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

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A B S T R A C T

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

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1. Introduction

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

Among the many management choices foresters have to make, the nature of the tree species is a most important one. Tree species identity, abundance and diversity can determine levels of resources available to understory vegetation and influence their spatial variation (Barbier et al., 2008), and can thus shape understory diversity and abundance (Barbier et al., 2009a). This may explain why tree species richness and dominance are used as biodiversity indicators in Europe and France (Ministerial Conference on the Protection of Forests in Europe, 2011; Ministère de l’Agriculture et de la Pêche, 2011). Herein, we define “dominance” as the relative abundance – in terms of cover or basal area – of the most abundant species. Yet, as with many indicators, tree species richness and dominance are not necessarily indicative of all components of
biodiversity. Furthermore, these indicators might show influences on biodiversity that work in unexpected directions. Also, other stand-level indicators related to tree species might be better indicators than richness or dominance for some components of floristic biodiversity (Barbier et al., 2009a). Finally, as mentioned by Glenn-Lewin (1977), these indicators might correlate with some components of biodiversity that is in fact due to responses to site type variations – and not to forest management choices. Indeed, when controlling for site type in some lowland French forests, Barbier et al. (2009a) found that indicators related to tree species richness and dominance had either negligible effects on floristic biodiversity or effects that were too noisy to conclude; in some cases, the direction of the effect was reversed compared to what was expected based on intuition. In contrast, indicators related to tree species abundance modeled variations in biodiversity more accurately and showed stronger, non-negligible effects.

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

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

Our second objective was to study the variation of the relationship between dendrometric indicators and biodiversity along various ecological gradients. Our approach is based on a comparison of the results of Barbier et al. (2009a) with those of Barbier et al. (2009a) with those of Barbier (2007): although the qualitative results in Barbier (2007) were similar to those of Barbier et al. (2009a), the magnitude of the relationships was lower. This discrepancy could have resulted from the inherent instability of the relationship according to the ecological context. Indeed, the 2009 study was carried out in a constant site type in one region with a rather limited variation in soil pH, whereas in 2007, there were no such controls. If relationships vary with ecological context or region, this could explain the lower magnitude of the effects Barbier found in 2007. We therefore had a second prediction in this study that the relationship between dendrometric indicators and biodiversity would depend on the position along various ecological gradients. This prediction was inspired firstly by general principles (e.g. Biggs et al., 2009) that point in this direction: most ecological relationships are not likely to be general across all ecological conditions but instead should depend on the ecological context. Secondly, it has been shown that relationships among vegetation strata or plant species vary along different ecological gradients (Callaway et al., 2002; Michalet al., 2002). Thirdly, the indicators that we study herein are what Austin and Smith (1989) called “indirect gradients”, where the variable (such as basal area, for example) affects the plants through other variables which have a direct physiological effect on them. In the case of basal area (and other measures of tree abundance) there is some prior knowledge that it influences both the level of transmitted light (Brown and Parker, 1994; Sonohat et al., 2004) and the proportion of precipitation that reaches the ground (Fig. 1 in Barbier et al., 2009b). Barbier et al. (2008) also reviewed knowledge on the impact of dominant tree species on different ecological mechanisms important for plants. These results show that dendrometric indicators are at most indirect gradients for floristic diversity. It is logical expect that the effect of dendrometric indicators on biodiversity should vary with the position along various ecological gradients, since (i) the relationship between direct gradients and floristic diversity can vary in shape – linear, Gaussian, asymmetric, sigmoidal.; (ii) floric diversity is likely to have limiting factors that depend on the ecological context and (iii) dendrometric indicators influence several of these mechanisms simultaneously. However, the relationship between tree species abundance and floristic biodiversity along ecological gradients is very much related to the stress-gradient hypothesis (e.g. Bertness and Callaway, 1994; Callaway et al., 2002; but see Maestre et al., 2009) which states that positive interactions between species (or between the abundance of one species and the biodiversity of one ecological group) should increase with ecological stress. It should be recognized that ecological stress is not a precise concept (Maestre et al., 2009), but is generally interpreted to refer to ecological conditions in which the productivity of a species is limited by the abiotic environment. The stress-gradient hypothesis not only predicts that relationships between indicators and biodiversity will vary along ecological gradients, but might determine in which direction the relationships occur.

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

To sum up, our objectives were to document how the current list of biodiversity indicators related to forest management can be improved by specifying for which ecological groups and in which ecological contexts these indicators have a non-negligible positive or negative statistical relationship with biodiversity – one that cannot be directly attributed to site type variation.

2. Material and methods

2.1. Study sites

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

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

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

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

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

2.2. Data collection

2.2.1. Dendrometric data

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

G is the total basal area on the plot. It is calculated with diam-
eter at breast height (dbh) and a weighting coefficient, provided
by the NFI. Tree censusing is typically done by counting all the trees in
a given dbh – actually circumference – interval in three circular
subplots centered on the plot center: a 6 m-radius subplot for
small trees (from 23.5 to 70.5 cm in circumference), 9 m-radius
subplot for medium trees (from 70.5 to 117.5 cm in circumference)
and 15 m-radius subplot for big trees (more than 117.5 cm in cir-
cumference). Floristic counts were done at a 15 m-radius subplot.

For each tree a weight was thus calculated according to the pro-
spection area corresponding to its dbh class. A change in weight
could occur if the plot size is reduced (for example, if a nearby for-
est path or any other obstacle precludes establishing a fully-sized
plot in the field), but also if there are too many trees of the same
species inside the same diameter class. G.spruce, G.fir, G.othersp
are the basal areas for (respectively) Norway spruce, silver fir
and other species. They are calculated from the same data, taking
tree species into account. G.BT, G.VBT, G.MT, G.ST are the basal
areas for (respectively) large trees (trees with dbh between 42.5
and 67.5 cm), very large trees (dbh bigger than 67.5 cm), medium
trees (dbh between 17.5 and 42.5 cm), and small trees (dbh smaller
than 17.5 cm). rs is tree species richness based on basal area counts.

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

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

2.2.2. Floristic data

The NFI relevés contain information relative to understory spe-
cies identification and abundance on each plot. Species identific-
tion data were coupled with autecological data from Philippe
Julve’s work on French vegetation and flora (http://philippe.
philippe.julve.pagesperso-orange.fr/). When faced with duplicates in-
side the database (for example different ecotypes of the same
species), the one most fitted to our study was retained. The data
regarding species abundance was also used but will not be pre-
sented in this paper, as work is still in progress.

Our analysis focused on the species richness of ecological
groups rather than on floristic diversity as a whole, based on the
considerations in, e.g. Barbier et al. (2009a) and Gosselin (2012).
Each ecological classification first separated woody and non-woo-
dy species. It secondly separated species based on Ellenberg values
(light and temperature; Ellenberg et al., 1992) and forest succes-
sion association (mature forest species, peri-forest species and
non-forest species; as in Barbier et al. 2009a). The number of spe-
cies in the intersection of these two types of groups (based on life
form, then on an ecological classification) gave the species richness
of the ecological groups. The use of successional status was moti-
vated by the wide variety of studies that have chosen to work with
this classification (Kwiatkowska, 1994; Kwiatkowska et al. 1997;
Spyreas and Matthews, 2006; Barbier et al. 2009a), while light
and temperature requirements were chosen because they could be
important factors to take into consideration in order to explain
the variations in biodiversity in response to dendrometric
indicators.

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

2.2.3. Climatic data

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

The values of these climatic variables are summarized in Table SM1. Tmin is the temperature for January and potential evapotranspiration, precipitation (PPT) and solar radiation were summed over the growing season, from May to September.

2.3. Data analysis

2.3.1. Statistical models

The premise of the study was a reflection on the general shape of the statistical models used to relate biodiversity to dendrometric indicators. Our first challenge was to include an ecological aspect in the statistical model used to estimate the relationship between biodiversity and ecological variables – excluding dendrometric indicators. By explicitly modeling the site type variation within the statistical biodiversity model, the models may separate the effect of abiotic variables from the effect of the dendrometric indicator on biodiversity. In order to achieve this goal, we chose the abiotic variables according to Austin and Van Niel (2011a,b): light above the canopy, temperature, reaction, precipitation and topography were included in the model. We did not include CO₂ levels, disturbance or biota variables, because CO₂ was assumed to be constant for the time span and spatial scale considered in the study, and both biota and disturbance are modeled through the dendrometric indicators.

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

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

The ecological variables introduced into the model were: soil pH as indicated by the Ellenberg values of the understory species (denoted as reaction), mean annual temperature (T), growing season precipitation (PPT), solar radiation (solrad), topography, aspect and slope. Temperature, reaction, precipitation and radiation were input into the model through an automatic restricted cubic spline transformation involving four knots, thus requiring the estimation of three parameters for each variable (Harrell, 2001). This transformation is classical for species distribution models; it allows the function to model a possible non-linear relationship between the transformed predictor and the explanatory variable.

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

\[
\text{rcs}(\text{reaction}) 4 + \text{rcs}(\text{scale}(\text{PPT}), 4) + \text{rcs}(\text{scale}(\text{T}), 4) + \text{rcs}(\text{scale}(\text{solrad}), 4) + \ldots + \text{topo0} + l(\text{sin}(\text{p min}(\text{slope}, \pi/4))) + \cos(\text{aspect}) + \text{"Indicator model"}
\]

where "rcs" is the R function for the restricted cubic spline transformation involving four knots (Harrell, 2001), "T" is the identity link, "pmin" is the parallel minimum function (giving the minimum value after comparing the elements of one or more vectors or matri-

Table 1

<table>
<thead>
<tr>
<th>Model</th>
<th>Variable content of the model in R syntax</th>
<th>Model symbol</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total cover</td>
<td>-C</td>
<td>C</td>
</tr>
<tr>
<td>Total basal area</td>
<td>-G</td>
<td>G</td>
</tr>
<tr>
<td>Cover per tree species</td>
<td>-C.spruce + C.fr + C.othersp</td>
<td>C.sp</td>
</tr>
<tr>
<td>Basal area per tree species</td>
<td>-G.spruce + G.fr + G.othersp</td>
<td>G.sp</td>
</tr>
<tr>
<td>Basal area per diameter class</td>
<td>-G.BT + G.VBT + G.MT + G.ST</td>
<td>G.D</td>
</tr>
<tr>
<td>Tree species richness</td>
<td>-RS</td>
<td>RS</td>
</tr>
<tr>
<td>Cover dominance</td>
<td>-Dominance.C + C</td>
<td>Dom.C</td>
</tr>
<tr>
<td>Basal area dominance</td>
<td>-Dominance.G + G</td>
<td>Dom.G</td>
</tr>
<tr>
<td>Null model</td>
<td>-1</td>
<td></td>
</tr>
</tbody>
</table>
2 ha = 0.1 and log( levels metric functions.

1.1 (Gelman et al., 2004). After convergence was reached, we asked 
ries, and a thinning parameter of 50. The convergence of the mod-
domains that the mode-based DIC did not have.

Indeed, the classical version of the DIC yielded incoherent, unstable 
set of parameters leading to the highest posterior probability.

domains in calculating the reference deviance not at the mean of the param-
spatial indices –, as discussed by Celeux et al. (2006), which consists 
Vrugt et al. (2009) based on four trajectories and 

groups successively to determine for each group which indica-

We addressed our two main predictions by using a mixture of 
atures based on models comparison and the analysis of the magni-
itude of the effects of the models. Our first prediction was that 
dendrometric models involving only tree abundance would be 
7.5% for C.othersp, 1.5 genera for tree species richness and 0.2 for 

dominance. For each parameter, we reported the mean 
for an increase in the ecological parameter of around one standard 
deviation. We chose the following increases for the different 
parameters: 10 m² ha⁻¹ for most basal area parameters 
(5 m² ha⁻¹ for G.othersp and G.ST, respectively basal area of 
areas other than fir or spruce and basal area of stems less than 
17.5 cm in dbh), 15% for all tree crown cover parameters, except 
7.5% for C.othersp, 1.5 genera for tree species richness and 0.2 for 
tree species dominance. For each parameter, we reported the mean 
value of the log of the multiplier of the mean corresponding to such 
a variation, its 95% confidence interval, and the probability of the 
significance test that the parameter was null. Levels of statistical 
significance for parameters were symbolized as follows: * = p < 0.01 and ** = p < 0.05. Inspired from Dixon and Peckmann 
2005), we also did an analysis based on equivalence and inequiv-
ulence tests to detect negligible effects: based on Bayesian param-
eter estimations as in Camp et al. (2008), the aim of this analysis 
was to identify (i) when the parameter has a high probability of being in an interval, called the negligible interval, that is a priori 
considered to represent negligible effects, (ii) when the parameter 
had a high probability of being below this interval and (iii) when 
the parameter had a high probability of being above it. Two negli-
gible intervals were distinguished: one for weak negligibility and 
one for strong negligibility. We denoted by 0 < b₁ < b₂ the levels 
associated to the two negligible intervals. We used the symbol 0 
to describes cases where P(b₂ < log(β) < b₁) ≥ 0.95 and 00 for 
the more stringent: P(b₁ < log(β) < b₂) ≥ 0.95. Similarly, we de-
noted by ‘−’ cases where P(β < −b₁) ≥ 0.95 and ‘−−’ cases where 
P(log(β) < −b₂) ≥ 0.95. These cases correspond to non-neg-
ligible negative and strongly non-negligible negative effects, 
respectively. We had similar notations − ‘++’ and ‘+++’ − for the po-
itive side. We chose b₁ = 0.1 and b₂ = 0.2 for species richness data, 
corresponding respectively to a multiplication of species richness by 
exp(0.1) ≈ 1.11 and exp(0.2) ≈ 1.22 at the upper side of the neg-
ligible interval.

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

(i) Model comparisons: for each category of dendrometric model 
between total abundance, abundance by tree species, abun-
dance by diameter class, Tree species richness and tree dom-
inance and abundance), either based on crown cover or on 
basal area, we recorded the number of times the category

<table>
<thead>
<tr>
<th>Ecological gradient involved in the interaction</th>
<th>Variable content of the model in R syntax</th>
</tr>
</thead>
<tbody>
<tr>
<td>Region (categorical variable with four levels; cf. text)</td>
<td>~&quot;Indicator model&quot; + &quot;Indicator model&quot;:Region</td>
</tr>
<tr>
<td>Aspect (including slope)</td>
<td>~&quot;Indicator model&quot; + ...</td>
</tr>
<tr>
<td>Reaction</td>
<td>~&quot;Indicator model&quot;</td>
</tr>
<tr>
<td>Elevaton</td>
<td>~&quot;Indicator model&quot; + &quot;Indicator model&quot;:(Reaction)</td>
</tr>
<tr>
<td>ETP</td>
<td>~&quot;Indicator model&quot; + &quot;Indicator model&quot;:(ETP)</td>
</tr>
<tr>
<td>SWC</td>
<td>~&quot;Indicator model&quot; + &quot;Indicator model&quot;:(SWC)</td>
</tr>
<tr>
<td>Tmin</td>
<td>~&quot;Indicator model&quot; + &quot;Indicator model&quot;:(Tmin)</td>
</tr>
<tr>
<td>PPT</td>
<td>~&quot;Indicator model&quot; + &quot;Indicator model&quot;:(PPT)</td>
</tr>
</tbody>
</table>

ETP stands for evapotranspiration, SWC for soil water content and ppt for precipitations, and toposimple equals one is there is a value for aspect and slope 0 otherwise (in the case of complex topographic conditions).
of model was the best, the second best, and so on. We also recorded the mean difference in DIC with the best model, over the 16 ecological groups studied. A model that had less difference in DIC and a higher rank was interpreted as being a better model than the others.

(ii) **Magnitude and significance of the effects:** for each dendrometric parameter among the floristic ecological groups, we recorded the number of times it was negative and significant to the 1% level, positive and significant to the 1% level, judged negligible, negative non-negligible, positive non-negligible or without enough information relative to negligibility of the effect. These parameters were grouped in the same categories as in (i) above, except that we also identified parameters for pure abundance (i.e. total abundance based either on crown cover or basal area).

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

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

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

Finally, we checked the statistical quality of our models by using the new goodness of fit p-values proposed by Gosselin (2011b), called the sampled posterior p-values. We applied these p-values on different aspects of normalized residuals (as described in Gosselin, 2011b): their skewness, their kurtosis – to diagnose the probability distribution used-, their correlation with the estimated mean – to diagnose general linearity problems – and with the covariates incorporated in the models (precipitation, solar radiation, reaction, temperature . . ). To detect potentially non-monotonic correlations between variables, we used the Hoeffding’s D statistic provided in the Hmisc R package (Harrell, 2001). We applied this method to the best model of each ecological group. We also checked the multi-collinearity of our variables of interest by calculating the variance inflation factor (VIF) of all the dendrometric variables we were interested in as a function of all the other variables in the model (Zuur et al., 2010).

3. Results

3.1. Choice of model

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

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

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

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

Dendrometric models formulated on abundance data were better models overall than those based on tree species richness (Table 3 and SM3–SM6). Indeed, the abundance-based models (i.e. G.sp and C.sp in Ab.SP and G.D) were the best for one third of the biodiversity ecological groups on average whereas the species richness model (RS) was the best for at most one sixth of the ecological groups. Furthermore, for the RS model, the mean difference in DIC from the DIC of the best model ranged from 40% to more than 150% more than for models based on abundance. Dom models (including Dom.C and Dom.G) involving both tree species
dominance and total tree species abundance were intermediate but rarely provided the best model.

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

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

An interaction between dendrometric variables and ecological context was detected for most of the ecological groups (cf. Table 6).

### Table 4

(A) Mean over the dendrometric variables in the abundance or RS or dominance models of the number of cases in each category of effect (classified either according to the negligibility of the effect or its 1% significance: cf. Section 2.3.2 “Analysis of model results”) over the 16 ecological groups and over the 15 cases analyzed in Tables SM 7–37. (B) Same information for the 5 dendrometric variables with the most significant relationships (corresponding to the sum of the last two lines). (C) Same information for the 5 dendrometric variables with the most non-negligible relationships (corresponding to the sum of lines 2 and 3).

<table>
<thead>
<tr>
<th>Level of significance</th>
<th>Ab.Tot</th>
<th>Ab.SP</th>
<th>G.D</th>
<th>RS</th>
<th>Dom</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Negligible</td>
<td>235.5</td>
<td>198.33</td>
<td>199</td>
<td>164.5</td>
<td>211</td>
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<td>Negative non-neg</td>
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<td>525</td>
<td>65</td>
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</tr>
<tr>
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<td>1.17</td>
<td>0</td>
<td>13.5</td>
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</tr>
<tr>
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<td>33.83</td>
<td>36.25</td>
<td>56</td>
<td>23.5</td>
</tr>
<tr>
<td>Positive significant</td>
<td>18.5</td>
<td>16.5</td>
<td>3.75</td>
<td>60.5</td>
<td>2</td>
</tr>
<tr>
<td>Negative significant</td>
<td>64.5</td>
<td>43.33</td>
<td>47</td>
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<td>58.5</td>
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<table>
<thead>
<tr>
<th>Level of significance</th>
<th>G.spruce</th>
<th>G.ST</th>
<th>C.spruce</th>
<th>G</th>
<th>C</th>
</tr>
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<tr>
<td>B</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Negligible</td>
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<td>146</td>
<td>209</td>
<td>237</td>
<td>234</td>
</tr>
<tr>
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<td>20</td>
<td>13</td>
<td>20</td>
<td>7</td>
<td>9</td>
</tr>
<tr>
<td>Positive non-neg</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>No info negligible</td>
<td>26</td>
<td>81</td>
<td>12</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Positive significant</td>
<td>20</td>
<td>1</td>
<td>25</td>
<td>8</td>
<td>29</td>
</tr>
<tr>
<td>Negative significant</td>
<td>88</td>
<td>97</td>
<td>71</td>
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</table>

<table>
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<tr>
<th>Level of significance</th>
<th>RS</th>
<th>G.spruce</th>
<th>C.spruce</th>
<th>G.ST</th>
<th>Dominance,G</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Negligible</td>
<td>147</td>
<td>195</td>
<td>209</td>
<td>146</td>
<td>119</td>
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<tr>
<td>Negative non-neg</td>
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<td>20</td>
<td>20</td>
<td>13</td>
<td>6</td>
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<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>No info negligible</td>
<td>65</td>
<td>26</td>
<td>12</td>
<td>81</td>
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<td>51</td>
<td>20</td>
<td>25</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Negative significant</td>
<td>23</td>
<td>88</td>
<td>71</td>
<td>97</td>
<td>31</td>
</tr>
</tbody>
</table>

Mostly only two ecological groups (peri-forest herbaceous species and intermediate light-demanding woody species) had DIC differences of more than −5 between the best interaction model and the best simple model, while five ecological groups (non-forest herbaceous species, heliophilous herbaceous species, cold-temperature herbaceous species, mid-temperature woody species and high-temperature woody species) had a DIC difference of less than −20.
Regarding the ecological groups and contexts in which each dendrometric variable was a non-negligible indicator of biodiversity (cf. Table 7), most ecological groups were indicated in specific ecological contexts, as hypothesized. Only in a few cases did dendrometric indicators indicate a non-negligible variation across all the plots analyzed (2 for C.spruce, 1 for G.ST, 1 for G.spruce, 2 for rs and 1 for Dominance.G). Indicators related to tree abundance mostly negatively impacted non-forest, high-light or low-temperature herbaceous species, mostly in northern aspects, at lower elevations and in more acidic conditions. We noticed a counter relationship of a positive non-negligible effect of some tree abundance attributes on south facing slopes for low-light herbaceous species. We also noticed a positive effect of the basal area of tree species other than spruce and fir on four ecological groups in the Internal Alps (results not shown). Spruce cover and basal area as well as the basal area of trees less than 17.5 cm in dbh (G.ST) were the most involved in relationships with biodiversity.

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

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

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

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 ecological group in general or in a given environmental context (with respect to reaction, aspect or elevation). We here distinguish negative and positive non-negligible cases for the cover of trees (C) and the tree species richness (RS) and indicate the mean estimate and 95% credibility interval for the natural logarithm of the multiplicative effect on mean species richness. Only in a few cases did den- drometric variable was a non-negligible indicator of biodiver- sity in response to total cover, fir cover and spruce cover along the reaction and aspect gradients.

<table>
<thead>
<tr>
<th>Variable in the model</th>
<th>Negative non-negligible effects</th>
<th>Positive non-negligible effects</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>h.HL at slope = 0.5 &amp; E/W aspect</td>
<td>-0.131 [-0.168; -0.0943]</td>
<td>h.LL at slope = 0.5 &amp; S aspect 0.177 [0.0999; 0.256]</td>
</tr>
<tr>
<td>h.NF at slope = 0.5 &amp; N aspect</td>
<td>-0.154 [-0.205; -0.102]</td>
<td></td>
</tr>
<tr>
<td>h.HL at slope = 0.5 &amp; N aspect</td>
<td>-0.202 [-0.253; -0.142]</td>
<td></td>
</tr>
<tr>
<td>h.HL at Reaction = 5</td>
<td>-0.144 [-0.179; -0.109]</td>
<td></td>
</tr>
<tr>
<td>h.NF at Reaction = 4.5</td>
<td>-0.16 [-0.209; -0.111]</td>
<td></td>
</tr>
<tr>
<td>h.HL at Reaction = 4.5</td>
<td>-0.201 [-0.255; -0.147]</td>
<td></td>
</tr>
<tr>
<td>h.LT at Reaction = 4.5</td>
<td>-0.147 [-0.199; -0.097]</td>
<td></td>
</tr>
<tr>
<td>h.HL at Elevation = 770 m</td>
<td>-0.172 [-0.215; -0.132]</td>
<td></td>
</tr>
<tr>
<td>rs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>h.HL</td>
<td>-0.208 [-0.307; -0.112]</td>
<td>w.LT 0.213 [0.0773; 0.348]</td>
</tr>
<tr>
<td>h.HL at slope = 0.5 &amp; E/W aspect</td>
<td>-0.237 [-0.347; -0.129]</td>
<td>h.MF on flat terrain 0.182 [0.0988; 0.263]</td>
</tr>
<tr>
<td>h.NF at slope = 0.5 &amp; N aspect</td>
<td>-0.292 [-0.464; -0.0978]</td>
<td>w.MF at slope = 0.5 &amp; E/W aspect 0.149 [0.0993; 0.207]</td>
</tr>
<tr>
<td>h.HL at slope = 0.5 &amp; N aspect</td>
<td>-0.413 [-0.612; -0.214]</td>
<td>w.LT at slope = 0.5 &amp; N aspect 0.403 [0.118; 0.608]</td>
</tr>
<tr>
<td>h.HL at Reaction = 5</td>
<td>-0.222 [-0.32; -0.12]</td>
<td>h.MF at Reaction = 5.5 0.211 [0.122; 0.307]</td>
</tr>
<tr>
<td>h.HL at Reaction = 4.5</td>
<td>-0.253 [-0.402; -0.104]</td>
<td>w.MF at Reaction = 4.5 0.173 [0.0972; 0.253]</td>
</tr>
<tr>
<td>h.HL at Elevation = 1120 m</td>
<td>-0.229 [-0.325; -0.13]</td>
<td>w.LT at Reaction = 4.5 0.308 [0.116; 0.513]</td>
</tr>
<tr>
<td>h.NF at Elevation = 770 m</td>
<td>-0.317 [-0.425; -0.22]</td>
<td>w.LT at Elevation = 1460 m 0.405 [0.256; 0.561]</td>
</tr>
<tr>
<td>h.HL at Elevation = 770 m</td>
<td>-0.379 [-0.511; -0.255]</td>
<td>h.MF at Elevation = 770 m 0.179 [0.099; 0.249]</td>
</tr>
<tr>
<td>h.LT at Elevation = 770 m</td>
<td>-0.249 [-0.356; -0.132]</td>
<td>w.MF at Elevation = 770 m 0.168 [0.0117; 0.22]</td>
</tr>
</tbody>
</table>

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 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 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 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 tree species richness.
The mean variation that is shared by the groups. Substantial variations of indicators are both ends of each gradient. We put in italics the cases where the standard deviation is log response of species richness to a substantive variation in the indicator between Mean (standard deviation) across 16 ecological groups of the difference of the mean abundance). heliophilous herbaceous species for spruce groups (peri-forest herbaceous species for small diameter tree dominance indicated – mostly negatively – partly different ecological groups. This is as having similar effects on floristic species composition. This is inspired firstly by general considerations as well as more specific results that point in this direction (cf. Section 1): most ecological relationships are not likely to be general across all ecological conditions but instead should depend on the ecological context. Our results partially confirmed our second prediction: the best models always included an interaction of dendrometric indicators with an ecological gradient (cf. Table 6). The relationships between individual indicators and the biodiversity of specific ecological groups were more often non-negligible in certain specific locations (Northern slopes and Jura for abundance measures; Jura, Northern Alps, Internal Alps for RS). However, overall, the frequency of non-negligible cases was less frequent in simple models (2.9% of all groups, 3.7% for herbaceous groups only) than in models analyzed in specific ecological contexts (3.7% of all groups, 5.4% for herbaceous groups only), the differences between these frequencies were non-significant. This result means that even if we demonstrated the importance of ecological context in the dendrometric indicator – biodiversity relationship, this importance is somewhat relative.

### 4.2. The relationship between dendrometric indicators and floristic biodiversity depends on the ecological group and the ecological context

Our second prediction was rather general; it stated that the relationship between dendrometric indicators and floristic biodiversity should depend on the ecological context. This prediction was inspired firstly by general considerations as well as more specific results that point in this direction (cf. Section 1): most ecological relationships are not likely to be general across all ecological conditions but instead should depend on the ecological context. Our results partially confirmed our second prediction: the best models always included an interaction of dendrometric indicators with an ecological gradient (cf. Table 6). The relationships between individual indicators and the biodiversity of specific ecological groups were more often non-negligible in certain specific locations (Northern slopes and Jura for abundance measures; Jura, Northern Alps, Internal Alps for RS). However, overall, the frequency of non-negligible cases was less frequent in simple models (2.9% of all groups, 3.7% for herbaceous groups only) than in models analyzed in specific ecological contexts (3.7% of all groups, 5.4% for herbaceous groups only), the differences between these frequencies were non-significant. This result means that even if we demonstrated the importance of ecological context in the dendrometric indicator – biodiversity relationship, this importance is somewhat relative.

### 4.3. Analysis of biodiversity relationships with indicators along gradients

In addition to studying the relationship between dendrometric indicators and floristic species richness in specific ecological conditions, we also used a rather novel type of analysis to study how these relationships vary among species groups along ecological gradients (cf. Table 8). This analysis allowed us to characterize cases where the indicator/biodiversity relationship was relatively stable across groups along the ecological gradient, but only in relative terms, i.e. in terms of the differences between the coefficients of the indicators between groups. In other words, there was a parallel shift of the relationship across groups along the gradient (bold cases in Table 8). This is similar to a null model in which different ecological groups respond differentially to an indicator, but with a difference in coefficients that remains constant along the gradient. This was the case for indicators based on spruce and fir crown cover measurements along the aspect and reaction gradients. These results could be translated in ecological terms as a global shift from negative interactions between canopy abundance and floristic biodiversity to more positive interactions from one side of the gradient to the other.

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

### Table 8

Mean (standard deviation) across 16 ecological groups of the difference of the mean log response of species richness to a substantive variation in the indicator between both ends of each gradient. We put in italics the cases where the standard deviation is

<table>
<thead>
<tr>
<th>Variable</th>
<th>N–S Aspect</th>
<th>+2 Reaction</th>
<th>+1380 m Elevation</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>0.1 (0.05)</td>
<td>0.19 (0.06)</td>
<td>0.04 (0.13)</td>
</tr>
<tr>
<td>C.fir</td>
<td>0.11 (0.05)</td>
<td>0.26 (0.09)</td>
<td>0.04 (0.15)</td>
</tr>
<tr>
<td>C.spruce</td>
<td>0.17 (0.1)</td>
<td>0.21 (0.06)</td>
<td>0.05 (0.12)</td>
</tr>
<tr>
<td>C.othersp</td>
<td>-0.03 (0.08)</td>
<td>0.05 (0.09)</td>
<td>0 (0.06)</td>
</tr>
<tr>
<td>G.BT</td>
<td>0.04 (0.06)</td>
<td>0.14 (0.11)</td>
<td>0.03 (0.13)</td>
</tr>
<tr>
<td>G.VBT</td>
<td>0.04 (0.1)</td>
<td>0.07 (0.09)</td>
<td>0.02 (0.05)</td>
</tr>
<tr>
<td>G.MT</td>
<td>0.1 (0.08)</td>
<td>0.12 (0.1)</td>
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</tr>
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<td>G.ST</td>
<td>0.12 (0.18)</td>
<td>0.07 (0.1)</td>
<td>-0.03 (0.09)</td>
</tr>
<tr>
<td>G.fir</td>
<td>0.05 (0.05)</td>
<td>0.11 (0.04)</td>
<td>0.02 (0.12)</td>
</tr>
<tr>
<td>G.spruce</td>
<td>0.14 (0.15)</td>
<td>0.13 (0.08)</td>
<td>0.04 (0.17)</td>
</tr>
<tr>
<td>G.othersp</td>
<td>-0.04 (0.17)</td>
<td>-0.02 (0.34)</td>
<td>-0.03 (0.17)</td>
</tr>
<tr>
<td>G</td>
<td>0.06 (0.07)</td>
<td>0.11 (0.05)</td>
<td>0.02 (0.13)</td>
</tr>
<tr>
<td>RS</td>
<td>0.09 (0.18)</td>
<td>0.09 (0.25)</td>
<td>0.12 (0.38)</td>
</tr>
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<td>Dominance.G</td>
<td>-0.04 (0.07)</td>
<td>-0.1 (0.07)</td>
<td>0.01 (0.19)</td>
</tr>
<tr>
<td>Dominance.C</td>
<td>0.02 (0.06)</td>
<td>0.09 (0.07)</td>
<td>-0.02 (0.14)</td>
</tr>
</tbody>
</table>
A third interesting case appeared where there was no central tendency in the variation in the indicator/biodiversity relationship among ecological groups along the gradient but instead a strong variance among ecological groups along the gradient (italic cases in Table 8). This occurred for most of the indicators along the elevation gradient as well as for some indicators along the aspect and reaction gradients. In this case, the indicator could very well be related to biodiversity in some regions of the ecological gradient, but the biodiversity/indicator relationship was unstable across ecological groups in relative terms along the ecological gradient.

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

Following other authors, Austin and Van Niel (2011a,b) made the point that species distribution models should incorporate topographic variables to better predict the future distribution of species in response to climate change. Our results on floristic biodiversity in forests are along the same lines but we go a step further: our results indicate that not only should we take into account topographic information, we should also take into account tree abundance and the interaction between tree abundance and topographic variables. Our results indicate that denser tree cover would decrease some floristic stand-level diversity in northern aspects while it would promote other components of floristic diversity in southern aspects. This can be interpreted in terms of the stress/facilitation hypothesis which states that positive interactions between species are more likely in more ecologically stressful conditions (Callaway et al., 2002; Callaway, 1997; Michalet et al., 2002). Indeed, if we had used the Index of Moisture Availability (IMA) as did Laughlin et al. (2005) (based on Batek et al., 1999), our aspect gradient would have been transformed into a water stress gradient since the IMA predicts greater water stress on steep south-facing slopes. However, other mechanisms may become limiting at certain points along the aspect gradient (e.g. light on northern aspects when tree abundance is high and light levels are reduced). Therefore, we should not too hastily explain the effect of such an indirect ecological gradient, in our case aspect, by a unique more direct ecological gradient (see also Soliveres et al., 2011). Michalet et al. (2002) observed that floristic species composition differed in fir and spruce stands in the French Alps on southern aspects but not on northern aspects. This seems to be a result qualitatively similar to ours in that it indicates an interaction of tree species effect on biodiversity along the aspect gradient. However, in our study, the species richness response of the ecological groups to fir abundance did not strongly differ from their response to spruce abundance along the aspect gradient. Therefore, our results are not completely in agreement with those of Michalet et al. (2002). One difference between Michalet et al. (2002)’s study and ours is that we investigated the impact of tree species abundance, and not tree species dominance in the stand. Also, while Michalet et al. studied species composition, we analyzed the species richness of ecological groups, which reflects presence-absence species composition only if the species inside each ecological group have homogeneous ecological behaviors.

Similar observations were made on the soil reaction gradient — indicative of soil pH. Here too, there was an opposite effect at each end of the gradient. The effects of tree abundance on the species richness of many ecological groups were mostly negative in more acidic conditions, while they were more positive in less acidic conditions (cf. Tables 8 and SM.35–SM.40). Ecologically interpreting this case in terms of stress is more difficult because soil pH should indicate stress at both ends of the gradient, where two different resources are involved (water and nutrients; Maestre et al., 2009). This should result in positive effects of tree abundance at both ends of the gradient, unless the stress-gradient hypothesis is refined as indicated by Maestre et al. (2009). Still our results appear to be in the opposite direction to those of Tyler (1989), who documented a more negative effect of tree crown cover on floristic diversity in less acidic conditions than in more acidic conditions. Similarly, we did not confirm the stress-facilitation hypothesis along the altitudinal gradient as did Callaway et al. (2002) (cf. Tables 8 and SM.28–SM.33). Our results therefore indicate that the “classic” stress-facilitation hypothesis appears on some gradients (here the aspect gradient) but not on others (elevation and reaction) for the species richness of ecological groups. This finding must still be verified through the analysis of the ecological group abundance and species abundance.

4.5. Implications for forest management and biodiversity indicators

One of the conclusions of our research is that not only should we consider all the ecological variables which are involved in the floristic biodiversity (trees, shrubs, herbaceous, etc., cf. Tables 8 and SM.28–SM.33). In this case, floristic biodiversity is an aggregate of floristic diversity, small diameter tree basal area and species richness of ecological groups. The species richness of biodiversity indicators to specify in which ecological contexts and ecological conditions to less acidic conditions) for the abundance of spruce trees (respectively, spruce basal area and cover, fir cover, and basal area of big trees). This means that if floristic biodiversity is the objective, managers should apply opposite guidelines in these contrasted ecological conditions.

Our results support our initial prediction (cf. also Barbier et al., 2008; Barbier et al., 2009a) which states that biodiversity indicators only reflect a part of the biodiversity in specific ecological conditions. Our work therefore promotes evaluating biodiversity indicators to specify in which ecological contexts and which component of biodiversity the indicator has a non-negligible relationship to the biodiversity that can be observed with species richness or species abundance.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.07.049.

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