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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ABSTRACT

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 compo-

nents 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

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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 relations among vegetation strata or plant species vary along different ecological gradients (Callaway et al., 2002; Michalet et 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.
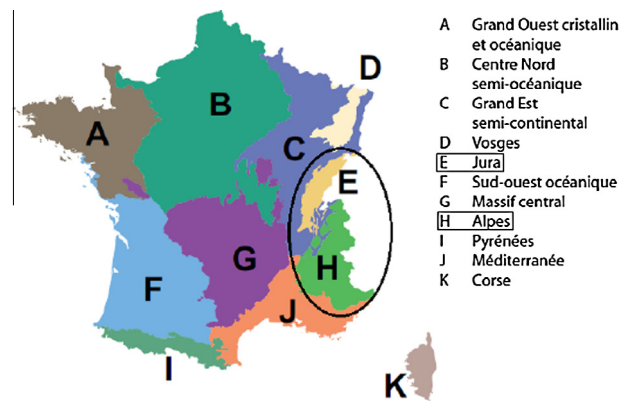

Fig. 1. List of great ecological regions (GRECOs) of France. The circled ones correspond to the study area.

A   Grand Ouest cristallin et océanique
B   Centre Nord semi-océanique
C   Grand Est semi-continental
D   Vosges
E   Jura
F   Sud-ouest océanique
G   Massif central
H   Alpes
I   Pyrénées
J   Méditerranée
K   Corse

(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) floristic 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,