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1 **Improving biodiversity indicators of sustainable forest management: tree genus abundance**  
2 **rather than tree genus richness and dominance for understory vegetation in French**  
3 **lowland oak hornbeam forests**

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26

27

28 **Abstract**

29 Two different biodiversity indicators based on tree species diversity are being used, in  
30 Europe and France respectively, without strong prior scientific validation: (1) tree species or  
31 genus richness as a positive indicator, and (2) relative abundance of the main species  
32 ("dominance") as a negative indicator. We tested the relevance of these ecological models as  
33 indicators of understory vegetation biodiversity in sustainable forest management by comparing  
34 them to other ecological models, mainly related to tree species composition and abundance. We  
35 have developed Bayesian statistical models for richness and abundance of ecological groups of  
36 understory vegetation species, classified according to successional status or shade tolerance. The  
37 count data probability distributions in the models were new to ecology. These models were fitted  
38 using data from 49 plots in mature lowland forests in the centre of France (Bassin Parisien) with  
39 similar site conditions. We used equivalence and inequivalence tests to detect negligible and non-  
40 negligible effects.

41 Tree genus richness and dominance resulted in models that were worse than ones based  
42 on the abundance of tree genus groups. Furthermore, the only significant results for dominance  
43 and tree genus richness were opposite to the ones implicitly assumed in the indicator system.  
44 However, the magnitude of the effects and which indicator provided the best statistical model  
45 varied among ecological groups of plants. Our results show the negative non-negligible effect of  
46 the basal area of undergrowth tree species on the cover of all ecological groups of herbaceous and  
47 woody species, and on the species richness of non-forest and peri-forest herbaceous and woody  
48 species. Compared to the literature, our sampling design strongly controlled forest and site type,  
49 thus removing to some degree the potential confusion between influences on biodiversity of  
50 management specific variables and other ecological variables. We discuss our results from both  
51 an ecological perspective and in terms of the value of these groups as indicators of sustainable

52 management. For example, the best-performing model was a multivariate model, which may be  
53 more difficult to explain to forest managers or policy-makers than an indicator simply based on  
54 tree genus richness.

55

56 **Key-words**

57 Deciduous forest; temperate forest; tree species; Bayesian count models; model comparison;  
58 ordered categorical data; equivalence tests; *Quercus*.

59

## 60 **Introduction**

61 Improving biodiversity is one of the main objectives of the international Convention on  
62 Biological Diversity and associated National Strategies. Part of these strategies are sectorial, i.e.  
63 they try to improve biodiversity assessment in each major domain of human activity. Forestry  
64 and forests are no exceptions. As a result, biodiversity has been identified as one of the six  
65 criteria of sustainable forest management in Europe (MCPFE, 2003). A dozen or so indicators for  
66 biodiversity have been defined, that partly vary among countries. By indicator, we mean any  
67 measurable correlate to the particular aspects of biodiversity being studied (Duelli and Obrist,  
68 2003). Yet, these indicators have not been defined thoroughly, since the information to interpret  
69 them as pressures on biodiversity is often lacking – e.g. what components of biodiversity do they  
70 indicate? What are the magnitude and direction of the relationship between indicator and  
71 biodiversity? In which ecological conditions is this relationship valid? (Lindenmayer et al., 2000,  
72 Duelli and Obrist, 2003). What's more, there have been few efforts to compare existing indicators  
73 with new, potentially more appropriate ones.

74 One of the main acts in forest management is the selection of tree species. Tree species  
75 identity, abundance and diversity can shape the mean level of resources available to understory  
76 vegetation as well as their spatial variation, and thus can influence understory diversity and  
77 abundance (Barbier et al., 2008, Mölder et al., 2008, Barbier et al., In Press). This may explain  
78 why tree species richness and dominance are used as indicators of biodiversity in Europe and  
79 France (MCPFE, 2003, Ministère de l'Agriculture et de la Pêche, 2006). Yet, the state of the  
80 literature seems to question this choice if tree species richness and dominance are used in  
81 sustainable management practices as indicators of larger components of biodiversity, here:  
82 understory vegetation diversity – i.e. the diversity of vascular plants and bryophytes growing on

83 the forest floor below 2 m. Indeed, when summarizing a series of results, Glenn Lewin (1977, p.  
84 158) stated that "relationships between [the diversity of] strata that do occur appear to be the  
85 result of local moisture gradients and substrate types". Actually, most of the work that has  
86 focused on dominant tree species identity or tree species diversity as indicators of understory  
87 diversity (cf. references quoted in the Discussion) was based on sampling schemes that included a  
88 substantial variation in site type conditions. This is reflected in some of the results, e.g. those in  
89 Mölder et al. (2008) where understory species richness was strongly related both to tree species  
90 richness and soil pH. In such conditions, these indicators – which may be more related to site  
91 type variations than to forest management (cf. Lindenmayer, 1999 and Gilliam, 2007 for similar  
92 examples) – may not qualify as valid biodiversity indicators of sustainable forest management.

93         The aim of this study was to test and compare the relevance of different ecological models  
94 related to tree species diversity and abundance as indicators of sustainable management for  
95 understory vegetation biodiversity variation. By ecological models, we mean the identity of the  
96 particular ecological factors that are included in a statistical model using floristic biodiversity as  
97 the response variable. Our general approach was to compare potential indicators based on  
98 ecological models involving tree species richness, abundance and composition, among  
99 themselves and with other potential indicators (e.g. humus type, date and site chemical  
100 characteristics). We defined these ecological models (cf. Tables 1 & 2) from those currently  
101 being used in sustainable management evaluations but also from those found in past studies.  
102 Most of these models involve variables that can be quantified based on dendrometric data such as  
103 those from the French Forest National Inventory (e.g. in terms of scale).

104         We first focused our attention on ecological models related to tree genus composition and  
105 abundance, partly corresponding to the domain covered by indicator 4.1 in Ministère de  
106 l'Agriculture et de la Pêche (2006). Our first model related to tree species was the (dominant)

107 Tree genus Group Identity (hereafter called *TGI*). *TGI* is not as such an indicator of forest  
108 biodiversity in Europe and France, although it is part of indicator 4.1.1 in France and is  
109 considered to be an indicator of forest resources – n° 1.1.4 (cf. MCPFE, 2003, Ministère de  
110 l'Agriculture et de la Pêche, 2006). Our second model related to the tree layer was total Tree  
111 Abundance, here basal area (hereafter called *TA*). A mix of *TGI* with *TA* – here interpreted as an  
112 additive effect of both factors: *TGI+TA* – is used in France as an indicator of biodiversity  
113 (Ministère de l'Agriculture et de la Pêche, 2006): it was our third model. Since much of the  
114 existing literature reports the effect of the abundance of particular tree species on floristic  
115 biodiversity, we constructed our fourth model on the absolute abundance of different tree genus  
116 groups, as did Korb et al. (2007), here with a grouping based on Successional/Structural status  
117 (model called *TGAS*, much as in Auclair and Goff, 1971). Here we distinguished Pioneer tree  
118 genera from ordinary Post-Pioneer tree genera, including oaks, and from Post-Pioneer tree genera  
119 that form dense undergrowth in deciduous French forests and have a higher tolerance to shade  
120 than other trees (*Carpinus betulus* and *Tilia sp.*; Rameau et al., 1989, Vera, 2000, but see  
121 Evstigneev, 1988 for hornbeam). Following Rice et al. (1984), Betts et al. (2005) and Barbier et  
122 al. (2008), we preferred to use absolute rather than relative abundance of groups of trees because  
123 (i) we assume that this value can lead to different management implications than those based on  
124 the relative abundance of trees; and (ii) we hypothesize that this value is more related to the effect  
125 of the tree canopy on ecological gradients such as light (e.g. Sonohat et al., 2004). Many different  
126 mechanisms can account for the effects of *TGI* and various measures of tree abundance on  
127 floristic biodiversity, such as differences in light, water and nutrients, or physical effects of the  
128 humus layer (cf. Michalet et al., 2002, Gilliam, 2007, Barbier et al., 2008).

129 Other ecological models based on tree species involve the notion of species diversity of  
130 the tree stand, with the underlying assumption that a more diverse tree stand might indicate more

131 diverse understory vegetation. We have retained as our fifth and sixth models the indicators used  
132 in France, i.e. Tree Genus Dominance (*TGD* in the model *TGI+TGD*; Ministère de l'Agriculture  
133 et de la Pêche, 2006) and Tree Genus Richness (*TGR*). Tree genus Dominance (*TGD*) was  
134 calculated as the maximum among the tree genera of their relative basal area in the plot, and Tree  
135 Genus Richness (*TGR*) was calculated as the genus richness of living trees and shrubs collected  
136 from the dendrometric relevé, including all woody material with diameter at breast height (DBH)  
137 > 2.5 cm. More precisely, model *mTGR4* – the minimum between Tree Genus Richness and 4 –  
138 is indicator n°4.1 in Ministère de l'Agriculture et de la Pêche (2006). Herein, we considered both  
139 *mTGR4* – our seventh model – and *TGR*, which varied between 1 and 8, with a mean of 4.3 (cf.  
140 Table 2). At least two mechanisms could explain the positive effect of tree species diversity on  
141 understory diversity: either the higher heterogeneity of resource levels under diverse tree stands  
142 (Brewer, 1980, Barbier, 2007, Mölder et al., 2008) or a common response of the richness of these  
143 two strata to the same environmental factors (cf. Glenn Lewin, 1977, Gilliam, 2007, Mölder et  
144 al., 2008).

145 Finally, we also included three models that are not linked to the tree layer, but which  
146 could account for potential biases in our sampling scheme. These were our three final non-null  
147 models:

- 148 – a model *Date* including the date of the floristic relevé;
- 149 – a model called *Block*, that incorporated the identity of the forest Block, distinguishing  
150 the Southern Block – corresponding to the Villefermoy forest – from the Northern Block;
- 151 – a model called *Soil* that included variables associated to site type – here two chemical  
152 properties of the organic-mineral layer, humus type and depth of dominant clay content (cf. Table  
153 2).

154           In this study, our first methodological choice was to test the relevance of these ecological  
155 models irrespective of site type variation (cf. above). We therefore decided to *control site type as*  
156 *much as possible*, in order to compare varying tree species identities, diversities and abundances  
157 on a similar site type. We did this by locating our study plots in a limited geographical area with  
158 the same climatic characteristics, by a priori controlling for site type when choosing forest plots,  
159 and by a posteriori quantifications of soil properties known to be relatively constant during the  
160 forest cycle, such as pH of the first mineral layer.

161           Our second methodological choice was to analyze vegetation diversity not as a whole but in  
162 separate ecological groups, which are known to have different ecological requirements (Gosselin  
163 and Gosselin, 2004). We assumed that model relevance, and direction and magnitude of effect  
164 within one model, would vary according to the understory ecological group considered.

165 Discrepancies or lack of correlation between total species richness and the diversity of particular  
166 ecological or functional groups were indeed frequent (Lindenmayer, 1999, Duelli and Obrist,  
167 2003). We therefore analyzed the understory abundance – here, percent cover – and species  
168 richness of ecological groups associated with the successional status, light requirements and life  
169 form of species. The use of the successional status of plants – or their association to particular  
170 phytosociological groups – is rather frequent in the forest ecology literature, either directly in the  
171 analyses (e.g. Kwiatkowska, 1994; Kwiatkowska et al., 1997; ; Spyreas and Matthews, 2006) or  
172 more indirectly, by restricting the analysis of vegetation to "forest" species only (Van Oijen et al.,  
173 2005), or in interpretations of the variations of total species richness (Mölder et al., 2008). Light  
174 preference was chosen because we assumed that light could be an important mechanism in  
175 explaining floristic diversity response to tree species identity or abundance.

176           Finally, we analyzed the data in a quantitative manner through the use of Bayesian parametric  
177 statistical models, based on improved probability distributions. For the analysis of the results, we

178 coupled the model comparison framework (Hilborn and Mangel, 1997; Spiegelhalter et al., 2002)  
179 with the analysis of the non-negligibility of the effects (Dixon and Pechmann, 2005). Among the  
180 ecological models analysed, this helped us distinguish those which incorporated a negligible  
181 effect from the ones where data were insufficient to discriminate between negligible and non-  
182 negligible effects.

183 As will be seen in the discussion, the study of the relationship between tree species and  
184 understory biodiversity is not new – and approaches are quite diverse. This is why we have  
185 adopted a pluralistic view of this relationship, without one preferred ecological model or  
186 hypothesis, that comes close to the multiple hypotheses framework of Chamberlin (1965; cf. also  
187 Hilborn and Mangel, 1997). Indeed, our aim was to find the best ecological models of  
188 biodiversity variation among the biodiversity indicators currently being used in France and the  
189 ecological models found in the literature, and to identify cases where the effects were non-  
190 negligible.

191

## 192 **Material and methods**

### 193 *Study area*

194 The study area encompassed ca 8,000 ha in two zones included in a large area about 50 km  
195 east and south-east of Paris, France, in the region called "Brie Francilienne", in the Seine et  
196 Marne administrative department. The forests studied ranged from 48°27' N to 48°51' N and from  
197 2°39' W to 2°57' W and were located on a plateau between 100 and 140 m above sea level. We  
198 focused on four different forests called Ferrières, Armainvilliers, Crécy, and Villefermoy – the  
199 latter was about 50 km south of the three others, which were relatively contiguous. This region  
200 had an oceanic-subcontinental climate characterized by a mean annual temperature of 10.6°C and  
201 a mean annual precipitation of about 660 mm (Météo France, 1996). In the plots studied, the soil

202 was composed of a layer of silt around 45 cm in depth above a clay layer. The substratum was  
203 limestone from the Oligocene (Ferrières, Armainvilliers, and Crecy) and the Cretaceous period  
204 (Villefermoy). The soil was brown-leached, with moderate discoloration due to waterlogging,  
205 with more intensive discoloration at a depth of around 20 cm. The soil was mildly acidic, with a  
206 neutroclinous to acidiclinous vegetation. The mean value of the pH KCl in the first mineral layer  
207 was 3.8 (Table 2). Layers with dominant clay texture appeared at an average depth of 46 cm in  
208 the plots studied (Table 2). All the plots were at least 50 m from the forest edge, to avoid  
209 interfering edge effects.

210 The forests we studied are almost exclusively composed of deciduous trees, mainly oaks  
211 (*Quercus petraea* and *Q. robur*) and hornbeam (*Carpinus betulus*), though other tree species such  
212 as lime (mainly *Tilia cordata*), birch (mainly *Betula pendula*) and aspen (*Populus tremula* and *P.*  
213 *canescens*) may be locally dominant or co-dominant. Sweet chestnut (*Castanea sativa*) was also  
214 frequent. Hardwood management in the area consisted in the conversion of old coppice-with-  
215 standards stands to even-aged oak high forests. Some of the stands, however, were being  
216 managed as uneven-aged oak high forests.

217

### 218 ***Data collection***

219 Forty-nine plots were selected for (i) a common forest site type, described above; and (ii)  
220 their inclusion in 9 forest stand types defined by oak age structure and tree species composition –  
221 three types corresponded to mixed hardwood stands with uneven-aged oak, four types to oak-  
222 hornbeam or pure oak stands with even-aged oak, and three types dominated either by hornbeam,  
223 lime or pioneer tree species. Because much of the existing literature concerns only mature stands,  
224 and due to results that indicate that tree species composition is well correlated with understory

225 biodiversity only in "mature" forest stands (Gilliam et al., 1995), we excluded young stands from  
226 our study, i.e. we did not consider stands at regeneration, seedling or thicket stages.

227 In each 20x20m square plot, vegetation was inventoried for 85 minutes once in May, June or  
228 early July, 1999, by one of two botanists.

229 Vascular plants and bryophytes were recorded only if they were rooted in the litter and soil,  
230 not if they were growing on woody and rocky substrates. We considered vegetation below 2 m in  
231 height. Botanical nomenclature followed Kerguélen (1999) for vascular plants, Corley et al.  
232 (1981) and Corley and Crundwell (1991) for mosses and Grolle (1983) for hepatics.

233 Identifications were made visually in the field, at the species level whenever possible. However,  
234 some species aggregates were defined because of identification problems (*Agrostis canina* + *A.*  
235 *stolonifera*, *Eurhynchium stokesii* + *E. praelongum*, *Juncus effusus* + *J. conglomeratus*, *Luzula*  
236 *multiflora* + *L. forsteri*, *Lythrum salicaria* + *Epilobium tetragonum* + *Hypericum tetrapterum*,  
237 *Populus tremula* + *P. canescens*, *Salix cinerea* + *S. aurita*, *Viola reichenbachiana* + *V.*  
238 *riviniana*). Six species were identified in the field as different from the others but they could not  
239 be named. Some taxa were determined only at the genus level (*Abies* sp., *Calypogeia* sp.,  
240 *Fissidens* sp., *Isothecium* sp., *Lophocolea* sp., *Plagiothecium* sp., *Trifolium* sp.). However, we  
241 have used the term "species richness" for what was actually taxon richness.

242 For each species present in a relevé, we coded the estimated abundance-dominance of the  
243 species in each of the following strata: <0.5 m; ≥ 0.5 and <2 m, and in each of the four square  
244 100 m<sup>2</sup> subplots in the a 20x20m square plot. Our data consisted in the mean over the plot of the  
245 sum of the cover of each species in these two strata in each subplot. The abundance-dominance of  
246 each species in each strata was rated using the Braun-Blanquet phytosociological classes. The  
247 cover of an individual reaching a given stratum was totally attributed to that stratum. These  
248 Braun-Blanquet classes were then transformed into numbers, according to one of the codings in

249 van der Maarel (1979) for classes 2 to 5, and according to calibrations we made between total  
250 estimated cover and the number of species in the classes  $i$ , + and 1, and the predicted cover in the  
251 four last classes (2 to 5). With this calibration,  $i$  became 0.05%; + became 1% for non bryophytes  
252 and 0.15% for bryophytes; 1 became 2.75% for non bryophytes and 1.15% for bryophytes ; 2, 3,  
253 4 and 5 became 17.5%, 37.5%, 62.5% and 87.5%, respectively.

254 In each plot, tree basal area at breast height ("G", in  $\text{m}^2 \cdot \text{ha}^{-1}$ ) was calculated species by  
255 species, in three different configurations: 1) four circles with 4 m radius at the center of each  
256 subplot for trees with  $2.5 \text{ cm} < \text{diameter at breast height (DBH)} < 7.5 \text{ cm}$ ; 2) the four square  $100$   
257  $\text{m}^2$  subplots for  $7.5 \text{ cm}$  to  $17.5 \text{ cm}$  DBH; and 3) the  $22 \text{ m}$  radius circle at the center of the plot for  
258 trees with  $\text{DBH} > 17.5 \text{ cm}$ . Specific parameters in the models were calculated from this  
259 dendrometric inventory (Table 2). Some shrubs were included in the dendrometric relevé; in our  
260 case, they however had a minor contribution to both basal area and "tree" genus richness data  
261 (mean richness of shrubs: 0.27 compared to a mean TGR of 4.6; cf. Table 2).

262 At each of the four  $100 \text{ m}^2$  subplots, a probe was used to measure the depth to which clay was  
263 dominant. The four values were averaged for each sampling plot. At each of the four  $100 \text{ m}^2$   
264 subplots a soil sample was taken at 5-10 cm, corresponding to the first organic-mineral layer (A  
265 layer), and then at 15-25 cm, corresponding to the first mineral layer (B layer). The four samples  
266 of the same layer were combined, then air-dried and sieved at 2 mm for laboratory analyses:  
267 pH KCl, total nitrogen (N) and organic carbon (C). Analytical methods followed ISO standards  
268 (anonymous, 1999).

269 The humus form was visually assessed in each plot, based on Brêthes et al. (1995), modified  
270 by Jabiol et al. (2000). Humus Index was then calculated as in Ponge et al. (2002).

271

272 ***Data analysis***

273 In our analyses we focused on two ecological characteristics of understory species and their  
274 life traits to define ecological groups: light preference and successional status, crossed with life  
275 form.

276 For light preference ("HELIO" classification), we distinguished three species classes  
277 according to light Ellenberg indicator values, "L" (Ellenberg et al., 1992): heliophilous ( $L \geq 7$ ,  
278 "helio"), intermediate-light ( $5 \leq L < 7$ , "mid"), and shade-tolerant species ( $L < 5$ , "shad"). Species  
279 without an L value were classified according to Rameau et al. (1989) and our own knowledge.  
280 For successional status of species ("SUCC" classification), we distinguished three classes: non  
281 forest species ("NF") whose habitats are not linked to forests, peri-forest species ("PF") whose  
282 habitats are found close to mature forests either temporally (in the early stages of succession) or  
283 spatially (along edges), and mature forest species ("AF") that reach their maximum abundance in  
284 mature forests. For this classification, we followed Julve (2002), Hodgson et al. (1995) and  
285 Rameau et al. (1989). These two classifications – HELIO and SUCC – were distinguished in each  
286 of the following life form groups: bryophytes, herbaceous (*i.e.* non woody vascular) plants and  
287 woody species. The latter distinction is frequent in the literature (e.g. Glenn-Lewin, 1977). Only  
288 groups which were represented by at least one species in more than 20 plots and more than 60  
289 subplots were taken into account in the analysis.

290

291 We analyzed the effect of our different ecological models on the species richness and cover of  
292 the understory species groups defined above, at the 400 m<sup>2</sup> scale. The effects of the model were:  
293 the intercept, the observer effect, and the parameters of the ecological model (cf. Table 1). We  
294 analyzed all the ecological groups of a given classification in the same statistical model, with

295 different estimated parameters for each group – except for the qualitative observer effects that  
296 were shared between ecological groups.

297 For species richness, the models were mostly equivalent to Poissonian generalized linear  
298 models, except that the Poisson distribution was replaced by a more flexible distribution – the  
299 Bernoulli/Double Polya mixture-Poisson-Negative Binomial family – allowing both under- and  
300 over- dispersion (Gosselin, Submitted a). This continuum of distributions uses different  
301 distributions according to an estimated dispersion parameter  $\sigma$  for each ecological group: if  
302 greater than 1.0, we use a negative binomial distribution, if equal to 1.0, we use the Poisson  
303 distribution, and if less than 1.0, the Bernoulli/double Polya mixture distribution parameterized  
304 so that the expected index of dispersion is asymptotically  $\sigma$  (cf. Gosselin, Submitted a). The link  
305 function was the logarithm.

306 Cover of the ecological groups was analyzed with the same framework, except that the  
307 underlying probability distribution was not a count data distribution but a cumulative logit  
308 distribution (Liu and Agresti, 2005). We distinguished five intervals of cover (0; ]0; 1], ]1; 5],  
309 ]5; 25], ]25;  $\infty$ [) and applied the cumulative logit through equations of the shape:

$$310 \quad P(Y > \alpha_i | \gamma) = \frac{1}{1 + \exp(\beta_i) / \gamma},$$

311 where  $Y$  is the cover value,  $\gamma$  is the positive quantity that incorporates the fixed effects through  
312 an exponential function,  $\{\alpha_1, \alpha_2, \alpha_3, \alpha_4\} = \{0; 1; 5; 25\}$  and  $\beta_1 < \beta_2 < \beta_3 < \beta_4$ . This distribution  
313 has the characteristic that the odds values of the cumulative probabilities  $P(Y > \alpha_i | \gamma)$  are equal  
314 to  $\gamma$ , and in particular do not depend on the cover class  $i$ . We used this distribution because we  
315 did not find any better alternative to model values that could be either null or positive and

316 simultaneously continuous. Our highest cut point,  $\alpha_4 = 25$ , was such that less than 5% of the  
317 data were above it.

318 In our Bayesian models, the priors of fixed effects were mostly weakly informative: the prior  
319 for fixed effects was a centered normal distribution with a standard deviation 3 times the inverse  
320 of the standard deviation of the associated ecological parameter. The priors for the other  
321 parameters – the dispersion parameter and the  $\beta_i$  for the cover models – were also chosen mostly  
322 non informative.

323 The Bayesian models were fitted through the adaptive MCMC described in Roberts and  
324 Rosenthal (In Press), based on three trajectories of 20,000 iterations, a burning period of 7,000  
325 iterations and a thinning parameter of 10. The convergence of the models was checked with the  
326 Rubin and Gelman Rhat quantity (Gelman et al., 2004), smaller than 1.1. The adequacy of the  
327 probability distributions with the data was qualified through sampled posterior predictive values  
328 (Johnson, 2007, Gosselin, Submitted b).

329 To compare our models one with each other, we used the DIC – Deviance Information  
330 Criterion (Spiegelhalter et al., 2002) –, which is the most common information criterion to  
331 compare models in a Bayesian setting. The smaller the DIC, the better the model.

332 The sign and magnitude of the effects of parameters in the ecological model were analyzed  
333 for the SUCC classification and for models used in current indicators (TGR, mTGR4, TA in  
334 TGI+TA and TGD in TI+TGD) as well as for the model that turned out to be the best (TGAS).  
335 For each parameter in these models we reported the multiplicative coefficient – of the mean fitted  
336 value for species richness and of the odds of cumulative probabilities  $P(Y > \alpha_i)$  for abundance  
337 data – associated with an increase of the ecological parameter of around one standard deviation,  
338 i.e.  $5 \text{ m}^2 \cdot \text{ha}^{-1}$  for basal area parameters, 1.5 genera for genus richness and 0.2 for tree genus

339 dominance. For each parameter we reported the mean value of the multiplier, its 95% confidence  
340 interval, and the probability of the significance test that the parameter was null. Levels of  
341 statistical significance for parameters were symbolized as follows: \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \*  
342 =  $p < 0.05$ . Inspired from Dixon and Pechmann (2005), we also did an analysis based on  
343 equivalence and inequivalence tests to detect negligible effects: based on Bayesian parameter  
344 estimation as in Camp et al. (2008), the aim of the analysis was to identify when the parameter  
345 has a high probability of being in an interval, called the negligible interval, that is *a priori*  
346 considered to be representing negligible effects, when the parameter had a high probability of  
347 being below this interval and when the parameter had a high probability of being above. We also  
348 distinguished two negligible intervals: one for weak negligibility and one for strong negligibility.  
349 Denoting by  $\beta$  one value of the multiplier stemming from the posterior distribution of the  
350 Bayesian model, and by  $0 < b_1 < b_2$  the levels associated to the two negligible intervals, we  
351 therefore used the symbol 0 to describes cases where  $P(-b_2 < \log(\beta) < b_2) \geq 0.95$  and 00 for the  
352 more stringent:  $P(-b_1 < \log(\beta) < b_1) \geq 0.95$ . Similarly, we denoted by "-" cases where  
353  $P(\log(\beta) < -b_1) \geq 0.95$  and "--" cases where  $P(\log(\beta) < -b_2) \geq 0.95$ . These cases correspond to  
354 non-negligible negative and strongly non-negligible negative effects, respectively. We had  
355 similar notations – "+" and "++" – for the positive side. We chose  $b_1 = 0.1$ , and  $b_2 = 0.2$  for  
356 species richness data, corresponding respectively to a multiplication of species richness by  
357  $\exp(0.1) \approx 1.11$  and  $\exp(0.2) \approx 1.22$  at the upper side of the negligible interval. For abundance  
358 data, we used  $b_1 = 0.25$ , and  $b_2 = 0.5$ , corresponding to divisions by  $\exp(0.25) \approx 1.28$  and  
359  $\exp(0.5) \approx 1.65$  of the odds value of the cumulative probabilities  $P(Y > \alpha_i)$ . For example, using

360  $b_2 = 0.5$ , an initial value of  $P(Y > \alpha_i) = 0.5$  (respectively  $P(Y > \alpha_i) = 0.1$ ) would be

361 transformed to  $P(Y > \alpha_i) = 0.38$  (respectively  $P(Y > \alpha_i) = 0.06$ ).

362

### 363 **Results**

364 The most frequent understory species – found in more than half of the plots – were *Rubus*

365 *fruticosus*, *Carpinus betulus*, *Quercus robur*, *Lonicera periclymenum*, *Populus tremula*\* *Populus*

366 *canescens*, *Tilia cordata*, *Castanea sativa*, *Fraxinus excelsior* for woody species, *Carex*

367 *pilulifera*, *Convallaria majalis*, *Dryopteris carthusiana*, *Dryopteris filix-mas* and *Luzula pilosa*

368 for herbaceous species, and *Atrichum undulatum*, *Dicranella heteromalla*, *Eurhynchium striatum*,

369 *Eurhynchium stokesii*, *Hypnum cupressiforme*, *Polytricum formosum* and *Thuidium tamariscium*

370 for bryophyte species. Mean plot richness levels were 10.1 ( $\pm 1.8$ ) for bryophytes, 9.1 ( $\pm 7.0$ ) for

371 herbaceous species and 9.3 ( $\pm 3.2$ ) for woody species.

372 The Bayesian models converged correctly according to the Rubin and Gelman Rhat quantity

373 and the goodness of fit diagnostics did not show significant departures from the uniform

374 distribution, except for intermediate light bryophyte and shade-tolerant herbaceous species

375 abundance. Observer effects were significant and rather strong for abundance data and

376 insignificant for species richness data. For species richness data for bryophyte and woody species

377 groups, dispersion parameters were below 1 – indicating underdispersion relative to the Poisson

378 distribution; they were mostly above 1 for herbaceous species groups – except for AF herbaceous

379 species (results not shown).

380 Overall, the best ecological models in terms of DIC were models including one form of tree

381 abundance and tree genus identity (TGAS, TGI+TA for abundance data; Tables 3 to 4 & S1 &

382 S2). Models associated to tree genus richness were less effective than these best models by more

383 than 5 DIC units – except for intermediate light bryophytes –, and often came close to the null  
384 model by less than 5 DIC units. This was also the case for the models including the effect of Date  
385 of sampling and the forest Block (models "Date" and "Block"). Models associated to tree genus  
386 dominance (*TGI+TGD*) were also less effective than the best models by more than 5 DIC units  
387 (except for shade-tolerant and AF herbaceous species richness and abundance, AF and shade-  
388 tolerant woody species richness, and AF bryophyte and intermediate light woody species  
389 abundance). They also came close to their baseline reference (*TGI*) by less than 5 DIC units in  
390 half of the cases for abundance data and in all cases for species richness data, with only one  
391 exception: intermediate light herbaceous species. The model with site effects fell in the middle  
392 and was much better than the null model for most groups. It was even the best model for some  
393 groups. The identity of the best model varied slightly according to the ecological group  
394 considered (Tables 3, 4, S1 & S2). TGAS was the best model or very close to the best model (less  
395 than 2 DIC units) for all the ecological groups with the following exceptions: AF and  
396 intermediate light bryophyte species richness, and shade-tolerant herbaceous species abundance.  
397 The best model was at more than 5 DIC units from the null model except for the abundance of  
398 intermediate light bryophytes.

399 The analysis of the magnitude and "non-negligibility" of the effects for the SUCC  
400 classification (Tables 5 and 6) produced the following results. The analyses for the basal area of  
401 Pioneer species (G.Pi) and of Post-Pioneer species including oaks (G.Qu) and Tree Genus  
402 Richness (TGR) were negligible (except for NF and PF herbaceous species, and AF herbaceous  
403 species only for G.Pi) for species richness data. For abundance data, the results were without  
404 information related to negligibility (except for AF bryophytes where the effect was negligible for  
405 TGR). This was not the case for the basal area of undergrowth tree species (G.Un) which  
406 included non-negligibly negative effects for all the ecological groups (except for AF woody

407 species richness and AF bryophytes for which the effect was negligible, and species richness of  
408 AF herbaceous species for which the negligibility of the effect could not be determined).  
409 Somewhat similar results were found for total basal area in the model TGI+TA. For the restricted  
410 Tree Genus richness (mTGR4) and tree genus dominance (TGD) the effects were without  
411 information relative to negligibility, except for AF bryophyte and woody species richness for  
412 mTGR4 (negligible effect) and NF herbaceous and AF woody species abundance (non-negligible  
413 negative for mTGR4, and non-negligible positive for TGD).

414 The negligible and non-negligible ecological effects of the Soil model (Tables S3 & S4)  
415 were:

- 416 – negligible effects of ClayDepth on all non-herbaceous species groups for species richness;  
417 of HUMUS, pH and C/N on AF bryophyte species richness; of C/N on AF herbaceous and AF  
418 and PF woody species richness;
- 419 – non-negligible negative effects of HUMUS and pH on PF and NF groups species richness,  
420 on AF and NF herbaceous species abundance; non-negligible negative effects of pH on the  
421 abundance of PF herbaceous and AF woody species.

422

## 423 **Discussion**

### 424 *Towards better indicator(s) of understory diversity and abundance*

425 Our results show that the currently preferred indicators of biodiversity – restricted tree  
426 genus richness (mTGR4) and tree genus dominance (TGD) (Ministère de l'Agriculture et de la  
427 Pêche, 2006) – are not among the best models for the ecological groups studied and generally do  
428 not show significant effects on biodiversity. However, our data did not give any information on  
429 negligibility, except for mature forest (AF) bryophyte and woody species richness for dominance,  
430 for which the effect was negligible, and for the abundance data of non-forest herbaceous (NF

431 herbaceous species) and AF woody species, which displayed a surprising significant, non-  
432 negligible behavior: a decrease (respectively increase) in abundance of these groups with the  
433 increase in restricted tree genus richness (resp. dominance). These surprising results might be  
434 associated with significant correlations of mTGR4 and TGD with the basal area of undergrowth  
435 trees (G.Un), respectively positive ( $\rho = 0.35^*$ ) and negative ( $\rho = -0.54^{***}$ ). Thus, these tree  
436 diversity indicators do not appear to be completely substantiated by our analyses, with two  
437 ecological groups actually showing reverse trends compared to what is generally expected.

438 We must insist that many other references in the literature found positive effects of tree  
439 species richness on understory biodiversity. Fourteen of the 36 correlations between TSR and  
440 understory species richness or diversity we found in the literature (e.g. Daubenmire and  
441 Daubenmire, 1968, Glenn-Lewin, 1977, p.159, references in Barbier et al., 2008, p.5, Mölder et  
442 al., 2008) were positive and significant at the 5% level; the mean coefficient of correlation was  
443 0.25. However, these results may be more related to site type variations than to management  
444 practices (cf. Glenn Lewin 1977, and Introduction section). Our results do not have this drawback  
445 since site type was carefully controlled, at least in terms of soil acidity (cf. Table 2); site type  
446 variations should be less likely to explain observed relationship between over- and understory in  
447 our study than in other studies.

448 Models involving (dominant) Tree Genus Identity (TGI) were better models of biodiversity  
449 variations than null models or models based on Tree Genus Richness (Tables 1 and 2). This  
450 recalls the old forest ecology topic of biodiversity differences among dominant tree species  
451 (Whittaker, 1956, Michalet et al., 2002, Barbier et al., 2008). Actually, the absence of strong  
452 correlations between canopy tree species and understory species (Whittaker, 1956, Daubenmire  
453 and Daubenmire, 1968) has been one of the arguments used to promote the ecological concepts

454 of a loose organization of communities and the individualistic behavior of species assemblages  
455 (Gleason, 1926). Yet, these analyses "appear to assume that interactions among species should be  
456 similar at all points along environmental axes and that groups of species should be associated at  
457 all points on a gradient if interdependence is to be accepted. However, virtually all types of  
458 ecological interactions have been shown to vary with changes in the abiotic environment , and a  
459 number of field experiments indicate that positive effects become stronger as abiotic stress  
460 increases" (Callaway, 1997). Interactions among plants have been shown to shift from  
461 competition to facilitation along environmental gradients, with stronger positive interactions in  
462 stressful abiotic conditions (Callaway, 1997, Michalet et al., 2002, Callaway et al., 2002). Also,  
463 some papers have noted differences in the floristic species composition under different dominant  
464 tree species; this difference tends to be strongest in specific site type conditions, especially in dry  
465 conditions, and may even occur between two tree species assumed to be in the same ecological  
466 group – *Abies alba* and *Picea abies* (Michalet et al., 2002). Other papers – reviewed in Barbier et  
467 al. (2008) – have stressed that the local species richness was lower in stands dominated by  
468 coniferous species than in stands dominated by hardwoods. Many different mechanisms can  
469 account for such an effect (cf. Michalet et al., 2002, Barbier et al., 2008).

470 Other ecological models based on tree genus composition explained much better the diversity  
471 variations for nearly all the ecological groups analyzed than the ones related to tree genus  
472 diversity. These were the models accounting for the abundance of tree genus groups (TGAS) and,  
473 for cover data, the model mixing dominant tree genus identity and total basal area (TGI+TA). We  
474 found similar results when distinguishing tree species according to the richness of their leaf litter  
475 (model TGAR, based on Aubert et al., 2004; Van Oijen et al., 2005; results not shown), which  
476 gave a tree grouping very close to the successional grouping used in TGAS. The results of these  
477 models are in agreement with other results in the literature showing the strong, negative effect of

478 the abundance of one or several undergrowth tree or shrub species on vascular understory  
479 biodiversity (Kwiatkowska, 1994; Kwiatkowska et al., 1997 for *Carpinus betulus*, Baker and van  
480 Lear, 1998 for *Rhododendron maximum*, Ammer & Stimm 1996 in Ewald, 2002 for *Acer*  
481 *pseudoplatanus*, Brewer, 1980 for *Acer saccharum* and *Fagus americana*; see also Barbier et al.,  
482 2008, p. 5, and Rogers et al., 2008; but see Van Oijen et al., 2005 for a positive effect of such tree  
483 species). Kwiatkowska et al. (1994, 1997) described the decline in the diversity of all understory  
484 species groups with the increasing abundance of *Carpinus betulus*. This corresponds to the  
485 transition phase of succession described in e.g. Spies (1997), where the dominance of the initial  
486 tree species declines in favor of newly established tree species, a process also called  
487 "mesification" (Rogers et al., 2008). We also found a negative effect of the basal area of  
488 undergrowth trees – here hornbeam and lime – on the species richness and abundance of nearly  
489 all the ecological groups. The effects tended to be logically ordered among ecological groups for  
490 species richness – with a higher impact for NF groups than for PF (peri-forest) and then AF  
491 groups (cf. Table 5) –, but less so for abundance data. Quantifications of these effects had rarely  
492 been made. Kwiatkowska et al. (1997) have analyzed the relationship between species richness  
493 and density and mean diameter of hornbeam saplings; here, we propose to use the basal area of  
494 undergrowth tree species to quantify understory diversity – as Baker and van Lear (1998) did –, a  
495 parameter that depends both on density and mean diameter.

496 Other authors (Ewald, 2002, Spyreas and Matthews, 2006, Rogers et al., 2008) have related  
497 understory biodiversity to total tree abundance – measured as density, cover, basal area at breast  
498 height, volume or biomass –, without any specific reference to the tree species composition.  
499 Although different results were found when using tree cover as a measure of tree abundance  
500 (Tyler, 1989), these publications generally reported a decrease in understory species richness  
501 with increasing abundance. Based on the analysis of different ecological groups, we either found

502 such a decline or no trend of diversity with total tree abundance (Tables 5 and 6). These are cases  
503 of a decrease in biodiversity that may be due to asymmetric competition by trees on understory  
504 plants, more likely to occur in mesic or humid conditions than under dry conditions (Ewald,  
505 2002). Although nestedness should be checked at the species level, our results for model  
506 (TGI+TA) probably point to a nested structure of communities with respect to basal area (here:  
507 TA), as in Spyreas and Matthews (2006), in the sense that the communities had monotonic  
508 species richness variations along the TA gradient, with less rich communities being composed of  
509 species that were also present in richer communities. Indeed, the ecological groups studied either  
510 did not depend on TA or declined in species richness and abundance with TA. In particular, as in  
511 Spyreas and Matthews (2006) and Rogers et al. (2008), NF and PF herbaceous species were the  
512 most impacted in terms of species richness and there was no sign of enrichment of forest species  
513 in high TA stands.

514 It may be useful to discuss these results in terms of successional models of forest vegetation  
515 and the associated debate about the "linkage" between forest strata (Spyreas and Matthews, 2006,  
516 Gilliam, 2007). The null model of succession as implicitly hypothesized by Spyreas and  
517 Matthews (2006) is a model of linkage between forest strata matching the relay floristics  
518 successional model sensu Egler (1954), where species frequency optima are placed continuously  
519 along the successional or basal area gradient. Here, mature forest species are assumed to be  
520 associated with older successional stages or stages with higher basal areas, or to increase in  
521 frequency in such contexts. This model fits neither the observations in our study nor in the many  
522 studies cited above. Actually, "mesification" –corresponding to an increase in the abundance of  
523 the overstory stratum or of undergrowth, mesophanerophytes and associated canopy cover – is a  
524 source of degradation rather than recovery, as hypothesized in the above null model (Spyreas and  
525 Matthews, 2006). Although for AF species richness our negligibility results are consistent with

526 Spyreas and Matthews (2006)'s "decoupling between strata" terminology, what we observe for  
527 abundance and PF and NF species richness data would be better termed "reversed coupling  
528 between strata" – except for AF bryophyte species (cf. line "G.Un" in Tables 5 & 6). Why is this  
529 so? The first possible explanation is simply that the null model of succession is wrong: the true  
530 model should be a nested successional model, where "all" the species are equally or more  
531 frequent in young, disturbed stands than in old, mesified stands (e.g. Clark et al., 2003, Redburn  
532 and Strong, 2008). More precisely, in both natural and artificial conditions, forest species  
533 frequency and richness would either decline or remain stable during succession or mesification,  
534 with all other species groups declining. The second explanation could be that natural succession  
535 and succession under altered conditions are fundamentally different. Altered conditions could  
536 include alterations in the disturbance regime, changes in ungulate densities or in the dispersal  
537 intensity of forest species due either to their low frequency in the landscape or to fragmentation  
538 (Rogers et al., 2008, Spyreas and Matthews, 2006). Natural succession would be close to the  
539 relay floristics model under a natural disturbance regime due to the more frequent removal of  
540 some forest species by natural disturbances such as fire. Altered succession on the other hand,  
541 would be nested as described in the above explanation. However, the relevance of the relay  
542 floristics or nested successional models might vary with site type, climatic fluctuations and  
543 historical and spatial contingencies (Veblen and Lorenz, 1986, Pickett et al., 2001 and Dovciak et  
544 al., 2005).

545

546 ***Statistical comments: negligibility and less than Poisson distributions***

547 For species richness data, we have used new probability distributions that allow us to account  
548 for both under- and over-dispersion relative to the Poisson distribution. As far as we know, this is  
549 the first time that such under-dispersed distributions have been used in regression models applied

550 to ecology. This has allowed us to reach more precise estimates, especially for bryophytes (cf.  
551 Gosselin, Submitted b). Indeed, for bryophyte and woody species groups, dispersion parameters  
552 were below 1 – indicating under-dispersion relative to the Poisson distribution.

553 Secondly, we have insisted on the interest of using statistical tools – in short equivalence  
554 tests – to detect cases where results are judged as biologically negligible from cases where they  
555 are not negligible or cases where information is insufficient to judge. This echoes many calls for  
556 the estimation of effects rather than the test of null hypotheses from specialists working across  
557 the borderline between statistics and ecology (Johnson, 1999, Anderson et al., 2000). The first  
558 advantage of equivalence tests is that they introduce a decision category that does not exist in  
559 point null hypothesis testing: the case where the estimate is judged negligible. This facilitates a  
560 more balanced decision: is there any non-negligible effect or not? A second advantage to the  
561 approach is in cases where the real effects are too small to be of biological or managerial  
562 relevance. With "insufficient" data, classical point null hypothesis testing may not conclude  
563 anything because the null hypothesis will not be rejected and a "need-for-more -data" syndrome  
564 may appear. In such situations, equivalence tests will more easily conclude that the effect is truly  
565 negligible. In our case, the number of clear decisions for species richness data was greater with  
566 equivalence tests than with point null hypothesis testing while it was the same for abundance data  
567 (cf. bold and underlined figures in Table 7). However, it is sometimes possible for the point null  
568 hypothesis to be rejected even though the effect is judged negligible: this occurred once in our  
569 analyses (Table 7). The reverse is logically impossible: an effect cannot be judged non-negligible  
570 and non-significant.

571

572 *Limitations of the present results and associated perspectives*

573           The small extent of the study site and the limited number of replicates are the first obvious  
574 limitations in our study. Furthermore, the sampling scheme was neither a random sample from  
575 deciduous stands in the region nor a completely controlled stratified sampling. All these  
576 elements, together with the levels of variability in the data, meant that many estimators could not  
577 be categorized as negligible or non-negligible (Tables 5 & 6). Yet, for the basal area of  
578 undergrowth tree species, the fact that our results strongly echo similar results found in other  
579 deciduous forests, where a transition phase seems to be under way (cf. above), gives us some  
580 confidence in our results.

581           Broader-scale studies in terms of number of replicates, extent of region and site variability  
582 are desirable, provided they incorporate ecological sources of variation such as site variability  
583 into the statistical model. One such study was attempted in Barbier (2007), and gave qualitatively  
584 similar results to those of the present study, i.e. TGAS was one of the best models, TGR and  
585 TGI+TGD were less effective with globally non-significant coefficients for TGR, and negative  
586 effects of shade tolerant trees on biodiversity were observed – except for mature forest  
587 herbaceous species.

588           If such tree abundance models are to be tested in other conditions, researchers should  
589 think further on the quantities used for tree abundance and/or on the ecological conditions under  
590 which the models should be used. Indeed, as pointed out by Daubenmire and Daubenmire (1968),  
591 quantities such as basal area or volume might be less representative of the impact of tree species  
592 on light availability than models based on cover. For example, if the sampling plots included an  
593 important ratio of senescent trees, there could be a high basal area but a low light interception.  
594 The relationship between basal area and light capture might thus vary among DBH classes, or  
595 across stand types, or in mixed stands.

596 Barbier (2007) did not have the opportunity to investigate interactions between tree species  
597 composition and site characteristics. Yet, many previous papers point in this direction (Tyler,  
598 1989, Michalet et al., 2002, Callaway, 1997, Callaway et al., 2002). This might partly relate to  
599 limiting ecological factors that vary with site type conditions (Härdtle et al., 2003). Similarly,  
600 relationships between parameters such as tree species richness and understory biodiversity might  
601 well depend on the successional status or the range of successional stages studied (Auclair and  
602 Goff, 1971, Gilliam et al., 1995). We could not deal with this question due to the limited scope of  
603 our sample.

604 Another obvious limitation of our study – and this is also true for almost all the literature  
605 on the subject – is that it was observational and not experimental. An experimental approach used  
606 by Kwiatkowska and Wyszomirski (1990) based on the cut of hornbeams has mostly  
607 corroborated observational results. This method could be generalized to other tree species or to  
608 experimental manipulations through tree cutting of other ecological parameters – e.g. tree genus  
609 richness. An alternative would be to use experimental plantations as in Scherer-Lorenzen et al.  
610 (2007).

611 In our study, we restricted our analyses to species richness and cover for only certain  
612 ecological classifications. Analyses should also be done at the species level and for other  
613 ecological groups that are relevant to the ecological questions (e.g. associated with leaf  
614 phenology, soil nutrient richness...). Also, analyses of conservation value of biodiversity (Duelli  
615 and Obrist, 2003), beta-diversity (Aubert et al., 2004) and evenness could enrich the analysis.

616 Another challenge is to use multivariate models such as the one implying the abundance  
617 of various groups of tree species (TGAS) in reports on sustainable forest management. It is  
618 indeed difficult to communicate a multivariate model in a report intended for the lay public. An

619 alternative might be to simulate the associated expected changes in components of biodiversity  
620 from the observed temporal changes in tree species abundances based on the statistical models.

621 Our study was also limited in that we considered only one broad taxonomic group, which  
622 is not necessarily indicative of other taxonomic groups. Indeed, some other taxonomic groups  
623 studied in the same plots – such as carabid beetles – did not show the same trends, either in terms  
624 of the best models or the direction of the effects (results not shown).

625 Finally and more generally, this paper has taken for granted that biodiversity could be  
626 accounted for chiefly with pressure-type indicators. Yet, this may not necessarily be the case  
627 since biodiversity states and variations are the result of the cumulative effects of different  
628 pressures. We therefore support the idea that biodiversity components should be directly  
629 monitored in sustainable forest management policy assessment. Yet, pressure level indicators or  
630 analyses of this type do offer the possibility to better interpret observed trends, and possibly to  
631 extrapolate to situations where only dendrometric and no biodiversity information is available.

632

### 633 ***Conclusions***

634 Our paper promotes testing biodiversity indicators based on parametric statistical models  
635 which are – to our knowledge – the only ones that allow the use of both model comparison  
636 techniques and the study of negligible effects. In particular, methods based simply on correlation  
637 coefficients and associated probabilities of significance are to our knowledge incapable of  
638 distinguishing the different situations of non-negligible trend as defined by Dixon and Pechmann  
639 (2005). Based on our results and on this discussion, we believe that for these oak-dominated  
640 types of forests with a potentially strong hornbeam component but without beech, TGAS models  
641 – and maybe even a simpler model with only the basal area of undergrowth trees – are better than

642 models based on tree genus diversity. The generalization of these results to broader sampling  
643 sites with more variable site conditions and tree species composition is desirable.

644

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654

#### 655 **References**

- 656 anonymous, 1999. *Qualité des sols*. AFNOR, Paris.
- 657 Anderson, D.R., Burnham, K.P., Thompson, W.L., 2000. Null hypothesis testing: Problems,  
658 prevalence, and an alternative. *Journal of Wildlife Management* 64, 912-923.
- 659 Aubert, M., Bureau, F., Alard, D., Bardat, J., 2004. Effect of tree mixture on the humic epipedon  
660 and vegetation diversity in managed beech forests (Normandy, France). *Canadian Journal of*  
661 *Forest Research* 34, 233-248.
- 662 Auclair, A.N., Goff, F.G., 1971. Diversity relations of upland forests in the western Great Lakes  
663 area. *The American Naturalist* 105, 499-528.
- 664 Baker, T.T., van Lear, D.H., 1998. Relations between density of rhododendron thickets and  
665 diversity of riparian forests. *Forest Ecology and Management* 109, 21-32.

666 Barbier, S., Balandier, P., Gosselin, F., Influence of several tree traits on rainfall partitioning in  
667 temperate and boreal forests: a review. *Annals of Forest Science* In Press.

668 Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation  
669 diversity and mechanisms involved - a critical review for temperate and boreal forests. *Forest*  
670 *Ecology and Management* 254, 1-15.

671 Barbier, S., 2007. Influence de la diversité, de la composition et de l'abondance des essences  
672 forestières sur la diversité floristique des forêts tempérées. Université d'Orléans, Orléans,  
673 <http://tel.archives-ouvertes.fr/tel-00238532/fr>.

674 Betts, M.G., Diamond, A.W., Forbes, G.J., Frego, K.A., Loo, J.A., Matson, B., Roberts, M.R.,  
675 Villard, M.A., Wissink, R., Wuest, L., 2005. Plantations and biodiversity: A comment on the  
676 debate in New Brunswick. *The Forestry Chronicle* 81, 265-269.

677 Brêthes, A., Brun, J.J., Jabiol, B., Ponge, J., Toutain, F., 1995. Classification of forest humus  
678 forms: A French proposal. *Annals of Forest Science* 52, 535-546.

679 Brewer, R., 1980. A half-century of changes in the herb layer of a climax deciduous forest in  
680 Michigan. *Journal of Ecology* 68, 823-832.

681 Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L.,  
682 Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., Cook, B.J., 2002.  
683 Positive interactions among alpine plants increase with stress. *Nature* 417, 844-848.

684 Callaway, R.M., 1997. Positive interactions in plant communities and the individualistic-  
685 continuum concept. *Oecologia* 112, 143-149.

686 Camp, R.J., Seavy, N.E., Gorresen, P.M., Reynolds, M.H., 2008. A statistical test to show  
687 negligible trend: Comment. *Ecology* 89, 1469-1472.

688 Chamberlin, T., 1965. The method of multiple working hypotheses. *Science* 148, 754-759.

689 Clark, D.F., Antos, J.A., Bradfield, G.E., 2003. Succession in sub-boreal forests of West-Central  
690 British Columbia. *Journal of Vegetation Science* 14, 721-732.

691 Corley, M.F.V., Crundwell, A.C., Dull, R., Hill, M.O., Smith, A.J.E., 1981. Mosses of Europe  
692 and the Azores ; an annotated list of species, with synonyms from the recent literature. *Journal of*  
693 *Bryology* 11, 609-689.

694 Corley, M.F.V., Crundwell, A.C., 1991. Additions and amendments to the mosses of Europe and  
695 the Azores. *Journal of Bryology* 16, 337-356.

696 Daubenmire, R., Daubenmire, J.B., 1968. Forest vegetation of eastern Washington and northern  
697 Idaho. *Technical Bulletin, Washington Agricultural Experiment Station, Pullman* 60, 104.

698 Dixon, P.M., Pechmann, J.H.K., 2005. A statistical test to show negligible trend. *Ecology* 86,  
699 1751-1756.

700 Dovciak, M., Frelich, L.E., Reich, P.B., 2005. Pathways in old-field succession to white pine:  
701 Seed rain, shade, and climate effects. *Ecological Monographs* 75, 363-378.

702 Duelli, P., Obrist, M.K., 2003. Regional biodiversity in an agricultural landscape: the  
703 contribution of seminatural habitat islands. *Basic and Applied Ecology* 4, 129-138.

704 Egler, F.E., 1954. *Vegetation Science Concepts I. Initial floristic composition, a factor in old-*  
705 *field vegetation development. Vegetatio* 4, 412-417.

706 Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1992. *Zeigerwerte von*  
707 *Pflanzen in Mitteleuropa. Verlag Goltze, Göttingen.*

708 Evstigneev, O.I., 1988. Developmental features of broadleaved trees under the forest canopy in  
709 various light conditions. *Botanicheskii Zhurnal (st. Petersburg)* 73, 1730-1736.

710 Ewald, J., 2002. Multiple controls of understorey plant richness in mountain forests of the  
711 Bavarian Alps. *Phytocoenologia* 32, 85-100.

712 Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. Bayesian Data Analysis. Chapman &  
713 Hall, Boca Raton.

714 Gilliam, F.S., Turrill, N.L., Adams, M.B., 1995. Herbaceous-layer and overstory species in clear-  
715 cut and mature central Appalachian hardwood forests. *Ecological Applications* 5, 947-955.

716 Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest  
717 ecosystems. *BioScience* 57, 845-858.

718 Gleason, H.A., 1926. The individualistic concept of the plant association. *Bulletin of the Torrey*  
719 *Botanical Club* 543, 7-26.

720 Glenn-Lewin, D.C., 1977. Species diversity in North American temperate forests. *Vegetatio* 33,  
721 153-162.

722 Gosselin, F., Gosselin, M., 2004. Analyser les variations de biodiversité : outils et méthodes. In:  
723 Gosselin M., Larroussinie O. (Eds.), *Biodiversité et gestion forestière : connaître pour préserver -*  
724 *synthèse bibliographique*. Coédition GIP Ecofor - Cemagref Editions, Antony, pp. 58-99.

725 Grolle, R., 1983. Hepatics of Europe including the Azores : an annotated list of species, with  
726 synonyms from the recent literature. *Journal of Bryology* 12, 403-459.

727 Härdtle, W., von Oheimb, G., Westphal, C., 2003. The effects of light and soil conditions on the  
728 species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-  
729 Holstein). *Forest Ecology and Management* 182, 327-338.

730 Hilborn, R., Mangel, M., 1997. *The ecological detective: confronting models with data*. Princeton  
731 University Press, Princeton (NJ).

732 Hodgson, J.G., Grime, J.P., Hunt, R., Thompson, K., 1995. *The electronic comparative plant*  
733 *ecology*. Chapman & Hall, London.

734 Jabiol, B., Höltermann, A., Gégout, J.C., Ponge, J.F., Brêthes, A., 2000. Typologie des formes  
735 d'humus peu actives. Validation par des critères macro- et micromorphologiques, biologiques et  
736 chimiques. *Etude et Gestion des Sols* 7, 133-154.

737 Johnson, D.H., 1999. The insignificance of statistical significance testing. *Journal of Wildlife*  
738 *Management* 63, 763-772.

739 Johnson, V.E., 2007. Bayesian Model Assessment Using Pivotal Quantities. *Bayesian Analysis* 2,  
740 719-734.

741 Julve, P., 2002. Index écologique et chorologique de la flore de France,  
742 <http://perso.wanadoo.fr/philippe.julve/catminat.htm#INDEXFLORE> .

743 Kerguélen, M., 1999. Index synonymique de la flore de France, [http://www2.dijon.inra.fr/flore-](http://www2.dijon.inra.fr/flore-france/)  
744 [france/](http://www2.dijon.inra.fr/flore-france/) .

745 Korb, J.E., Daniels, M.L., Laughlin, D.C., Fulé, P.Z., 2007. Understory communities of warm-  
746 dry, mixed-conifer forests in southwestern Colorado. *Southwestern Naturalist* 52, 493-503.

747 Kwiatkowska, A.J., Spalik, K., Michalak, E., Palinska, A., Panufnik, D., 1997. Influence of the  
748 size and density of *Carpinus betulus* on the spatial distribution and rate of deletion of forest-floor  
749 species in thermophilous oak forest. *Plant Ecology* 129, 1-10.

750 Kwiatkowska, A.J., Wyszomirski, T., 1990. Species deletion in *Potentillo albae-Quercetum*  
751 phytocoenoses reversed by the removal of *Carpinus betulus*. *Vegetatio* 87, 115-126.

752 Kwiatkowska, A.J., 1994. Changes in the species richness, spatial pattern and species frequency  
753 associated with the decline of oak forest. *Vegetatio* 112, 171-180.

754 Lindenmayer, D.B., Margules, C.R., Botkin, D.B., 2000. Indicators of biodiversity for  
755 ecologically sustainable forest management. *Conservation Biology* 14, 941-950.

756 Lindenmayer, D.B., 1999. Future directions for biodiversity conservation in managed forests :  
757 indicator species, impact studies and monitoring programs. *Forest Ecology and Management* 115,  
758 277-287.

759 Liu, I., Agresti, A., 2005. The analysis of ordered categorical data: An overview and a survey of  
760 recent developments. *Test* 14, 1-73.

761 MCPFE, 2003. Improved pan-European indicators for sustainable forest management as adopted  
762 by the MCPFE Expert Level Meeting. Ministerial Conference on the Protection of Forests in  
763 Europe, Vienna.

764 Météo France, 1996. Normales climatiques. Période 1961 - 1990. Tome 1. Stations de Métropole.  
765 Météo France, Paris, France.

766 Michalet, R., Rolland, C., Joud, D., Gafta, D., Callaway, R.M., 2002. Associations between  
767 canopy and understory species increase along a rainshadow gradient in the Alps: Habitat  
768 heterogeneity or facilitation? *Plant Ecology* 165, 145-160.

769 Ministère de l'Agriculture et de la Pêche, 2006. Les indicateurs de gestion durable des forêts  
770 françaises - Edition 2005. MAP, Paris.

771 Mölder, A., Bernhardt-Römermann, M., Schmidt, W., 2008. Herb-layer diversity in deciduous  
772 forests: Raised by tree richness or beaten by beech? *Forest Ecology and Management* 256, 272-  
773 281.

774 Pickett, S.T., Cadenasso, M.L., Bartha, S., 2001. Implications from the Buell-Small Succession  
775 Study for vegetation restoration. *Applied Vegetation Science* 4, 41-52.

776 Ponge, J.F., Chevalier, R., Loussot, P., 2002. Humus index: an integrated tool for the assessment  
777 of forest floor and topsoil properties. *Soil Science Society of America Journal* 66, 1996-2001.

778 Rameau, J.C., Mansion, D., Dumé, G., Timbal, J., Lecoite, A., Dupont, P., Keller, R., 1989.  
779 Flore forestière française. Guide écologique illustré. Tome 1 : Plaines et collines. Institut pour le  
780 Développement Forestier, Paris.

781 Redburn, M.J., Strong, W.L., 2008. Successional development of silviculturally treated and  
782 untreated high-latitude *Populus tremuloides* clearcuts in northern Alberta, Canada. Forest  
783 Ecology and Management 255, 2937-2949.

784 Rice, J., Anderson, B.W., Ohmart, R.D., 1984. Comparison of the importance of different habitat  
785 attributes to avian community organization. Journal of Wildlife Management 48, 895-911.

786 Roberts, G.O., Rosenthal, J.S., Examples of adaptive MCMC. Journal of Computational and  
787 Graphical Statistics In Press.

788 Rogers, D.A., Rooney, T.P., Olson, D., Waller, D.M., 2008. Shifts in Southern Wisconsin forest  
789 canopy and understory richness, composition, and heterogeneity. Ecology 89, 2482-2492.

790 Scherer-Lorenzen, M., Schulze, E.D., Don, A., Schumacher, J., Weller, E., 2007. Exploring the  
791 functional significance of forest diversity: A new long-term experiment with temperate tree  
792 species (BIOTREE). Perspectives in Plant Ecology, Evolution and Systematics 9, 53-70.

793 Sonohat, G., Balandier, P., Ruchaud, F., 2004. Predicting solar radiation transmittance in the  
794 understory of even-aged coniferous stands in temperate forests. Annals of Forest Science 61, 629-  
795 641.

796 Spiegelhalter, D., Best, N., Carlin, J.B., van der Linde, A., 2002. Bayesian measures of model  
797 complexity and fit (with Discussion). Journal of the Royal Statistical Society, Series B 64, 583-  
798 616.

799 Spies, T.A., 1997. Forest stand structure, composition, and function. In: Kohn K.A., Franklin J.F.  
800 (Eds.), Creating a forestry for the 21st century - The science of ecosystem management. Island  
801 Press, Washington D.C., pp. 11-30.

802 Spyreas, G., Matthews, J.W., 2006. Floristic conservation value, nested understory floras, and the  
803 development of second-growth forest. *Ecological Applications* 16, 1351-1366.

804 Tyler, G., 1989. Interacting effects of soil acidity and canopy cover on the species composition of  
805 field-layer vegetation in oak/hornbeam forests. *Forest Ecology and Management* 28, 101-114.

806 van der Maarel, E., 1979. Transformation of cover-abundance values in phytosociology and its  
807 effects on community similarity. *Vegetatio* 39, 97-144.

808 Van Oijen, D., Feijen, M., Hommel, P., Den Ouden, J., De Wall, R., 2005. Effects of tree species  
809 composition on within-forest distribution of understory species. *Applied Vegetation Science* 8,  
810 155-166.

811 Veblen, T.T., Lorenz, D.C., 1986. Anthropogenic disturbance and recovery patterns in montane  
812 forests, Colorado Front Range. *Physical Geography* 7, 1-24.

813 Vera, F.W.M., 2000. *Grazing Ecology and Forest History*. CABI Publishing, New York.

814 Whittaker, R.H., 1956. *Vegetation of the Great Smoky Mountains*. *Ecological Monographs* 6, 1-  
815 80.

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817

818 **Table 1. Summary statistics of the quantitative ecological variables used in ecological models (BA is basal area at breast**  
 819 **height). SD is standard deviation.**

820

Ecological variable	Definition and units	Mean	SD	Range
Date	Number of days (from the 1 <sup>st</sup> June 1999)	11.3	14.4	-15 – 55
G	Total BA (m <sup>2</sup> .ha <sup>-1</sup> )	29.6	6.9	13.9 – 44.0
G.Pi	BA of "Pioneer trees" ( <i>Betula sp.</i> and <i>Populus sp.</i> ) (m <sup>2</sup> .ha <sup>-1</sup> )	4.9	5.9	0.0 – 21.9
G.Qu	BA of "Oaks" or post-pioneer tree genera ( <i>Quercus petraea</i> and <i>Q. robur</i> ; also including tree genera not in G.Pi and G.Un) (m <sup>2</sup> .ha <sup>-1</sup> )	14.6	7.8	0.6 – 30.5
G.Un	BA of "undergrowth" tree genera ( <i>Carpinus betulus</i> and <i>Tilia sp.</i> ) (m <sup>2</sup> .ha <sup>-1</sup> )	10.12	8.4	0.0 – 32.2
TGR	Tree genus richness in the dendrometric relevé (varying radius sampling, up to 1520 m <sup>2</sup> ) (# of species)	4.6	1.5	1 – 8

TGD	Tree genus dominance: calculated as $\max(G.Pi, G.Qu, G.Un)/G$	0.6	0.2	0.3 – 1.0
pH.KCl.A	pH KCl of the organic-mineral layer of the soil (5-10 cm deep)	3.8	0.3	3.2 – 4.7
pH.KCl.B	pH KCl of the first mineral layer of the soil (15-25 cm deep)	3.7	0.1	3.6 – 3.9
C/N.A	Ratio of organic C over total Nitrogen in the organic-mineral layer	16.6	1.0	14.0 – 19.0
HUMUS	Humus index (cf. text)	5.1	1.3	2.0 – 6.2
ClayDepth	Depth in the soil at which clay was dominant (cm)	45.6	4.7	31.2 – 57.5

821 **Table 2. Definition of the specific parameters identifying the ecological models (cf. Table 1**  
 822 **for the definition of variables).**

Model acronym	Ecological parameters specific to the model (not including the intercept)
<i>TGI</i>	~TGI  Tree genus identity of the group which has the highest G in the plot, among Pi, Qu or Un as defined for TGAS
<i>TA</i>	~G
<i>TGI+TA</i>	~TGI+G  Addition of the TGI and G effects– with no interaction
<i>TGAS</i>	~G.Pi+G.Qu+G.Un
<i>TGI+TGD</i>	~TGI+TGD
<i>TGR</i>	~TGR
<i>mTGR4</i>	~min(TGR,4)  Minimum between TGR and 4
<i>Date</i>	~ Date
<i>Block</i>	~ Identity of the forest Block (two levels: between Southern Block and Northern Block)
<i>Soil</i>	~ pH.KCl.A+C/N.A+HUMUS+ClayDepth
<i>null</i>	0

823 Table 3. Differences in DIC (Deviance Information Criterion) values between the different  
824 ecological models and the null model, for species richness data for the ecological groups by  
825 successional classification (SUCC): "AF" for mature forest, "PF" for peri-forest and "NF" for  
826 non-forest species. The smaller the DIC, the better the model with respect to the others. Within  
827 each ecological group, the model with the smallest DIC was underlined and the DIC values  
828 within 5 units to this model were put in bold. For each line, the column "Sum" gives the (sum of)  
829 DIC differences over ecological groups.  
830

Model							
Acronym	Bryophytes		Herbaceous		Woody		Sum
	AF	AF	PF	NF	AF	PF	
TGI	-3.4	-12.8	-4.9	-12.4	<b>-4.7</b>	-6.5	-44.7
TA	-2.8	-5.5	-11.5	-17.4	-2.2	-19.7	-59.0
TGI+TA	-3.9	-14.3	<b>-13.9</b>	-23.1	<b>-4.8</b>	-21.9	-82.0
TGAS	-4.9	<u><b>-21.0</b></u>	<u><b>-18.2</b></u>	<u><b>-35.7</b></u>	<u><b>-9.1</b></u>	<u><b>-32.6</b></u>	<u><b>-121.4</b></u>
TGI+TGD	-3.1	-15.2	-6.5	-16.5	<b>-4.7</b>	-8.7	-54.8
TGR	-1.4	0.0	0.0	0.0	-1.5	0.0	-2.7
mTGR4	-0.3	-0.6	-0.0	-1.2	-0.2	-2.5	-4.8
Date	0.2	-2.6	-0.9	-0.8	-0.5	-0.1	-4.7
Block	-6.1	0.0	-0.6	-0.5	-0.4	-1.8	-9.3
Soil	<u><b>-19.5</b></u>	-3.9	-9.0	-13.9	<b>-8.9</b>	-12.7	-68.0
null	0	0	0	0	0	0	0

831

832 Table 4. Differences in DIC (Deviance Information Criterion) values between the different  
 833 ecological models and the null model, for abundance data for the ecological groups by  
 834 successional classification (SUCC). The rest of the legend is the same as in Table 3.  
 835

Model Acronym	Bryophytes		Herbaceous			Woody		Sum
	AF	AF	PF	NF	AF	PF		
TGI	<b>-10.1</b>	<b>-8.8</b>	-9.4	-7.9	-13.8	-6.6	-56.6	
TA	-5.3	-5.5	-17.6	-21.4	-26.6	-10.4	-86.8	
TGI+TA	<b>-12.5</b>	<b>-10.1</b>	<b>-23.0</b>	-23.8	<b>-30.7</b>	-15.6	-115.7	
TGAS	<b><u>-14.9</u></b>	<b><u>-9.0</u></b>	<b><u>-26.4</u></b>	<b><u>-29.4</u></b>	<b><u>-33.9</u></b>	<b><u>-21.2</u></b>	<b><u>-134.8</u></b>	
TGI+TGD	<b>-11.8</b>	<b>-9.1</b>	-15.6	-22.3	-22.5	-7.4	-88.7	
TGR	-0.1	-0.2	0.1	-0.7	-0.6	-0.3	-1.8	
mTGR4	-1.2	-0.1	-1.1	-6.8	-8.5	-0.5	-18.2	
Date	-1.1	-4.4	-0.4	-0.8	-0.0	-2.0	-8.7	
Block	-0.9	-2.1	-1.4	-0.7	-1.1	0.1	-6.1	
Soil	<b>-12.9</b>	<b><u>-10.9</u></b>	-8.9	-11.4	-16.2	-5.9	-66.2	
null	0	0	0	0	0	0	0	

836

837

838 Table 5. Analysis of the multiplicative effect of a given variation of selected ecological  
839 parameters on the species richness of the ecological groups by successional classification  
840 (SUCC). Variations were an addition of  $5 \text{ m}^2 \cdot \text{ha}^{-1}$  for basal area data (G.Pi, G.Qu, G.Un, G), of  
841 1.5 genera for TGR and mTGR4 and of 0.2 for TGD (Tree Genus Dominance). Levels of  
842 statistical significance of parameters are symbolized as follows: \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  
843  $p < 0.05$ . "0" and "00" indicate that the effect has a P-value of at least 0.95 of being negligible, at  
844 two different levels (cf. text). "-" and "--" indicate that the effect has a P-value of at least 0.95 of  
845 being negative and non-negligible, at two different levels (cf. text). The rest of the legend is the  
846 same as in Table 3.

Model	Bryophytes		Herbaceous		Woody	
Acronym	AF	AF	PF	NF	AF	PF
G.Pi	1.01 <sup>00</sup> [0.94;1.08]	1.18 [1.00;1.38]	0.96 [0.67;1.37]	0.97 [0.63;1.41]	1.05 <sup>0</sup> [0.92;1.21]	0.98 <sup>0</sup> [0.88;1.09]
G.Qu	0.99 <sup>00</sup> [0.93;1.06]	1.06 <sup>0</sup> [0.91;1.22]	0.85 [0.62;1.14]	0.81 [0.58;1.08]	1.06 <sup>0</sup> [0.93;1.20]	0.89 <sup>*,0</sup> [0.81;0.98]
G.Un	1.03 <sup>00</sup> [0.99;1.07]	0.83 <sup>**</sup> [0.75;0.92]	0.62 <sup>***,-</sup> [0.48;0.79]	0.40 <sup>***,-</sup> [0.29;0.53]	0.93 <sup>0</sup> [0.85;1.01]	0.80 <sup>***,-</sup> [0.75;0.85]
G in TGI+TA	1.02 <sup>00</sup> [0.97;1.07]	0.93 <sup>0</sup> [0.83;1.04]	0.67 <sup>**,-</sup> [0.50;0.88]	0.57 <sup>**,-</sup> [0.40;0.81]	0.98 <sup>0</sup> [0.89;1.08]	0.84 <sup>***,-</sup> [0.78;0.92]
TGR	0.97 <sup>00</sup> [0.91;1.03]	1.01 <sup>0</sup> [0.87;1.17]	1.02 [0.73;1.41]	0.98 [0.65;1.45]	1.07 <sup>0</sup> [0.96;1.19]	1.00 <sup>0</sup> [0.90;1.14]
mTGR4	0.97 <sup>0</sup> [0.86;1.08]	0.90 [0.68;1.19]	0.91 [0.42;1.75]	0.57 [0.19;1.40]	1.02 [0.82;1.31]	0.84 [0.67;1.05]
TGD in	1.00 <sup>00</sup> [0.94;1.07]	1.14 [0.96;1.36]	1.24 [0.86;1.79]	1.55 [0.98;2.53]	0.99 <sup>0</sup> [0.87;1.13]	1.11 [0.96;1.27]
TGI+TGD						

848 Table 6. Analysis of the multiplicative effect of a given variation of selected ecological  
 849 parameters on the odds value of the cumulative probabilities  $P(Y > \alpha_i)$  for abundance data of the  
 850 ecological groups by successional classification (SUCC). Variations were an addition of  $5 \text{ m}^2 \cdot \text{ha}^{-1}$   
 851 for basal area data (G.Pi, G.Qu, G.Un, G), of 1.5 genera for TGR and mTGR4 and of 0.2 for  
 852 TGD (Tree genus Dominance). The rest of the notation is as in Table 5.

Model						
Acronym	Bryophytes		Herbaceous		Woody	
	AF	AF	PF	NF	AF	PF
	1.90	1.01	0.92	0.82	0.49	1.15
G.Pi	[0.92;3.93]	[0.46;2.21]	[0.47;1.81]	[0.36;1.86]	[0.24;1.00]	[0.51;2.54]
	0.96	0.69	0.68	0.61	0.54	0.53
G.Qu	[0.53;1.75]	[0.34;1.37]	[0.38;1.22]	[0.31;1.21]	[0.27;1.05]	[0.24;1.10]
	1.14 <sup>0</sup>	0.48 <sup>**,-</sup>	0.31 <sup>***,-</sup>	0.23 <sup>***,-</sup>	0.31 <sup>***,-</sup>	0.35 <sup>***,-</sup>
G.Un	[0.74;1.74]	[0.30;0.75]	[0.20;0.49]	[0.13;0.40]	[0.20;0.49]	[0.22;0.56]
	1.09	0.69	0.40 <sup>***,-</sup>	0.30 <sup>***,-</sup>	0.36 <sup>***,-</sup>	0.41 <sup>***,-</sup>
G in TGI+TA	[0.68;1.76]	[0.40;1.13]	[0.24;0.63]	[0.17;0.52]	[0.21;0.60]	[0.24;0.71]
	1.08 <sup>0</sup>	0.98	1.01	0.74	0.77	1.18
TGR	[0.66;1.75]	[0.58;1.67]	[0.59;1.74]	[0.39;1.38]	[0.43;1.38]	[0.67;2.12]
	1.41	0.88	0.56	0.19 <sup>**,-</sup>	0.14 <sup>**,-</sup>	0.57
mTGR4	[0.51;3.75]	[0.29;2.67]	[0.19;1.66]	[0.05;0.61]	[0.03;0.50]	[0.18;1.75]
	0.78	0.50	10.1 <sup>**;++</sup>	60.8 <sup>***;++</sup>	13.23 <sup>**;++</sup>	2.73
TGD in	[0.14;3.87]	[0.09;2.97]	[1.80;53]	[8.0;486]	[2.28;82]	[0.43;17]
TGI+TGD						

853 Table 7. Synthesis of the correspondences between classical statistical significance – based on the  
 854 rejection of classical point null hypotheses ( $p=0.05$ ) – and equivalence and inequivalence tests –  
 855 giving results about the weak negligibility, non weak negligibility or lack of information about  
 856 the negligibility of the effects. Each cell contains the number of cases met in Tables 5 and 6, for  
 857 Species Richness (in sub-column SR) and Abundance data (in sub-column A). Grey cells  
 858 correspond to cases that are impossible.  
 859

	Non significant effect		Significant effect		Total count	
	SR	A	SR	A	SR	A
Negligible effect	18	2	1	0	<b><u>19</u></b>	<b><u>2</u></b>
Non negligible effect	0	0	6	14	<b><u>6</u></b>	<b><u>14</u></b>
Without information	16	26	1	0	17	26
Total count	34	28	<b><u>8</u></b>	<b><u>14</u></b>	42	42

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