



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



Adriano Mazziotta^{a,*}, Jacob Heilmann-Clausen^a, Hans Henrik Bruun^b, Örjan Fritz^c, Erik Aude^d, Anders P. Tøttrup^a

^a Center for Macroecology Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

^b Section for Ecology and Evolution, Department of Biology, University of Copenhagen, Copenhagen, Denmark

^c Naturcentrum AB, Sweden

^d HabitatVision A/S, Denmark

ARTICLE INFO

Article history:

Received 18 July 2016

Received in revised form 17 September 2016

Accepted 19 September 2016

Keywords:

Bryophytes

Forest restoration

Lichens

Space-for-time substitution

Vascular plants

Wood-inhabiting fungi

ABSTRACT

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.

© 2016 Elsevier B.V. All rights reserved.

* Corresponding author at: Center for Macroecology Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, Copenhagen, Denmark.

E-mail addresses: a_mazziotta@hotmail.com, adriano.mazziotta@snm.ku.dk (A. Mazziotta), jheilmann-clausen@snm.ku.dk (J. Heilmann-Clausen), hbruun@bio.ku.dk (H.H. Bruun), orjan.fritz@naturcentrum.se (Ö. Fritz), eau@habitatvision.dk (E. Aude), aptottrup@snm.ku.dk (A.P. Tøttrup).

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

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 (Brümeliš 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°50'N, 10°15'E, 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 km²; 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 petraea*, *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≤yrs≤140} = 53%, %SA(2013)_{yrs>235} = 31%). The set-aside regime will increase SA to the

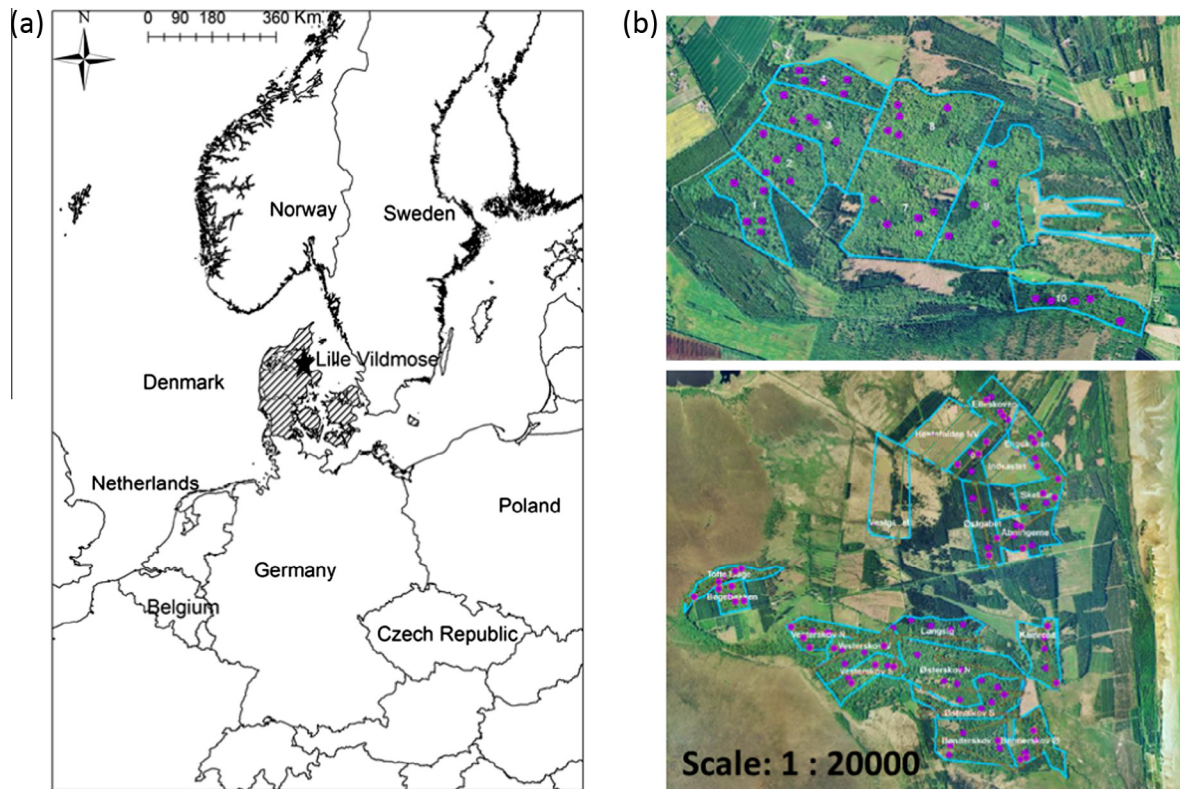


Fig. 1. Study area. (a) Location of the Lille Vildmose reserve in Denmark; (b) aerial photograph showing the monitoring scheme in the two forest sites (above, Høstemark Skov, below, Tofte Skov) consisting of polygons (blue) and sample plots (pink) (scale 1:20,000). Polygons in open areas do not contain any sample plot. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

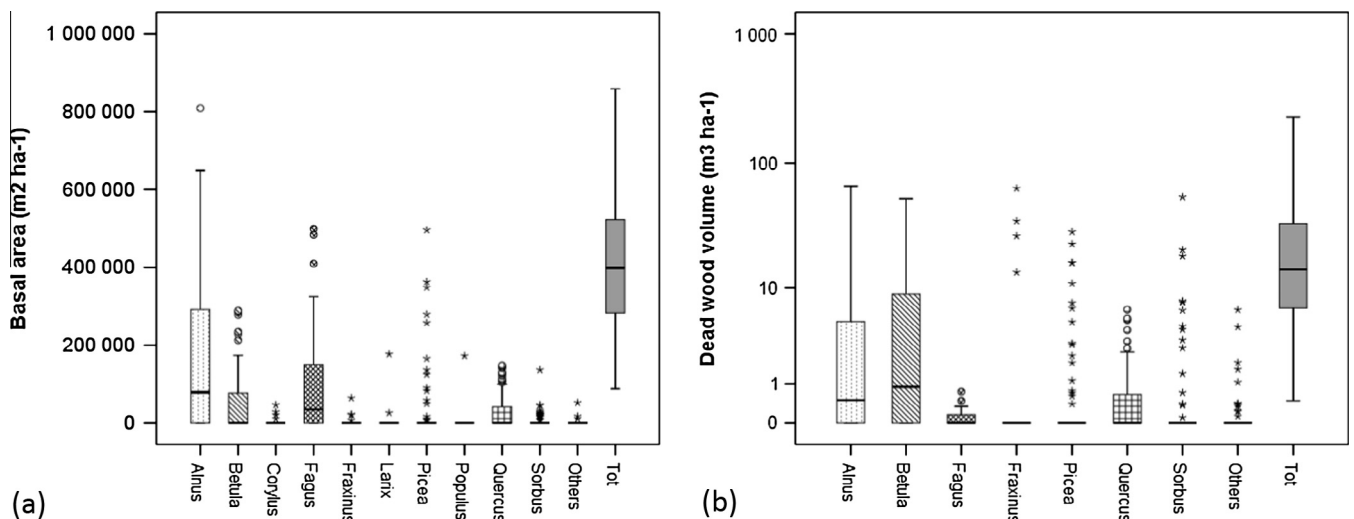


Fig. 2. Current variability (i.e., pre-restoration conditions in 2013) in the measured cumulative values of (a) basal area and (b) deadwood volume for tree genera in the plots of the study area for different tree genera in Lille Vildmose. Box plots show the distribution of cumulative values (mean, interquartile range, ○ outliers; ★ extreme values) of plots. “Others” for basal area (BA) indicates the sum of genera (i.e., *Juniperus*, *Pinus*, *Salix*) with BA < 10⁵ m². For deadwood (DW), “Others” include genera (i.e., *Corylus*, *Juniperus*, *Larix*, *Pinus*, *Populus*, *Salix*) with DW < 10² m³. Note the logarithmic scale for deadwood in (b).

level of old-growth forests for all the stands by the end of the 21st century (medianSA(2100) = 216 years, minSA(2100) = 116, maxSA(2100) = 322).

2.3. Data collection

In the two forest areas we sampled species and environmental data using a stratified random scheme (Fig. 1b). First we defined

22 polygons on a map to represent various forest types and variation in drainage levels (Fig. 1b). The variation in drainage levels partly reflect natural topographic variation, but are also highly influenced by former drainage by ditching in most of the area. In each polygon, we randomly placed 5 circular sample plots (radius 15 m), settled at a minimum distance of 30 m from each other and with a 15 m minimum buffer distance from forest edges with the purpose to sample homogeneous forest habitats (Fig. 1b). In each

of the 102 forest plots, we recorded species incidence (presence-absence; species lists in Data in Brief DiB_A.xls) for each ecological group, i.e. vascular plants, wood-inhabiting fungi, and epiphytic bryophytes and lichens with the following procedures during 2013:

- Vascular plants (215 species, 87.4% of the richness estimated by a homogeneous model where all species have equal detection probability; Lee and Chao, 1994) were recorded in a 5 m circular plot concentric with the study plot. Vegetation was monitored in the field in summer.
- Fruit bodies of wood-inhabiting fungi (193 species, 88.2% of the estimated richness) were recorded per each deadwood item in the plot, on two occasions (August, October) to cover early and late phenology.
- Epiphytic bryophytes (61 species, 91.0% of the estimated richness) and lichens (120 species, 94.4% of the estimated richness) were recorded on all standing live and dead trees with DBH ≥ 10 cm from 0 up to 2 m height in each plot. Stumps taller than 1.5 m were also inspected, whereas lying wood was excluded from the survey; epiphytes were surveyed in April, August and October.

Species identification in all the surveys was carried out in the field if possible. Specimens were taken for later microscopic identification if needed.

In order to capture environmental gradients explaining species richness (Table “Richness_Env” in DiB_A.xls), the following variables associated with resources and disturbances were measured across sample plots during the species sampling in 2013, mainly following the standard protocols given by Fredshavn et al. (2011): (1) dimensions and tree species for all deadwood items with diameter ≥ 10 cm and length ≥ 1 m; (2) all living trees with diameter ≥ 10 cm identified and their DBH; tree DBH was used to calculate living volumes according to allometric formulas by Zianis et al. (2005) (maximum height for each tree species was obtained at plot level from Riis et al. (2009a,b)); (3) number of trees with rotten parts in each plot, i.e. living trees with visible and substantial decay (area >100 m²) by wood-decomposing fungi; (4) water level (WL) averaged from 4 different measures, each taken 5 m from the center of the plot. If WL was above ground, water surface depth was measured as a positive value. Otherwise, a small hole was dug and distance from the ground level to the raised water surface was measured as a negative value. If no water rose when 40 cm depth was reached, the value was recorded as “ >-40 cm”. Maximum WLs were measured for all the plots on 24–25th February 2013, two days without precipitation. Future WLs by 2050 (year of achievement of pre-disturbance hydrological conditions) were estimated by means of hydrological models using the predicted drainage depth (described in Riis et al. (2009a,b)); (5) stand age for each plot was taken from the forestry maps of the area and yearly incremented during restoration.

2.4. Modelling restoration targets

The water level (WL) is of direct importance for plants, as a proxy for soil moisture in each plot, and of indirect importance for epiphytes, as a proxy for air humidity. The stand age (SA) is directly important for epiphytes and fungi, as a proxy for density of old trees and structures. The tree basal area (BA), and its diversity in terms of substrates of tree genera, are of direct importance for epiphytes, as a proxy for inhabitable bark area, and indirectly important for vascular plants and epiphytes, by differently altering understory light conditions and microclimate (models including also canopy cover as predictor showed less predictive power than models including only the effects of BA). The deadwood volume

(DW) is directly important for wood-inhabiting fungi as a resource. BA and DW of each tree species are differently affected by SA and WL (in Appendix A, Supplementary Table A). The current variability in the values of BA and DW for tree genera in the plots is reported in Fig. 2. Future BAs and DWs were projected for two restoration goals: when only the WL is restored (by 2050) and when also each stand has achieved old-growth structure (SA > 100 years by 2100). First (1) for each tree genus we modelled the dependency between current (=2013) BA/DW (response variables) and SA or WL or their interaction (predictors) (Supplementary Table B, see below); second (2), we made use of the equations' coefficients estimated in (1) to project the future BA/DW under restored hydrological gradient and old SA profile (Fig. 3).

In (1) the choice of the predictor to model was based on its independent importance for the response variable, evaluated through multilayer perceptron, a neural network technique accounting for non-linearity minimizing the prediction error of the dependent variable (Schalkoff, 1992), as in Supplementary Table A; we chose to model the interaction term SAxWL, as better capturing the whole effect of restoration actions, when its importance was comparable to the single predictors, as in the case of *Alnus* and total BA, while we modelled deadwood volume of *Betula* with SA as this relationship better reflected *Betula*'s heliophilous characteristics. The functions' shape and parameters best approximating the dependencies of living BA/DW from SA/WL were the ones highly ranked by the CurveFinder tool in the curve fitting software CurveExpert 1.4 (Hyams, 2005), i.e. with comparatively low standard error and residuals. Among the highly ranking models (Supplementary Table B) we chose those better describing forest compositions through the existing variability in the environmental gradients.

2.5. Modelling species richness

For each ecological group we first estimated the Kendall rank correlations between species richness and all the collected environmental variables (Supplementary Table C). To predict species richness (response variable) under current and projected environmental predictors, we used the following procedure: (1) we ran full linear models containing all the environmental predictors, removing less-important predictors showing strong collinearity (high Variance Inflation Factor, VIF > 2.5); (2) we evaluated the competing models including all the remaining predictors through a multi-model inference procedure, and selected the best models balancing high likelihood and numbers of predictors (with limited differences in corrected Akaike Information Criterion (AICc) from the model with the lowest AICc value, i.e. $\Delta AICc < 2.0$); (3) for the best models describing species richness, we applied geographically weighted regression (GWR) to account for spatial autocorrelation and spatial patterns across the sample plots (Fotheringham et al., 2002) (Fig. 4; Supplementary Table D). GWR fits “local” linear regressions (with an adaptive spatial kernel) for each plot estimating separate slopes and intercepts, and makes the residuals in the model spatially independent. Therefore this technique improves the predictive power of our space-for-time approach. We retained environmental variables substantially improving the GWR models even if only marginally significant ($P < 0.1$). To account for spatial variability in the explanatory power of the GWR models, we provided both overall model explained variance (r^2) and average variances across the plots accompanied by coefficients of variation at 95% level (Supplementary Table D). We did not include interaction terms, as they were poorly improving r^2 or highly redundant (VIF > 2.5). GWRs were performed using SAM (Rangel et al., 2010), Generalized estimating equations (GEE) (Hardin and Hilbe, 2003), accounting for the spatial correlation in the response variables, were run for testing differences in BAs and DWs (predicted values

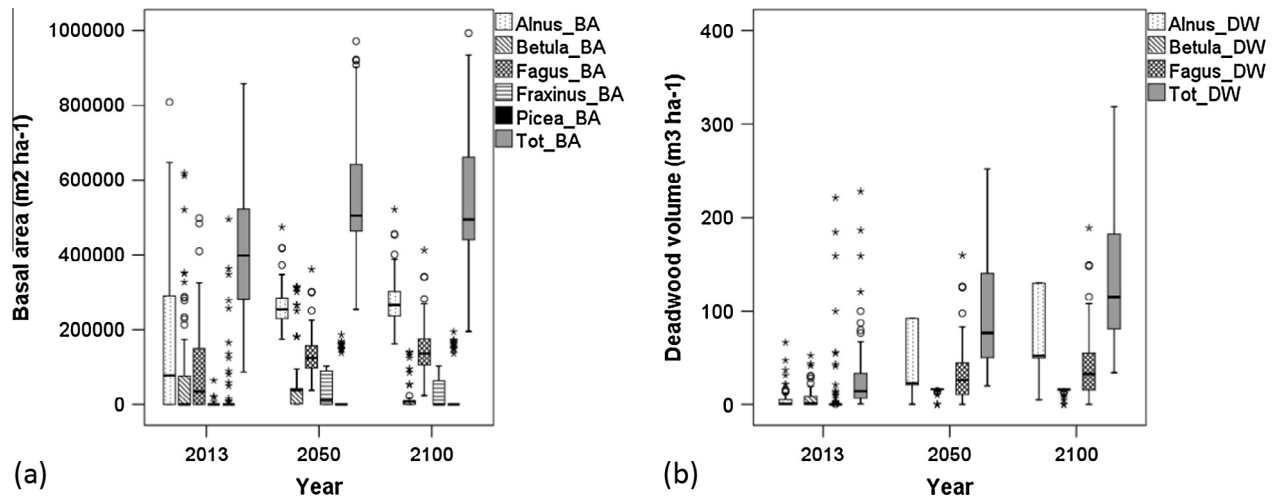


Fig. 3. Predicted effects of restoration on forest trees. Predicted effect of restoration on levels of (a) basal area (BA) and (b) deadwood volume (DW) for different tree genera affected by changes in water level and stand age in Lille Vildmose. Boxplots show the distribution of cumulative values (median, interquartile range, \circ outliers, \star extremes) across plots. Measured cumulative values are provided at present in the pre-restoration conditions (2013), predicted values when only water level is restored at the target level (2050) and when both water level and stand age are restored (2100).

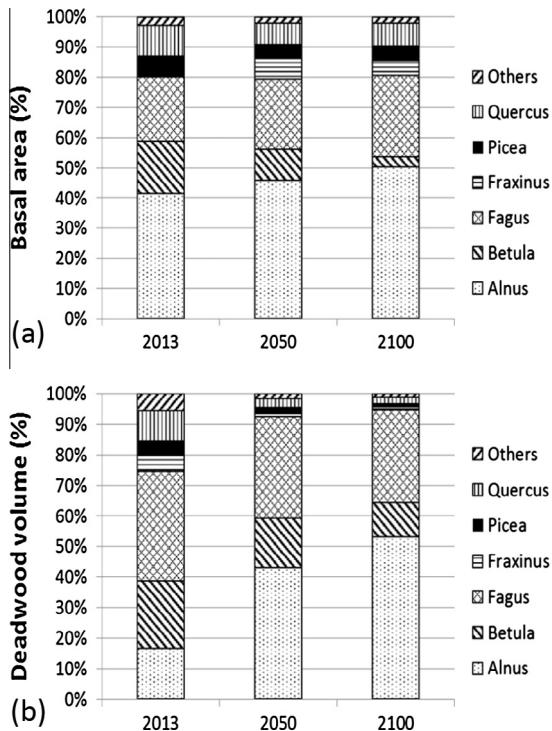


Fig. 4. Predicted effects of restoration on forest characteristics. Predicted changes induced by forest restoration in the proportions of (a) basal area and (b) deadwood volume for different tree genera in the Lille Vildmose. Average measured values are provided at present in the pre-restoration conditions (2013), average predicted values when only water level is restored (2050) and when both water level and stand age are restored (2100).

in [Supplementary Table E](#), details in [Supplementary Table F](#)) and in species richness ([Supplementary Tables G and H](#)) (continuous response variables) between restoration phases (categorical predictor) using SPSS (IBM Corp., 2011).

Even though our models were based on environmental gradients of proven importance for forest biodiversity, the choice of using few predictors goes in the direction of finding common drivers of environmental change induced by restoration, but it is still a simplification of all the processes going on in the real forest.

Furthermore, while our approach and predictions allow exportable conclusions on the effects of forest restoration, species-environmental curves are tailored on the area under study and should not be used for any forecast outside the lengths of the explored current and future environmental gradients.

3. Results

3.1. Environmental projections under restoration scenarios

In 2013 the mean standing living volume of the current forest was $210.8 \text{ m}^3 \text{ ha}^{-1}$ (S.D. = $93.0 \text{ m}^3 \text{ ha}^{-1}$) and the mean deadwood volume was $27.9 \text{ m}^3 \text{ ha}^{-1}$ (S.D. = $37.9 \text{ m}^3 \text{ ha}^{-1}$). When the natural water level (WL) was restored, the total forest basal area (BA), and consequently the total accumulated deadwood volume (DW), were projected to be significantly higher than in the pre-restoration levels (respectively, an average +43% in BA and +245% in DW by 2050). When also the stand age (SA) was restored by 2100, BA remained practically stable, being reduced only by 6% respect to 2050, but the deadwood volume increased by 131%, achieving an average of $132.8 \text{ m}^3 \text{ ha}^{-1}$ (S.D. = $65.4 \text{ m}^3 \text{ ha}^{-1}$) (Fig. 3a and b).

For the living tree BA, the models predicted the restored forest landscape to be dominated by alder (almost 50% of the total BA by 2100) and beech (c. 25%), the highest proportions of other species being oak (c. 7%), ash and spruce (both c. 5% of the total) (Fig. 4a). Approaching a higher WL and SA, the forest showed a slow turnover in the dominance of living tree species. Compared to pre-restoration levels the most dramatic changes were an increase in the proportions of the hygrophilous alder (overall, an average +9% in the BA by 2100, from an average 40% in 2013) and ash (+4.6% by 2100, from only 0.3% in 2013), but even beech, already well represented in the pre-restoration forest (21% of the BA), showed a marked increase (+5% by 2100). The light-demanding oak (10% of the BA in 2013 and not affected by restoration, but slightly, −3%, lower proportion by 2100) and birch (overall −13% by 2100, from 17% of the BA in 2013), both decreased in relative proportions. Finally, the spruce BA did not significantly increase, but slightly decreased (−2% by 2100, from a 6% pre-restoration level) likely as an effect of the higher WL (Fig. 4a).

For the DW, the restored forests were dominated by alder (more than 50% of the total volume by 2100) and beech (30%), with an

important fraction of birch (11%) (Fig. 4b). The higher WL and SA were likely to provoke also a slow turnover in the dominance of DW tree genera, with the most dramatic changes being a strong relative increase in alder DW (+37% by 2100) and a decrease in the relative proportion of birch and beech DW (respectively, –10% and –4% by 2100). Both the species were well represented in the pre-restoration forest (respectively, birch 21% and beech 34% of the DW in 2013). Even though ash, oak and spruce DW fractions were unaffected by restoration, their relative proportions dropped in the landscape when alder became dominant (Fig. 4b; respectively, for ash –4% by 2100, this fraction being 5% of the DW in 2013; for oak, –7%, 9% in 2013; for spruce, –4%, 5% in 2013).

BAs and DWs for oak and the other less represented tree genera remained unaffected by changes in WL and SA (Supplementary Table A) hence are not reported in Fig. 3, even if they changed their relative proportions in the forest (Fig. 4).

The Shannon index for tree species diversity was predicted to decrease across the restoration phases for both living and dead tree fractions (for BA: $H'_{2013} = 1.51$; in restored conditions $H'_{2100} = 1.38$; for DW: $H'_{2013} = 1.80$; $H'_{2100} = 1.22$).

3.2. Predictors of species richness

Under the pre-restoration conditions, species richness of vascular plants was positively associated with high WL, high SA, more living ash and more trees with rotten parts, but negatively with beech BA (Fig. 5; Supplementary Table C). Bryophyte richness was positively associated with alder and beech BA, as well as higher tree richness, while lichen richness was positively affected by SA, but negatively by spruce or birch BA. Finally, species richness of wood-inhabiting fungi was higher in stands where the DW fraction was dominated either by beech, alder or birch (Fig. 5; Supplementary Table C).

3.3. Projections of species richness under restoration scenarios

The joint increase in WL and SA were projected to modify species richness of different organism groups, mediated by changes in

forest composition affecting living tree BA and DW, as described above. When the natural WL was restored by 2050, the species richness of plants, fungi and lichens was projected to be significantly higher than in the pre-restoration levels (Fig. 6). However, the increase in the mean number of species was much higher for fungi (+178%) than for plants (+90%) and only limited for lichens (+20%). Plants were projected to reach a richness plateau within the first restoration phase that was not significantly modified when the forest reached old-growth structure. In contrast, fungi and lichens further increased their mean richness levels from the first to the second restoration phase (respectively, +299% and +43% of the species by 2100 respect to 2013). Finally, the models predicted bryophytes to maintain stable species richness throughout the restoration process (Fig. 6).

4. Discussion

Our space-for-time approach projected a marked increase in species richness of vascular plants, epiphytic lichens and wood-inhabiting fungi as a result of the restoration of hydrology and old-growth structures in a forest formerly managed for timber production. Furthermore, species richness of groups associated with different habitat features was differentially affected by restoration. Plant richness stabilized by 2050 most likely due to the faster recovery of soil moisture; a slower recovery was indicated for lichens and wood-inhabiting fungi, probably caused by the slower process of substrate formation via stand ageing.

In the year of our survey (2013), land-use had already changed considerably since 1990, when forestry operations were reported to have been terminated in most parts (Møller, 1990). This time lag apparently was enough to recover the living tree volume, but not the deadwood volume at a level comparable with old growth forest reserves with a longer history of minimum intervention. The current standing living volume (c. $210 \text{ m}^3 \text{ ha}^{-1}$) is at the low end of the range of values reported from nemoral forest reserves in Europe ($201\text{--}674 \text{ m}^3 \text{ ha}^{-1}$ cf., Christensen et al., 2005). This probably reflects poor growing conditions in Lille Vildmose, which beds for a considerable intermixing of less productive tree species,

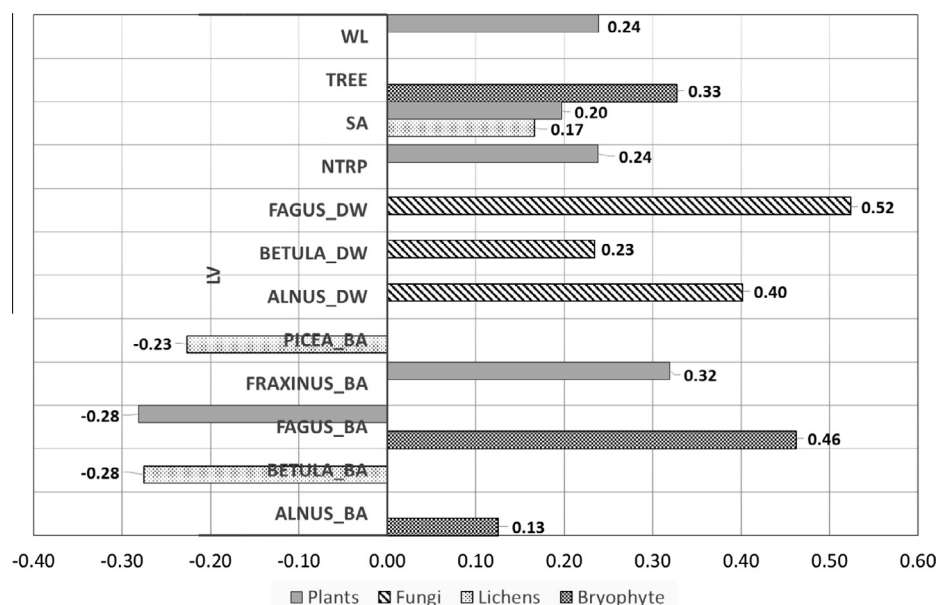


Fig. 5. Predictors of species richness in Lille Vildmose (LV). Values of the standard coefficients, estimated through Geographically Weighted Regression models, showing the median effect (positive or negative) of the main environmental gradients (predictors) on the species richness of four ecological groups in the plots of the whole LV. Abbreviations for the predictors: WL = water level, Tree = N. of tree species, SA = Stand Age, NTRP = N. trees with rotten parts, X_DW = deadwood for the X tree-genus; X_BA = basal area for the X tree-genus.

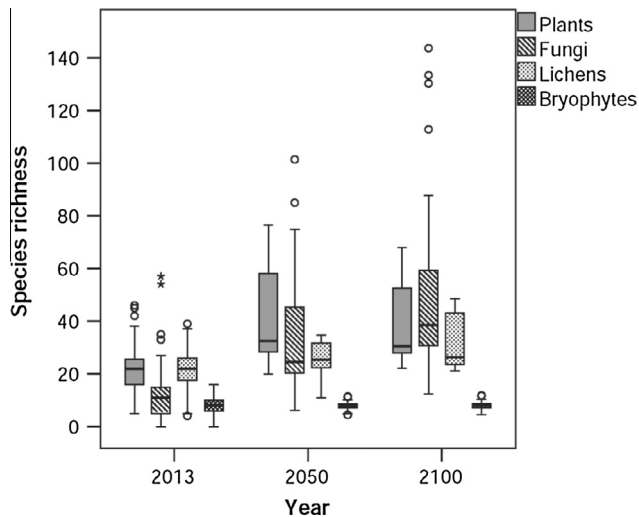


Fig. 6. Predicted effects of forest restoration for species richness. Predicted effects of changes in water level, stand age and forest structure for species richness of four ecological groups in Lille Vildmose. Box plots show the distribution of values (median, interquartile range, \circ outliers, \star extremes) across plots. Measured values are provided at present in the pre-restoration conditions (2013), predicted values when only water level is restored (2050) and when both water level and stand age are restored (2100).

as alder and birch. The current deadwood levels (c. $30 \text{ m}^3 \text{ ha}^{-1}$) are much lower than in Danish forest reserves with comparable living tree volume (e.g., Møns Klinteskov, living volume = $201 \text{ m}^3 \text{ ha}^{-1}$, deadwood = $73 \text{ m}^3 \text{ ha}^{-1}$; Christensen et al., 2005), which probably reflects impact of rather recent timber production in the study area.

By the end of this century, the basal area is projected to increase by c. 35%, as a result of the free development of forest stands in the reserve, and the deadwood by c. 375%. However, while our model predicts the basal area to be stabilized already by 2050, which seems highly realistic as many stands are likely to approach the gap-initiation phase increasing tree mortality rate (Peterken and Jones, 1987), deadwood is projected to increase up to 2100 (final mean volume c. $130 \text{ m}^3 \text{ ha}^{-1}$). Already by 2050 the mean deadwood volume (c. $96 \text{ m}^3 \text{ ha}^{-1}$) is comparable with other nemoral forests ($73\text{--}234 \text{ m}^3 \text{ ha}^{-1}$; Christensen et al., 2005) and considerably above the $30\text{--}50 \text{ m}^3 \text{ ha}^{-1}$ interval reported to be critical for maximizing deadwood biodiversity in lowland oak-beech forests (Müller and Büttler, 2010). Hence, according to our framework, passive restoration via the cessation of forestry is predicted to restore deadwood levels within normal successional times (Meyer and Schmidt, 2011).

In our model, the increase in soil moisture predicts substantial changes in the forest composition compared to the pre-restoration level, transforming several stands into alder carr, a forest type dominated by alder (c. +10% in basal area by 2100) occurring in habitats with high, often stagnant groundwater levels (Douda et al., 2009). However, for other tree species the changes in microclimate induced by increase in stand age are projected to be more important than their tolerance for soil moisture: the persistence of the hygrophilous birch is finally limited by its heliophilous preferences not favoured in old stands, while beech increases thanks to its shade-tolerant nature despite its low tolerance for high soil moisture.

Even though the restored forest is expected to harbour more tree biomass and deadwood along with old-growth structures, as the restoration proceeds towards a more mature successional state, our model predicted the forest to become more homogeneous in composition, both in terms of basal area and deadwood.

Whether this decrease in tree diversity with larger dominance of the shade-tolerant beech and the hydrophilic alder will actually occur is however an open question. As the forest reaches old growth conditions, gap dynamics in combination with continued high browsing pressure is likely to create and maintain large canopy gaps, possibly allowing regeneration of light-demanding species (ash, birch and oak) (Brunet et al., 2014). Presently, these processes can be observed only locally in the area, hence have minimal weights in the models. An obvious weakness with all static modelling approaches is the inability to incorporate unpredicted anomalous events. Currently, an outbreak of ash-dieback is evident in the study area, and the final mortality rate is unknown, hence it is uncertain if ash will be able to gain territory in 2050 as the model predicts. In this context, the incorporation in the model of other disturbance factors, such as climate (windstorms), forest fires, and human impacts (the fluctuation of deer population) would require a precise knowledge of the past frequency of these phenomena, acting at a scale from centuries to millennia (Overballe-Petersen et al., 2014). The analysis of disturbance dynamics is out of the scope of the present research focusing on the direct effects of current restoration actions for biodiversity.

The environmental factors affecting species richness in the forest-dwelling groups were related to substrate availability, in terms of living bark surface or deadwood volume. The importance of these factors for forest biodiversity has been shown in several previous studies (e.g., McGee and Kimmerer, 2002; Fritz and Heilmann-Clausen, 2010). As a result of the general positive relationship with stand age, these substrates were projected to increase in abundance throughout the forest succession, explaining the modelled increase in species richness, in agreement with other studies (for epiphytes: Fritz et al., 2009; for wood-inhabiting fungi: Heilmann-Clausen and Christensen, 2005).

Stand age was projected to have positive effect on the richness of vascular plants and epiphytic lichens, likely for different reasons: old stands offer a higher substrate density, quality and diversity for epiphytes, but higher habitat heterogeneity, in terms of light availability and microhabitat diversity, for plants. They host higher amounts of veteran trees, which are key elements for epiphytic lichens and bryophytes (Fritz et al., 2009), due to differences in bark chemistry, nutrient availability and variety in special microhabitats, including rot holes and dead branches (Fritz and Brunet, 2010). The process of gap-formation in mature stands promotes heterogeneity in light availability (Collins and Pickett, 1987), supporting richness of understory plants (Douda et al., 2012) and of epiphytic lichens (Barkman, 1958). We found lower lichen richness in stands hosting coniferous trees, likely as a result of their effective role in decreasing light availability all year around (Ódor et al., 2013). Moreover, usually coniferous trees inhabit less epiphyte species than deciduous trees (Coote et al., 2008). At present, lichen diversity is limited in stands with coniferous trees (planted and naturally regenerating spruce) or birch. Under the future restoration scenario, these trees will be limited by higher water level and stand age. Active removal of non-indigenous coniferous tree species, especially in large monospecific stands, can benefit both lichens and bryophytes.

The raise in water level, modifying humidity in air and soil, is expected to gradually change the local communities for all the ecological groups, making room for hygrophilous species confined to humid forest refugia and increasing the frequency of the hygrophilous elements already present. For vascular plants, the projected increase in soil moisture is likely to increase richness (Härdtle et al., 2003), by reducing the dominance of a number of a potentially dominant plant species and, thus, creating open habitat for a larger suite of plants species associated with swamp forests (Schuster and Diekmann, 2005; Axmanová et al., 2012). In addition the projected increase in stand age is likely to increase plant

richness as a result of natural forest succession (Douda et al., 2012). This modelled plant sensitivity to both restoration components would explain why their projected richness increase was immediately higher than for other ecological groups and stabilized as the forest approaches the gap-initiation phase (Peterken and Jones, 1987). The increase in beech basal area, according to our model incompatible with the development of a diverse herb layer (cf., Mölder et al., 2008), is expected to be counterbalanced by the process of gap-formation in the canopy, sustained by tree ageing and deer browsing (Naaf and Wulf, 2007). Finally, other studies have shown that plants have increased in diversity with more wind-throw and deadwood (von Oheimb et al., 2007), which is expected also in old-growth swamp forests like Lille Vildmose (Löhmus and Kraut, 2010).

Somewhat surprisingly, we found no change in epiphytic bryophyte species richness with restoration. This projection probably reflects the lower species richness of bryophytes, and their more limited affiliation to forest structural variation than other groups. In fact, many of the surveyed epiphytic bryophytes are not obligate epiphytes but can survive (or even thrive) on the ground floor as well (rocks, stones, soil), in contrast to almost all of the surveyed epiphytic lichens. Further, the high browsing pressure may limit the most desiccation-sensitive epiphytic bryophytes in the study site. Grazing limits regrowth of tree, shrub and liana layers, which results in more desiccation (Yates et al., 2000), but also in more light in the forest, which would instead explain the positive response for lichens in the model. In fact, like epiphytic bryophytes, some epiphytic lichens are associated with high humidity but others also with the higher light availability in browsed forests (Barkman, 1958). In our study area the disturbance maintained by deer browsing keeps the area relatively open, providing good light conditions for understory plants and epiphytes, but reducing air humidity, which seems to be more important to bryophytes than to lichens. From a historical perspective, livestock grazing activity in the Danish forest started 6000 years ago, and has already become integrated in the dynamics of natural disturbances and climate change altering the forest composition and structure over millennia (Overballe-Petersen et al., 2014). Whether the actual grazing pressure in the study area is beyond natural levels is debated (Buchwald, 2012), however it is more stable than it would be if regulated only by natural predation, being contained by tight regulation of hunting activities.

Our space-for-time approach predicts the potential effects of forest restoration, considering a limited local species pool nested within the regional species pool of Denmark, from which different species can colonize the forest reserve. Most likely both the local and the regional pools have been considerably impoverished in the past, and specialized species may have died out or have become very rare in the anthropogenic matrix before the positive effects of restoration start to appear (Cornell and Harrison, 2014). In particular, the current lack of bryophytes specialized in old tree habitats, may indicate that past timber extraction has depleted this species pool even more than other groups in NW Europe (Heilmann-Clausen et al., 2014). The long term development of the local species pool hence depends on the overall conservation actions taken for forest biodiversity at national and international scales, and more locally in the landscape surrounding the study area. If appropriate measures are taken (Petersen et al., 2016) this would result in larger connectivity in old growth habitats increasing dispersal within the regional species pool, and potentially even the recolonization from regionally extinct specialists. Hence the actual gain in species richness from improved local conditions could be higher than projected, if local communities are presently not saturated.

The goals of ecological restoration differ among projects (cf. Benayas et al., 2009; Maanaviija et al., 2014), but in the present

case increasing the biodiversity value of the area is the primary target. However, high site biodiversity is not necessarily coupled with high site naturalness. Restoration should not aim only for high site biodiversity, but for a pristine-like community, which may have lower alpha-diversity than the community in the degraded ecosystem state, but yet contribute to landscape scale diversity (gamma-diversity) by supporting populations of species highly sensitive to human disturbance (Maanaviija et al., 2014).

5. Conclusions

Reversing the effects of a long history of management for timber extraction in the area increased availability and diversity of suitable forest habitat, and hence the local species richness for three of four of the organism groups, compared to the pre-restoration conditions. The projected speed and magnitude of the potential increase in species richness differed between groups, with vascular plants responding most quickly, due to a positive effect of recovered hydrology, and wood-inhabiting fungi responding most slowly, due to the slow build-up of deadwood pools.

We suggest applying our space-for-time approach as a tool to assess biodiversity responses in similar projects under open-ended restoration actions, 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 (Hughes et al., 2011).

Conflict of interest

The authors declare that they have no conflict of interests.

Acknowledgements

We thank the Aage V. Jensen Foundation for funding. AM, APT, HHB and JHC acknowledge the Danish National Research Foundation for funding the Center for Macroecology, Evolution and Climate (grant no. DNRF96). We are thankful to Andreas Malmqvist (Naturcentrum AB, Sweden) for participating in epiphytes' surveys. We thank the COWI consulting group (Denmark) for release of measured and projected data on the current and future water level.

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.2016.09.028>.

References

- Anonymous, 2011. <http://ec.europa.eu/environment/life/project/Projects/index.cfm?fuseaction=search.dspPage&n_proj_id=4035&docType=pdf>.
- Axmanová, I., Chytrý, M., Zelený, D., Li, C.-F., Vymazalová, M., Danihelka, J., Horsák, M., Kočí, M., Kubešová, S., Lososová, Z., Otýpková, Z., Tichý, L., Martynenko, V.B., Baisheva, E.v.Z., Schuster, B., Diekmann, M., 2012. The species richness-productivity relationship in the herb layer of European deciduous forests. *Global Ecol. Biogeogr.* 21, 657–667.
- Banet, A.L., Trexler, J.C., 2013. Space-for-time substitution works in everglades ecological forecasting models. *PLoS One* 8, e81025.
- Barkman, J.J., 1958. *Phytosociology and Ecology of Cryptogamic Epiphytes, Including a Taxonomic Survey and Description of Their Vegetation Units in Europe*. Van Gorcum and Company. N.V., Assen, Netherlands.
- Benayas, J.M. Rey, Newton, A.C., Diaz, A., Bullock, J.M., 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* 325, 1121–1124.
- Brumelis, G., Jonsson, B.G., Kouki, J., Kuuluvainen, T., Shorohova, E., 2011. Forest naturalness in northern Europe: perspectives on processes, structures and species diversity. *Silva Fenn.* 45, 807–821.
- Brunet, J., Bukina, Y., Hedwall, P.-O., Holmström, E., von Oheimb, G., 2014. Pathogen induced disturbance and succession in temperate forests: evidence from a 100-year data set in southern Sweden. *Basic Appl. Ecol.* 15, 114–121.

- Buchwald, E., 2012. Flora og vegetation på Tofte-ejendommen. In: Hald-Mortensen, P. (Ed.), Tofte Skov og Mose – status 2012, pp. 154–210.
- Bütler, R., Angelstam, P., Schlaepfer, R., 2004. Quantitative snag targets for the three-toed woodpecker, *Picoides tridactylus*. Ecol. Bull. 51, 219–232.
- Christensen, M., Emborg, J., 1996. Biodiversity in natural versus managed forest in Denmark. For. Ecol. Manage. 85, 47–51.
- Christensen, M., Hahn, K., Mountford, E.P., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S., Vrska, T., 2005. Dead wood in European beech (*Fagus sylvatica*) forest reserves. For. Ecol. Manage. 210, 267–282.
- Collins, B.S., Pickett, S.T.A., 1987. Influence of canopy opening on the environment and herb layer in a northern hardwoods forest. Vegetatio 70, 3–10.
- Coote, L., Smith, G.F., Kelly, D.L., O'Donoghue, S., Dowling, P., Iremonger, S., Mitchell, F.J.G., 2008. Epiphytes of Sitka spruce (*Picea sitchensis*) plantations in Ireland and the effects of open spaces. Biodivers. Conserv. 17, 953–968.
- Cornell, H.V., Harrison, S.P., 2014. What are species pools and when are they important? Annu. Rev. Ecol. Evol. Syst. 45, 45–67.
- Crites, S., Dale, M.R., 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. Can. J. Bot. 76, 641–651.
- Douda, J., Čejková, A., Douda, K., Kochánková, J., 2009. Development of alder carr after the abandonment of wet grasslands during the last 70 years. Ann. For. Sci. 66, 1–13.
- Douda, J., Doudová-Kochánková, J., Boulbík, K., Drašnarová, A., 2012. Plant species coexistence at local scale in temperate swamp forest: test of habitat heterogeneity hypothesis. Oecologia 169, 523–534.
- Fotheringham, A.S., Brunsdon, C., Charlton, M.E., 2002. Geographically Weighted Regression: The Analysis of Spatially Varying Relationships. Wiley, Chichester.
- Fredshavn, J.R., Ejrnæs, R., Nygaard, B., 2011. Teknisk anvisning til kortlægning af terrestriske naturtyper. Danmarks Miljøundersøgelser, Teknisk Anvisning TA-N3 ver. 1-04.
- Fritz, Ö., Brunet, J., 2010. Epiphytic bryophytes and lichens in Swedish beech forests—effects of forest history and habitat quality. Ecol. Bull. 53, 95–107.
- Fritz, Ö., Heilmann-Clausen, J., 2010. Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (*Fagus sylvatica*). Biol. Conserv. 143, 1008–1016.
- Fritz, Ö., Niklasson, M., Churski, M., 2009. Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. Appl. Veg. Sci. 12, 93–106.
- Görn, S., Fischer, K., 2015. Measuring the efficiency of fen restoration on carabid beetles and vascular plants: a case study from north-eastern Germany. Restor. Ecol. 23, 413–420.
- Halme, P., Allen, K.A., Auniš, A., Bradshaw, R.H.W., Brümelis, G., Čada, V., Clear, J.L., Eriksson, A., Hannon, G., Hyvärinen, E., Ikauniece, S., Iršėnaitė, R., Jonsson, B.G., Junninen, K., Karekela, S., Komonen, A., Kotiaho, J.S., Kouki, J., Kuuluvainen, T., Mazziotta, A., Mönkkönen, M., Nyholm, K., Oldén, A., Shorohova, E., Strange, N., Toivanen, T., Vanha-Majamaa, I., Wallenius, T., Ylisirniö, A., Zin, E., 2013. Challenges of ecological restoration: lessons from forests in northern Europe. Biol. Conserv. 167, 248–256.
- Hardin, J.W., Hilbe, J.M., 2003. Generalized Estimating Equations. Chapman and Hall/CRC, Boca Raton, FL, USA.
- Härdtle, W., von Oheimb, G., Westphal, C., 2003. The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-Holstein). For. Ecol. Manage. 182, 327–338.
- Heilmann-Clausen, J., Aude, E., van Dort, K., Christensen, M., Piltaver, A., Veerkamp, M., Walley, R., Siller, I., Standovár, T., Ódor, P., 2014. Communities of wood-inhabiting bryophytes and fungi on dead beech logs in Europe - reflecting substrate quality or shaped by climate and forest conditions? J. Biogeogr. 41, 2269–2282.
- Heilmann-Clausen, J., Christensen, M., 2005. Wood-inhabiting macrofungi in Danish beech-forests – conflicting diversity patterns and their implications in a conservation perspective. Biol. Conserv. 122, 633–642.
- Hughes, F.M.R., Stroh, P.A., Adams, W.M., Kirby, K.J., Mountford, J.O., Warrington, S., 2011. Monitoring and evaluating large-scale, “open-ended” habitat creation projects: a journey rather than a destination. J. Nat. Conserv. 19, 245–253.
- Hyams, D., 2005. CurveExpert 1.3: a comprehensive curve fitting package for Windows.
- IBM Corp., 2011. IBM SPSS Statistics for Windows, Version 20.0. IBM Corp, Armonk, NY.
- Lee, S.-M., Chao, A., 1994. Estimating population size via sample coverage for closed capture-recapture models. Biometrics 50, 88–97.
- Löhmus, A., Kraut, A., 2010. Stand structure of hemiboreal old-growth forests: characteristic features, variation among site types, and a comparison with FSC-certified mature stands in Estonia. For. Ecol. Manage. 260, 155–165.
- Maanaviija, L., Aapala, K., Haapalehto, T., Kotiaho, J.S., Tuittila, E.S., 2014. Impact of drainage and hydrological restoration on vegetation structure in boreal spruce swamp forests. For. Ecol. Manage. 330, 115–125.
- Maron, M., Rhodes, J.R., Gibbons, P., 2013. Calculating the benefit of conservation actions. Conserv. Lett. 6, 359–367.
- McGee, G.G., Kimmerer, R.W., 2002. Forest age and management effects on epiphytic bryophyte communities in Adirondack northern hardwood forests, New York, USA. Can. J. For. Res. 32, 1562–1576.
- Meyer, P., Schmidt, M., 2011. Accumulation of dead wood in abandoned beech (*Fagus sylvatica* L.) forests in northwestern Germany. For. Ecol. Manage. 261, 342–352.
- Mölder, A., Bernhardt-Römermann, M., Schmidt, W., 2008. Herb-layer diversity in deciduous forests: raised by tree richness or beaten by beech? For. Ecol. Manage. 256, 272–281.
- Møller, P.F., 1990. Naturskove i Danmark. En foreløbig opgørelse over danske naturskove udenfor statsskoven. DGU Intern rapport, 39.
- Müller, J., Bütler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eur. J. For. Res. 129, 981–992.
- Naaf, T., Wulf, M., 2007. Effects of gap size, light and herbivory on the herb layer vegetation in European beech forest gaps. For. Ecol. Manage. 244, 141–149.
- Ódor, P., Király, I., Tinya, F., Bortignon, F., Nascimbene, J., 2013. Patterns and drivers of species composition of epiphytic bryophytes and lichens in managed temperate forests. For. Ecol. Manage. 306, 256–265.
- Overballe-Petersen, M.V., Raulund-Rasmussen, K., Buttenschön, R.M., Bradshaw, R.H.W., 2014. The forest Gribskov, Denmark: lessons from the past qualify contemporary conservation, restoration and forest management. Biodivers. Conserv. 23, 23–37.
- Paillet, Y., Bergès, L., Hjältén, J., Odor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastião, M.-T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv. Biol. 24, 101–112.
- Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., 2015. Quantifying the recovery of old-growth attributes in forest reserves: a first reference for France. For. Ecol. Manage. 346, 51–64.
- Peterken, G.F., Jones, E.W., 1987. Forty years of change in Lady Park Wood: the old-growth stands. J. Ecol. 75, 477–512.
- Petersen, A.H., Strange, N., Anthon, S., Bjørner, T.B., Rahbek, C., 2016. Conserving what, where and how? Cost-efficient measures to conserve biodiversity in Denmark. J. Nat. Conserv. 29, 33–44.
- Pickett, S.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In: Long-Term Studies in Ecology. Springer, New York, New York, NY, pp. 110–135.
- Rangel, T.F., Diniz-Filho, J.A.F., Bini, L.M., 2010. SAM: a comprehensive application for spatial analysis in macroecology. Ecography 33, 46–50.
- Ranius, T., Kindvall, O., 2004. Modelling the amount of coarse woody debris produced by the new biodiversity-oriented silvicultural practices in Sweden. Biol. Conserv. 119, 51–59.
- Riis, N., Møller, P.F., Aaby, B., 2009a. Naturforbedring Af Høstemark Skov I Lille Vildmose. Grøn Driftsplan Med Skitseprojekt. Aage V. Jensen Naturfond.
- Riis, N., Møller, P.F., Aaby, B., 2009b. Naturforbedring Af Tofte Skov I Lille Vildmose. Grøn Driftsplan Med Skitseprojekt. Aage V. Jensen Naturfond.
- Schalkoff, R., 1992. Pattern Recognition: Statistical, Structural and Neural Approaches. Wiley, New York.
- Schuster, B., Diekmann, M., 2005. Species richness and environmental correlates in deciduous forests of Northwest Germany. For. Ecol. Manage. 206, 197–205.
- von Oheimb, G., Friedel, A., Bertsch, A., Härdtle, W., 2007. The effects of windthrow on plant species richness in a Central European beech forest. Plant Ecol. 191, 47–65.
- Yates, C.J., Norton, D.A., Hobbs, R.J., 2000. Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south-western Australia: implications for restoration. Austral Ecol. 25, 36–47.
- Zianis, D., Muukkonen, P., Mäkipää, R., Mencuccini, M., 2005. Biomass and Stem Volume Equations for Tree Species in Europe. Silva Fenn. Monogr. 4, 63p.