

413   natural forests, not to speak of unmanaged forests, which allow the persistence of dispersal

414   limited species (e.g. Boch et al. 2013; Boch et al. 2021). The positive response of

415   tracheophytes in plantations may seem surprising, but probably reflects a higher share of

416   disturbance tolerant herbs in more disturbed sites, as shown in several individual studies

417   (Boch et al. 2013). In addition, the semi-natural category encompasses a wide range of

418   management types (Trentanovi et al. 2023), and unmanaged forests in our dataset have

419   mostly been recently abandoned, which may cause a decrease in the biodiversity of

420   tracheophytes during the first decades after abandonment (e.g. Paillet et al. 2010).

421

422   Deadwood volume, followed by diversity of tree species, were two indicators that often

423   correlated with scaled species richness, both in univariate and multivariate analyses.

424   Deadwood and diversity of tree species have complementary roles for biodiversity (Storch et

425   al. 2023). Deadwood provides a substrate and a resource for numerous species that depend

426   on it for part of their life cycle (Lassauce et al. 2011; Müller et al. 2019; Müller et al. 2015;

427   Parajuli & Markwith 2023), but also for facultative species (Graf et al. 2022). Indeed, the

428   richness of bryophytes, fungi and lichens, and to a lesser extent birds, correlated positively

429   to deadwood volume in our analyses. Surprisingly however, saproxylic beetles richness did

430   not correlate significantly to deadwood volume despite a weak positive effect. It is likely that,

431   for this group in particular, deadwood does not act as a universal indicator that could be

432   transposed in all situations (see also Zeller et al. 2023). For example, Lassauce et al. (2011)

433   showed that the correlation between richness of saproxylic beetles and deadwood volume

434   was higher in boreal than in temperate forests, a result that was however not confirmed by

435   Parajuli and Markwith (2023). Müller et al. (2015) showed compensation effects between

436   deadwood and temperature, supporting that the influence of deadwood on saproxylic beetle

437   richness declines with increasing temperature, both in geographical space, but also locally in

438   relation to canopy openness (e.g. Koch Widerberg et al. 2012). It is also possible that the

22

439   observed deadwood volumes (mean 40 m^3/ha, Table 3) lead to relatively poor beetle

440   communities. However, in most cases, the mean deadwood values in our dataset were

441   above the average deadwood volume per European country (which was 11.5m3/ha on

442   average, but varied from 2.3 to 28m3/ha between countries, Forest Europe 2020).

443   Consequently, while the positive role of deadwood for biodiversity remains unchallenged, its

444   use as an indicator should probably be refined by a better integration of the context

445   (macroclimate, microclimate, position on the deadwood volume gradient) in the relation. It is

446   also true that deadwood quality (e.g. including size and decay stage Vítková et al. 2018) is

447   as much relevant as its quantity. Some saproxylic beetle species (e.g. the red-listed species

448   *Rosalia alpina*, Campanaro et al. 2017) develop in large logs, snags and standing dead trees

449   within canopy gaps. In most of the sampling units we analyzed, deadwood was represented

450   by relatively small fragments (mostly around 15-20 cm diameter) likely deriving from thinning

451   processes occurring in closed forests (Burrascano et al. 2023). Further, many rare taxa

452   depend on the occurrence of tree-related microhabitats (Larrieu et al. 2018), such as the

453   protected umbrella species *Osmoderma eremita,* which larvae develop in large cavities in

454   living trees (Dubois et al. 2009). Since several tree-related microhabitats are very scarce in

455   managed forests (Paillet et al. 2017), and not readily quantified as part of the deadwood pool

456   (Müller et al. 2014), their role is not currently taken into consideration.

457   Diversity of tree species also showed positive correlation with the biodiversity of several

458   taxonomic and functional groups (bryophytes, fungi, lichens and more marginally

459   tracheophytes). Different tree species provide different habitat conditions for epiphytic and

460   saproxylic species living in forests (e.g. Boch et al. 2021; Cavard et al. 2011; Leidinger et al.

461   2021). These conditions encompass direct biotic interactions, different chemical properties of

462   the bark and wood, decomposition rates as well as differential light interception (Gosselin et

463   al. 2017; Zeller et al. 2023). This in turn provides niche heterogeneity for several species and

464   thus enhances biodiversity and confirms the role of diversity of tree species as a biodiversity

465   indicator.

466

23

467   Among the other indicators, forest fragmentation showed negative effects on tracheophytes

468   and birds, and a positive effect on bryophytes, and marginally on beetles and fungi. It should

469   be noted that since it is based on forest area density (European Commission et al. 2019), it

470   represents forest cover rather than its discontinuity and configuration, but has the advantage

471   of being calculable and homogeneous across Europe. Besides, the landscapes surrounding

472   our sampling units presented a high forest cover (77% on average, in a 500 ha buffer,

473   Table 1). Thus, the observed correlations reflect that forest area density could have been

474   beneficial for forest interior species that are sensitive to edge effects (bryophytes or lichens),

475   but detrimental to non-forest, open habitat or light demanding species, such as

476   tracheophytes and open-habitat birds (but see Bełcik et al. 2020, who show an increase

477   before a plateau in taxonomic diversity with increasing forest area in agricultural

478   landscapes). The inferences on the effect of fragmentation on biodiversity, based on the

479   Single Large vs Several Small principle (Diamond 1975), support that large continuous

480   habitat should have a greater effect on biodiversity conservation, compared to several small

481   ones. However, recent multitaxa studies proved the disproportionately high value of small

482   patches, harboring richer assemblages, even when focusing only on protected species (Riva

483   & Fahrig 2022). Besides, it has been highlighted that biodiversity conservation in human-

484   modified forest landscapes is better achieved maintaining at least 40% of forest cover, rather

485   than focusing on fragmentation and configuration (Arroyo-Rodríguez et al. 2020). Hence, the

486   role of fragmentation, as it is currently estimated, should be probably be reconsidered to take

487   into account both the amount of forest cover and the value of the patches.

488

489   Contrary to the previous indicators, threatened species and birds are based on direct

490   biodiversity sampling (other than trees). These indicators directly describe the evolution of a

491   small part of the biodiversity, but generally correlate poorly to the richness of other taxa and

492   most of the results observed are linked to the fact that these indicators represent subsets of

493   larger groups (evidently forest birds vs. birds). However, despite several pieces of evidence

494   showing that congruence between taxa is generally small, especially in forests (Burrascano

495   et al. 2018; Westgate et al. 2017), forest birds positively correlated to beetles and fungi.

496   Probably these groups respond to the same favorable habitat conditions, but this was not

497   reflected in the multivariate analyses.

498   The proportion of IUCN-protected areas around the plots positively influenced the richness

499   of bryophytes and lichens, highlighting the positive effects of protection for these groups, but

500   surprisingly had a negative effect on birds (see Honkanen et al. 2010).

501   Finally, invasive tree species did not show any correlation with biodiversity, apart from a

502   marginal positive effect on tracheophytes supporting high local tracheophyte diversity to be

503   often an indicator of disturbance. Despite the negative effects of invasive species

504   introduction on native flora, fauna and mycota, this effect is rather limited in our dataset

505   since it contains very few invasive species in total (maximum one tree species per plot)

506   reflecting that no projects targeted the effects of plantations rich in, or dominated by,

507   introduced tree species on biodiversity. This limited gradient probably does not allow to show

508   significant effects on biodiversity. In addition, an indicator on introduced species rather than

509   invasive ones – as it is defined in Forest Europe's indicators – may perform better.

510

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

512   *improvements*

513   Our study is one of the first to test Forest Europe indicators against multitaxonomic data at

514   the European level. During the model selection process, the best single variable models

515   were more often involving naturalness (tracheophytes, bryophytes and lichens) followed by

516   forest birds (birds and beetles) and deadwood (fungi). However, the multivariate models did

517   perform better than single ones (except for beetles), and often the best ones combined

518   several indicators to reflect variations of the *indicandum*. Only beetles were best indicated by

519   forest birds, but with a low magnitude, and birds by three combined indicators (including

520   forest birds and threatened species). The magnitude of the effects in the multivariate models

521   were comparable to those of single variable models (Appendix 3) which confirmed that

522   indicators were not collinear.

523   We studied only total richness as a response variable, and evidently, the results may be

524   different for other, more specialized groups, or other metrics of biodiversity (abundance,

525   occurrence of individual species, functional diversity). Such approach remains to be tested

526   (see e.g. Lelli et al. 2019) but was beyond the scope of the present study. In addition, some

527   of the references we used were probably incomplete regarding some groups: e.g. almost no

528   lichens are included in the list we used for red-listed species, but the proportion of

529   threatened species at the national levels may be high.

530   We limited our approach to the strict definition of the indicators as used in Forest Europe, but

531   higher performance could probably be reached by at least two improvements. First, adding

532   context to the indicators could probably reveal that they need to be adapted locally

533   (Chiarucci et al. 2012; Honkanen et al. 2010). Examples of context could be: elevation

534   (mountain vs. lowlands), biome (Mediterranean, temperate, boreal) and European forest

535   types. Second, most of the metrics we used are abundance metrics (apart from tree species

536   richness) that quantify habitat available for species. However, indicators based on diversity

537   of resources (following the heterogeneity-diversity theory, Tews et al. 2004) could perform

538   better, e.g. in the case of deadwood and saproxylic beetles (Bouget et al. 2013), or tree-

539   related microhabitats and birds and bats (Paillet et al. 2018). It would then be interesting to

540   assess the performance of other indicator metrics vs. the current ones in assessing forest

541   biodiversity.

542

543   **Conclusions: towards new indicators definitions and better reporting**

544   Many forest biodiversity indicators are proxies based on pre-existing data mostly issued from

545   National Forest Inventories (Tomppo et al. 2010). Despite recent progresses based on

546   international initiatives (namely the Essential Biodiversity Variables, GEOBON, IPBES),

547   monitoring the state and trends of forest biodiversity solely based on proxies is not

548   satisfactory: while proxies are generally easier to measure than species themselves, they

549   are prone to demographic effects such as extinction debts or colonization credits. In other

550   words, the presence of a given habitat - such as deadwood - does not guarantee the

26

551   presence of the species that depend on it (e.g. Paillet et al. 2018). In addition, the response

552   of biodiversity to a given indicator depends on the taxonomic or functional group studied

553   (Zeller et al. 2022), so no indicator may represent biodiversity overall. This was confirmed by

554   our analyses. We showed that, while some indicators performed correctly for several

555   taxonomic and functional groups in terms of significance and magnitude, we did not highlight

556   a predominant role of one indicator over the others.

557   Stevenson et al. (2021) claimed that indicators were often implemented without clear

558   considerations of their purposes and utility in terms of decision-making. We argue that, while

559   combinations of current Forest Europe indicators are useful to delineate general trends in

560   biodiversity, taking into account context and analyzing the performance of other - more

561   diversity-driven - metrics would help better reporting on biodiversity (e.g. Alterio et al. 2023;

562   Paillet et al. 2018). Such improvements would also be beneficial to the use of indicators

563   beyond general trends to include evaluating management and policy actions, decisions, or

564   set biodiversity targets (Stevenson et al. 2021). For example, we showed that larger

565   negative effects on biodiversity were observed in planted forests. This poses key challenges

566   for making the 3 billion trees planting promoted by the European Forest Strategy for 2030 a

567   beneficial action for biodiversity in forests (Sills et al. 2020), if high growing rate plantations

568   such as introduced Douglas fir (*Pseudotsuga menziesii*) or eucalyptus (*Eucalyptus* spp.) are

569   promoted against semi-natural forests. Conversely, promoting old-growth and unmanaged

570   forests, as well as restoration of monocultures and conversions towards semi-natural forests,

571   could have a positive effect on biodiversity. It is crucial to assess and balance these potential

572   effects with the use of current data available and biodiversity indicators before taking actions

573   or to modulate actions in favor of biodiversity against detrimental ones.

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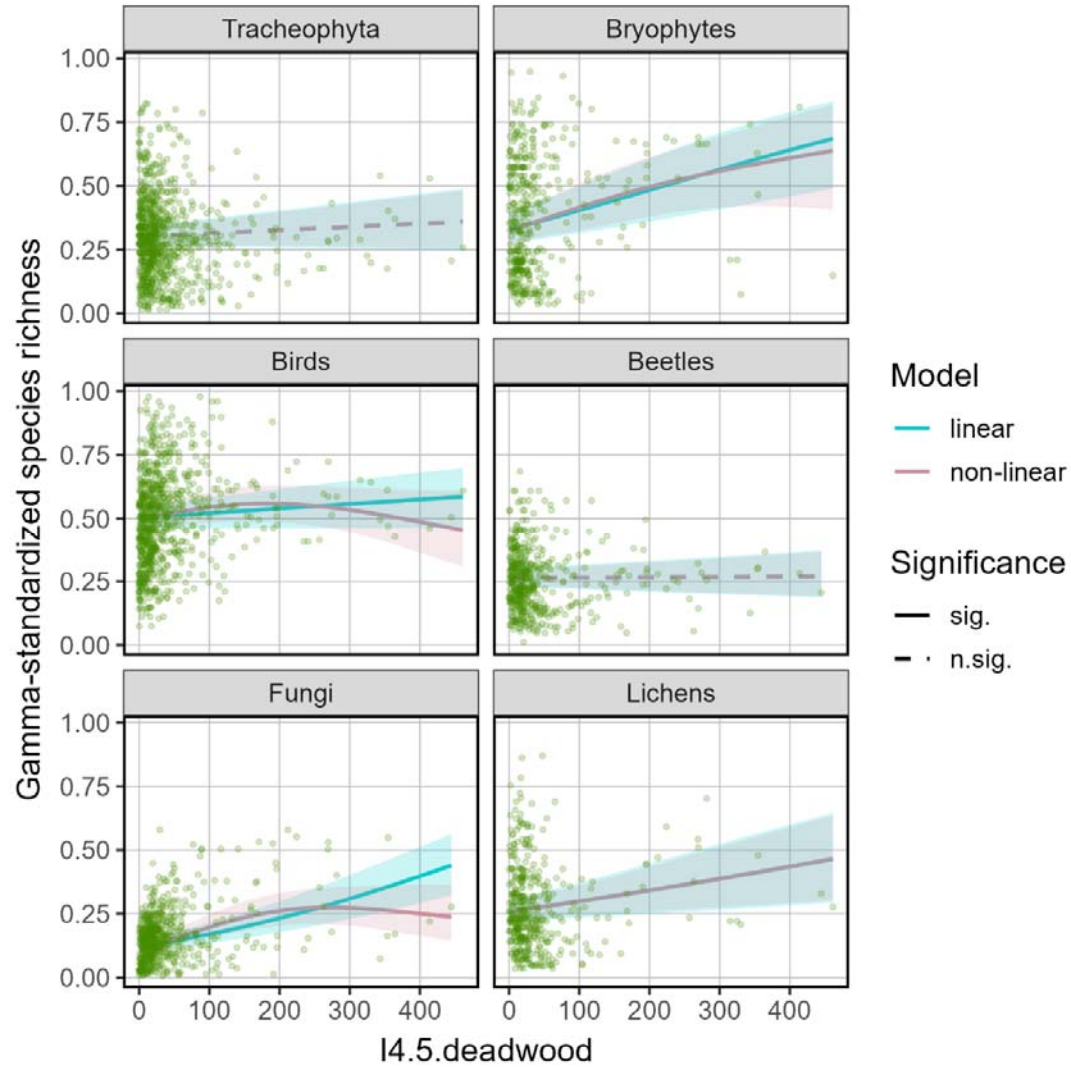756

757 **Appendices**

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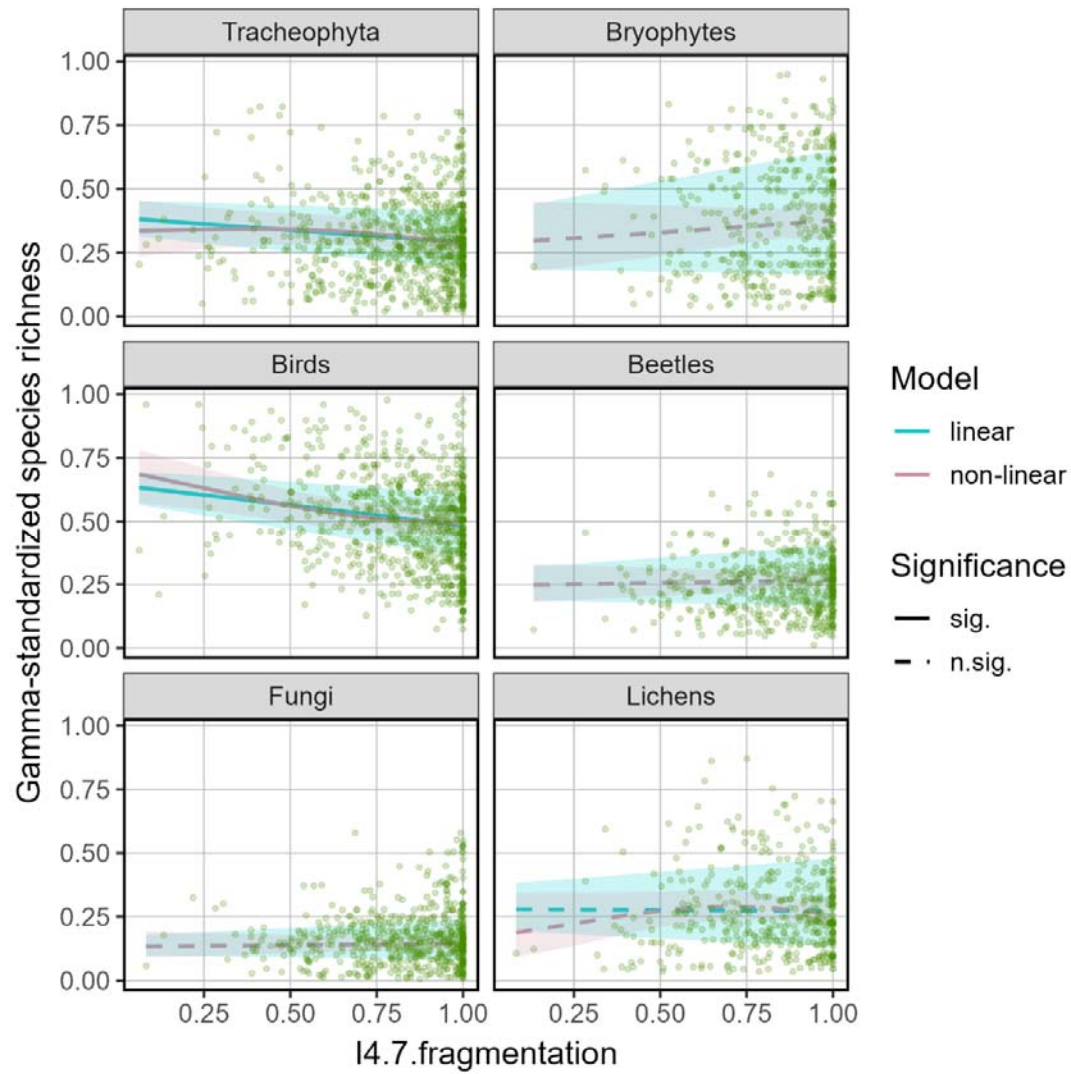
759 between standardized species richness and several Forest Europe's biodiversity indicators.
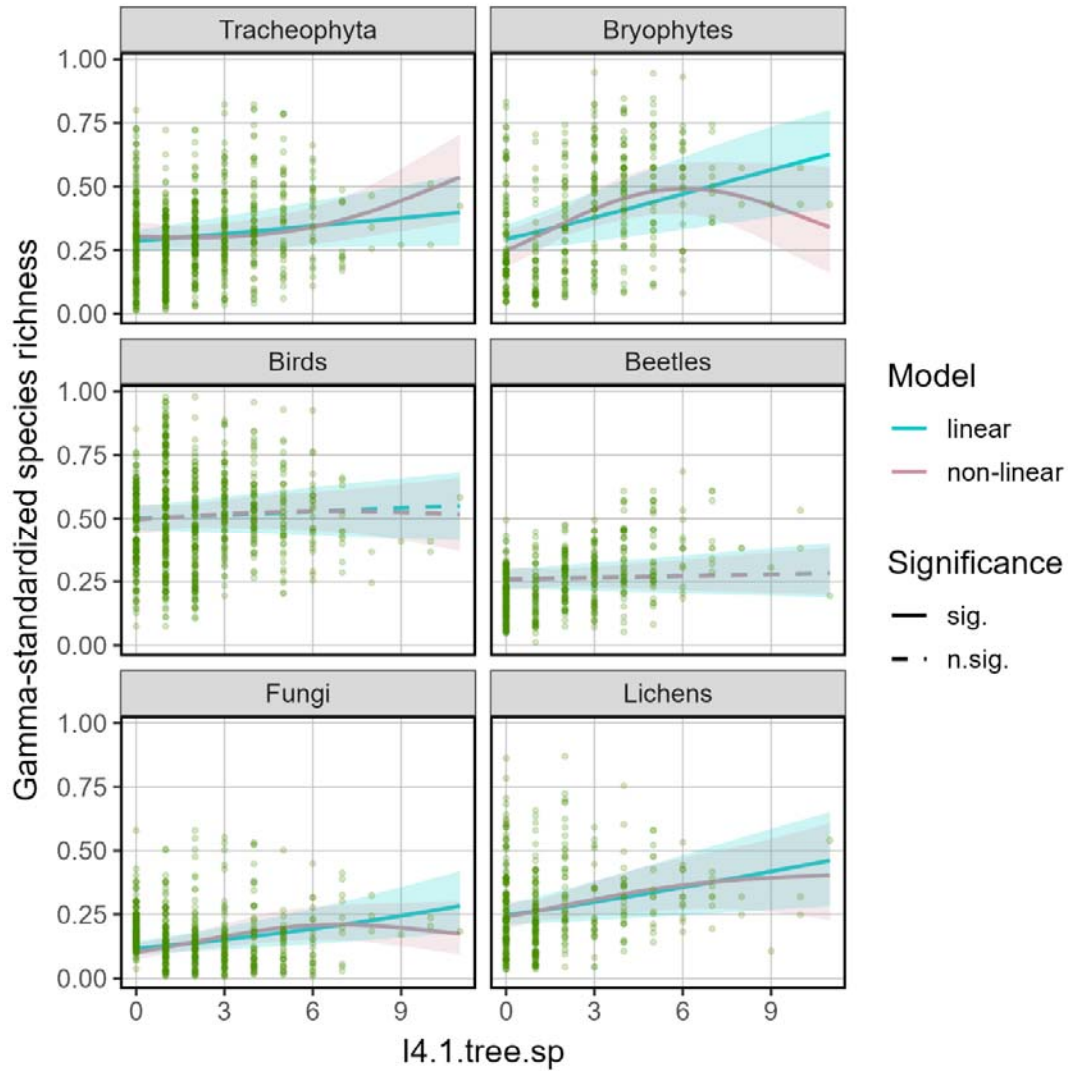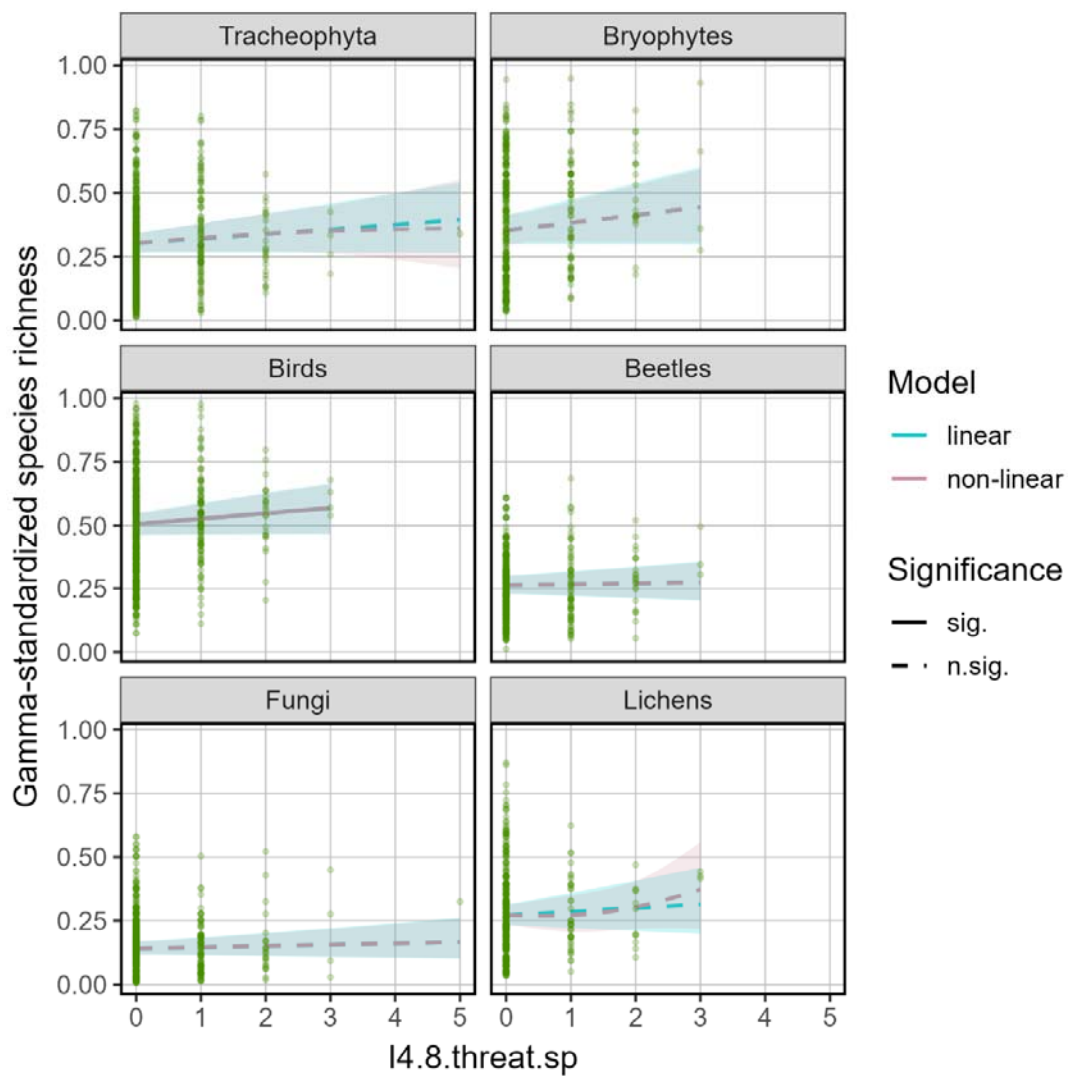

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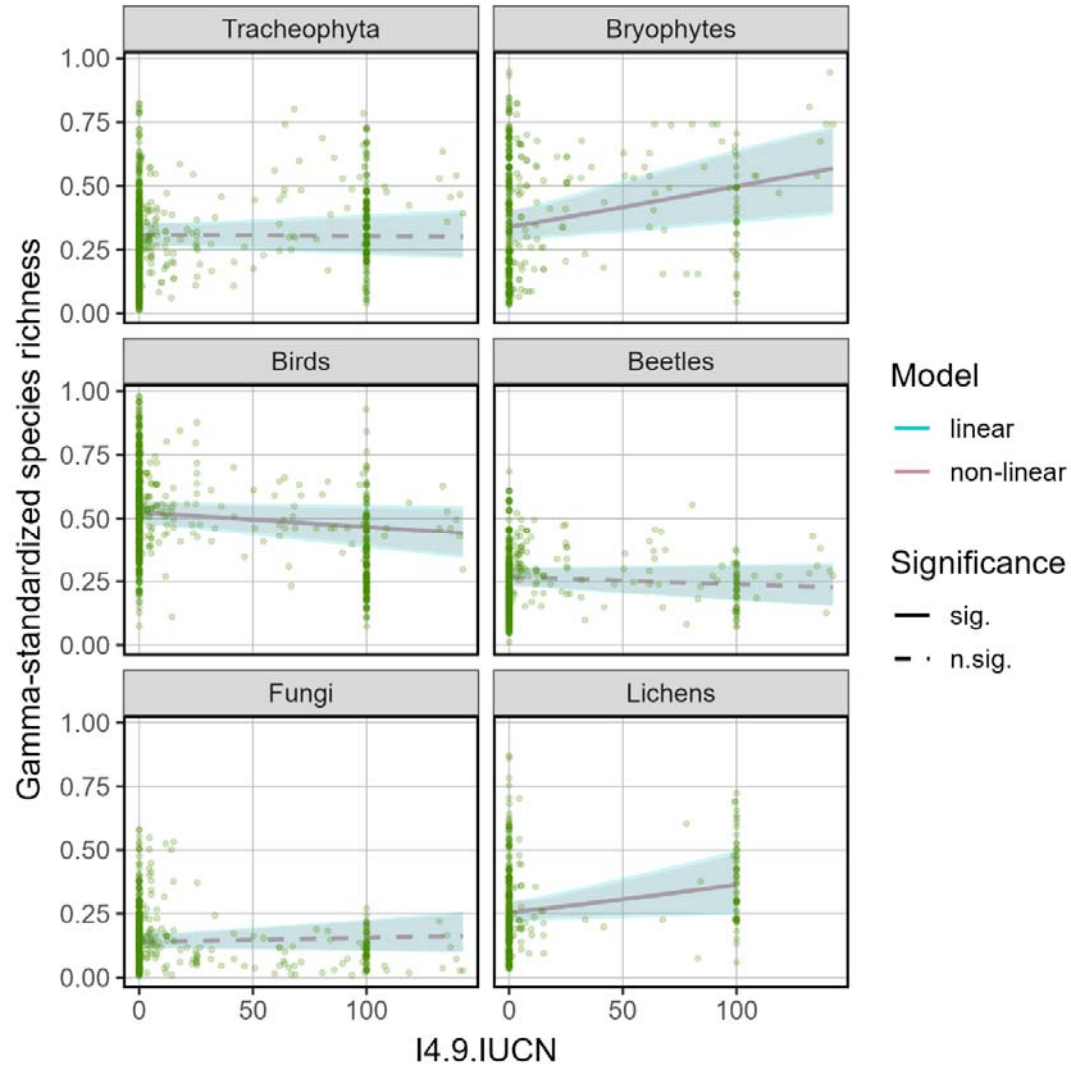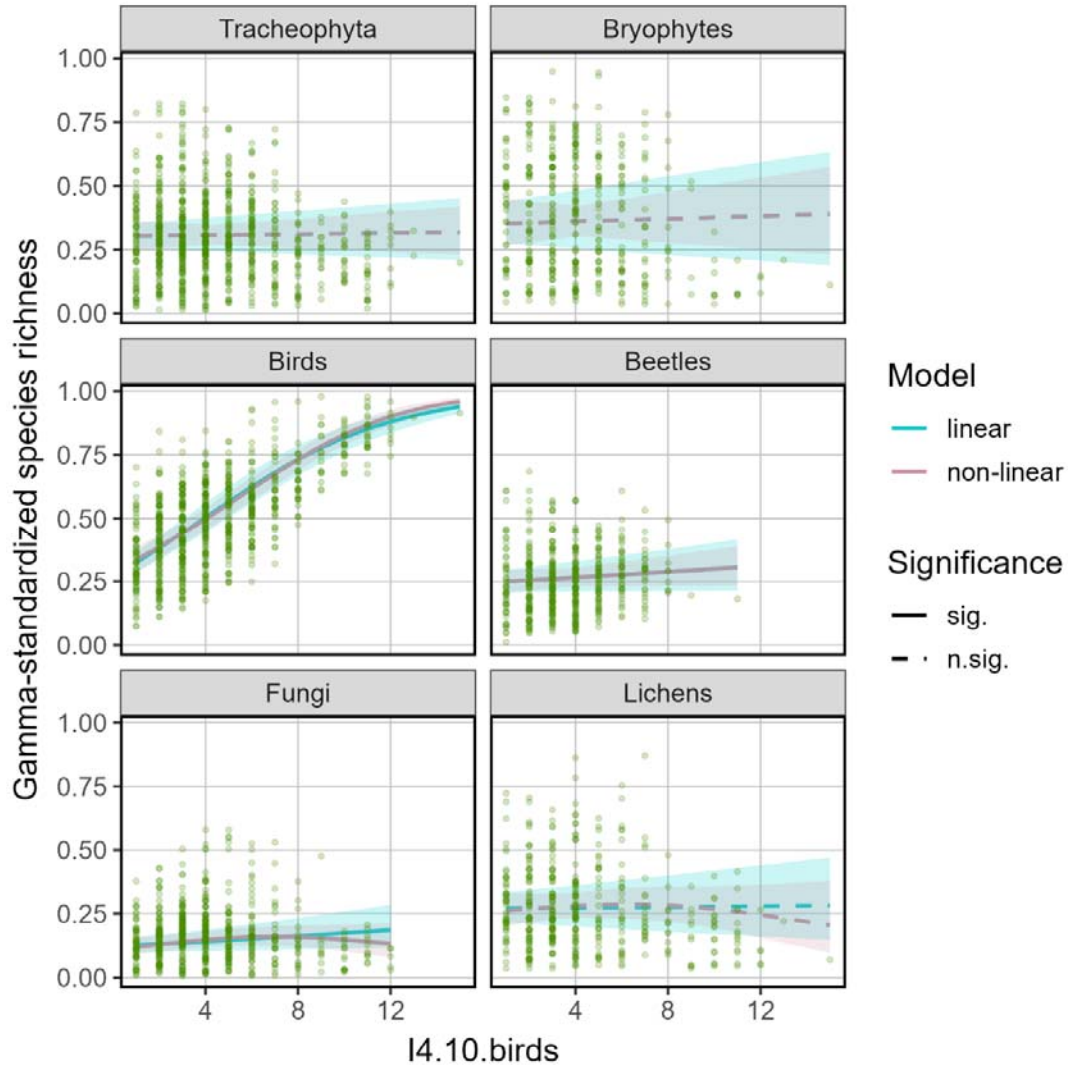
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770 Appendix 2: Correlation between indicators of Forest Europe from the tracheophytes

771 dataset. Figures on the right are Pearson correlation coefficients, biplots on the left and

772 histograms on the diagonal represent the distribution of the data. Regeneration (4.2) and

773 Naturalness (4.3) are categorical variables not represented here.
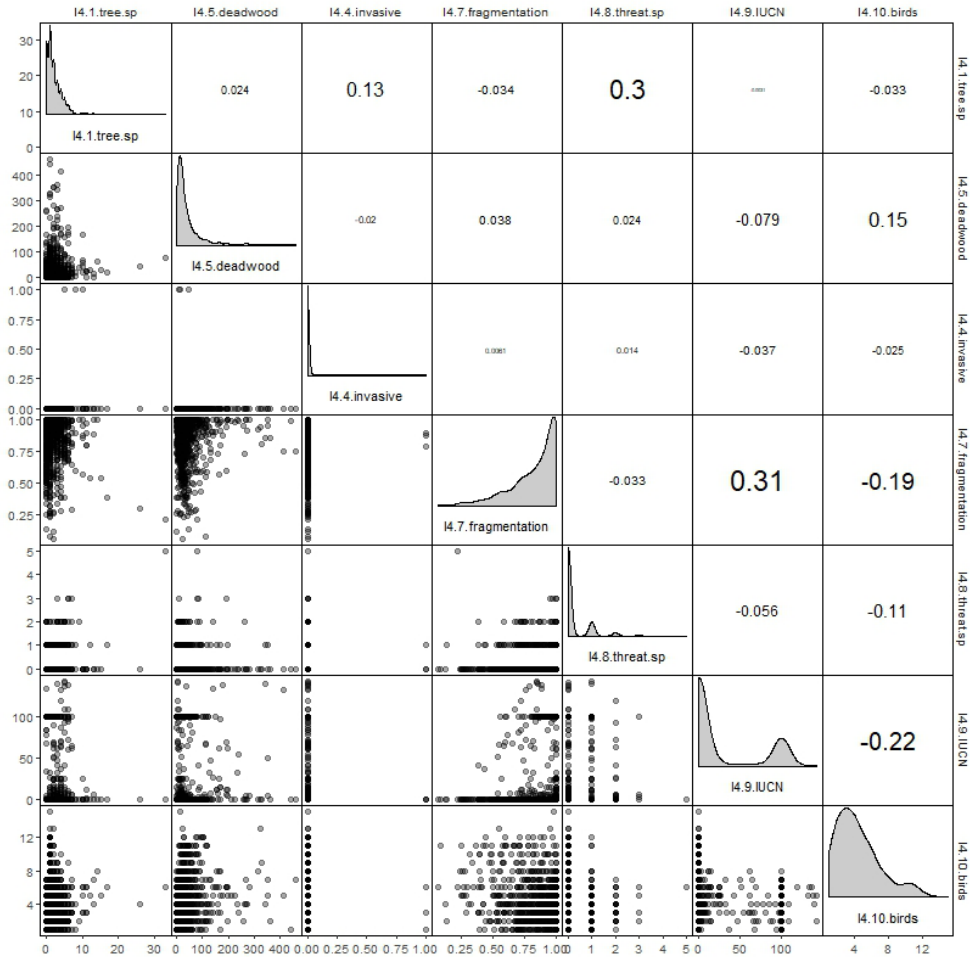
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776 Appendix 3: Standardized richness estimates table for all single generalized mixed models

777 with beta error distribution and logit link. Intercept for I4.2.Regeneration is "Coppice", and for

778 I4.3.Naturalness "Plantation" (PLA). S.N = semi-natural forest, UNM = Unmanaged forests.

779 se = standard error of the mean, pl = critical probability, (*) p<0.1, * p<0.05, ** p<0.01, ***

780 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	

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