



Original articles

Stand height and cover type complement forest age structure as a biodiversity indicator in boreal and northern temperate forest management



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ABSTRACT

Forest age structure is one of the main indicators of biodiversity in temperate and boreal forests worldwide. This indicator was mainly chosen for the conservation of a subset of rare or sensitive species related to the oldest age classes, not to capture variability across the entire biodiversity spectrum, but is often considered as such. In this study, we analysed alpha and beta diversity in temporary plots of western Quebec, Canada, to consider biodiversity indicators complementary to existing forest age structure targets. Our analysis revealed that considered individually, stand characteristics such as cover type and height are better predictors of changes in site-level contribution to tree beta diversity than age. We also show that plots belonging to different age classes can be similar in terms of tree alpha diversity. Height class was found to have a more significant impact on tree alpha diversity than expected: height was more important than age in coniferous forests, and in deciduous and mixedwood stands it frequently complemented age in explaining the observed diversity patterns. Our results suggest that forest age structure target levels should not be used as the sole indicator of ecosystem sustainability, and that some mature secondary stands can provide significant contributions to biodiversity. We propose that more efficient trade-offs between forest exploitation, ecosystem functioning and environmental conservation can be attained if: (i) forest age structure targets are complemented by cover type and stand height; or (ii) complementary biodiversity indicators of ecosystem sustainability are implemented.

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1. Introduction

Forests provide several fundamental ecosystem services worldwide (Gamfeldt et al., 2013). They contribute to climate change mitigation through the sequestration of CO₂ (Canadell and Raupach, 2008), help sustain local livelihoods (Scherr et al., 2003), provide fresh water supplies (Jones et al., 2009), and harbour numerous endangered species (Myers et al., 2000). Due to the ecological and socio-economic importance of forest ecosystems, a number of management practices at the international and governmental levels have been proposed to help ensure the sustainability of their exploitation. These range from voluntary mechanisms, such as the United Nations Programme on Reducing Emissions

from Deforestation and Forest Degradation (UN-REDD) and forest sustainability certifications granted, for instance, by the Forest Stewardship Council, to governmentally-enforced regulations. While the facultative sustainability mechanisms mentioned above are quite widespread (Auld et al., 2008), only governmentally-enforced practices are truly mandatory.

By agreeing to the Montréal Process (Montréal Process Working Group, 2015), a group of countries accounting for 90% of the world's temperate and boreal forests have agreed to adopt a number of recommendations and follow several indicators for the conservation and sustainable management of temperate and boreal forests. One of the main recognized indicators is forest age structure, of which the proportion of the oldest age classes is the most critical component in a forest management context. Granting oldest stands such an influential position is not without cause. Older forests are associated with critical habitats for species of conservation concern (Drapeau et al., 2016) and epiphytic lichens and bryophytes (e.g. Fritz et al., 2009), improved recreational value (Englin et al.,

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2006), and increased carbon stores (Goulden et al., 2011). These broad links to forest management objectives, coupled with its fairly inexpensive estimation process and its straightforward implementation within timber supply models (Buongiorno and Gilles, 2003), likely justify the widespread use of forest age as a proxy of biodiversity.

Still, using age structure targets do not necessarily capture all facets of biodiversity, and could be complemented or even replaced by different indicators of ecosystem sustainability (Chapin et al., 1996). In particular, variables other than stand age have been documented to have a significant impact on biodiversity. Height class and canopy cover density are linked to stand structural development (Harper et al., 2002), and cover type (deciduous, mixedwood or coniferous trees) is an indicator of the type of species community found in the study area. Recent studies also show that for many potentially sensitive species, habitat quality is not primarily related to forest age, but to particular micro-habitats that could be present or not within a given forest age class. For example, Thompson et al. (2016) found that the presence of large white pines was more important than stand age for cavity nesters in central Ontario mixedwood forests, and Luszcz and Barclay (2016) found that some forest-dwelling bat species in southwestern British Columbia were influenced by forest composition, but not by stand age. These studies confirm that the assumption that relationships between biodiversity and forest stand characteristics are driven primarily by forest age is an oversimplification. This suggests that there is a need to develop complementary indicators that are adapted to capture the effect of forest management practices on overall forest biodiversity.

Biodiversity can be considered as a triumvirate of compositional, structural and functional attributes (Redford and Richter, 1999), and it can be further classified as alpha (local diversity), gamma (regional diversity) and beta diversity (spatial differentiation) (Whittaker, 1972). Measurements of tree biodiversity at the stand- or site-scale, such as species richness and Shannon's diversity, are indicators of alpha diversity. Equally important to consider when examining the performance of biodiversity indicators are the variation in biodiversity between sites at the landscape level, which relates to beta diversity (Whittaker, 1972). Recently, total variance of the sampled community data has been proposed as a useful indicator of beta diversity that is independent from alpha diversity measurements (Legendre and de Cáceres, 2013), which is very advantageous when partitioning diversity into alpha and beta components (Jost, 2007). This methodology also allows researchers to estimate each site's local contribution to beta diversity (LCBD), an indicator of the ecological uniqueness of a site with regards to its contribution to beta diversity. LCBD could therefore complement alpha diversity indicators by identifying sites worth protecting due to their unusual species compositions and degraded sites that require ecological restoration interventions. Despite its recent origin, LCBD studies have already been published in areas as distinct as limnology (Anton-Pardo et al., 2015) and urban forestry (Yang et al., 2015).

The concept of functional diversity, which is the variation or dispersion of functional traits in an ecological group (Laliberté and Legendre, 2010), could potentially complement more traditional biodiversity indicators, such as the previously mentioned species richness and Shannon's diversity. The implementation of functional diversity is still poorly developed within a forest management context (Mori et al., 2016). Functional traits refer to the phenotypic attributes of an organism linked to its effect on ecosystem processes and its response to environmental changes (Hooper et al., 2005; Mori et al., 2013). Functional diversity is considered to be the component of biodiversity most significantly linked to overall ecosystem service performance (Balvanera et al., 2006) and it has been found to be a good predictor of temperate and boreal forest

productivity (Paquette and Messier, 2011). Moreover, functional diversity has been proposed as a proxy for quantifying ecological resilience because of its ability to capture the capacity of communities to respond to a range of disturbances (Standish et al., 2014; Suding et al., 2008).

The aim of this study was to examine the potential of developing a biodiversity indicator complementary to conventional forest age structure targets. In order to do this, we used data from temporary sampling plots of western Québec (eastern Canada) to assess how these targets, originally designed to protect a subset of sensitive species within boreal and northern temperate hardwood forests, capture: (i) variability of diversity at the landscape scale using a novel indicator of beta diversity, local contribution to beta diversity (LCBD); and (ii) variability of overall compositional, structural and functional biodiversity at the site level (alpha diversity). First, we estimated beta diversity, determined each plot's LCBD and assessed which variables best explained variability in LCBD. Then, we calculated three measures of tree alpha diversity (site-level compositional, structural and functional diversity) and we compared the influence of stand-level variables (age included) on these measures of tree diversity. We further explored the forest management implications of our results.

2. Methodology

2.1. Study area

We used data from temporary sample plots located in western Québec, Canada (Fig. 1). These plots are distributed across a latitudinal gradient that ranges from the northern temperate forest to the southern boreal forest and encompass a number of distinct climates,

forest communities, prevalent natural disturbances and forest management practices. Six distinct bioclimatic domains are included in this latitudinal gradient: sugar maple (*Acer saccharum*)-basswood (*Tilia americana*), sugar maple-bitternut hickory (*Carya cordiformis*), sugar maple-yellow birch (*Betula alleghaniensis*), balsam fir (*Abies balsamea*)-yellow birch, balsam fir-white birch (*Betula papyrifera*) and black spruce (*Picea mariana*)-feathermoss (Robitaille and Saucier, 1998). Sample points located to the north of the northern limit of the harvestable boreal forest were excluded from our analyses.

A total of 99,429 sampling plots from this database were used. Within each circular plot of 400 m², all trees with a diameter at breast height (DBH) greater than 9 cm are identified, their DBH measured and the overall percentage of defoliation estimated (MFFP, 2016). At the centre of each 400 m² plot is a smaller 40 m² circular plot where saplings (DBH ≤ 9 cm) are identified and counted by DBH class. Plots are sampled randomly according to a stratified sampling design: 15 plots are sampled per strata, which are defined according to forest age and composition. Sampling effort varies between main vegetation zones (deciduous, coniferous and mixed). Stand age class is determined through visual inspection of the plot and core-based ageing of three trees per plot, cover type is estimated according to the basal area occupied by coniferous species (deciduous: <25%; mixedwood: 25–50%; coniferous: >75%), and height class is the mode of the photo-interpreted height of all trees in the plot. Data examined was collected between 1970 and 2012 (MFFP, 2016).

2.2. Beta diversity analysis

Beta diversity was estimated according to the methodology proposed by Legendre and de Cáceres, (2013) using the R scripts provided therein. Beta diversity was measured as the total variance

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