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

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Abstract

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

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

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

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

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

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

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

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

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

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

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

Our second methodological choice was to analyze vegetation diversity not as a whole but in separate ecological groups, which are known to have different ecological requirements (Gosselin and Gosselin, 2004). We assumed that model relevance, and direction and magnitude of effect within one model, would vary according to the understory ecological group considered. Discrepancies or lack of correlation between total species richness and the diversity of particular ecological or functional groups were indeed frequent (Lindenmayer, 1999, Duelli and Obrist, 2003). We therefore analyzed the understory abundance – here, percent cover – and species richness of ecological groups associated with the successional status, light requirements and life form of species. The use of the successional status of plants – or their association to particular phytosociological groups – is rather frequent in the forest ecology literature, either directly in the analyses (e.g. Kwiatkowska, 1994; Kwiatkowska et al., 1997; ; Spyreas and Matthews, 2006) or more indirectly, by restricting the analysis of vegetation to "forest" species only (Van Oijen et al., 2005), or in interpretations of the variations of total species richness (Mölder et al., 2008). Light preference was chosen because we assumed that light could be an important mechanism in explaining floristic diversity response to tree species identity or abundance.

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

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

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

Material and methods

Study area

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

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

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

Data collection

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

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

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

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

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

For each species present in a relevé, we coded the estimated abundance-dominance of the species in each of the following strata: <0.5 m; ≥ 0.5 and <2 m, and in each of the four square 100 m² subplots in the a 20x20m square plot. Our data consisted in the mean over the plot of the sum of the cover of each species in these two strata in each subplot. The abundance-dominance of each species in each strata was rated using the Braun-Blanquet phytosociological classes. The cover of an individual reaching a given stratum was totally attributed to that stratum. These Braun-Blanquet classes were then transformed into numbers, according to one of the codings in

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

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

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

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

Data analysis

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

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

We analyzed the effect of our different ecological models on the species richness and cover of the understory species groups defined above, at the 400 m² scale. The effects of the model were: the intercept, the observer effect, and the parameters of the ecological model (cf. Table 1). We analyzed all the ecological groups of a given classification in the same statistical model, with

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

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

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

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

where Y is the cover value, γ is the positive quantity that incorporates the fixed effects through 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 has the characteristic that the odds values of the cumulative probabilities $P(Y > \alpha_i | \gamma)$ are equal to γ , and in particular do not depend on the cover class i . We used this distribution because we did not find any better alternative to model values that could be either null or positive and

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

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

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

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

The sign and magnitude of the effects of parameters in the ecological model were analyzed for the SUCC classification and for models used in current indicators (TGR, mTGR4, TA in TGI+TA and TGD in TI+TGD) as well as for the model that turned out to be the best (TGAS). For each parameter in these models we reported the multiplicative coefficient – of the mean fitted value for species richness and of the odds of cumulative probabilities $P(Y > \alpha_i)$ for abundance data – associated with an increase of the ecological parameter of around one standard deviation, i.e. 5 m².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

$b_2 = 0.5$, an initial value of $P(Y > \alpha_i) = 0.5$ (respectively $P(Y > \alpha_i) = 0.1$) would be transformed to $P(Y > \alpha_i) = 0.38$ (respectively $P(Y > \alpha_i) = 0.06$).

Results

The most frequent understory species – found in more than half of the plots – were *Rubus fruticosus*, *Carpinus betulus*, *Quercus robur*, *Lonicera periclymenum*, *Populus tremula** *Populus canescens*, *Tilia cordata*, *Castanea sativa*, *Fraxinus excelsior* for woody species, *Carex pilulifera*, *Convallaria majalis*, *Dryopteris carthusiana*, *Dryopteris filix-mas* and *Luzula pilosa* for herbaceous species, and *Atrichum undulatum*, *Dicranella heteromalla*, *Eurhynchium striatum*, *Eurhynchium stokesii*, *Hypnum cupressiforme*, *Polytrichum formosum* and *Thuidium tamariscium* for bryophyte species. Mean plot richness levels were 10.1 (± 1.8) for bryophytes, 9.1 (± 7.0) for herbaceous species and 9.3 (± 3.2) for woody species.

The Bayesian models converged correctly according to the Rubin and Gelman Rhat quantity and the goodness of fit diagnostics did not show significant departures from the uniform distribution, except for intermediate light bryophyte and shade-tolerant herbaceous species abundance. Observer effects were significant and rather strong for abundance data and insignificant for species richness data. For species richness data for bryophyte and woody species groups, dispersion parameters were below 1 – indicating underdispersion relative to the Poisson distribution; they were mostly above 1 for herbaceous species groups – except for AF herbaceous species (results not shown).

Overall, the best ecological models in terms of DIC were models including one form of tree abundance and tree genus identity (TGAS, TGI+TA for abundance data; Tables 3 to 4 & S1 & S2). Models associated to tree genus richness were less effective than these best models by more

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

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

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

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

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

Discussion

Towards better indicator(s) of understory diversity and abundance

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

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

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

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

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

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

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

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

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

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

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

Statistical comments: negligibility and less than Poisson distributions

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

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

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

Limitations of the present results and associated perspectives

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

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

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

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

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

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

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

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

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

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

Conclusions

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

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

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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</i> <i>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

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

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

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

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>	-9.0	<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

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 m².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						
Acronym	Bryophytes		Herbaceous		Woody	
	AF	AF	PF	NF	AF	PF
	1.01 ⁰⁰	1.18	0.96	0.97	1.05 ⁰	0.98 ⁰
G.Pi	[0.94;1.08]	[1.00;1.38]	[0.67;1.37]	[0.63;1.41]	[0.92;1.21]	[0.88;1.09]
	0.99 ⁰⁰	1.06 ⁰	0.85	0.81	1.06 ⁰	0.89 ^{*,0}
G.Qu	[0.93;1.06]	[0.91;1.22]	[0.62;1.14]	[0.58;1.08]	[0.93;1.20]	[0.81;0.98]
	1.03 ⁰⁰	0.83 ^{**}	0.62 ^{***,-}	0.40 ^{***,-}	0.93 ⁰	0.80 ^{***,-}
G.Un	[0.99;1.07]	[0.75;0.92]	[0.48;0.79]	[0.29;0.53]	[0.85;1.01]	[0.75;0.85]
	1.02 ⁰⁰	0.93 ⁰	0.67 ^{**,-}	0.57 ^{**,-}	0.98 ⁰	0.84 ^{***,-}
G in TGI+TA	[0.97;1.07]	[0.83;1.04]	[0.50;0.88]	[0.40;0.81]	[0.89;1.08]	[0.78;0.92]
	0.97 ⁰⁰	1.01 ⁰	1.02	0.98	1.07 ⁰	1.00 ⁰
TGR	[0.91;1.03]	[0.87;1.17]	[0.73;1.41]	[0.65;1.45]	[0.96;1.19]	[0.90;1.14]
	0.97 ⁰	0.90	0.91	0.57	1.02	0.84
mTGR4	[0.86;1.08]	[0.68;1.19]	[0.42;1.75]	[0.19;1.40]	[0.82;1.31]	[0.67;1.05]
TGD in	1.00 ⁰⁰	1.14	1.24	1.55	0.99 ⁰	1.11
TGI+TGD	[0.94;1.07]	[0.96;1.36]	[0.86;1.79]	[0.98;2.53]	[0.87;1.13]	[0.96;1.27]

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						
TGI+TGD	[0.14;3.87]	[0.09;2.97]	[1.80;53]	[8.0;486]	[2.28;82]	[0.43;17]

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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