



HAL
open science

**Tree species diversity and abundance as indicators of
understory diversity in French mountain forests:
Variations of the relationship in geographical and
ecological space**

C. Zilliox, Frédéric Gosselin

► **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

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

5 Christophe Zilliox ^{1,2} & Frédéric Gosselin ^{1,*}

6 1 : IRSTEA, UR EFNO, Domaine des Barres, F-45290 Nogent-sur-Vernisson, France

7 2 : AgroParisTech, GEEFT, BP 7355, 34086 Montpellier Cedex 4, France

8

9 * : corresponding author ; e-mail: frederic.gosselin@irstea.fr; phone: +33 2 38 95 03 58

10

11

12

13

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

16

17

Available at:

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

19

12713005070

20

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 ± 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 MétéoFrance, 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 CO₂ levels, disturbance or biota
282 variables, because CO₂ 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: $10 \text{ m}^2 \cdot \text{ha}^{-1}$ for most basal area parameters ($5 \text{ m}^2 \cdot \text{ha}^{-1}$ 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

712 **References:**

713 Auclair, A. N. and F. G. Goff, 1971. Diversity relations of upland forests in the western Great
714 Lakes area. *The American Naturalist*, 105(946), 499-528.

715 Austin, M. P. and K. P. Van Niel, 2011a. Impact of landscape predictors on climate change
716 modelling of species distributions: A case study with *Eucalyptus fastigata* in southern New
717 South Wales, Australia. *Journal of Biogeography*, 38(1), 9-19.

718 Austin, M. P. and K. P. Van Niel, 2011b. Improving species distribution models for climate
719 change studies: Variable selection and scale. *Journal of Biogeography*, 38(1), 1-8.

720 Austin, M. P. and T. M. Smith, 1989. A new model for the continuum concept. *Vegetatio*,
721 83(1-2), 35-47.

722 Barbier, S., 2007. Influence de la diversité, de la composition et de l'abondance des essences
723 forestières sur la diversité floristique des forêts tempérées. Ph.D thesis Thesis, Université
724 d'Orléans, Orléans.

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

728 Barbier, S., R. Chevalier, P. Loussot, L. Bergès and F. Gosselin, 2009a. Improving
729 biodiversity indicators of sustainable forest management: tree genus abundance rather than
730 tree genus richness and dominance for understory vegetation in French lowland oak hornbeam
731 forests. *Forest Ecology and Management*, 258(), S176-S186.

732 Barbier, S., P. Balandier and F. Gosselin, 2009b. Influence of several tree traits on rainfall
733 partitioning in temperate and boreal forests: a review. *Annals of Forest Science*, 66(602).

734 Batek, M. J., A. J. Rebertus, W. A. Schroeder, T. L. Haithcoat, E. Compas et al., 1999.
735 Reconstruction of early nineteenth-century vegetation and fire regimes in the Missouri
736 Ozarks. *Journal of Biogeography*, 26(2), 397-412.

737 Bertness, M. D. and R. Callaway, 1994. Positive interactions in communities. *Trends in*
738 *Ecology and Evolution*, 9(5), 187-191.

739 Biggs, R., S. R. Carpenter and W. A. Brock, 2009. Spurious certainty: How ignoring
740 measurement error and environmental heterogeneity may contribute to environmental
741 controversies. *BioScience*, 59(1), 65-76.

742 Brosofske, K. D., J. Chen and T. R. Crow, 2001. Understory vegetation and site factors:
743 implications for a managed Wisconsin landscape. *Forest Ecology and Management*, 146(1-3),
744 75-87.

745 Brown, M. J. and G. G. Parker, 1994. Canopy light transmittance in a chronosequence of
746 mixed-species deciduous forests. *Canadian Journal of Forest Research*, 24(8), 1694-1703.

747 Callaway, R. M., 1997. Positive interactions in plant communities and the individualistic-
748 continuum concept. *Oecologia*, 112(2), 143-149.

749 Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie et al., 2002. Positive
750 interactions among alpine plants increase with stress. *Nature*, 417(6891), 844-848.

751 Camp, R. J., N. E. Seavy, P. M. Gorresen and M. H. Reynolds, 2008. A statistical test to show
752 negligible trend: Comment. *Ecology*, 89(5), 1469-1472.

753 Cavaignac, S., 2009. Les sylvoécórégions (SER) de France métropolitaine, Etude de
754 définition, French National Forest Inventory, Nogent sur Vernisson.

755 Celeux, G., F. Forbesy, C. P. Robertz and D. M. Titteringtonx, 2006. Deviance information
756 criteria for missing data models. *Bayesian Analysis*, 1(4), 651-674.

757 Dixon, P. M. and J. H. K. Pechmann, 2005. A statistical test to show negligible trend.
758 *Ecology*, 86(7), 1751-1756.

759 Douguédroit, A. and M. F. de Saintignon, 1970. Méthode d'étude de la décroissance des
760 températures en montagne de latitude moyenne: Exemple des alpes françaises du sud. *Revue*
761 *de géographie alpine*, 58, 453-472.

762 Duelli, Peter and Martin K. Obrist, 2003. Biodiversity indicators: the choice of values and
763 measures. *Agriculture, Ecosystems & Environment*, 2063, 1-12.

764 Dufour-Kowalski, S., B. Courbaud, P. Dreyfus, C. Meredieu and F. De Coligny, 2012.
765 Capsis: An open software framework and community for forest growth modelling. *Annals of*
766 *Forest Science*, 69(2), 221-233.

767 Ellenberg, H., H. E. Weber, R. Düll, V. Wirth, W. Werner et al., 1992, *Zeigerwerte von*
768 *Pflanzen in Mitteleuropa*, vol. 18 (). Verlag Goltze, Göttingen.

769 Ewald, J., 2000. The partial influence of Norway spruce stands on understorey vegetation in
770 montane forests of the Bavarian Alps. *Mountain Research and Development*, 20(4), 364-371.

771 Gelman, A., J. B. Carlin, H. S. Stern and D. B. Rubin, 2004, *Bayesian Data Analysis* ().
772 Chapman & Hall, Boca Raton.

773 Glenn-Lewin, D. C., 1977. Species diversity in North American temperate forests. *Vegetatio*,
774 33, 153-162.

775 Gosselin, F., 2011a. Propositions pour améliorer l'équipement biométrique du détective
776 écologique. Application à la modélisation de la relation entre gestion forestière et biodiversité.
777 HDR Thesis, Université Pierre et Marie Curie, Paris.

778 Gosselin, F., 2011b. A New Calibrated Bayesian Internal Goodness-of-Fit Method: Sampled
779 Posterior p-values as Simple and General p-values that Allow Double Use of the Data. *Plos*
780 *One*, 6(3), e14770.

781 Gosselin, F., 2012. Improving Approaches to the Analysis of Functional and Taxonomic
782 Biotic Homogenization: beyond Mean Specialization. *Journal of Ecology*, 100(6), 1289-1295.

783 Harrell, F. E., 2001, *Regression Modeling Strategies, With Applications to Linear Models,*
784 *Logistic Regression, and Survival Analysis*. Springer, New York, USA.

- 785 Hicks, D. J., 1980. Intrastrand distribution patterns of southern Appalachian forest herbaceous
786 species. *American Midland Naturalist*, 104(2), 209-223.
- 787 Ingerpuu, N., K. Vellak, J. Liira and M. Partel, 2003. Relationships between species richness
788 patterns in deciduous forests at the north Estonian limestone escarpment. *Journal of*
789 *Vegetation Science*, 14(5), 773-780.
- 790 Kwiatkowska, A. J., 1994. Changes in the species richness, spatial pattern and species
791 frequency associated with the decline of oak forest. *Vegetatio*, 112(2), 171-180.
- 792 Kwiatkowska, A. J., K. Spalik, E. Michalak, A. Palinska and D. Panufnik, 1997. Influence of
793 the size and density of *Carpinus betulus* on the spatial distribution and rate of deletion of
794 forest-floor species in thermophilous oak forest. *Plant Ecology*, 129(1), 1-10.
- 795 Laughlin, D. C., J. D. Bakker and P. Z. Fule, 2005. Understorey plant community structure in
796 lower montane and subalpine forests, Grand Canyon National Park, USA. *Journal of*
797 *Biogeography*, 32(12), 2083-2102.
- 798 Lindenmayer, D. B., C. R. Margules and D. B. Botkin, 2000. Indicators of biodiversity for
799 ecologically sustainable forest management. *Conservation Biology*, 14(4), 941-950.
- 800 Lindenmayer, D. B. and G. E. Likens, 2011. Direct Measurement Versus Surrogate Indicator
801 Species for Evaluating Environmental Change and Biodiversity Loss. *Ecosystems*, 14(1), 47-
802 59.
- 803 Lindh, B. C., 2005. Effects of conifer basal area on understory herb presence, abundance, and
804 flowering in a second-growth Douglas-fir forest. *Canadian Journal of Forest Research*, 35(4),
805 938-948.
- 806 Maestre, F. T., R. M. Callaway, F. Valladares and C. J. Lortie, 2009. Refining the stress-
807 gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*,
808 97(2), 199-205 DOI 10.1111/j.136.
- 809 McCune, B. and J. A. Antos, 1981. Diversity relationships of forest layers in the Swan Valley,
810 Montana. *Bulletin of the Torrey Botanical Club*, 108(3), 354-361.

811 Michalet, R., Rolland, C., Joud, D., Gafta, D. and Callaway, R. M., 2002. Associations
812 between canopy and understory species increase along a rainshadow gradient in the Alps:
813 Habitat heterogeneity or facilitation? *Plant Ecology*, 165(2), 145-160.

814 Ministère de l'Agriculture et de la Pêche, 2011. Les indicateurs de gestion durable des forêts
815 françaises métropolitaines - Edition 2010, MAP, Paris.

816 Ministerial Conference on the Protection of Forests in Europe, 2011. State of Europe's forests
817 2011 - Status and trends in Sustainable Forest Management in Europe.

818 Mitchell, P. L. and K. J. Kirby, 1989, Ecological effects of forestry practices in long-
819 established woodland and their implications for nature conservation (). Oxford Forestry
820 Institute, Oxford.

821 Moir, W. H., 1966. Influence of ponderosa pine on herbaceous vegetation. *Ecology*, 47(6),
822 1045-1048.

823 Mölder, A., M. Bernhardt-Römermann and W. Schmidt, 2008. Herb-layer diversity in
824 deciduous forests: Raised by tree richness or beaten by beech? *Forest Ecology and*
825 *Management*, 256(3), 272-281.

826 Morneau, F., C. Duprez and J. C. Hervé, 2008. Mixed-species forests in metropolitan France -
827 Characterization based on national forest inventory findings. *Revue Forestiere Francaise*,
828 60(2), 107-120.

829 Ohlemüller, R., P. Bannister, K. J.M. Dickinson, S. Walker, B. J. Anderson et al., 2004.
830 Correlates of vascular plant species richness in fragmented indigenous forests: Assessing the
831 role of local and regional factors. *Community Ecology*, 5(1), 45-54.

832 Pitkanen, S., 2000. Effect of tree stand and site variables on alpha diversity of ground
833 vegetation in the forests of Northern Karelia. *Journal of Environmental Management*, 58(4),
834 289-295.

835 Rice, W. R., 1989. Analyzing tables of statistical tests. *Evolution*, 43, 223-225.

836 Rigler, F. H., 1982. Recognition of the possible: an advantage of empiricism in ecology.
837 *Canadian Journal of Fisheries and Aquatic Sciences*, 39(9), 1323-1331.

838 Soliveres, S., D. J. Eldridge, F. T. Maestre, M. A. Bowker, M. Tighe et al., 2011.
839 Microhabitat amelioration and reduced competition among understorey plants as drivers of
840 facilitation across environmental gradients: Towards a unifying framework. *Perspectives in*
841 *Plant Ecology, Evolution and Systematics*, 13(4), 247-258.

842 Sonohat, G., P. Balandier and F. Ruchaud, 2004. Predicting solar radiation transmittance in
843 the understory of even-aged coniferous stands in temperate forests. *Annals of Forest Science*,
844 61, 629-641.

845 Specht, R. L. and D. G. Morgan, 1981. The balance between the foliage projective covers of
846 overstorey and understorey strata in Australian vegetation. *Australian Journal of Ecology*, 6,
847 193-202.

848 Spiegelhalter, D.J., N.G. Best, J. B. Carlin and A. van der Linde, 2002. Bayesian measures of
849 model complexity and fit (with Discussion). *Journal of the Royal Statistical Society, Series B*,
850 64(4), 583-616.

851 Spyreas, G. and J. W. Matthews, 2006. Floristic conservation value, nested understory floras,
852 and the development of second-growth forest. *Ecological Applications*, 16(4), 1351-1366.

853 Tyler, G., 1989. Interacting effects of soil acidity and canopy cover on the species
854 composition of field-layer vegetation in oak/hornbeam forests. *Forest Ecology and*
855 *Management*, 28(2), 101-114.

856 Vockenhuber, E. A., C. Scherber, C. Langenbruch, M. Meißner, D. Seidel et al., 2011. Tree
857 diversity and environmental context predict herb species richness and cover in Germany's
858 largest connected deciduous forest. *Perspectives in Plant Ecology, Evolution and Systematics*,
859 13(2), 111-119.

860 Vrugt, J. A., C. J.F. Ter Braak, C. G.H. Diks, B. A. Robinson, J. M. Hyman et al., 2009.
861 Accelerating Markov chain Monte Carlo simulation by differential evolution with self-
862 adaptive randomized subspace sampling. *International Journal of Nonlinear Sciences and*
863 *Numerical Simulation*, 10(3), 273-290.

864 Weiner, J., 1995. On the practice of ecology. *Journal of Ecology*, 83, 153-158.

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	

869

870

871

872

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.

896

897

898

899

900

901

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	Δ 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]	
h.HL at Reaction=4.5		
	-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]
h.NF at Elevation=770m		w.LT at Elevation=1460m	
	-0.317 [-0.425; -0.22]		0.405 [0.256; 0.561]
h.HL at Elevation=770m		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)	0.19 (0.08)	<i>0.04 (0.13)</i>
C.fir	0.11 (0.05)	0.26 (0.09)	<i>0.04 (0.15)</i>
C.spruce	0.17 (0.1)	0.21 (0.06)	<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)	0.14 (0.13)	<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)	0.12 (0.1)	<i>0.05 (0.18)</i>
G.ST	0.12 (0.18)	0.07 (0.1)	-0.03 (0.09)
G.fir	0.05 (0.05)	0.11 (0.04)	<i>0.02 (0.12)</i>
G.spruce	0.14 (0.15)	0.13 (0.08)	<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)	0.11 (0.05)	<i>0.02 (0.13)</i>
RS	<i>0.09 (0.18)</i>	<i>0.09 (0.25)</i>	0.12 (0.38)
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>

941

942

943