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► **To cite this version:**

C. Zilliox, Frédéric Gosselin. Tree species diversity and abundance as indicators of understory diversity in French mountain forests: Variations of the relationship in geographical and ecological space. *Forest Ecology and Management*, 2014, 321, pp.105-116. 10.1016/j.foreco.2013.07.049 . hal-01094414

**HAL Id: hal-01094414**

**<https://hal.science/hal-01094414v1>**

Submitted on 12 Dec 2014

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1 Tree species diversity and abundance as indicators of understory  
2 diversity in French mountain forests: variations of the relationship  
3 in geographical and ecological space

4

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14 Published in Forest Ecology and Management (vol. 321,  
15 pages 105-116, doi: 10.1016/j.foreco.2013.07.049)

16

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Available at:

18 <http://www.sciencedirect.com/science/article/pii/S03781>

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12713005070

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21 **Abstract.** Trees are one of the main components of forest ecosystems; they modify resource  
22 levels (light, nutrients, water) that affect understory vegetation composition and diversity.  
23 Tree species diversity is used as a biodiversity indicator in various European and French  
24 monitoring schemes for sustainable forest management. Moreover, tree species basal area has  
25 been found to better indicate floristic biodiversity than tree species richness or diversity.  
26 Herein we empirically check this finding by analyzing data from mountain spruce-fir forests  
27 in France with Bayesian statistical models. We insist on the magnitude of the relationship and  
28 its variation in geographical and ecological space. Our results indicate that both tree species  
29 abundance (based on cover or basal area) and tree species richness and dominance are good  
30 indicators of some parts of understory vascular plant species richness. The effect of  
31 dendrometric indicators on floristic biodiversity varied among ecological groups and along  
32 ecological gradients such as aspect, soil acidity, region and altitude. As a result, plots with  
33 north-facing and south-facing slopes exhibited opposite relationships of species richness with  
34 tree species abundance, and so did plots located on acidic and basic sites. We discuss these  
35 results in light of other empirical results relating positive interactions between species and  
36 abiotic stress. Our study supports evaluating biodiversity indicators to determine when they  
37 actually have non-negligible relationships with biodiversity, i.e. for which ecological groups  
38 and in which ecological contexts.

39 **Keywords.** Biodiversity; indicator; monitoring; ecological gradient; vegetation; vascular  
40 plants

41 1. Introduction  
42

43 Biodiversity conservation is one of the main objectives stated in the international  
44 Convention on Biological Diversity and in associated national strategies. Some of these  
45 strategies are sectorial, i.e. they aim to improve biodiversity assessment in specific fields of  
46 human activity. Forestry is no exception and biodiversity has been included as one of the six  
47 criteria for sustainable forest management in Europe (Ministerial Conference on the  
48 Protection of Forests in Europe, 2011). A dozen or so biodiversity indicators have been  
49 defined, which vary somewhat among countries. By indicator, we mean any measurable  
50 correlate to the particular components of biodiversity being studied (Duelli and Obrist, 2003).  
51 Though the creation of such indicators can be a significant step towards better monitoring and  
52 conservation of our forest resources, their present form is incomplete. They do not explicitly  
53 target specific components of forest biodiversity in specific ecological conditions where the  
54 indicator/target component relationship has been established as valid. Furthermore, they do  
55 not give information about the magnitude and direction of their relationship with biodiversity  
56 (Lindenmayer et al., 2000, Duelli and Obrist, 2003, Lindenmayer and Likens, 2011). In other  
57 words, we lack information regarding which specific component of forest biodiversity these  
58 indicators can effectively help monitor and in which ecological conditions.

59 Among the many management choices foresters have to make, the nature of the tree  
60 species is a most important one. Tree species identity, abundance and diversity can determine  
61 levels of resources available to understory vegetation and influence their spatial variation  
62 (Barbier et al., 2008), and can thus shape understory diversity and abundance (Barbier et al.,  
63 2009a). This may explain why tree species richness and dominance are used as biodiversity  
64 indicators in Europe and France (Ministerial Conference on the Protection of Forests in  
65 Europe, 2011, Ministère de l'Agriculture et de la Pêche, 2011). Herein, we define  
66 “dominance” as the relative abundance – in terms of cover or basal area – of the most  
67 abundant species. Yet, as with many indicators, tree species richness and dominance are not  
68 necessarily indicative of all components of biodiversity. Furthermore, these indicators might  
69 show influences on biodiversity that work in unexpected directions. Also, other stand-level  
70 indicators related to tree species might be better indicators than richness or dominance for  
71 some components of floristic biodiversity (Barbier et al., 2009a). Finally, as mentioned by  
72 Glenn-Lewin (1977), these indicators might correlate with some components of biodiversity  
73 that is in fact due to responses to site type variations – and not to forest management choices.  
74 Indeed, when controlling for site type in some lowland French forests, Barbier et al. (2009a)

75 found that indicators related to tree species richness and dominance had either negligible  
76 effects on floristic biodiversity or effects that were too noisy to conclude; in some cases, the  
77 direction of the effect was reversed compared to what was expected based on intuition. In  
78 contrast, indicators related to tree species abundance modeled variations in biodiversity more  
79 accurately and showed stronger, non-negligible effects.

80 Our present study can be seen as a follow-up to the study by Barbier et al. (2009a) on the  
81 empirical comparison through statistical models of various stand-level indicators of  
82 understory biodiversity related to tree species abundance, composition and diversity. Our  
83 work is therefore included in the field of empirical studies, which are a vital part to ecology as  
84 well as to any other science (e.g. Rigler 1982, Weiner 1995). We chose to work with vascular  
85 plants for several reasons: first, because extensive data were available; second, because  
86 vascular plants are a relatively diversified group and one that has an important functional role  
87 in forest ecosystems; third, because vascular plants are a well-known taxonomic group, that  
88 allow to define a priori ecologically more homogenous groups of species. Indeed, our  
89 response variable was the species richness of certain ecological groups of vascular plants.

90 Our first objective was to verify in mountain spruce-fir forests the results Barbier et al.  
91 (2009a) found for deciduous lowland forests: i.e. that indicators based on tree species  
92 abundance (quantified by crown cover or basal area) would be better indicators of understory  
93 biodiversity than richness or dominance.

94 Our second objective was to study the variation of the relationship between dendrometric  
95 indicators and biodiversity along various ecological gradients. Our approach is based on a  
96 comparison of the results of Barbier et al. (2009a) with those of Barbier (2007): although the  
97 qualitative results in Barbier (2007) were similar to those of Barbier et al. (2009a), the  
98 magnitude of the relationships was lower. This discrepancy could have resulted from the  
99 inherent instability of the relationship according to the ecological context. Indeed, the 2009  
100 study was carried out in a constant site type in one region with a rather limited variation in  
101 soil pH, whereas in 2007, there were no such controls. If relationships vary with ecological  
102 context or region, this could explain the lower magnitude of the effects Barbier found in 2007.  
103 We therefore had a second prediction in this study that the relationship between dendrometric  
104 indicators and biodiversity would depend on the position along various ecological gradients.  
105 This prediction was inspired firstly by general principles (e.g. Biggs et al., 2009) that point in  
106 this direction: most ecological relationships are not likely to be general across all ecological  
107 conditions but instead should depend on the ecological context. Secondly, it has been shown  
108 that relations among vegetation strata or plant species vary along different ecological

109 gradients (Callaway et al., 2002, Michalet et al., 2002). Thirdly, the indicators that we study  
110 herein are what Austin and Smith (1989) called "indirect gradients", where the variable (such  
111 as basal area, for example) affects the plants through other variables which have a direct  
112 physiological effect on them. In the case of basal area (and other measures of tree abundance)  
113 there is some prior knowledge that it influences both the level of transmitted light (Brown and  
114 Parker, 1994, Sonohat et al. 2004) and the proportion of precipitation that reaches the ground  
115 (Figure 1 in Barbier et al. 2009b). Barbier et al. (2008) also reviewed knowledge on the  
116 impact of dominant tree species on different ecological mechanisms important for plants.  
117 These results show that dendrometric indicators are at most indirect gradients for floristic  
118 diversity. It is logical expect that the effect of dendrometric indicators on biodiversity should  
119 vary with the position along various ecological gradients, since (i) the relationship between  
120 direct gradients and floristic diversity can vary in shape – linear, Gaussian, asymmetric,  
121 sigmoidal...; (ii) floristic diversity is likely to have limiting factors that depend on the  
122 ecological context and (iii) dendrometric indicators influence several of these mechanisms  
123 simultaneously. However, the relationship between tree species abundance and floristic  
124 biodiversity along ecological gradients is very much related to the stress-gradient hypothesis  
125 (e.g. Bertness and Callaway, 1994, Callaway et al., 2002; but see Maestre et al., 2009) which  
126 states that positive interactions between species (or between the abundance of one species and  
127 the biodiversity of one ecological group) should increase with ecological stress. It should be  
128 recognized that ecological stress is not a precise concept (Maestre et al., 2009), but is  
129 generally interpreted to refer to ecological conditions in which the productivity of a species is  
130 limited by the abiotic environment. The stress-gradient hypothesis not only predicts that  
131 relationships between indicators and biodiversity will vary along ecological gradients, but  
132 might determine in which direction the relationships occur.

133         As in Barbier et al. (2009a), we also placed special emphasis on the magnitude of the  
134 relationship between floristic biodiversity and biodiversity indicators. However, we changed  
135 several parameters: we studied mountain forests rather than lowland forests; we included  
136 much more ecological variation in the data and modeled it explicitly in the statistical models;  
137 and we increased the number of plots.

138

139         To sum up, our objectives were to document how the current list of biodiversity  
140 indicators related to forest management can be improved by specifying for which ecological  
141 groups and in which ecological contexts these indicators have a non-negligible positive or

142 negative statistical relationship with biodiversity – one that cannot be directly attributed to site  
143 type variation

144

## 145 2. Material and methods

### 146 2.1 Study sites

147 The study sites were located in the Alps and Jura great ecological regions (GRECOs;  
148 cf. Figure 1), as defined by the NFI. We used the compiled data from the NFI plots, from 2006  
149 to 2010. The GRECOs in France, which are determined according to topography, climate and  
150 the geological features of the terrain, each contain several sylvo-ecoregions (SER), which are  
151 defined in NFI documentation as the largest geographical zones inside which the factors  
152 determining forest production or forest habitat distribution vary in a homogeneous fashion  
153 with precise values, resulting in an original combination of these factors, i.e. different from  
154 adjacent SERs (Cavaignac, 2009).

155 For the study we regrouped the SERs of our study area according to an external-internal  
156 geographic location of SERs inside the Alps GRECO, with three SERs located in internal  
157 Alps (H22:Northern internal Alps, H41:Southern mid-Alps, H42:Southern internal Alps), two  
158 in external Alps (H21:Northern external Alps, H30: Southern external Alps) and one in pre-  
159 northern Alps (H10: pre-Northern Alps), while Jura was left untouched and contains two  
160 SERs (E10: First plateau of Jura, E20:second plateau and Haut-Jura). These four groups  
161 defined the variable called Region.

162 We focused on tree stands dominated by Norway spruce and silver fir (*Picea abies* and  
163 *Abies alba*). This choice was made because our study was included in a broader project to test  
164 biodiversity indicators for inclusion in the tree growth simulation tool CAPSIS (Dufour-  
165 Kowalski et al., 2012) for spruce/fir stands. For the selected plots, following Vallet et al.  
166 (2011), stands were considered to be pure stands of either species when the basal area of one  
167 species (either spruce or fir) was greater than 80% of the total basal area of the plot. Stands  
168 were considered to be mixed when the basal area of both species combined was greater than  
169 80% of the total basal area of the plot and each of them had a greater basal area than all the  
170 other species combined (excluding spruce and fir).

171 After this initial selection, we removed plots according to two specific criteria.  
172 We first removed winter relevés (when data was collected during December, January or  
173 February) and plots where the operator indicated frozen or snow-covered soil to avoid floristic  
174 inventories performed under non-adequate weather conditions. A total of 32 plots were thus  
175 removed from the dataset.

176 We then removed the NFI "simplified plots", which are plots that are not fully-sized,  
177 generally because of a forest edge, road, or other element which reduces the size of the plot.  
178 Simplified plots could not be used in the study because there is no indication as to how the  
179 simplification was performed, and this prevented further calculations. Plots with reduced sizes  
180 were removed, based on the values of tree weight (cf. below), which changes when the plot is  
181 downsized. We ended up with a total of 475 plots.

182

## 183 2.2 Data collection

### 184 2.2.1 Dendrometric data

185 Dendrometric data were taken from NFI relevés. They are summarized in Table SM1  
186 (in the Supplementary Material). The definitions of the variables presented in Table SM1 are  
187 listed below. C is the total tree crown cover on the plot and is the sum of all individual tree  
188 covers on the plot, each cover being defined as the ratio of the total surface area of the tree  
189 crown's vertical projection to the total plot surface area (0.2 ha). C.spruce, C.fir, C.othersp are  
190 the tree crown covers for (respectively) Norway spruce, silver fir and other species. They are  
191 calculated from the same cover data, taking tree species into account. Cover was visually  
192 estimated by NFI observers.

193 G is the total basal area on the plot. It is calculated with diameter at breast height (dbh)  
194 and a weighting coefficient, provided by the NFI. Tree censusing is typically done by  
195 counting all the trees in a given dbh – actually circumference – interval in three circular  
196 subplots centered on the plot centre: a 6m-radius subplot for small trees (from 23.5 to 70.5 cm  
197 in circumference), 9m-radius subplot for medium trees (from 70.5 to 117.5cm in  
198 circumference) and 15m-radius subplot for big trees (more than 117.5 cm in circumference).  
199 Floristic counts were done at a 15m-radius subplot. For each tree a weight was thus calculated  
200 according to the prospection area corresponding to its dbh class. A change in weight could  
201 occur if the plot size is reduced (for example, if a nearby forest path or any other obstacle  
202 precludes establishing a fully-sized plot in the field), but also if there are too many trees of the  
203 same species inside the same diameter class. G.spruce, G.fir, G.othersp are the basal areas for  
204 (respectively) Norway spruce, silver fir and other species. They are calculated from the same  
205 data, taking tree species into account. G.BT, G.VBT, G.MT, G.ST are the basal areas for  
206 (respectively) large trees (trees with dbh between 42.5 and 67.5 cm), very large trees (dbh  
207 bigger than 67.5 cm), medium trees (dbh between 17.5 and 42.5 cm), and small trees (dbh  
208 smaller than 17.5 cm).



209 rs is tree species richness based on basal area counts.

210 Dominance.C is the tree cover of the most abundant tree species divided by the total tree  
211 cover on the plot and Dominance.G is the basal area percentage of the most abundant tree  
212 species.

213 Aspect is the magnetic azimuth of the plot's largest slope, measured with an accuracy of  
214  $\pm 5$  degrees, and only in non-complex topographical situations, as defined by the NFI protocol.  
215 Elevation is the elevation reported by the NFI for the plot (in m). Reaction is the estimation of  
216 soil pH derived from the mean of the Ellenberg indicator values for the plants on the plot. The  
217 mean function we used was weighted by the abundance of each plant on the plot, based on  
218 abundance-dominance with the Braun-Blanquet method as recorded by the NFI floristic  
219 relevé and then transformed into cover as in Barbier et al. (2009a). It follows the same order  
220 as pH: a low reaction means that the plant is adapted to acidic soils, and a higher value  
221 indicates adaptation to basic soils (Ellenberg et al., 1992).

222

### 223 2.2.2 Floristic data

224 The NFI relevés contain information relative to understory species identification and  
225 abundance on each plot. Species identification data were coupled with autecological data from  
226 Philippe Julve's work on French vegetation and flora ([http://philippe.julve.pagesperso-  
227 orange.fr/](http://philippe.julve.pagesperso-orange.fr/)). When faced with duplicates inside the database (for example different ecotypes of  
228 the same species), the one most fitted to our study was retained. The data regarding species  
229 abundance was also used but will not be presented in this paper, as work is still in progress.

230 Our analysis focused on the species richness of ecological groups rather than on  
231 floristic diversity as a whole, based on the considerations in e.g. Barbier et al. (2009a) and  
232 Gosselin (2012). Each ecological classification first separated woody and non-woody species.  
233 It secondly separated species based on Ellenberg values (light and temperature; Ellenberg et  
234 al., 1992) and forest succession association (mature forest species, peri-forest species and  
235 non-forest species; as in Barbier et al. 2009a). The number of species in the intersection of  
236 these two types of groups (based on life form, then on an ecological classification) gave the  
237 species richness of the ecological groups. The use of successional status was motivated by the  
238 wide variety of studies that have chosen to work with this classification (Kwiatkowska, 1994;  
239 Kwiatkowska et al. 1997; Spyreas and Matthews, 2006; Barbier et al. 2009a), while light and  
240 temperature requirements were chosen because they could be important factors to take into

241 consideration in order to explain the variations in biodiversity in response to dendrometric  
242 indicators.

243         The Ellenberg values estimated by Julve were based on the ecological requirements of  
244 German flora, and extrapolated to France. For example, in the original classification from 1 to  
245 9, plants range from extreme shade tolerance to extreme heliophilous behavior. After  
246 regrouping the values, values 1 to 3 grouped the shade-tolerant species, 4 to 6 the intermediate  
247 species, and 7 to 9 the heliophilous ones. The temperature scale follows the same pattern,  
248 from cold-adapted to warm-adapted species. The statistical summary for the species richness  
249 of these ecological groups can be found in Table SM2.

250

### 251 2.2.3 Climatic data

252         The meteorological data, obtained from MeteoFrance, included maximum, minimum  
253 and mean temperatures for each month and the whole year, as well as mean precipitation for  
254 each month and the whole year, for the 2005-2010 period. They were extracted based on the  
255 approximate position of the plot given by the NFI, which corresponds to the coordinates of  
256 the node to which the plot is linked – the plot is at a maximum of 640m from the node. The  
257 data required two corrections: a correction based on topography and exposure, and another  
258 one based on elevation. As in Michalet et al. (2002), the results from Douguédroit and de  
259 Saintignon (1970) were applied to a correction of the decrease in temperature with elevation,  
260 with the lapse rates taking into account exposure and topographical situation. The lapse rates,  
261 i.e. the rate at which temperature linearly decreases with increasing elevation, were calculated  
262 for minimum and maximum temperatures in January and July for valley bottoms and south-  
263 facing slopes. By taking means between these extreme situations, we determined the rate to  
264 use for each situation in order to obtain our temperature data. In addition to these climatic  
265 data, global solar radiation (solrad), soil water capacity (SWC) and potential  
266 evapotranspiration (ETP) were calculated as explained in the Supplementary Material.  
267 The values of these climatic variables are summarized in Table SM1. Tmin is the temperature  
268 for January and potential evapotranspiration, precipitation (PPT) and solar radiation were  
269 summed over the growing season, from May to September.

270

## 271 2.3 Data analysis

### 272 2.3.1 Statistical models

273         The premise of the study was a reflection on the general shape of the statistical models  
274 used to relate biodiversity to dendrometric indicators. Our first challenge was to include an

275 ecological aspect in the statistical model used to estimate the relationship between  
276 biodiversity and ecological variables - excluding dendrometric indicators. By explicitly  
277 modeling the site type variation within the statistical biodiversity model, the models may  
278 separate the effect of abiotic variables from the effect of the dendrometric indicator on  
279 biodiversity. In order to achieve this goal, we chose the abiotic variables according to Austin  
280 and Van Nielb (2011): light above the canopy, temperature, reaction, precipitation and  
281 topography were included in the model. We did not include CO<sub>2</sub> levels, disturbance or biota  
282 variables, because CO<sub>2</sub> was assumed to be constant for the time span and spatial scale  
283 considered in the study, and both biota and disturbance are modeled through the dendrometric  
284 indicators.

285 The dendrometric indicators selected were mostly inspired from Barbier et al. (2009a), with  
286 the general goal of comparing tree species richness and dominance indicators with indicators  
287 based on tree abundance (cf. Table 1). We added two points to this general objective:  
288 whenever possible, we compared models based on cover data to similar models based on  
289 basal area data (see below); and we added models which included the basal area of different  
290 diameter classes. The latter addition was due to the inclusion of this work in a larger project  
291 on tree stand simulators developed to test silvicultural scenarios which are mainly based on  
292 diameter classes. Finally, we also added the interactions between the dendrometric models  
293 and certain ecological gradients (see below).

294 The effect of both ecological variables and indicators on the species richness of the  
295 different ecological groups was modeled through Bayesian models similar to Generalized  
296 Additive Models (GAMs; Harrell, 2001). Since we were analyzing count data, the models we  
297 used were mostly equivalent to Poisson GAMs, except that the Poisson distribution was  
298 replaced by a more flexible distribution in the Bernoulli/Double Polya mixture-Poisson-  
299 Negative Binomial family – which allows for both under- and over-dispersion relative to the  
300 Poisson distribution (Gosselin, 2011a; Gosselin, Unpublished). This meant that, conditional  
301 on all the covariates, the variance of the model could be smaller or larger than the mean. The  
302 link function was the classical logarithm link function for Poisson GAMs.

303 The ecological variables introduced into the model were: soil pH as indicated by the  
304 Ellenberg values of the understory species (denoted as *reaction*), mean annual temperature  
305 (*T*), growing season precipitation (*PPT*), solar radiation (*solrad*), topography, aspect and  
306 slope. Temperature, reaction, precipitation and radiation were input into the model through an  
307 automatic restricted cubic spline transformation involving four knots, thus requiring the  
308 estimation of three parameters for each variable (Harrell, 2001). This transformation is

309 classical for species distribution models; it allows the function to model a possible non-linear  
310 relationship between the transformed predictor and the explanatory variable.

311 Topography was taken into account through a variable denoted as *topo0* with a 1  
312 value for flat positions and 0 otherwise (see Fig. SM1). This allowed us to model the  
313 difference between flat topographies and the other topographies. Finally, aspect was taken into  
314 account through a cosine function multiplied by a variable related to slope such that the  
315 variable was equal to zero for zero slope (no aspect effect) and equal to 1 for slopes of 45°  
316 and steeper. All these variables were put into the model as a linear combination of the  
317 logarithm of the mean, The effect of the indicators we wanted to test (see Table 1) was added  
318 to this linear combination either alone or in interaction with another ecological variable (see  
319 Table 2). The formula for the logarithm of the mean, using a R-like syntax, was therefore:

320 
$$rsc(scale(reaction),4) + rsc(scale(PPT),4) + rsc(scale(T),4) + rsc(scale(solrad),4) + \dots$$
  
$$\dots + topo0 + I(\sin(pmin(slope, \pi / 4)) * \cos(aspect)) + \text{"Indicator model"}$$

321 where "rsc" is the R function for the restricted cubic spline transformation involving four  
322 knots (Harrell, 2001), "I" is the identity link, "pmin" is the parallel minimum function (giving  
323 the minimum value after comparing the elements of one or more vectors or matrices), "sin"  
324 and "cos" are respectively the sine and cosine trigonometric functions.

325 Another parameter – related to the index of dispersion of the model – was also estimated as a  
326 constant. The priors probability distributions of the fixed effects – i.e. the probability  
327 distributions of the corresponding statistical parameters, before the data is taken into account  
328 – were mostly weakly informative, often with a normal distribution of mean 0 and a standard  
329 deviation of 2 as prior distributions.

330 This model structure was used throughout with variations only in the “Indicator model”,  
331 which we now come to. The indicator models were either the models specified in Table 1 or  
332 the models in Table 1 plus the interaction of this model with one of the ecological variables in  
333 Table 2. As the ecological variable itself was often already present in the model, and to  
334 compare models on similar grounds, the simple ecological effect itself was not included in the  
335 model. The ecological variables investigated either corresponded to geographic regions as  
336 advocated by Biggs et al. (2009), ecological variables related to ecological stress (especially  
337 water stress) as studied by Michalet et al. (2002) and Callaway et al. (2002) (precipitation,  
338 temperature, exposure,...) and soil pH, inspired from Tyler (1989). The aspect model  
339 included a slope component because aspect effect was modulated by the value of the slope.

340 The simple models were then tested on the successional ecological groups  
341 successively to determine for each group which indicators gave the best results. For each  
342 ecological group, we then compared the best indicator model, first without interaction and  
343 then in interaction with the ecological variables in Table 2. We selected four ecological  
344 variables that involved the best models for further analyses (see Results section).

345 The Bayesian models were fitted through an adaptation of the algorithm proposed by Vrugt et  
346 al. (2009) based on four trajectories, and a thinning parameter of 50. The convergence of the  
347 models was checked with the Rubin and Gelman Rhat quantity, below 1.1 (Gelman et al.,  
348 2004). After convergence was reached, we asked each model to estimate 2,000 values of the  
349 parameters.

350 To compare our models with each other, we used a modified version of the DIC –  
351 Deviance Information Criterion (Spiegelhalter et al., 2002) –, as discussed by Celeux et al.  
352 (2006), which consists in calculating the reference Deviance not at the mean of the parameters  
353 but at an estimate of its mode – which here corresponded to the set of parameters leading to  
354 the highest posterior probability. Indeed, the classical version of the DIC yielded incoherent,  
355 unstable results with negative values for the number of parameters, a problem that the mode-  
356 based DIC did not have.

357

### 358 2.3.2 Analysis of model results

359 For each model, the direction and magnitude of the effects of the indicator parameters were  
360 analyzed with the same methods as in Barbier et al. (2009a). For each indicator parameter we  
361 studied the effect on the mean fitted value for species richness of an increase in the ecological  
362 parameter of around one standard deviation. We chose the following increases for the  
363 different parameters: 10 m<sup>2</sup>.ha<sup>-1</sup> for most basal area parameters (5 m<sup>2</sup>.ha<sup>-1</sup> for G.othersp and  
364 G.ST, respectively basal area of species other than fir or spruce and basal area of stems less  
365 than 17.5 cm in dbh), 15% for all tree crown cover parameters, except 7.5% for C.othersp, 1.5  
366 genera for tree species richness and 0.2 for tree species dominance. For each parameter, we  
367 reported the mean value of the log of the multiplier of the mean corresponding to such a  
368 variation, its 95% confidence interval, and the probability of the significance test that the  
369 parameter was null. Levels of statistical significance for parameters were symbolized as  
370 follows: \*\* =  $p < 0.01$  and \* =  $p < 0.05$ . Inspired from Dixon and Pechmann (2005), we also  
371 did an analysis based on equivalence and inequivalence tests to detect negligible effects:  
372 based on Bayesian parameter estimations as in Camp et al. (2008), the aim of this analysis

373 was to identify (i) when the parameter has a high probability of being in an interval, called the  
374 negligible interval, that is a priori considered to represent negligible effects, (ii) when the  
375 parameter had a high probability of being below this interval and (iii) when the parameter had  
376 a high probability of being above it. Two negligible intervals were distinguished: one for  
377 weak negligibility and one for strong negligibility. We denoted by  $0 < b_1 < b_2$  the levels  
378 associated to the two negligible intervals. We used the symbol 0 to describes cases where  $P(-$   
379  $b_2 < \log(\beta) < b_2) \geq 0.95$  and 00 for the more stringent:  $P(-b_1 < \log(\beta) < b_1) \geq 0.95$ . Similarly,  
380 we denoted by "-" cases where  $P(\log(\beta) < -b_1) \geq 0.95$  and "--" cases where  $P(\log(\beta) < -b_2) \geq$   
381  $0.95$ . These cases correspond to non-negligible negative and strongly non-negligible negative  
382 effects, respectively. We had similar notations - "+" and "++" - for the positive side. We chose  
383  $b_1 = 0.1$  and  $b_2 = 0.2$  for species richness data, corresponding respectively to a multiplication  
384 of species richness by  $\exp(0.1) \approx 1.11$  and  $\exp(0.2) \approx 1.22$  at the upper side of the negligible  
385 interval.

386

387 We addressed our two main predictions by using a mixture of analyses based on  
388 models comparison and the analysis of the magnitude of the effects of the models. Our first  
389 prediction was that dendrometric models involving only tree abundance would be more robust  
390 than those with either tree species richness or stand dominance. Our analyses relied on two  
391 forms of evidence, both for dendrometric models without interaction with other ecological  
392 variables and those with interaction either with aspect, altitude, reaction or region, which were  
393 the most active variables among those tested (listed in Table 3; cf. Results section):

394 (i) model comparisons: for each category of dendrometric model (between Total Abundance,  
395 Abundance by tree species, Abundance by diameter class, Tree species richness and Tree  
396 dominance and abundance), either based on crown cover or on basal area, we recorded the  
397 number of times the category of model was the best, the second best, and so on. We also  
398 recorded the mean difference in DIC with the best model, over the 16 ecological groups  
399 studied. A model that had less difference in DIC and a higher rank was interpreted as being a  
400 better model than the others;

401 (ii) magnitude and significance of the effects: for each dendrometric parameter among the  
402 floristic ecological groups, we recorded the number of times it was negative and significant to  
403 the 1% level, positive and significant to the 1% level, judged negligible, negative non  
404 negligible, positive non negligible or without enough information relative to negligibility of  
405 the effect. These parameters were grouped in the same categories as in (i) above, except that

406 we also identified parameters for pure abundance (i.e. total abundance based either on crown  
407 cover or basal area).

408 Our second prediction stated that dendrometric indicators would have relationships  
409 with biodiversity that would depend on the ecological context. To tackle this prediction,  
410 having selected the best four ecological variables (reaction, altitude, exposure and region; cf.  
411 below), we compared the difference in DIC between the best model with interaction and the  
412 best model without interaction. When the DIC value for the model with interaction was lower  
413 by at least 5 DIC units from the model without an interaction, we interpreted this as an  
414 indication of an interaction with the ecological gradient.

415 We then analyzed the magnitude of the effect of the dendrometric parameters on floristic  
416 diversity in different ecological contexts to interpret the direction of this interaction. To do  
417 this, for each dendrometric parameter we listed the ecological groups and ecological contexts  
418 in which the relationship between the dendrometric parameter and the species richness of the  
419 ecological group was judged negative non-negligible or positive non-negligible (cf. above).  
420 For each dendrometric parameter, we also identified the ecological groups that were still  
421 significantly negative non-negligible or positive non-negligible after the multi-comparison  
422 correction proposed by Rice (1989). The estimators were taken at flat positions and at slope =  
423 50% and aspects East or West, South and North aspect for aspect/slope models, and as the  
424  $\text{mean}+1*\text{sd}$  and  $\text{mean}-1*\text{sd}$  for elevation and reaction gradients.

425 To more collectively analyze the dependence of the indicator-biodiversity relationship on the  
426 ecological context, we calculated the mean and standard deviation across ecological groups of  
427 the difference at both ends of the ecological gradient in the mean effect of a typical variation  
428 of the indicator on the log of the mean species richness. The differences taken were the  
429 difference between South and North aspect at slope = 50% for aspect/slope models and as the  
430  $\text{mean}+2*\text{sd}$  and  $\text{mean}-2*\text{sd}$  for elevation and reaction gradients.

431 Finally, we checked the statistical quality of our models by using the new goodness of fit p-  
432 values proposed by Gosselin (2011b), called the sampled posterior p-values. We applied these  
433 p-values on different aspects of normalized residuals (as described in Gosselin, 2011b): their  
434 skewness, their kurtosis – to diagnose the probability distribution used -, their correlation with  
435 the estimated mean – to diagnose general linearity problems – and with the covariates  
436 incorporated in the models (precipitation, solar radiation, reaction, temperature...). To detect  
437 potentially non-monotonous correlations between variables, we used the Hoeffding's D  
438 statistic provided in the Hmisc R package (Harrell, 2001). We applied this method to the best  
439 model of each ecological group. We also checked the multi-collinearity of our variables of

440 interest by calculating the variance inflation factor (VIF) of all the dendrometric variables we  
441 were interested in as a function of all the other variables in the model (Zuur et al., 2010).

442

### 443 3. Results

#### 444 3.1 Choice of model

445 To determine which ecological gradients to include in interactions with our  
446 dendrometric models, the simple models were first tested on the successional ecological  
447 groups to determine which indicators gave the best results (Table SM.7). These indicators  
448 were then run with the ecological variables in interaction as indicated in Table 2. Table SM.8  
449 gives the results of this first comparison. The best models were: the "region:G.D" model for  
450 mature forest and peri-forest herbaceous species, the "region:G.sp" model for non-forest  
451 herbaceous species, the "region:RS" model for mature forest woody species and the  
452 "reaction:G.sp" model for peri-forest woody species. Altogether, the aspect, elevation,  
453 reaction and region variables performed best (see Table SM.8).

454 Furthermore, the goodness-of-fit checks of the best models of each group revealed  
455 some significant departures from the probabilistic hypotheses in the models for more than half  
456 of the ecological groups (9 over 16; Table SM.9). These departures involved the probability  
457 distribution for species richness (4 cases) – indicating a problem in the probability distribution  
458 used for these ecological groups –, the log link function (4 cases) or the relationships with  
459 some ecological variables (8 cases in total) – indicating that more complex relationships  
460 might be warranted for these groups.

461 Finally, regarding multicollinearity, some dendrometric variables in the simple models  
462 had mildly problematic levels of VIF between 2 and 3 for the cover of spruce and fir (C.fir  
463 and C.spruce) and for the total cover and dominance based on cover (C and Dominance.C) in  
464 the Cover dominance model. For the first two, the problem was not strongly exacerbated in  
465 the models with interaction. The other dendrometric variables had non problematic VIF  
466 values below 2 (Zuur et al., 2010).

467

468 3.2 Prediction 1: dendrometric models based on abundance (i.e. basal area and tree cover) are  
469 better than those based on dominance or tree species richness

470 Dendrometric models formulated on abundance data were better models overall than those  
471 based on tree species richness (Table 3 and Tables SM3 to SM6). Indeed, the abundance-  
472 based models (i.e. G.sp and C.sp in Ab.SP and G.D) were the best for one third of the



473 biodiversity ecological groups on average whereas the species richness model (RS) was the  
474 best for at most one sixth of the ecological groups. Furthermore, for the RS model, the mean  
475 difference in DIC from the DIC of the best model ranged from 40% to more than 150% more  
476 than for models based on abundance. Dom models (including Dom.C and Dom.G) involving  
477 both tree species dominance and total tree species abundance were intermediate but rarely  
478 provided the best model.

479 However, analysis of the significance and magnitude of the effects of the parameters in these  
480 different models tempered the above results. Indeed, overall, the parameters in the tree species  
481 richness models had the highest chance of involving a non-negligible relationship, whatever  
482 the context (Table 4). Moreover, this result was not due to abundance parameters involving  
483 more cases where there was not enough information to conclude. Rather the reverse was true.  
484 The result was tempered for statistically significant results: the best variables were those  
485 based on absolute abundance in the tree stand. Furthermore, when only herbaceous floristic  
486 biodiversity was analyzed, leaving aside woody ecological groups, tree species richness  
487 models were slightly surpassed by abundance models, by tree species or by diameter class for  
488 the mean of significant results, although they still involved the most non-negligible  
489 relationships on average (cf. Table 5). Also, for the five dendrometric variables that involved  
490 the greatest number of significant results or the most number of non-negligible results,  
491 dendrometric variables involving abundance data (total abundance, spruce abundance or  
492 abundance of trees less than 17.5cm dbh) appeared among the first (cf. Tables 4 & 5). Tree  
493 species richness was still a good dendrometric variable. Overall, tree species richness had  
494 more positive than negative significant or non-negligible effects for woody floristic ecological  
495 groups, but the reverse was true when the analysis was restricted to herbaceous ecological  
496 groups (compare Tables 4 & 5). Variables related to tree abundance had mostly negative  
497 effects on floristic biodiversity (see Table 4).

498

499 3.3 Prediction 2 : : dendrometric indicators have relationships with biodiversity that depend  
500 on the ecological context:

501 An interaction between dendrometric variables and ecological context was detected for most  
502 of the ecological groups (cf. Table 6). Only two ecological groups (peri-forest herbaceous  
503 species and intermediate light-demanding woody species) had DIC differences of more than -  
504 5 between the best interaction model and the best simple model, while five ecological groups  
505 (non-forest herbaceous species, heliophilous herbaceous species, cold-temperature herbaceous

506 species, mid-temperature woody species and high-temperature woody species) had a DIC  
507 difference of less than -20.

508 Regarding the ecological groups and contexts in which each dendrometric variable was a non-  
509 negligible indicator of biodiversity (cf. Table 7), most ecological groups were indicated in  
510 specific ecological contexts, as hypothesized. Only in a few cases did dendrometric indicators  
511 indicate a non-negligible variation across all the plots analyzed (2 for C.spruce, 1 for G.ST, 1  
512 for G.spruce, 2 for rs and 1 for Dominance.G). Indicators related to tree abundance mostly  
513 negatively impacted non-forest, high-light or low-temperature herbaceous species, mostly in  
514 northern aspects, at lower elevations and in more acidic conditions. We noticed a counter  
515 relationship of a positive non-negligible effect of some tree abundance attributes on south  
516 facing slopes for low-light herbaceous species. We also noticed a positive effect of the basal  
517 area of tree species other than spruce and fir on four ecological groups in the Internal Alps  
518 (results not shown). Spruce cover and basal area as well as the basal area of trees less than  
519 17.5 cm in dbh (G.ST) were the most involved in relationships with biodiversity.

520 The picture was somewhat different for tree species richness indicators: they mostly had  
521 positive non-negligible effects on the species richness of herbaceous and woody forest species  
522 as well as low-temperature woody species. Tree species richness had noticeable negative  
523 effects on some herbaceous species groups, mostly for groups and in ecological conditions for  
524 which there was also a negative impact of tree abundance indicators.

525 In addition, stand dominance based on basal area had a negative effect on low-temperature  
526 woody species in many ecological contexts and on forest herbaceous species in two ecological  
527 contexts.

528

529 Finally, by analyzing the variation across ecological groups of their response to each  
530 dendrometric ecological indicator along ecological gradients (cf. Table 8), we detected  
531 unilateral variations in biodiversity in response to total cover, fir cover and spruce cover along  
532 the reaction and aspect gradients. Slightly less strong results were detected for equivalent  
533 basal area data as well as for the basal area of trees between 17.5 and 42.5 dbh. A slight  
534 reverse trend was found for tree species richness based on cover for the aspect gradient and  
535 for tree species dominance for the reaction gradient. Another, “variational” response, where  
536 there was no strong central trend and considerable variation among ecological groups, was  
537 detected for most cases along the elevation gradient as well as for some other cases along the  
538 aspect and reaction gradients, especially for tree species richness. This means that while some

539 species groups had a response to the indicator that increased rather strongly along the  
540 gradient, other species groups decreased strongly.

541

#### 542 4. Discussion

##### 543 4.1 Identifying the best dendrometric indicators of floristic variables

544 Our first prediction was that models involving tree abundance could account for variations in  
545 floristic species richness better than models involving either tree species richness or  
546 dominance. At the statistical model level, our prediction was met. This was not completely the  
547 case at the individual predictor level, where variables in abundance models were on average  
548 associated with fewer non-negligible effects than tree species richness variables. Finally, the  
549 two best abundance variables, basal area of the smallest diameter class and spruce cover,  
550 competed well with tree species richness in terms of non-negligible or significant results. Our  
551 results are therefore less clear-cut than Barbier et al. (2009a) where the analyses based on  
552 model comparisons and magnitude of the effects clearly converged. Nonetheless, our results  
553 support considering models based on tree abundance as indicators of floristic biodiversity, as  
554 suggested by many previous studies (Moir, 1966, McCune and Antos, 1981, Specht and  
555 Morgan, 1981, Pitkanen, 2000, Brososke et al., 2001, Ohlemüller et al., 2004, Laughlin et al.,  
556 2005, Lindh, 2005, references in Barbier 2009 and Vockenhuber et al., 2011). Our results also  
557 suggest, however, that tree species richness may be a good univariate indicator of biodiversity  
558 for some ecological groups, in accordance with previous results in the literature (Auclair and  
559 Goff, 1971, Hicks, 1980, Ingerpuu et al., 2003, Vockenhuber et al., 2011 and references in  
560 Barbier et al., 2008).

561 We are unsure at this stage why spruce abundance and small diameter tree abundance are  
562 better indicators than the abundance of other tree species or diameter classes. Spruce  
563 abundance performance in our study is all the more surprising that Mitchell and Kirby (1989),  
564 when summarizing the literature, listed spruce and fir as having similar effects on floristic  
565 species composition. This is not what we have found, although we did not analyze species  
566 composition directly nor did we analyze the effect of spruce stand dominance, but rather the  
567 effect of spruce abundance. It should be noted that spruce abundance and small diameter tree  
568 abundance indicated – mostly negatively – partly different ecological groups (peri-forest  
569 herbaceous species for small diameter tree abundance, heliophilous herbaceous species for  
570 spruce abundance).

571 Multivariate models such as ours should be further studied to determine whether they are  
572 better than univariate models of abundance or than univariate models involving the relative  
573 abundance of some tree species, a commonly used variable in forest ecology (Ewald, 2000,  
574 Mölder et al., 2008). We promote using absolute abundance rather than relative abundance  
575 because it is more directly linked with ecological mechanisms, even though it has yet to be  
576 confirmed as a better indicator. In any case, we advise testing abundance-based as well as  
577 diversity-based dendrometric quantities as biodiversity indicators.

578

579 4.2 The relationship between dendrometric indicators and floristic biodiversity depends on the  
580 ecological group and the ecological context

581 Our second prediction was rather general; it stated that the relationship between dendrometric  
582 indicators and floristic biodiversity should depend on the ecological context. This prediction  
583 was inspired firstly by general considerations as well as more specific results that point in this  
584 direction (cf. Introduction section): most ecological relationships are not likely to be general  
585 across all ecological conditions but instead should depend on the ecological context. Our  
586 results partially confirmed our second prediction: the best models always included an  
587 interaction of dendrometric indicators with an ecological gradient (cf. Table 6). The  
588 relationships between individual indicators and the biodiversity of specific ecological groups  
589 were more often non-negligible in certain specific locations (Northern slopes and Jura for  
590 abundance models; Jura, Northern Alps, Internal Alps for RS). However, overall, though the  
591 frequency of non-negligible cases was less frequent in simple models (2.9% of all groups,  
592 3.7% for herbaceous groups only) than in models analyzed in specific ecological contexts  
593 (3.7% of all groups, 5.4% for herbaceous groups only), the differences between these  
594 frequencies were non-significant. This result means that even if we demonstrated the  
595 importance of ecological context in the dendrometric indicator – biodiversity relationship, this  
596 importance is somewhat relative.

597

598 4.3 Analysis of biodiversity relationships with indicators along gradients

599 In addition to studying the relationship between dendrometric indicators and floristic species  
600 richness in specific ecological conditions, we also used a rather novel type of analysis to study  
601 how these relationships vary among species groups along ecological gradients (cf. Table 8).  
602 This analysis allowed us to characterize cases where the indicator/biodiversity relationship

603 was relatively stable across groups along the ecological gradient, but only in relative terms,  
604 i.e. in terms of the differences between the coefficients of the indicators between groups. In  
605 other words, there was a parallel shift of the relationship across groups along the gradient  
606 (bold cases in Table 8). This is similar to a null model in which different ecological groups  
607 respond differentially to an indicator, but with a difference in coefficients that remains  
608 constant along the gradient. This was the case for indicators based on spruce and fir crown  
609 cover measurements along the aspect and reaction gradients. These results could be translated  
610 in ecological terms as a global shift from negative interactions between canopy abundance  
611 and floristic biodiversity to more positive interactions from one side of the gradient to the  
612 other.

613 In other cases, not only was the relative difference between estimators constant along the  
614 gradient, but the estimators themselves were relatively constant in absolute terms. This  
615 indicates that the relationship was stable between the indicator and biodiversity along the  
616 gradient. For example, this was the case for the basal area of very large trees or the crown  
617 cover of trees other than spruce and fir along the elevation gradient.

618 A third interesting case appeared where there was no central tendency in the variation in the  
619 indicator/biodiversity relationship among ecological groups along the gradient but instead a  
620 strong variance among ecological groups along the gradient (*italic cases in Table 8*). This  
621 occurred for most of the indicators along the elevation gradient as well as for some indicators  
622 along the aspect and reaction gradients. In this case, the indicator could very well be related to  
623 biodiversity in some regions of the ecological gradient, but the biodiversity/indicator  
624 relationship was unstable across ecological groups in relative terms along the ecological  
625 gradient.

626

627 4.4 Two contrasted gradients for the relationship between tree abundance indicators and  
628 herbaceous groups: aspect and soil reaction gradients

629 Following other authors, Austin and Van Niela (2011) made the point that species distribution  
630 models should incorporate topographic variables to better predict the future distribution of  
631 species in response to climate change. Our results on floristic biodiversity in forests are along  
632 the same lines but we go a step further: our results indicate that not only should we take into  
633 account topographic information, we should also take into account tree abundance and the  
634 interaction between tree abundance and topographic variables. Our results indicate that denser  
635 tree cover would decrease some floristic stand-level diversity in northern aspects while it

636 would promote other components of floristic diversity in southern aspects. This can be  
637 interpreted in terms of the stress/facilitation hypothesis which states that positive interactions  
638 between species are more likely in more ecologically stressful conditions (Callaway et al.,  
639 2002, Callaway, 1997, Michalet et al., 2002). Indeed, if we had used the Index of Moisture  
640 Availability (IMA) as did Laughlin et al. (2005, based on Batek et al., 1999), our aspect  
641 gradient would have been transformed into a water stress gradient since the IMA predicts  
642 greater water stress on steep south-facing slopes. However, other mechanisms may become  
643 limiting at certain points along the aspect gradient (e.g. light on northern aspects when tree  
644 abundance is high and light levels are reduced). Therefore, we should not too hastily explain  
645 the effect of such an indirect ecological gradient, in our case aspect, by a unique more direct  
646 ecological gradient (see also Soliveres et al., 2011).

647 Michalet et al. (2002) observed that floristic species composition differed in fir and spruce  
648 stands in the French Alps on southern aspects but not on northern aspects. This seems to be a  
649 result qualitatively similar to ours in that it indicates an interaction of tree species effect on  
650 biodiversity along the aspect gradient. However, in our study, the species richness response of  
651 the ecological groups to fir abundance did not strongly differ from their response to spruce  
652 abundance along the aspect gradient. Therefore, our results are not completely in agreement  
653 with those of Michalet et al. (2002). One difference between Michalet et al. (2002)'s study  
654 and ours is that we investigated the impact of tree species abundance, and not tree species  
655 dominance in the stand. Also, while Michalet et al. studied species composition, we analyzed  
656 the species richness of ecological groups, which reflects presence-absence species  
657 composition only if the species inside each ecological group have homogeneous ecological  
658 behaviors.

659         Similar observations were made on the soil reaction gradient – indicative of soil pH.  
660 Here too, there was an opposite effect at each end of the gradient. The effects of tree  
661 abundance on the species richness of many ecological groups were mostly negative in more  
662 acidic conditions, while they were more positive in less acidic conditions (cf. Table 8 & Tables  
663 SM.35 to SM.40). Ecologically interpreting this case in terms of stress is more difficult  
664 because soil pH should indicate stress at both ends of the gradient, where two different  
665 resources are involved (water and nutrients; Maestre et al., 2009). This should result in  
666 positive effects of tree abundance at both ends of the gradient, unless the stress-gradient  
667 hypothesis is refined as indicated by Maestre et al. (2009). Still our results appear to be in the  
668 opposite direction to those of Tyler (1989), who documented a more negative effect of tree  
669 crown cover on floristic diversity in less acidic conditions than in more acidic conditions.

670 Similarly, we did not confirm the stress-facilitation hypothesis along the altitudinal gradient as  
671 did Callaway et al. (2002) (cf. Table 8 & Tables SM.28 to SM.33). Our results therefore  
672 indicate that the “classic” stress-facilitation hypothesis appears on some gradients (here the  
673 aspect gradient) but not on others (elevation and reaction) for the species richness of  
674 ecological groups. This finding must still be verified through the analysis of the ecological  
675 group abundance and species abundance.

676

#### 677 4.5 Implications for forest management and biodiversity indicators

678 Of course, as for many observational ecological results, our results should be checked with  
679 other observational data, other methods of analysis and with experimental data before they  
680 can be applied with confidence in management. For example, we did not integrate all the  
681 interesting ecological groups nor did we analyze abundance data. Our study was also limited  
682 because we considered only one broad taxonomic group (understory vascular plant), which is  
683 not necessarily indicative of all forest biodiversity. Work should be pursued in these directions  
684 and our results should therefore not be unduly generalized.

685 Should our results be confirmed, we could say that variables such as spruce abundance, small  
686 diameter tree basal area and tree species richness have a non-negligible relationship with the  
687 species richness of relatively numerous floristic ecological groups. The relationships we  
688 found were mostly negative for spruce abundance and small diameter tree abundance but can  
689 be both negative and positive for tree species richness. Secondly, some of the abundance  
690 parameters had interactions with some of the ecological gradients that were in the same  
691 direction for the different ecological groups. This resulted, for example, in effects that  
692 globally changed from negative to positive from northern aspects to southern aspects  
693 (respectively, from acidic conditions to less acidic conditions) for the abundance of spruce  
694 trees (respectively, spruce basal area and cover, fir cover, and basal area of big trees). This  
695 means that if floristic biodiversity is the objective, managers should apply opposite guidelines  
696 in these contrasted ecological conditions.

697

698 Our results support our initial prediction (cf. also Barbier et al., 2008, Barbier et al., 2009a)  
699 which states that biodiversity indicators only reflect a part of the biodiversity in specific  
700 ecological conditions. Our work therefore promotes evaluating biodiversity indicators to  
701 specify in which ecological contexts and for which component of biodiversity the indicator  
702 has a non-negligible relationship and whether the relationship is positive or negative.

703

704 Acknowledgements. This work was supported by the French Ministry of Agriculture through  
705 grant n° E 23/2010 and FP7-KBBE project "ARANGE" (n° 289437). We thank Benoît  
706 Courbaud, Thomas Cordonnier and Valentine Lafond for comments on dendrometric  
707 indicators for silvicultural models. Patrick Vallet and Maude Toigo provided useful help on  
708 the NFI database. We thank Vincent Boulanger (ONF) and two anonymous reviewers for their  
709 help in improving the manuscript. We thank Vicki Moore for correcting the English.

710

711

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865 Zuur, Alain F., Elena N. Ieno and Chris S. Elphick, 2010. A protocol for data exploration to  
866 avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3-14.

867 Table 1. Dendrometric variables used in the dendrometric indicator models without  
 868 interaction with ecological gradients

Model	Variable content of the model in R syntax	Model symbol
Total cover	~C	C
Total basal area	~G	G
Cover per tree species	~C.spruce + C.fir + C.othersp	C.sp
Basal area per tree species	~G.spruce + G.fir + G.othersp	G.sp
Basal area per diameter class	~G.BT + G.VBT + G.MT + G.ST	G.D
Tree species richness	~rs	RS
Cover dominance	~Dominance.C + C	Dom.C
Basal area dominance	~Dominance.G + G	Dom.G
Null model	~1	

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873 Table 2. Shape of the dendrometric indicator models with interactions with ecological  
 874 gradients. The “indicator model” is one of the models in Table 1.

Ecological gradient involved in the interaction	Variable content of the model in R syntax
Region (categorical variable with four levels; cf. text)	~"Indicator model"+ "Indicator model":Region ~"Indicator model"+ ...
Aspect (including slope)	... "Indicator model":((1-topo0)*toposimple*slope*2/π+... ... (1-topo0)* toposimple*slope*2/π*cos(aspect))
Reaction	~"Indicator model"+ "Indicator model":(Reaction)
Elevation	~"Indicator model"+ "Indicator model":(Elevation)
ETP	~"Indicator model"+ "Indicator model":(ETP)
SWC	~"Indicator model"+ "Indicator model":(SWC)
Tmin	~"Indicator model"+ "Indicator model":(Tmin)
PPT	~"Indicator model"+ "Indicator model":(PPT)

875 ETP stands for evapotranspiration, SWC for soil water content and ppt for precipitations, and toposimple equals one is there  
 876 is a value for aspect and slope and 0 otherwise (in the case of complex topographic conditions)  
 877

878 Table 3. Number of times – over the 16 ecological groups – that each group of models was  
 879 ranked first, second, third or fourth compared to the other groups in terms of DIC comparison  
 880 for the no-interaction models. For the two groups that included two models (Ab.SP and Dom),  
 881 the best of the two models was considered. The last line gives the mean DIC difference  
 882 between the best model in the category and the best model in total: the largest the difference,  
 883 the furthest the model from the best model in total.

Rank	Ab.SP	G.D	Dom	RS
First	6	6	2	2
Second	3	3	7	3
Third	3	4	7	2
Fourth	4	3	0	9
Mean DIC difference	10.18	8.653	12.73	18.77

884 Ab.SP stands for both C.sp and G.sp models, and Dom stands for both Dom.C and Dom.G models.  
 885



886 Table 4. (A). Mean over the dendrometric variables in the abundance or RS or dominance  
 887 models of the number of cases in each category of effect (classified either according to the  
 888 negligibility of the effect or its 1% significance: cf. section 2.3.2 “Analysis of model results”)  
 889 over the 16 ecological groups and over the 15 cases analyzed in Tables SM 10 to 40. (B)  
 890 Same information for the 5 dendrometric variables with the most significant relationships  
 891 (corresponding to the sum of the last two lines). (C) Same information for the 5 dendrometric  
 892 variables with the most non-negligible relationships (corresponding to the sum of lines 2 and  
 893 3).

894

**A**

Level of significance	Ab.Tot	Ab.SP	G.D	RS	Dom
negligible	235,5	198,33	199	164,5	211
negative non-neg	8	7,67	5,25	6,5	5,5
positive non-neg	0,5	1,17	0	13,5	0
no info negligible	0,5	33,83	36,25	56	23,5
positive significant	18,5	16,5	3,75	60,5	2
negative significant	64,5	43,33	47	12,5	58,5

**B**

Level of significance	G.spruce	G.ST	C.spruce	G	C
negligible	195	146	209	237	234
negative non-neg	20	13	20	7	9
positive non-neg	1	0	1	0	1
no info negligible	26	81	12	0	1
positive significant	20	1	25	8	29
negative significant	88	97	71	76	53

**C**

Level of significance	RS	G.spruce	C.spruce	G.ST	Dominance.G
negligible	147	195	209	146	119
negative non-neg	13	20	20	13	6
positive non-neg	16	1	1	0	0
no info negligible	65	26	12	81	19
positive significant	51	20	25	1	1
negative significant	23	88	71	97	31

895 Ab.SP corresponds to C.sp and G.sp models, and Ab.Tot to C and G models.

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902 Table 5. (A). Mean over the dendrometric variables in the abundance or RS or dominance  
 903 models of the number of cases in each category of effect (classified either according to the  
 904 negligibility of the effect or its 1% significance: cf. section 2.3.2 “Analysis of model results”)  
 905 over the 9 herbaceous ecological groups and over the 15 cases analyzed in Tables SM 7 to 37.  
 906 (B) Same information for the 5 dendrometric variables with the most significant relationships  
 907 (corresponding to the sum of the last two lines). (C) Same information for the 5 dendrometric  
 908 variables with the most non-negligible relationships (corresponding to the sum of lines 2 and  
 909 3).

910

**A**

Level of significance	Ab.Tot	Ab.SP	G.D	RS	Dom
negligible	130,5	106,83	107	89,5	123
negative non-neg	8	7,33	5	6,5	2
positive non-neg	0,5	0,67	0	5,5	0
no info negligible	0,5	21,17	23,5	33,5	10
positive significant	17	10,67	3,25	24,5	2
negative significant	47,5	28	36,25	12,5	29

**B**

Level of significance	G.ST	C.spruce	C	G.spruce	G
negligible	70	108	129	96	132
negative non-neg	12	20	9	19	7
positive non-neg	0	1	1	1	0
no info negligible	53	8	1	21	0
positive significant	0	24	26	20	8
negative significant	79	54	47	49	48

**C**

Level of significance	C.spruce	G.spruce	RS	G.ST	C
negligible	108	96	75	70	129
negative non-neg	20	19	13	12	9
positive non-neg	1	1	5	0	1
no info negligible	8	21	42	53	1
positive significant	24	20	11	0	26
negative significant	54	49	23	79	47

911 Ab.SP corresponds to C.sp and G.sp models, and Ab.Tot to C and G models.

912

913 Table 6. DIC difference between the best interaction model and the best model without  
 914 interaction, for each ecological group, together with the identity of the best indicator model  
 915 and ecological gradient involved in the best interaction model.

Ecological group	$\Delta$ DIC	Type of model	Type of gradient
h.MF	-9.36	G.D	reaction
h.PF	-1.5	G.D	aspect
H.NF	-38.64	C	altitude
w.MF	-7.83	C	reaction
w.PF	-10.91	Dom.G	altitude
h.HL	-29.07	C	altitude
h.IL	-4.36	G.D	aspect
h.LL	-6.31	C	reaction
w.HL	-16	C.sp	reaction
w.IL	-8.02	Dom.G	altitude
h.HT	-14.98	Dom.G	region
h.IT	-8.25	G.D	aspect
h.LT	-40.58	C.sp	altitude
w.HT	-7.2	G.sp	reaction
w.IT	-29.14	Dom.G	altitude
w.LT	-28.93	Dom.G	altitude

916 h. and w. respectively stand for herbaceous and woody species; MF, NF and PF for mature forest, non-forest and peri-forest  
 917 species; HL, IL and LL for high-light, intermediate-light and low-light species; HT, IT and LT for high-temperature,  
 918 intermediate-temperature and low-temperature species. The names of the gradients refer to the models defined in Table 2.  
 919

920

921 Table 7. List of the cases where each dendrometric variable in the models in Table 1 had a non-negligible effect on the species richness of an  
 922 ecological group in general or in a given environmental context (with respect to reaction, aspect or elevation). We here distinguish negative and  
 923 positive non negligible cases for the Cover of trees (C) and the tree species richness (RS) and indicate the mean estimate and 95% credibility  
 924 interval for the natural logarithm of the multiplicative effect on mean species richness of a non-negligible increase in the dendrometric parameter.  
 925 The lines in bold indicate the ecological groups and ecological contexts that were still significantly negative non-negligible or positive non-  
 926 negligible after the multi-comparison correction proposed by Rice (1989), at the level of each dendrometric parameter. See Tables SM.10 and  
 927 SM.11 to SM.41 for further results.

928

Variable in the model	Negative non-negligible effects	Positive non-negligible effects
C	h.HL at slope=0.5 & E/W aspect	h.LL at slope=0.5 & S aspect
		0.177 [0.0991; 0.256]
	h.NF at slope=0.5 & N aspect	
		-0.154 [-0.205; -0.102]
	h.HL at slope=0.5 & N aspect	
		-0.202 [-0.263; -0.142]
	h.HL at Reaction=5	
		-0.144 [-0.179; -0.109]
	h.NF at Reaction=4.5	
	-0.16 [-0.209; -0.111]	
<b>h.HL at Reaction=4.5</b>		
	-0.201 [-0.255; -0.147]	
h.LT at Reaction=4.5		
	-0.147 [-0.199; -0.097]	
h.HL at Elevation=770m		
	-0.172 [-0.215; -0.132]	
rs	h.HL	w.LT
		0.213 [0.0773; 0.348]
	h.HL at slope=0.5 & E/W aspect	h.MF on flat terrain
		0.182 [0.0988; 0.263]
	h.NF at slope=0.5 & N aspect	w.MF at slope=0.5 & E/W aspect
		0.149 [0.0993; 0.207]
h.HL at slope=0.5 & N aspect	w.LT at slope=0.5 & N aspect	
	0.403 [0.118; 0.668]	
h.HL at Reaction=5	h.MF at Reaction=5.5	
	0.211 [0.122; 0.307]	
	-0.222 [-0.32; -0.12]	

h.HL at Reaction=4.5		w.MF at Reaction=4.5	
	-0.253 [-0.402; -0.104]		0.173 [0.0972; 0.253]
h.HL at Elevation=1120m		w.LT at Reaction=4.5	
	-0.229 [-0.325; -0.13]		0.308 [0.116; 0.513]
<b>h.NF at Elevation=770m</b>		<b>w.LT at Elevation=1460m</b>	
	-0.317 [-0.425; -0.22]		0.405 [0.256; 0.561]
<b>h.HL at Elevation=770m</b>		h.MF at Elevation=770m	
	-0.379 [-0.511; -0.255]		0.179 [0.109; 0.249]
h.LT at Elevation=770m		w.MF at Elevation=770m	
	-0.249 [-0.356; -0.132]		0.168 [0.117; 0.22]

929 h. and w. respectively stand for herbaceous and woody species; MF, NF and PF for mature forest, non-forest and peri-forest species; HL, IL and LL for high-light, intermediate-light and low-light  
930 species; HT and LT for high-temperature and low-temperature species. We here considered the simple models as well as the Aspect, Altitude and Reaction models defined in Table 2. We recall  
931 that a positive non-negligible effect means that there is a probability of 0.95 that the effect of adding a “non-negligible” variation of a given dendrometric parameter results in at least an  
932  $\exp(0.1)$  multiplication of the mean of species richness. We chose the following “non-negligible” increases for the different parameters: 15% for tree crown cover parameters, and 1.5 genera for  
933 tree species richness.  
934

935 Table 8. Mean (Standard deviation) across 16 ecological groups of the difference of the mean  
 936 log response of species richness to a substantive variation in the indicator between both ends  
 937 of each gradient. We put in italics the cases where the standard deviation is above 0.1 –  
 938 indicating a strong variation in this difference among groups – and in bold those for which the  
 939 absolute value of the mean is above 0.1 – indicating a strong mean variation that is shared by  
 940 the groups. Substantial variations of indicators are the same as those mentioned in Table 7.

Variable	N-S aspect	+2 reaction	+1380m elevation
C	0.1 (0.05)	<b>0.19 (0.08)</b>	<i>0.04 (0.13)</i>
C.fir	<b>0.11 (0.05)</b>	<b>0.26 (0.09)</b>	<i>0.04 (0.15)</i>
C.spruce	<b>0.17 (0.1)</b>	<b>0.21 (0.06)</b>	<i>0.05 (0.12)</i>
C.othersp	-0.03 (0.08)	0.05 (0.09)	0 (0.06)
G.BT	0.04 (0.06)	<b>0.14 (0.13)</b>	<i>0.03 (0.13)</i>
G.VBT	0.04 (0.1)	0.07 (0.09)	0.02 (0.05)
G.MT	0.1 (0.08)	<b>0.12 (0.1)</b>	<i>0.05 (0.18)</i>
G.ST	<b>0.12 (0.18)</b>	0.07 (0.1)	-0.03 (0.09)
G.fir	0.05 (0.05)	<b>0.11 (0.04)</b>	<i>0.02 (0.12)</i>
G.spruce	<b>0.14 (0.15)</b>	<b>0.13 (0.08)</b>	<i>0.04 (0.17)</i>
G.othersp	<i>-0.04 (0.17)</i>	<i>-0.02 (0.34)</i>	<i>-0.03 (0.17)</i>
G	0.06 (0.07)	<b>0.11 (0.05)</b>	<i>0.02 (0.13)</i>
RS	<i>0.09 (0.18)</i>	<i>0.09 (0.25)</i>	<b>0.12 (0.38)</b>
Dominance.G	-0.04 (0.07)	-0.1 (0.07)	<i>0.01 (0.19)</i>
Dominance.C	0.02 (0.06)	0.09 (0.07)	<i>-0.02 (0.14)</i>

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