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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**

4
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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 m² 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 m^2 subplots for 7.5 cm to 17.5 cm DBH; and 3) the 22 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 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 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 m² 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 σ 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 σ (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; ∞ [) 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, γ 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 γ , 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 β_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 β 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 (± 1.8) for bryophytes, 9.1 (± 7.0) for

371 herbaceous species and 9.3 (± 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

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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 st June 1999)	11.3	14.4	-15 – 55
G	Total BA (m ² .ha ⁻¹)	29.6	6.9	13.9 – 44.0
G.Pi	BA of "Pioneer trees" (<i>Betula sp.</i> and <i>Populus sp.</i>) (m ² .ha ⁻¹)	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 ² .ha ⁻¹)	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 ² .ha ⁻¹)	10.12	8.4	0.0 – 32.2
TGR	Tree genus richness in the dendrometric relevé (varying radius sampling, up to 1520 m ²) (# 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	-4.7	-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	-13.9	-23.1	-4.8	-21.9	-82.0
TGAS	-4.9	<u>-21.0</u>	<u>-18.2</u>	<u>-35.7</u>	<u>-9.1</u>	<u>-32.6</u>	<u>-121.4</u>
TGI+TGD	-3.1	-15.2	-6.5	-16.5	-4.7	-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>-19.5</u>	-3.9	-9.0	-13.9	-8.9	-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	-10.1	-8.8	-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	-12.5	-10.1	-23.0	-23.8	-30.7	-15.6	-115.7	
TGAS	<u>-14.9</u>	<u>-9.0</u>	<u>-26.4</u>	<u>-29.4</u>	<u>-33.9</u>	<u>-21.2</u>	<u>-134.8</u>	
TGI+TGD	-11.8	-9.1	-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	-12.9	<u>-10.9</u>	-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 ⁰⁰ [0.94;1.08]	1.18 [1.00;1.38]	0.96 [0.67;1.37]	0.97 [0.63;1.41]	1.05 ⁰ [0.92;1.21]	0.98 ⁰ [0.88;1.09]
G.Qu	0.99 ⁰⁰ [0.93;1.06]	1.06 ⁰ [0.91;1.22]	0.85 [0.62;1.14]	0.81 [0.58;1.08]	1.06 ⁰ [0.93;1.20]	0.89 ^{*,0} [0.81;0.98]
G.Un	1.03 ⁰⁰ [0.99;1.07]	0.83 ^{**} [0.75;0.92]	0.62 ^{***,-} [0.48;0.79]	0.40 ^{***,-} [0.29;0.53]	0.93 ⁰ [0.85;1.01]	0.80 ^{***,-} [0.75;0.85]
G in TGI+TA	1.02 ⁰⁰ [0.97;1.07]	0.93 ⁰ [0.83;1.04]	0.67 ^{**,-} [0.50;0.88]	0.57 ^{**,-} [0.40;0.81]	0.98 ⁰ [0.89;1.08]	0.84 ^{***,-} [0.78;0.92]
TGR	0.97 ⁰⁰ [0.91;1.03]	1.01 ⁰ [0.87;1.17]	1.02 [0.73;1.41]	0.98 [0.65;1.45]	1.07 ⁰ [0.96;1.19]	1.00 ⁰ [0.90;1.14]
mTGR4	0.97 ⁰ [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 ⁰⁰ [0.94;1.07]	1.14 [0.96;1.36]	1.24 [0.86;1.79]	1.55 [0.98;2.53]	0.99 ⁰ [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 m².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 ⁰	0.48 ^{**,-}	0.31 ^{***,-}	0.23 ^{***,-}	0.31 ^{***,-}	0.35 ^{***,-}
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 ^{***,-}	0.30 ^{***,-}	0.36 ^{***,-}	0.41 ^{***,-}
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 ⁰	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 ^{**,-}	0.14 ^{**,-}	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 ^{**;++}	60.8 ^{***;++}	13.23 ^{**;++}	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	<u>19</u>	<u>2</u>
Non negligible effect	0	0	6	14	<u>6</u>	<u>14</u>
Without information	16	26	1	0	17	26
Total count	34	28	<u>8</u>	<u>14</u>	42	42

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