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Restoring hydrology and old-growth structures in a former production forest: Modelling the long-term effects on biodiversity

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A B S T R A C T

The biodiversity value of production forests is substantially lower than that of natural forests. This is related to differences in hydrology, stand age and amounts of old trees and deadwood. Using a predictive model framework we show that restoring hydrology and old-growth characteristics in a forest formerly managed for timber extraction results in changes to forest composition and structure, ultimately increasing its biodiversity value.

We inventoried biodiversity and stand variables in 102 sample plots in a temperate mixed broadleaved forest, which is in focus of a LIFE+ programme aiming to restore hydrology and old-growth structure. We collected presence/absence data for four organism groups (vascular plants, epiphytic bryophytes and lichens, wood-inhabiting fungi) and measured environmental variables associated with species occurrence and influenced by restoration (dead or living tree characteristics, stand age, water level). We investigated biodiversity consequences of restoration towards pristine environmental characteristics by using a space-for-time substitution model. We evaluated how and through what mechanisms species richness is likely to react when pre-forestry hydrological conditions and old-growth structures are restored.

The model results show that reversing the effects of a long history of management for timber extraction increased availability of suitable habitat, and hence the local species richness for three of four of the organism groups, compared to the pre-restoration conditions. Furthermore, the increase in soil moisture shifted the forest plots towards an alder carr, while the stand ageing process sustained the shade-tolerant beech despite its low tolerance for high soil humidity. Our prediction shows an increase in species richness for plants directly driven by the restoration of natural water level, and for fungi as an indirect effect of a change in suitable substrate availability. Lichens responded positively to both processes. Plants stabilized their richness levels earlier than tree-dwelling organisms, as water level recovered faster than old-growth structures. The projection of stable bryophytes richness values under restoration is potentially biased by their lower diversity and more limited affiliation to forest structural variation than other groups.

We suggest applying our space-for-time approach as a tool to assess forest and biodiversity responses in similar restoration projects involving management actions of open-ended habitat creation, promoting development of natural processes in the long-term. This modelling tool turns to be especially relevant in dynamic habitats where the outcomes for biodiversity are uncertain.

1. Introduction

Production forest differs substantially from natural forest, not least in stand structure, deadwood amount and soil disturbance, and this difference is also reflected in its more limited biodiversity value (Christensen and Emborg, 1996; Paillet et al., 2010). In

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temperate deciduous swamp forests, recovery of naturalness involves restoring natural water levels and tree age profiles, as these are among the most important environmental factors affecting their biodiversity value (Brūmelis et al., 2011). Restoring forest naturalness can be achieved through quitting drainage by filling ditches, and old-growth structures will slowly recover after abandonment of timber extraction (Paillet et al., 2015) or it can be actively created e.g. by killing trees and creating gaps (see Halme et al., 2013).

Restoration affects groups of species in different ways (Görn and Fischer, 2015). Restored hydrology in forest is likely to enhance species richness for vascular plants, epiphytic lichens and ground bryophytes (Härdtle et al., 2003), whereas an increase in stand age is expected to increase richness of epiphytic bryophytes and lichens (in beech forest, Fritz et al., 2009; in humid forests, Crites and Dale, 1998) by increasing substrate amounts and quality through recovery of old-growth structures (Fritz and Heilmann-Clausen, 2010). Similarly, restoring deadwood is expected to increase richness for fungi depending on it as a resource (Müller and Bütler, 2010).

An assessment of the long-term effects of restoration on biodiversity is beyond the possibilities of a standard monitoring programme, but visible and measurable forest structural patterns can be translated into quantitative targets for biodiversity management (Bütler et al., 2004). As such, they may also be modelled in time, allowing the prediction of future habitat suitability under restoration scenarios (Ranius and Kindvall, 2004). If links between habitat suitability and biodiversity are well understood, the biodiversity response can be evaluated against pre-restoration conditions (Maron et al., 2013).

In this study, we model how forest biodiversity reacts to recently initiated open-ended ecological restoration in a forest reserve formerly used for timber extraction. We characterize how, and through what mechanisms, restoration of hydrological gradient and old-growth structure affect key forest habitats and consequently species richness. We investigate the response of four groups of organisms associated with different habitats, and responding differently to changes in the forest: wood-inhabiting fungi, epiphytic lichens and bryophytes, vascular plants.

Our approach was to first project changes in living tree basal area and deadwood volumes determined by an increase in stand age and water level. Then, we evaluated the effects of the recovery of the environmental conditions for biodiversity through space-for-time substitution (Pickett, 1989; Banet and Trexler, 2013), a technique used in predictive modelling when long time-series are not available, as follows: (1) we modelled species richness for each ecological group through a curve-fitting correlative approach. This implies estimation of the spatial relationships between current richness and the environmental gradients measured in the sample plots of the reserve; (2) we employed these spatially-explicit correlative models to generate projections of future species richness under the restored values of the environmental gradients. We limited our analysis of restoration effects to species richness, our study focusing more on the mechanisms driving forest change via restoration actions, rather than exploring the separate effects for all the species and biodiversity components.

We hypothesize that: (1) an increase in water level will increase species richness in most groups, because many forest species are hygrophilous (e.g. Härdtle et al., 2003 for vascular plants, epiphytic lichens and ground bryophytes); (2) an increase in forest age following the cessation of forestry will increase richness of groups associated with these resources (e.g. Crites and Dale, 1998; Fritz et al., 2009 for epiphytes; Müller and Bütler, 2010 for wood-inhabiting fungi); (3) species richness would increase faster in groups with many species directly benefiting from moistening soil, like plants, if compared with groups, where the proportion of species benefiting from moistening via slowly accumulating woody debris is greater, like wood-inhabiting fungi.

2. Materials and methods

2.1. Study area

Our study area was the forest of Lille Vildmose nature reserve in Denmark (56°509N, 10°159E, Fig. 1a), officially protected 2007 (World Database of Protected Areas, WDPA). Lille Vildmose (7800 ha) is the largest protected area in Denmark and includes conifer plantations, grasslands, lakes, moors, an intact raised bog and several old-growth forests remnants, aggregated in two more coherent forest complexes (maximum distance between sites 10 km): Tofte Skov (500 ha) and Høstemark Skov (133 ha) (Fig. 1b). Both sites are protected under the Habitat Directive since 1998 (WDPA). Our study plots fall into three vegetation types: mixed swampy deciduous forest (60 plots with current median water level (WL) across study plots = −4.9 cm, interquartile range (−16.69; 0)), almost pure beech (i.e., 25 plots with more than 45% of the basal area represented by beech, with lower WL = −21.3 cm, interquartile range (−30.13; −11.75)), mixed deciduous-coniferous forest (17 plots with the lowest WL = −29.0 cm, interquartile range (−40; −16.63)). The dominant tree genera in the plots are *Alnus*, *Betula*, *Fagus* and *Quercus*, and the old-growth part is mainly dominated by *Fagus* and *Quercus* (Fig. 2). Due to high browsing pressure from red deer *Cervus elaphus* under fence in the study area (about 10 adults per km^2; Buchwald, 2012), the forests are relatively open.

2.2. The restoration project

The study area consists of near-natural mixed deciduous forest, with some introduced conifers intermixing. All forests have been subjected to timber extraction in the past, mainly as high forest, but some stands have been subject also to coppicing almost 100 years ago. Further, some stands have been affected by active tree planting, or by selective cutting of certain tree species homogenizing the stand structure. In a natural state the forests in Lille Vildmose would be more humid than today, due to flatness of the area and a high ground water table, but drainage has been pursued to increase timber production. In 2009 open-ended restoration projects were initiated in both of the forest complexes, with the aims to recover natural hydrology and allow a free stand development with only minimal interventions to counteract the impact of past management for timber extraction, e.g. removal of invasive Sitka spruce (*Picea sitchensis*) (Riis et al., 2009a,b). The water level (WL) will be gradually raised on 770 ha, achieving the natural pre-drainage level by 2050. This is attained by filling ditches or blocking their outlets; in addition, the study area is adjacent to a European Union's LIFE+ Nature and Biodiversity funding programme 2011–2016, with the objective to preserve and restore large raised bogs between the forest complexes (Anonymous, 2011). Riis et al. (2009a,b) predicted a decrease in drainage depth by 2050 causing an increase in WL (current median WL across study plots = −14.7 cm, interquartile range (−25.31; −3.44); predicted future median level = −10.3 cm (−16.77; −2.72)). Especially in the areas where the WL raise will be highest, beech mortality is expected to make room for the more hygrophilous trees, alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), birch (*Betula pendula* and *B. pubescens*) and oak (*Quercus petrea*, *Q. robur*, *Q. rubra*). The gradual abandonment of production forestry over the last decades has already partly resulted in a high stand age (SA) in most of the area (medianSA(2013) = 129 yrs, minSA(2013) = 29 yrs, maxSA(2013) = 235 yrs; $\%SA(2013)_{yrs<100} = 16\%$, $\%SA(2013)_{105\leqslant yrs\leqslant 140} = 53\%$, $\%SA(2013)_{yrs=235} = 31\%$). The set-aside regime will increase SA to the