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Biodiversity response to forest structure and management: Comparing species richness, conservation relevant species and functional diversity as metrics in forest conservation

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A R T I C L E I N F O

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A B S T R A C T

Aim: We investigated the consistency between richness and trait-based diversity metrics in capturing the effects of management-related habitat factors on biodiversity. The choice of biodiversity metrics can substantially affect the evaluation of conservation tools. However, the relative sensitivity of different metrics is not well investigated, especially in a multi-taxon framework.
Location: European beech forests in Denmark.
Methods: We studied 20 beech stands comprising four management types (from intensively managed to long unmanaged stands). We analyzed how management-related environmental variables were reflected in the measure of: (i) species richness, (ii) number of conservation-relevant species (red-listed species and old-growth forest indicators) and (iii) functional diversity targeting five organism groups with different habitat requirements, i.e. vascular plants, epiphytic lichens and bryophytes, saproxylic fungi and breeding birds.
Results: Plain species richness at stand level was generally misleading, as it did not capture changes in the number of conservation relevant species with changes in management-related environmental variables. The interpretation of functional responses was most informative for the better known vascular plants, while responses were more fragmented for the other organism groups. Overall, however, functional responses were consistent with a loss of specialization and progressive simplification of species assemblages from long-unmanaged to intensively managed stands.
Conclusions: Our findings suggest that the occurrence of conservation-relevant species is a sound and relevant metric for planning and evaluating conservation actions, especially for less studied organism groups (e.g., saproxylic fungi and epiphytes). The functional approach is promising, but presupposes the availability of databases of relevant traits.

1. Introduction

European beech forest is a fundamental type of natural vegetation in temperate Europe (Brunet et al., 2010). However, a long history of human use including modern forestry (Bengtsson et al., 2000) has led to substantial habitat loss and changes in forest structure and dynamics (e.g., Paillet et al., 2010; Burrascano et al., 2013). Human intervention has generated a simplification of forest ecosystems, with a consequent decrease of several sensitive and narrow-range species depending on structures and processes of old-growth forests (e.g., Brunet et al., 2010; Paillet et al., 2010, Sabatini et al., 2018). For instance, certain epiphytic bryophytes and lichens, which inhabit old and damaged trees, are threatened due to the removal of their habitat trees in production forests (Fritz and Brunet, 2010). To counteract biodiversity loss, various measures have been suggested, spanning from the segregation of non-intervention forest reserves to the integration of wildlife-friendly

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elements, such as leaving retention trees and dead wood to support habitat specialists, in so-called “near-natural” forestry (Bauhus et al., 2009). While forest reserves represent a land-sparing approach, “near-natural” forestry is cognizant with a land-sharing philosophy, resting on the assumption that silviculture can be optimized to protect most forest biodiversity without major consequences for economic outcomes. However, knowledge of the impacts of “near-natural” forestry on biodiversity is limited in the temperate zone. Therefore it is debated how the two approaches can be combined and balanced to provide cost-effective conservation (Kraus and Krumm, 2013).

So far, the effects of management on biodiversity have been investigated mostly with a focus on stand-level species richness (Paillet et al., 2010; Chaudhary et al., 2016), probably because it represents the simplest way to measure biodiversity (Colwell and Coddington, 1994). Nevertheless, it presents relevant shortcomings. Firstly, species richness is highly prone to scale issues, which may result in misleading conclusions for conservation (Gotelli and Colwell, 2001; Chiarucci et al., 2011). In fact, fine-scale partitioning of resources may generate patterns of species diversity not properly addressed if focusing only on one fixed spatial scale (e.g., Standovár et al., 2006). Further, high species richness within stands (i.e., alpha-diversity) may mask lower levels of diversity across stands (i.e., beta-diversity) with homogenization at regional level (i.e., gamma-diversity) (Schall et al., 2018). Secondly, species richness may be misleading if adopted as an indicator for the conservation status of the forests. For instance, Boch et al. (2013) suggested species richness of vascular plants as indicator for disturbance by management. Indeed, plants may benefit from resource increase (such as light or nutrients) following moderate disturbance by management or other human uses (Roberts, 2004; Christensen and Heilmann-Clausen, 2009).

To account for these shortcomings, many researchers have focused on subsets of conservation-relevant species (Dolman et al., 2012). Red-listed species have been used to assess the conservation value of forests (Flensted et al., 2016), while other studies have focused on species with specific habitat requirements and/or particular biological attributes. For example, cavity-nesting birds have been adopted as target species to indicate critical thresholds of veteran trees and microhabitat abundance (Winter and Möller, 2008). These target species are often associated with old-growth forests conditions, including stand continuity (Hermy and Honnay, 1999; Schmidt et al., 2014). In many cases, however, the links between species and habitat conditions remain poorly understood or the bioindication is so obviously circular that the indicators have little relevance (Nordén et al., 2014; Halme et al., 2017).

Recently, functional approaches have been proposed as an alternative way to assess the impact of forest management on biodiversity (e.g., Giordani et al., 2012; Aubin et al., 2013). By focusing on the “kinds” of species rather than their numbers, a functional approach potentially gives a better understanding of the mechanisms driving habitat changes and species assemblages (Pausas and Verdú, 2010), allowing also comparisons across different ecosystems, regions and management systems. This approach may therefore be suitable to capture ecosystem properties and the effects of disturbances (e.g., Bässler et al., 2016a, 2016b). Despite these potentials, the reliability of functional measures is still not well known.

In all, choosing one metric of biodiversity over another may have substantial consequences on the evaluation of conservation tools. However, the consistency of different metrics is still scarcely investigated, especially in a multi-taxon framework, limiting applicability in practice.

The aim of our study was to investigate if different metrics of diversity show consistent patterns along a management-related environmental gradient, from long unmanaged to even-aged managed stands of European beech. We investigated how different diversity metrics (i.e., total species richness, richness of conservation-relevant species, and functional diversity) were related to this gradient, and hence may be indicative for the variation of forest attributes (i.e., structural and environmental ones) across five organism groups (vascular plants, epiphytic lichens and bryophytes, saproxylic fungi and birds).

We expected a non-consistency among the compared metrics, as well as among organism groups. Concerning the (1) total species richness (at stand level), we expected vascular plants to be favoured by human disturbance, in contrast to the other organism groups, but with a weak response of birds more likely depending on habitat suitability on a higher spatial scale than the stand level. Nevertheless, accounting only for the (2) richness of conservation-relevant species we hypothesised a general decrease from the long-unmanaged to the managed stands. Consistent with this trend we expected a homogenization of (3) functional diversity (at single-trait level) for all the organism groups, with a trend towards more generalist strategies, broad ecological niches and higher dispersal ability as response of disturbance by management.

2. Materials and methods

2.1. Study area

The study was conducted in Gribskov, one of the largest coherent forests in Denmark, covering an area of almost 6.000 ha. The terrain is undulating (9–89 m a.s.l.), with numerous boggy depressions. The topsoils are generally developed as mor or moder on glacial sandy to gravelly deposits stemming from the Weichelian glaciation. The forests are shaped by two centuries of timber oriented forestry, with European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) dominating and largely found as even-aged monocultures. European beech established in the area almost 6000 yrs ago, but became dominant only within the last 1000 yrs (Overballe-Petersen et al., 2013), while Norway spruce was introduced with modern forestry during the latest 250 yrs (Rune, 2009). Only small remnants of old-growth forests are left, mainly as stands smaller than 5 ha. The climate is temperate with an average annual precipitation of 697 mm and an annual mean temperature of 7.7 °C.

2.2. Data collection

Twenty forest stands, each 3 ha in size, were selected based on existing information and field visits during winter/spring 2015, using a stratified random sampling design to secure a balanced representation of management impact over space and time in the study landscape. The stands were selected to represent four broad classes based on management history and structural attributes in five replicates. Each class was defined based on detailed information in Graae and Buchwald (1997): (1) stands unmanaged for more than 50 years with dominant trees older than 200 years; (2) stands unmanaged for less than 50 years with dominant trees older than 100 years; (3) extensively managed biodiversity stands with dominant trees older than 100 years, and components of structural heterogeneity, in the form of a multi-layered canopy and the presence of at least some coarse woody debris (CWD); and (4) intensively managed stands with dominant trees older than 100 years, a simple structure with one or two dominant tree layers and no or little CWD. All selected stands were dominated by European beech (> 60% of basal area). Due to the rarity of long-unmanaged stands, these were selected first. In the second step, the topography, geography and general growth conditions (soil type) of the long unmanaged stands were used to guide the selection of stands in the other management categories, which were aggregated in four clusters containing one or two replicates of each management type (Fig. 1). To account for random and non-random spatial effects, we selected forest stands occurring in clusters where each of the four management levels is represented.

To sample the stands and collect species data, we randomly placed ten 50 m transects and ten circular plots with 5 m radius, respecting a minimum distance of 30 m between the plots. Up to five of the random plots were subsequently substituted with an equal number of plots

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