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Red-listed species and forest continuity – A multi-taxon approach to conservation in temperate forests

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ABSTRACT

The conservation status of European temperate forests is overall unfavorable, and many associated species are listed in national or European red-lists. A better understanding of factors increasing survival probability of red-listed species is needed for a more efficient conservation effort. Here, we investigated the importance of current forest cover, historical forest cover and a number of soil and climate variables on the incidence and richness of red-listed forest species in Denmark. We considered eight major taxa separately (mammals, saproxylic beetles, butterflies, vascular plants and four groups of fungi), using mainly citizen science data from several national mapping projects. Taxa were selected to represent important forest habitats or properties (soil, dead wood, forest glades and landscape context) and differ in dispersal potential and trophic strategy. For all groups, presence and richness of red-listed species was positively related with current forest cover, but - for most taxa - forest cover 200 years ago was an even better predictor. The intersection of past and current deciduous forest was used to identify the area of continuous, lost and new forest. Continuous and lost deciduous forest cover were strong predictors of red-listed species occurrence in most groups, but surprisingly species richness of butterflies and hydnoid fungi, and presence of mammals, was significantly, positively affected by coniferous forest area. The positive effect of lost deciduous forests on red-listed species, suggest an extinction debt of at least 200 years, with some areas hosting more red-listed species than the current area of old forest can sustain in the long run. Our results suggest that current priorities for forest conservation in Denmark are not efficient in protecting red-listed forest species, and that more focus should be put on conserving deciduous forest with long continuity. Furthermore, a multi-taxa approach including a wide array of organism groups with contrasting habitat affiliations, results in a more comprehensive understanding of the requirements of red-listed forest species and necessitate a more focused approach to conservation planning.

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1. Introduction

Due to historical loss of natural forest areas, many forest species in Europe are nationally or internationally threatened. Red-listed forest species often have specific habitat requirements and in order to ensure their survival, it is necessary to understand the factors affecting - negatively or positively - their survival probability. In temperate Europe, forest areas have been fragmented and lost to farmland with the increasing size of the human population (Kaplan et al., 2009). The forest area is now slowly increasing throughout Europe (Vilén et al., 2012), but most of the new forests

are plantations, predominantly of conifers (McGrath et al., 2015), and decades to centuries are needed before they can support old growth forest habitats like veteran trees or large decaying logs (Nordén et al., 2014). Remaining old forestlands have typically experienced drainage and planting, and have been subject to coppicing, clear cutting or shelterwood forestry in order to promote production. As a consequence most of the current forest area in Europe lacks naturalness and ecological continuity (Bengtsson et al., 2000; Pătru-Stupariu et al., 2013). During the last decades, the extent of protected forest areas has increased in Europe, and recovery of old growth attributes and diversity has been reported from protected and managed forests (Vandekerkhove et al., 2011). Overall, the conservation status of temperate forests in Europe is however still considered unfavorable (EEA, 2015), and

focused conservation efforts are needed to halt further biodiversity loss.

In Denmark the forest area reached a modern minimum around 1810, due to clearance for agriculture and centuries of logging and grazing in remaining woodlands (Mather et al., 1998; Fritzbøger, 2005). The resulting landscape was highly fragmented with forests constituting isolated patches in a farmland matrix. Since the foundation of the Danish Forest Protection act in 1805, the forest area has been quadrupled to now cover 14% of the country, mainly due to reforestation with introduced conifers in heathland and dunes on sandy soils. As a consequence of this forest history only a small percentage of the current Danish forest area can be classified as continuous forest (i.e. dating back to before 1800) (Naturstyrelsen, 2013). A very similar overall forest development has been reported from the Netherlands, the British Isles, Germany and Belgium (Buis, 1985; Watts, 2006; Schmidt et al., 2014; De Keersmaeker et al., 2015).

The relationship between forest area and species richness of different organism groups has been analyzed in numerous studies (e.g. Fahrig, 2003; Tikkanen et al., 2009; Martensen et al., 2012), some with special focus on forest fragmentation (Kolb and Diekmann, 2004; Hanski et al., 2013), others emphasizing the importance of forest history and continuity (Graae et al., 2004; Hermy and Verheyen, 2007) or remaining old growth structures (Fritz et al., 2008). Most of these studies have found a positive signal of intact forests areas on species richness of forest specialist or red-listed species, but they are typically restricted to single groups of organisms, and of limited relevance for more specific site selection and conservation planning.

It is well known that ecosystem changes resulting from land use or climate change may not be fully apparent for several decades, owing to long response times in ecological systems (Dullinger et al., 2013). Among insects, delays in extinction are known to extend well beyond 100 years, while even longer delays to forest fragmentation have been reported among forest plants (Tilman et al., 1994; Hanski, 2000; Vellend et al., 2006; Bulman et al., 2007). Similar time scales may be needed for formation of specific forest habitats in reforested or heavily managed forest areas (Nordén et al., 2014), and delays in recolonization of forest specialists into such areas may be substantial, especially for slow dispersing species (Jacquemyn et al., 2001). In addition other biotic and abiotic factors, e.g. climate and soil conditions may influence the value of old and new forest for biodiversity (e.g. De Keersmaeker et al., 2014; Heilmann-Clausen et al., 2014), which may further complicate efficient conservation planning.

The principle of complementary site selection is a cost-effective way to cover biodiversity in a conservation network (e.g. Pressey et al., 2007). Despite its statistical effectiveness, complementarity also has weaknesses, e.g. if species distribution patterns are incompletely known or changing over time. Further, there are often legislative or political constraints to reserve network selection which may lead to a quest for compromises. In this study we do not attempt to identify a cost-effective reserve network but rather to inform conservation planning on a general level, by investigating the major drivers of red-listed species in selected species groups with complementary habitat needs (cf. Maes and Bonte, 2006; Simila et al., 2006).

Our overall objective was to investigate the importance of forest history, soil and environmental variables for the presence and richness of red-listed forest species, with the aim to evaluate and qualify conservation planning, both in Denmark and in adjacent regions (especially Northern Germany, Benelux, Great Britain and S. Sweden) with comparable forest history and biodiversity. We included nationally red-listed species from eight different organism groups: mammals, saproxylic beetles, butterflies, four groups of fungi and vascular plants. As elaborated in the next section, the eight organism groups differ in their habitat requirements, and hence we expected them to show different relationships to the included forest variables. Following the species-area relationship, we expected (1) to find a general increase in the number of red-listed species with an increase in general forest area in all groups, but (2) to find a better fit with the historic or continuous deciduous forest area in groups dependent on old growth forest habitats or forest continuity (saproxylic beetles and fungi, mycorrhizal *Phlegmacium* & *Ramaria* species and vascular plants). Finally, we expected (3) to detect an influence from soil type variables on soil and root associated organisms (vascular plants and the three groups of non-saproxylic fungi). Since climate is known to be an important driver of biodiversity, we included annual precipitation and temperature as co-variables to account for possible effects. Similarly, we added distance to coast as a co-variable because coastal forests in Denmark seem to have suffered less from human impact, including air pollution, than inland forests.

2. Materials and methods

2.1. Study area

For this study we used datasets covering the entire country of Denmark, a total area of 43,094 km^2. The climate in Denmark is temperate with an average annual temperature of 8.3 °C and an average annual precipitation of 593 mm (climate normals 1961–1990, data available from www.dmi.dk).

The forest area in Denmark was estimated to 6081 km^2 or 14.1% of the total land area in 2013, following the FAO forest definition (Nord-Larsen et al., 2014). Of the forest area, 39.5% is pure coniferous forest, 40.8% is pure deciduous forest and 11.3% is mixed forests. The remaining 8.4% consist of work areas, roads and temporarily non-vegetated areas. The natural climax vegetation in most of the area is nemoral mixed forests composed of *Acer* spp., *Alnus glutinosa*, *Betula* spp., *Carpinus betulus*, *Corylus avellana*, *Crataegus* spp., *Fagus sylvatica*, *Fraxinus excelsior*, *Prunus* spp., *Quercus* spp., *Tilia* spp. and *Ulmus* spp. *Juniperus communis*, *Taxus baccata* and *Pinus sylvestris* are the only native conifers occurring in the area, but *Picea abies*, native to nearby parts of South Sweden and North Germany, is now the most common tree species (Nord-Larsen et al., 2014).

2.2. GIS work

All data was gridded in ArcGIS using a 10 × 10 km grid. The same grid has been used in several biological atlas surveys in Denmark and consists of 633 grid cells (Lund, 2002; Larsen et al., 2008). On the original grid, the grid cells along the border between UTM zones 32 and 33 have been modified, so that area and shape deviate somewhat from the standard 10 × 10 km cells. Since not all data on the explanatory variables included in this study was available in all 633 grid cells, 146 cells where omitted from the final dataset used in the statistical analyses, leaving 487 cells in the final grid (Fig. 1). The omitted cells include two of the rare important calcareous areas in Denmark (Høje Møn, Himmerland) known to host many red-listed species associated with calcareous soils. In all other aspects we consider the reduced dataset as representative for Danish forests in general.

2.3. Species data

We selected eight organism groups to represent the width of Danish forest biodiversity in respect to ecosystem functions and habitat requirements. Saproxylic fungi and beetles were selected to represent biodiversity connected to dead wood and veteran trees. The latter group has a preference for sun-exposed and
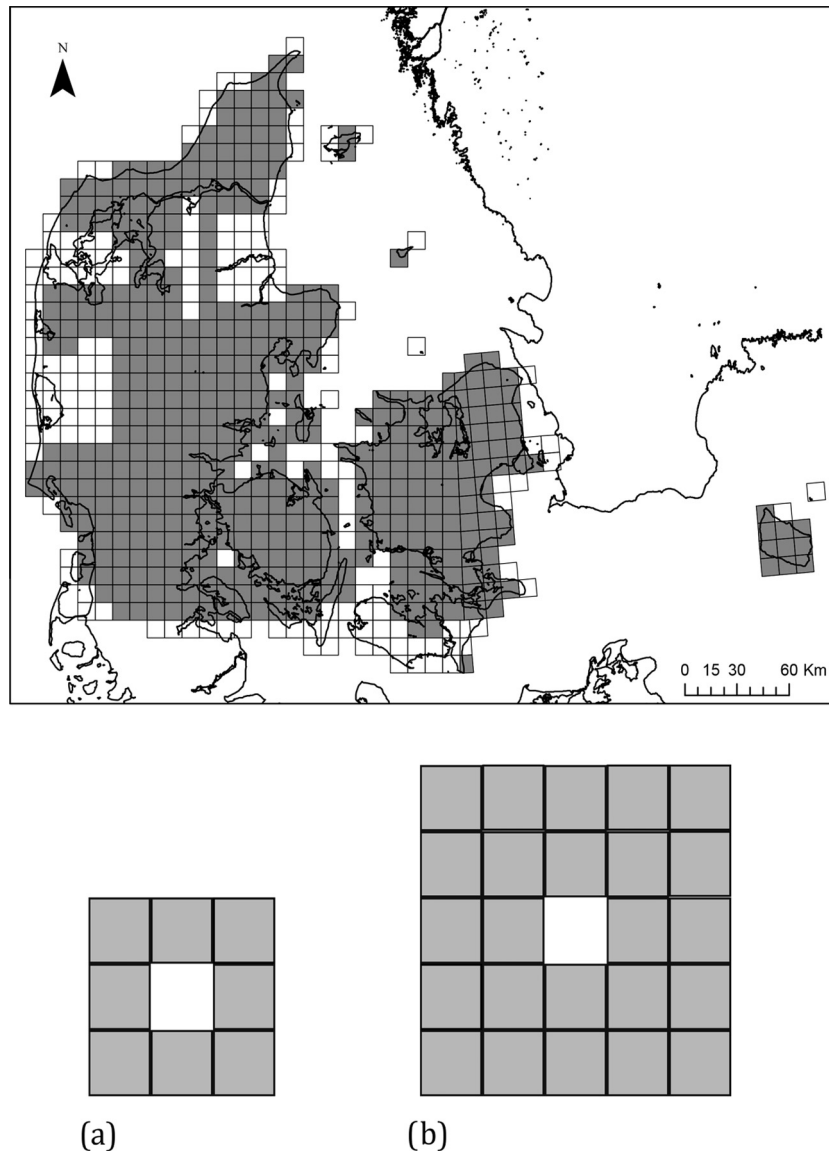
Fig. 1. Top: The 10 × 10 km grid covering Denmark - the grey cells outline the part of the grid that was used in this study. Bottom: Measures of connectivity with gridded data, taking onset in the white cell in the center, (a) 30 × 30 km and (b) 50 × 50 km.

standing dead wood habitats, while the former in general depend on lying dead wood and shady conditions (Stokland et al., 2012). Vascular plants and soil saprotrophic fungi were selected to represent autotrophic and saprotrophic soil biodiversity, respectively. Two groups of mycorrhizal fungi were selected to represent biotrophic biodiversity associated with tree roots, while mammals and butterflies were selected to represent mobile species depending on varied forest landscapes with structural variation and forest glades (Table 1). Within all included groups only forest dependent species were included; while species associated with non-forest habitats (e.g. grasslands) were excluded.

For each species group, presence-absence data per 10 × 10 km grid cell for all red-listed species (Wind and Pihl, 2004) was extracted from appropriate reliable sources. The selection of data was restricted to organism groups with complete or almost complete distribution data available. Data were selected to represent true presence-absence data with high confidence at the rather coarse grid scale used. In the original selection (Johannsen et al., 2013), epiphytic lichens and invertebrates of forest wetland habitats were considered, but they were excluded in the present analysis due to insufficient coverage. Data on all fungal groups

was extracted from the database of the Danish Mycological Society (2014), with half the data stemming from the Danish Fungal Atlas, a citizen science project that ran from 2009 to 2013, collecting more than 250,000 validated species records. A similar amount of data was extracted from other databases, including an extensive database containing almost 20,000 records of red-listed species, updated yearly from 1994 to 2009 by Jan Vesterholt†. During the atlas project, competitions and intensive recording camps were organized in order to ensure completeness in the sampling of red-listed species (Frøslev et al., 2014). Data on butterflies was collated from databases of two entomological societies, one national atlas survey, two major citizen science databases, and one private specimen collection. The full dataset contained 427,000 validated species records (for further details see Eskildsen et al. (2015)). Data on beetles was compiled using updated versions of the catalogue of Danish beetles (Hansen, 1964, 1996), the Danish Red List (http://redlist.dmu.dk), a national public database (www.fugleognatur.dk) and private records held by Denmark's top coleopterists Jan Pedersen, Ole Martin and Ole Mehl†. Even though these data do not stem from a specific atlas project, they are based on very comprehensive efforts made by

Table 1
Organism groups included in this study, with the total number of species and occupied grid cells (out of the 487 cells in the final grid) indicated for each group. In addition living substrate, specific habitat requirements and data sources are given (Johannsen et al., 2013).

Organism group	Number of species	Grid cells where present	Substrate	Specific habitats	Longevity and dispersal	Source
Hydnoid thelephoroid mycorrhizal fungi (family *Bankeraceae*)	19	76	Living roots of trees	Forests and plantations on nutrient poor sandy or calcareous soil, poor in nitrogen and with a thin humus layer	Decades, dispersal by wind borne spores	Danish Mycological Society (2014)
Mycorrhizal *Phlegmacium* & *Ramaria* species (Cortinarius subg. *Phlegmacium* and mycorrhizal members of *Ramaria*)	52	88	Living roots of trees	Old deciduous forest on mineral rich/calcareous soil,	Decades, dispersal by wind borne spores	Danish Mycological Society (2014)
Soil saprotrophic fungi (*Leucoagaricus* s.l. and *Lepiota* s.l)	25	91	Soil	Coniferous and deciduous forest and scrubs on undisturbed +/− calcareous mull soils	Few to many years, dispersal by wind-borne spores	Danish Mycological Society (2014)
Saproxylic beetles (*Elateridae, Eucnemidae, Lucanidae, Cetoniidae, Cerambycidae, Prostomidae, Tenebrionidae* and *Melandryidae*)	55	82	Dead wood	Forests with veteran trees and dead wood, many species with a preference for semi-open conditions	One to few years, active but in some species very local dispersal of adult individuals	Various sources[a]
Saproxylic fungi (Polypores + *Hericiaceae*)	35	194	Dead wood	Forests with veteran trees and dead wood	Decades, dispersal by wind-borne spores	Danish Mycological Society (2014)
Butterflies (Lepidoptera: Papilionoidea and Hesperioidea)	12	328	Living plants	Forest glades rich in flowering plants	One year, active dispersal of adult individuals	Various sources[b]
Vascular plants	25	170	Soil	Continuous forests with natural glades, mainly on mineral-rich soils	Few years to decades or more, dispersal by spores, seeds and vegetative means	Hartvig and Vestergaard (2015)
Mammals (pine-marten, dormouse + five bat species)	7	191	Mixed	Large forest landscapes, with veteran trees, wetlands and/or varied undergrowth	Few to many years, dispersal by adult individuals	Petersen et al. (2012)

[a] Data compiled by PFT from various sources (see text).
[b] Data compiled by AE from various sources (see text).

numerous amateur entomologists over many years and must be regarded as having almost complete coverage for the included families. Data on vascular plants (a selection of 25 red-listed obligate forest species, of which two were woody plants and 8 were orchids) were extracted from the Atlas Flora Danica survey running 1992–2012, which collected almost 1 million records of vascular plants and obtained complete coverage on a 10 × 10 km grid design (Hartvig and Vestergaard, 2015). Data on mammals was extracted from the Danish Mammal Atlas, a citizen science project that ran 2000–2003 (Baagøe and Jensen, 2007), but updated with additional data from scientific and volunteer based recordings both before and after the intensive mapping period. In the atlas project alone, more than 50,000 records of mammals were obtained (Baagøe and Jensen, 2007). All surveys and atlas projects used the same 10 × 10 grid design as in the present study.

The final dataset included distribution data on 230 species (see Appendix A for a full species list) in the categories Critically Endangered (CR), Endangered (EN) and Vulnerable (VU) and Near Threatened (NT) following the current Danish red list (Wind and Pihl, 2004, with updates until 2010). Only records from 1990 or later was included in the dataset, except for saproxylic beetles, were records back to 1980 was included, if deemed likely to represent still surviving populations.

2.4. Forest variables and connectivity measures

Eleven different forest type variables were extracted for the analyses, divided across three variable sets and gridded, so that the area of each forest type was calculated for each grid cell using ArcGIS (Table 2). As a measure of forest connectivity, the current

and historical forest areas in neighbouring grid cells were also considered, at two different spatial scales. One considering only the neighbouring quadrats (8 quadrats in total, Fig. 1a) and the second including the next row of neighbours (24 quadrats in total, Fig. 1b), in both cases excluding the center grid cell.

The second variable set was constructed by combining historical and current forest areas, the latter containing data on forest type (coniferous or deciduous) (Table 2). The area with coniferous forest was negligible until the 1850's and we therefore assumed all historical forest (mapped between 1760 and 1820) to be deciduous. Coniferous forest area was taken directly from the GIS layer, while new and lost deciduous forests were calculated based on the difference between the current deciduous area and the total historical forest area. Hence, new and lost deciduous forest excludes each other at grid cell level, since the area or deciduous forest per grit cell has either increased or declined since the historic map.

Finally, a third variable set was constructed by combining current forest cover with the detailed Danish soil type map (measured at one meter depth) supplied by the Geological Survey of Denmark and Greenland (Jakobsen et al., 2011). The map information included more than 50 different soil types, which we divided into five coarser soil classes of assumed biological relevance - gravel, sand, clay, lime and peat (Appendix B).

2.5. Climate variables and distance to coast

Data on precipitation and temperature was supplied by the Danish Meteorological Institute (DMI) and included monthly average values for 1989–2010 (Scharling, 2012). The data was

Table 2
11 forest variables used in the analyses, divided into three different datasets with maximum, mean and median values as well as the method used to derive these.

Variable set	Forest variable	Max. - Mean - Median area (km^2)	Method
Simple forest area	Current forest[a]	56.1 - 11.1 - 9	
	- 30 × 30 km	275.3 - 81.7 - 74.3	
	- 50 × 50 km	542 - 193.8 - 170.6	
	Historic forest area[b]	56.2 - 5.5 - 1.5	
	- 30 × 30 km	209.7 - 41.4 - 28.9	
	- 50 × 50 km	418.8 - 99.8 - 80.3	
Complex forest area	Coniferous forest	42 - 5.5 - 3	
	New deciduous forest	11.6 - 1.5 - 0.6	Current forest - historic forest
	Lost deciduous forest	29.4 - 2 - 0	Historic forest - current forest
	Continuous deciduous forest	26.8 - 3.5 - 1.3	Overlap between current and historic forest
Forest area divided on soil types	Forest on gravel	25.5 - 0.6 - 0.1	Current forest cover intersected with detailed
	Forest on lime	4.8 - 0.2 - 0.1	Danish soil type map[c]
	Forest on clay	29.3 - 2.9 - 1	
	Forest on sand	40.1 - 5.2 - 2.3	
	Forest on peat	10.9 - 0.8 - 03	

[a] FOT-Danmark (Geo Danmark) 2010.
[b] The Royal Danish Academy (VSK) 1760–1820.
[c] Soil type map GEUS_j25, 1:25,000 (Jakobsen et al., 2011).

converted to the same 10 × 10 km grid used for the other variables, and the average annual value was calculated for each grid cell. The precipitation ranged from 452 mm to 792 mm per year (mean = 573 mm) in the study area, while the average annual temperature varied from 8.0 °C to 9.3 °C (mean = 8.6 °C).

The last variable included was the distance from the forest to the nearest coast. This variable was included because coastal habitats in Denmark tend to suffer less from cultivation and impact from eutrophication compared to inland habitats (Ejrnæs et al., 2012). Distance to coast was calculated as the distance between the center of the 10 × 10 km cell and the center of the cells along the coastline. The grid cells along the coastline were all set to have a distance of zero kilometers to the coast. The distance to coast ranged from 0 km to 65 km (mean = 14.8 km).

2.6. Data analysis

A preliminary examination of the species distribution datasets showed a strongly zero-inflated distribution in most groups. For this reason the dataset was split into a presence-absence part (presence = 1, absence = 0) and a quantitative part (species richness), which only contained grid cells where species were recorded as present. As well as adjusting for the zero-inflated distribution and simplifying the modeling, this approach also made it possible to test whether occurrence and richness were explained by different factors.

All statistical analyses were performed in R, version 3.0.2 (R Core Team, 2013). Both datasets were analyzed using generalized linear models (GLMs), since it can be used for non-linear relationships and for both binomial and count data (Augustin et al., 1996; Echeverría et al., 2007). All forest areas were log-transformed, because of the expected species-area relationship and because it showed a better fit in all models (based on Akaike Information Criteria (AIC) values, (Freckleton, 2009; Grueber et al., 2011; Diniz-Folhi et al., 2013)). In the GLM models, the family was set to 'binomial' for the presence-absence dataset and 'poisson' for the richness dataset.

Separate models where fitted for each of the eight organism groups and tested on both the presence-absence and richness data set. No complete model with all variables included was tested, due to the fact that both the complex forest variables and the soil type variables added up to the same total forest area. We first fitted four simple models incorporating only one or few variables: (1) Historic forest area, (2) Historic forest area + connectivity, (3) Current forest area, (4) Current forest area + connectivity. Subsequently we fitted four complex models involving multiple variables: (5) Complex forest area, (6) Forest area divided on soil type, (7) Complex forest area + climate and distance to coast, (8) Forest area divided on soil type + climate and distance to coast. Based on the low effects of forest connectivity detected in the first simple models, we did not include connectivity in the complex models.

The drop1 function in R was used to achieve the lowest possible AIC value for each of the models by omitting insignificant variables. The different models were then compared using the AIC value to find the model that best explained the presence and richness for the different organism groups. The Likelihood-ratio test (LRT) value provided by the drop1 function was used to examine which of the variables in the final model explained most of the observed variation.

The GLM model assumes that observed data (here species counts) are independent, but when it comes to species data, however, this is rarely the case due to different factors, such as dispersal limitations, metapopulation structures and bias associated with collection of the species data. To test if data was spatially independent, each of the organism groups was tested for spatial autocorrelation (SAC) using Moran's I (Miller et al., 2007; Siesa et al., 2011; Liu and Slik, 2014). If SAC was found present in the data, it was taken into account by fitting an additional term as explanatory variable within the GLM models (an autocovariate). The autocovariate was calculated based on the species count and the longitude-latitude coordinates. This was done through a distance-weighted function, where each grid cell was given a value equal to the number of species in that cell and the coordinates were used for spatial measures, so that it could be estimated how much the species count in one cell correlated with the species counts in neighbouring cells (R-Package spdep, Dormann et al., 2007; Crase et al., 2012). The organism groups that didn't show SAC were fitted with the regular models described above. The SAC was only taken into account for the species richness dataset and not for the presence-absence one, because this was the form of the original dataset and what we found most relevant to look into regarding SAC.

3. Results

3.1. Overall species richness and correlations

Of the 487 quadrats in the grid, 79 cells had no red-listed species observed at all while only six cells had at least one species from all organism groups. The grid cell with the highest number
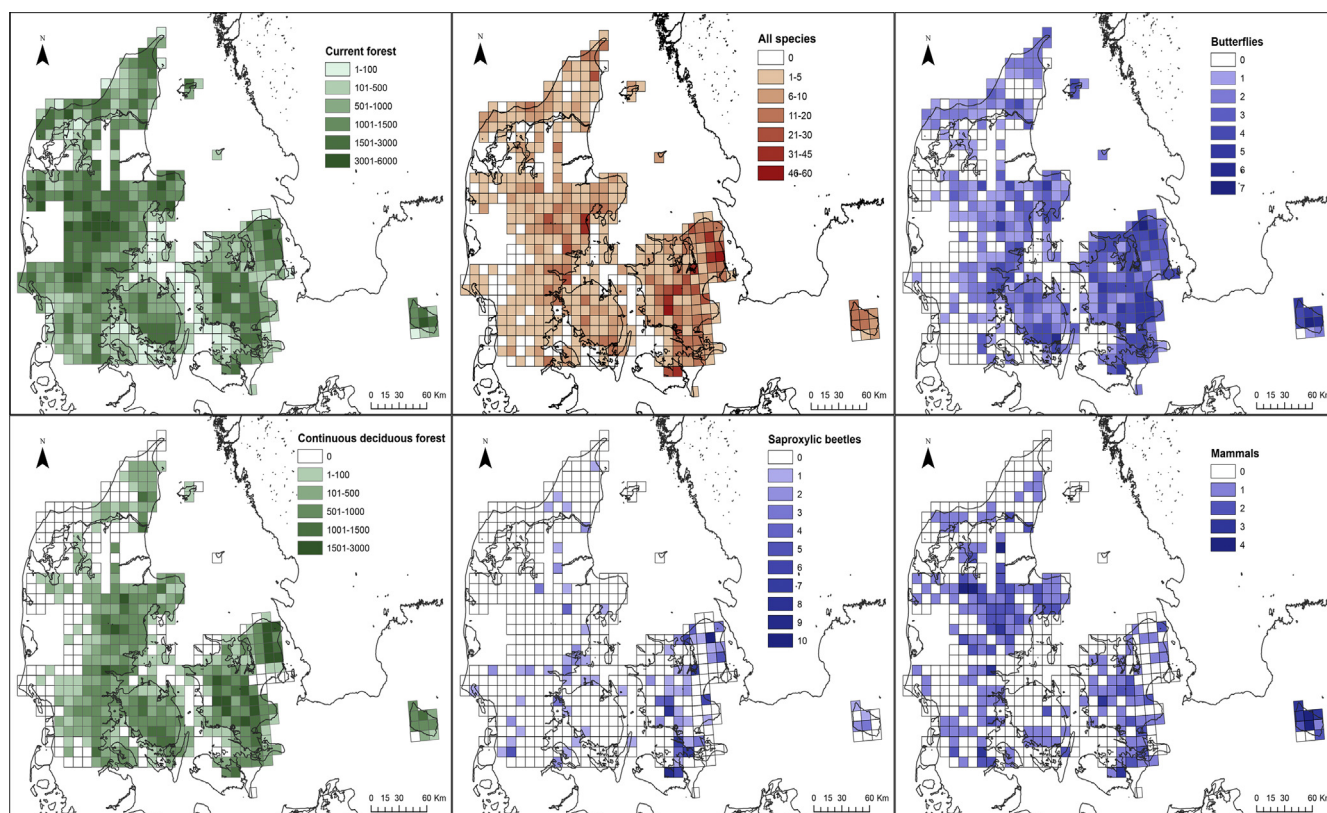
Fig. 2. Maps showing the distribution of total and continuous deciduous forest in Denmark (left column) and the number of red-listed species recorded across all eight organism groups analyzed in this dataset and for three selected organism groups (central and right column). The three groups were selected to highlight the variation in distribution patterns among groups.

of red-listed species had 52 species with the dominant organism group being saproxylic fungi (23 species).

The different organism groups showed very different distribution and richness patterns (Fig. 2). Some (e.g. butterflies, vascular plants, mammals) showed even distribution patterns while others (e.g. saproxylic beetles, soil saprotrophic fungi) showed a clustered distribution with distinct hotspots. Butterflies had the widest overall distribution, having one or more species present in 328 out of the 487 grid cells (Table 1). Despite variation in distribution patterns, species richness per grid cell was generally significantly positively correlated between organism groups, except for hydnoid fungi that were not correlated with the two groups of saproxylic organisms (Table C.2). Based on Moran's I, all groups except hydnoid fungi and mycorrhizal *Phlegmacium/Ramaria* species showed positive spatial autocorrelation in their species distribution patterns (Table C.4) meaning that the species from all six organism groups were clustered in distribution rather than random or dispersed (see Appendix D for Moran's I correlograms).

Current forest was present in all grid cells while historic forest was only present in 350 cells. Several forest variables were highly correlated. Historic forest area was strongly positively correlated with both continuous (Pearson's correlation coefficient $r = 0.92$, $n = 487$, $p < 0.0001$) and lost deciduous forest ($r = 0.92$, $n = 487$, $p < 0.0001$), but only weakly so with current forest cover ($r = 0.45$, $n = 487$, $p < 0.0001$), which was strongly positively correlated with coniferous forest cover ($r = 0.90$, $n = 487$, $p < 0.0001$) and less strongly with new deciduous forest ($r = 0.40$, $n = 487$, $p < 0.0001$). Of the different soil types, forest on clay showed a strong positive correlation with continuous forest ($r = 0.80$, $n = 487$, $p < 0.0001$) and historic forest ($r = 0.76$, $n = 487$, $p < 0.0001$), while forest on sand was positively correlated with

coniferous forest ($r = 0.87$, $n = 487$, $p < 0.0001$) and current forest ($r = 0.73$, $n = 487$, $p < 0.0001$) (Table C.3). Because the variables mentioned here do not appear in the same models, the strong correlations do not affect the results.

3.2. Presence-absence models

The presence/absence of seven out of the eight organism groups was best explained (based on the AIC value) by the model including the complex forest area variables (e.g. the coniferous and deciduous forest variables) as well as climate and distance to coast. Soil saprotrophic fungi was the only group that was better explained by the model including soil type, climate and distance to coast (Table 3).

In the final models, five organism groups showed a strong positive response to the continuous deciduous forest area while three organism groups were positively affected by coniferous forest area (Table 4). Other important significant variables in the models were forest growing on clay for soil saprotrophic fungi, and lost and new deciduous forest for saproxylic fungi. Of the climatic variables, temperature had a significant negative effect on vascular plants, while rainfall had a significant negative effect on butterflies and saproxylic fungi. Distance to coast had a negative effect on hydnoid fungi and vascular plants.

3.3. Species richness models

Four of the organism groups showed a noticeable difference in significant explanatory variables when comparing richness with presence-absence models. For mycorrhizal *Phlegmacium* & *Ramaria* species forest on clay and temperature were most efficient in

Table 3
Table showing AIC-values for the eight different models tested for each organism group and for both presence-absence (P/A) and richness. The lowest AIC values for each organism group are highlighted by bold lettering. The AIC values for the first four models (separated by the vertical line) are based on the full model, while the values for the last four models, are the lowest possible based on the drop1 function in R. This means that not all variables necessarily are included in the final model (see Table 4).

		Historic forest	Historic forest + connectivity	Current forest	Current forest + connectivity	Coniferous + deciduous	Soil structures	Soil structures + climate + distance to coast	Coniferous + deciduous + climate + distance to coast
Hydnoid thelephoroid mycorrhizal fungi	P/A	425.85	407.26	359.79	341.16	354.26	375.51	362.16	**328.66**
	Richness	319.74	319.26	327.52	326.13	310.31	321.37	318.94	**309.2**
Mycorrhizal *Phlegmacium* & *Ramaria* species	P/A	360.44	359.11	424.64	428.51	353.91	375.64	374.73	**350.94**
	Richness	557.11	531.85	572.87	556.97	534.73	516.5	**492.65**	520.92
Soil saprotrophic fungi	P/A	441.67	445.5	463.2	456.37	437.95	421.17	**393.1**	407.79
	Richness	381.71	385.21	388.17	389.51	381.32	375.82	**355.02**	365.48
Saproxylic beetles	P/A	389.21	392.43	421.73	418.86	388.37	399.65	393.9	**384.9**
	Richness	313.83	317.64	320.45	324.02	304.5	317.96	317.96	**297.99**
Saproxylic fungi	P/A	584.94	586.7	639.2	638.31	569.07	581.96	548.92	**525.53**
	Richness	728.63	732.35	736.33	739.02	**721.99**	735.68	731.16	**721.99**
Butterflies	P/A	552.97	556.8	578.28	578.78	541.97	555.76	467.49	**435.97**
	Richness	1027.4	1030.3	1016.6	1018.6	1022.6	1027.9	1027.9	**1012.2**
Vascular plants	P/A	609.26	613.04	593.95	588.06	598.1	604.79	557.28	**550.55**
	Richness	469.88	473.37	**464.33**	466.88	469.7	469.5	469.5	469.7
Mammals	P/A	587.32	589.08	541.13	542.23	521.46	583.2	566.38	**520.29**
	Richness	471.44	475.21	**470.5**	474.27	471.26	471.26	471.26	471.26

explaining species richness, while for vascular plants and mammals the current forest area showed the best model fit, although for mammals, the effect was not significant. For saproxylic beetles, richness was best explained by lost and new deciduous forest area. For the other four organism groups the same overall model explained both presence and richness.

In the final models (lowest AIC, Table 4) the variables that explained most of the variation in species richness were with some exceptions very similar to the ones explaining presence-absence patterns. However, for most organism groups, climate and distance to coast explained less variation in species richness. Also the area of continuous deciduous forest had smaller effects in the richness models, and was a strong positive predictor only for saproxylic fungi, while species richness in hydnoid fungi was negative affected. The area of coniferous forest remained a strong predictor of species richness for hydnoid fungi and butterflies but not for mammals.

4. Discussion

4.1. Overall importance of forest area and connectivity

In accordance with expectations, and the theory on species-area relationship (Arrhenius, 1921), all investigated groups of red-listed forest species responded positively to forest area. More interestingly, the historic forest area (200 years ago) was overall a better predictor of red-listed species than the current forest area, indicating old growth forests to be important for red-listed species. While forest connectivity (30 × 30 or 50 × 50 km scale) did not markedly help in explaining presence or richness of red-listed species, a signal of spatial autocorrelation was significant in six of eight organism groups. In other words, red-listed species richness tended to be clustered at landscape scale, independent of forest connectivity. We cannot completely rule out that this reflect bias in data, i.e. uneven but clustered sampling effort across Denmark (e.g. close to University cities), but believe that most of the signal reflects real biodiversity patterns in the Danish landscapes, i.e. spatial or temporal patterns in forest habitat quality that are not reflected in the coarse forest history variables explored in this study (cf. Graae, 2000). In an analytical context, the important point is that

these effects, irrespective of their nature, are accounted for by the spatial autocorrelation terms, and hence maximize the signals of the included spatially explicit predictor variables.

4.2. Forest continuity and extinction debt

The presence of red-listed species in organism groups dependent on old growth forest habitats or forest continuity (saproxylic beetles and fungi, mycorrhizal *Phlegmacium* & *Ramaria* species and vascular plants) was best explained by models including at least one of the variables lost deciduous forest and continuous deciduous forest. The effect was strongest and most consistent in saproxylic fungi and beetles, two species groups that are highly dependent on the continuous presence of dead wood and veteran trees in the forest (Similä et al., 2003; Penttilä et al., 2006; Bässler et al., 2010). Even though forest continuity is no guarantee for the presence of such habitats, it is a prerequisite for their formation (Nordén et al., 2014). For vascular plants the affinity to old deciduous forest most likely reflects dispersal limitation as reported from several targeted studies (e.g. Hermy et al., 1999), while mycorrhizal *Phlegmacium* & *Ramaria* species are assumed to depend on certain stable soil conditions that are present only in old forests (e.g. Nitare, 2000), even if the underlying mechanisms are not well studied (Nordén et al., 2014). Lost or continuous deciduous forest was also found to be important explanatory variables for the presence of mammals and butterflies. For mammals (including five bat species) the importance of veteran trees supplying cavities is a likely explanation for the importance of continuous deciduous forest, while for butterflies, the importance of continuous deciduous forests is most likely related to some species being dependent on the continuous presence of suitable forest glades over time (Eskildsen et al., 2015). Unfortunately, data on habitat abundance (amount of dead wood, abundance of old trees, etc.) was not available for this study, but could have provided deeper insight into interactions between forest continuity and actual habitat presence in Denmark and how this affects the presence of dependent red-listed species.

In cultivated landscapes, biodiversity extinction debts are often present (Honnay et al., 1999; Metzger et al., 2009), reflecting a

Table 4
Best model for each organism group for presence-absence and richness respectively. Based on lowest AIC value (Table 2) and showing significance levels (∗<0.05, ∗∗<0.01, ∗∗∗<0.001), sign (+/−) and LRT (likelihood ratio test) values for each variable as well as a pseudo R-squred for the full model.

	Presence-absence		Richness	
	Lowest AIC model	Likelihood Ratio Test (LRT value)	Lowest AIC model	Likelihood Ratio Test (LRT value)
Hydnoid thelephoroid mycorrhizal fungi (family *Bankeraceae*)	$R^2 = 0.24$		$R^2 = 0.26$	
	Coniferous forest*** (+)	48.19	Coniferous forest*** (+)	14.11
	Distance to coast*** (−)	26.28	Continuous deciduous*** (−)	13.10
	New deciduous** (+)	9.29	Rainfall (−)	3.11
	Lost deciduous** (+)	8.45		
Mycorrhizal *Phlegmacium* & *Ramaria* species (Cortinarius subg. *Phlegmacium* and mycorrhizal members of *Ramaria*)	$R^2 = 0.26$		$R^2 = 0.29$	
	Continuous deciduous*** (+)	43.64	Forest on clay*** (+)	52.94
	Lost deciduous*** (+)	12.56	Temperature*** (−)	27.29
	New deciduous** (+)	9.34	Forest on peat** (−)	9.76
	Distance to coast* (−)	4.91	Forest on gravel** (+)	9.50
			Forest on sand* (−)	6.23
			Distance to coast* (−)	4.17
			Forest on lime* (−)	3.96
Soil saprotrophic fungi (*Leucoagaricus* s.l. and *Lepiota* s.l)	$R^2 = 0.17$		$R^2 = 0.27$	
	Forest on clay*** (+)	35.28	Forest on clay*** (+)	22.64
	Distance to coast** (−)	8.13	Rainfall** (−)	9.59
	Rainfall* (−)	5.45	Temperature* (−)	6.02
	Forest on gravel* (+)	5.45	Forest on sand* (+)	5.68
			Forest on lime* (−)	5.47
Saproxylic beetles	$R^2 = 0.14$		$R^2 = 0.31$	
	Continuous deciduous*** (+)	46.33	Lost deciduous*** (+)	28.14
	Rainfall* (−)	4.46	New deciduous*** (+)	17.74
			Rainfall* (−)	6.29
			Temperature (+)	2.62
Saproxylic fungi (Polypores + *Hericiaceae*)	$R^2 = 0.29$		$R^2 = 0.43$	
	Lost deciduous*** (+)	23.83	Continuous deciduous*** (+)	23.52
	Rainfall*** (−)	23.67	Lost deciduous*** (+)	10.83
	Continuous deciduous*** (+)	22.64	New deciduous** (+)	10.11
	New deciduous*** (+)	21.66	Coniferous forest* (−)	5.03
	Distance to coast* (−)	4.05		
Butterflies	$R^2 = 0.30$		$R^2 = 0.38$	
	Rainfall*** (−)	72.72	Coniferous forest* (+)	6.94
	Continuous deciduous*** (+)	20.65	Continuous deciduous* (+)	6.19
	Coniferous forest*** (+)	15.22	Temperature (+)	1.12
	New deciduous** (+)	10.71	Rainfall (−)	0.10
	Lost deciduous** (+)	9.47		
	Distance to coast (−)	3.28		
	Temperature (−)	2.72		
Vascular plants	$R^2 = 0.14$		$R^2 = 0.19$	
	Temperature*** (−)	32.32	Current forest** (+)	8.31
	Distance to coast*** (−)	16.04		
	Lost deciduous*** (+)	12.71		
	New deciduous*** (+)	12.54		
	Continuous deciduous** (+)	8.31		
	Rainfall** (−)	7.89		
Mammals (pine-marten, dormouse + five bat species)	$R^2 = 0.21$		$R^2 = 0.22$	
	Continuous deciduous*** (+)	31.04	Current forest (+)	2.76
	Coniferous forest*** (+)	20.78		
	New deciduous** (+)	9.34		
	Lost deciduous** (+)	8.39		
	Distance to coast (+)	3.55		
	Rainfall (−)	2.82		

delayed responsiveness of certain species to habitat degradation or fragmentation in the past (Ranius et al., 2008; Kuussaari et al., 2009). Extinction debts imply that surviving old forest fragments may contain more species than their size or available habitats allow for, and hence they are prone to lose species in the long run, unless actions are taken to counteract this. The significance of lost deciduous forest as a positive predictor in several taxonomic groups in this study, suggests the presence of an unpaid extinction debt, most distinctly in saproxylic beetles and fungi. Previous studies on forest biodiversity have found similar results and various time-lags between habitat loss and species loss. For instance, Junninenand Komonen (2011) and Paltto et al. (2006) found a

time-lag of 120–150 years for saproxylic fungi and vascular plants in Fennoscandia. In our study the historical forest area included was from before 1820 indicating a time-lag in these organism groups in Denmark that may be more than 200 years.

4.3. Coniferous forest

In contrast to all other groups, the presence or richness of hydnoid thelephoroid fungi, butterflies and mammals showed a positive response to the coniferous forest area, which results from plantations since 1750. Hydnoid thelephoroid fungi are ectomycorrhizal with both deciduous and coniferous trees,

typically on extremely nutrient poor sandy or calcareous, humus poor soils (Nitare, 2000; van der Linde et al., 2009) and their preference for coniferous forests, which are typically planted on nutrient-poor sandy soils is therefore expected. In contrast, the butterflies included in our study are all naturally associated with warm, flower-rich forest glades or meadows and many require the existence of specific host plants. These habitat elements were part of the traditional deciduous forest landscape in southern Scandinavia until forest grazing and hay-meadows disappeared in the 19th and 20th centuries (Fritzbøger, 2005; Nilsson et al., 2008), but are not typically associated with coniferous forests, where intensive management and drainage makes the forest floor darker and less suitable for both host and nectar plants. Most of the coniferous forest in Denmark was however planted on former dunes, heathlands, grassland and on drained forest meadows and mires, which were often important and extensive habitats for butterflies in the past. Thus, the observed affinity of butterflies for landscapes rich in conifers could represent a historical legacy, potentially as an extinction debt (but see Krauss et al., 2010). It is possible that landscapes rich in coniferous plantations may present more suitable butterfly habitats than traditionally believed, due to the presence of clear-cuts, firebreaks, road verges and remaining patches of natural vegetation, that benefit host and nectar plants as shown in a study from southern France (van Halder et al., 2008). For presence of red-listed mammals we first interpreted the positive effect of coniferous forest to relate to the pine marten, which is generally considered to prefer coniferous forest habitats in Europe (Brainerd and Rolstad, 2002), but the effect was consistent also if this species was excluded from the dataset. This shows that even for red-listed bats and the dormouse, incidence was positively affected by large coniferous forest areas in the landscape.

4.4. Soil types and their link to forest history

Soil type variables were found to be more important predictors than forest history variables in two organism groups, soil saprotrophic fungi (presence and richness) and mycorrhizal *Phlegmacium* & *Ramaria* species (richness). In both cases forest on clay soils was an especially important explaining factor with a positive model effect. Both organism groups are known to have a preference for base rich soils (Nitare, 2000; Vellinga, 2004; Jeppesen and Frøslev, 2011), so these connections are not surprising and make sense biologically. It is important to note that the clear signal of soil type variables on fungal presence and richness does not rule out an importance of forest continuity per se for the two fungal groups, as continuous deciduous forest and forest on clay were very strongly correlated. At least for mycorrhizal *Phlegmacium* & *Ramaria* species a strong importance of habitat continuity has been suggested (Nitare, 2000), while evidence of continuous forest being important for the included soil saprotrophic fungi is more disputable (Vellinga, 2004).

The correlations between soil types and forest types also give an interesting insight into the Danish landscape history. While continuous and lost deciduous forests were strongly positively correlated with clayey soils, current and coniferous forest showed a strong positive correlation with sandy soils. This reflects a change in land-use with reforestation concentrated to old heathlands and disconnected to areas rich in continuous forests. Similar reforestation patterns have been reported from Belgium (De Keersmaeker et al., 2015) and may well be characteristic for larger parts of NW Europe. If this is indeed the case, the implications for slow-colonizing or dispersal limited forest species may well be more serious than current forest distribution suggest, resulting in a larger recolonization credit than if reforestation was done adjacent to existing continuous forests.

4.5. Climate and distance to coast

Climate variables (rainfall, temperature or both) were important predictors of the presence of butterflies, vascular plants and saproxylic fungi, and in all three groups our results indicate that areas with a continental climate (i.e. drier and/or cooler) appear more suitable for the threatened species. It is beyond the scope of this study to investigate whether this reflects differences in land-use or biodiversity across this climatic gradient, even if the potential implications are considerable in the context of climate change.

We found that proximity to the coast was an important predictor of richness for vascular plants and hydnoid fungi. Coastal forests tend to be less intensively managed, and may therefore provide more high-quality habitats for species sensitive to forest management. In addition, coastal forests in Denmark are often affected by erosion and strong winds that create more open conditions, and large variation in soil conditions spanning from freshly exposed mineral soils rich in base cations to more soils maintained by constant removal of leaf litter by strong winds. In combination these conditions are likely to benefit red-listed forest plants. For hydnoid fungi, that are known to be very sensitive to eutrophication (Arnolds, 2010; Lilleskov et al., 2011), a main factor behind coastal preference may be the lower nitrogen deposition in these areas (Vesterholt et al., 2000).

4.6. Conservation implications

Our study confirms that continuous forests are important for conservation of threatened forest biodiversity. Similar results have been found in several studies on red-listed forest species (e.g. Hermy et al., 1999; Fritz et al., 2008) and for richness of forest species in general (Peterken and Game, 1984; Dzwonko, 1993). In this light, it is problematic that less than half of the protected non-intervention forests in Denmark have continuity back to the 18th century (Johannsen et al., 2013). Hence, we strongly support that future efforts to select conservation areas should focus on continuous forest, both when enlarging existing reserves, and when selecting new conservations areas. Our study also indicates limited value of reforestation when it comes to protection of red-listed forest species. So far, reforestation has been a highly prioritized mean to halt forest biodiversity loss in Denmark, even though the price per area unit is considerably higher than the estimated or realized cost for setting aside non-intervention forests (Johannsen et al., 2013). Furthermore, several species associated with old trees have limited dispersal capacities, and reforestation will be pointless unless in close proximity to existing habitats, even when the newly planted trees reach appropriate ages (e.g. Hedin et al., 2008). The positive effect of coniferous forests on red-listed mammals, butterflies and hydnoid thelephoroid fungi indicate that the current strategy of active transformation of former heathland plantations to deciduous or mixed forests (Skov-og Naturstyrelsen, 2002) should be reconsidered. For both butterflies and mammals the most important conservation measure is the maintenance and recreation of flower rich forest glades in a generally varied forest landscape. Except for drainage and reforestation of forest glades and other open nature types, forestry is not a main threat for these organisms. For hydnoid thelephoroid fungi continued forestry or corresponding natural disturbances may even be a prerequisite for some of these species since they rely on infertile, mineral soils with a thin humus layer.

We believe that our more detailed results are relevant also in other regions with a forest history similar to the Danish, and more generally we suggest that our multitaxa approach to forest conservation is replicated in other regions. Too often conservation efforts are focused on a limited number of species groups (typically vascular plants, birds, butterflies and dragonflies), disregarding the

sometimes conflicting requirements of species-rich but often less known groups. Several other authors (e.g. Maes and Bonte, 2006; Larsen et al., 2009; Dolman et al., 2012) have explored similar approaches to multitaxa conservation planning, and have shown these to be both cost-effective and to give a more balanced perspective than approaches based on single species or species groups. This perspective is highly relevant in relation to forest ecosystems that are often highly complex, but often rather poor in traditional indicator taxa. One important challenge is of course that the amount of resources needed to collect primary biodiversity data increases with the number of organism groups covered, unless a targeted cost-effective protocol has been developed. In this study we addressed this challenge by using citizen science data, but in general such data has limited geographical resolution, which is the reason why we worked on gridded data using a 10 km resolution. However, even at this scale data might be incomplete, and in our study we had to exclude freshwater invertebrates and epiphytic lichens from the final analyses because the available distribution data was considered insufficient. As a consequence biodiversity related to natural forest wetlands and living trunks of veteran trees were not represented in our setup, while biodiversity related to soil, roots, dead wood, tree cavities, forest glades and landscape configuration were represented by one or more organism groups. Further work is needed to test the validity of our multitaxa approach to site selection and conservation monitoring in temperate forests, both at the landscape and local scale, but even with the broadly explorative approach presented in this study, we have shown new directions for forest conservation in Denmark that partly conflict with current conservation strategies.

Acknowledgements

Appendix A. Full species list

Hydnoid thelephoroid mycorrhizal fungi
Bankera fuligineoalba
Bankera violascens
Hydnellum aurantiacum
Hydnellum auratile
Hydnellum caeruleum
Hydnellum concrescens
Hydnellum ferrugineum
Hydnellum gracilipes
Hydnellum peckii
Hydnellum scrobiculatum
Hydnellum spongiosipes
Phellodon confluens
Phellodon melaleucus
Phellodon niger
Phellodon tomentosus

Appendix A. (*continued*)

Sarcodon imbricatus
Sarcodon lepidus
Sarcodon scabrosus
Sarcodon squamosus

Other mycorrhizal fungi
Cortinarius albertii
Cortinarius arcuatorum
Cortinarius aureocalceolatus
Cortinarius balteatocumatilis
Cortinarius bergeronii
Cortinarius caesiocortinatus
Cortinarius caesiostramineus
Cortinarius catharinae
Cortinarius cisticola
Cortinarius cliduchus
Cortinarius coerulescentium
Cortinarius cyanites
Cortinarius elegantissimus
Cortinarius eucaeruleus
Cortinarius flavovirens
Cortinarius fulvocitrinus
Cortinarius gracilior
Cortinarius humolens
Cortinarius langeorum
Cortinarius lilacinovelatus
Cortinarius maculosus
Cortinarius magicus
Cortinarius multiformium
Cortinarius nanceiensis
Cortinarius nymphicolor
Cortinarius odoratus
Cortinarius olearioides
Cortinarius osmophorus
Cortinarius platypus
Cortinarius porphyropus
Cortinarius rufo-olivaceus
Cortinarius saporatus
Cortinarius selandicus
Cortinarius sodagnitus
Cortinarius splendens
Cortinarius suaveolens
Cortinarius subporphyropus
Cortinarius subtortus
Cortinarius talus
Cortinarius variiformis
Cortinarius vesterholtii
Cortinarius xanthochlorus
Cortinarius xantho-ochraceus
Ramaria botrytis
Ramaria fagetorum
Ramaria fennica
Ramaria flavescens
Ramaria flavicingula
Ramaria formosa
Ramaria krieglsteineri
Ramaria pallida
Ramaria sanguinea

Soil saprotrophic fungi
Cystolepiota adulterina
Cystolepiota hetieri

Appendix A. (continued)

Cystolepiota icterina
Cystolepiota moelleri
Echinoderma boertmannii
Echinoderma calcicola
Echinoderma hystrix
Echinoderma perplexum
Echinoderma pseudoasperulum
Lepiota cingulum
Lepiota echinella
Lepiota fuscovinacea
Lepiota grangei
Lepiota griseovirens
Lepiota ignivolvata
Lepiota ochraceofulva
Lepiota poliochloodes
Lepiota pseudolilacea
Lepiota subgracilis
Lepiota tomentella
Lepiota xanthophylla
Leucoagaricus badhamii
Leucoagaricus sublittoralis
Leucocoprinus brebissonii
Melanophyllum eyrei

Saproxylic beetles
Abdera biflexuosa
Allecula morio
Allecula rhenana
Ampedus erythrogonus
Ampedus nigerrimus
Ampedus praeustus
Ampedus quercicola
Ampedus sanguineus
Anisoxya fuscula
Anoplodera sexguttata
Arhopalus ferus
Cerambyx scopolii
Corymbia scutellata
Crepidophorus mutilatus
Dinoptera collaris
Dorcus parallelipipedus
Elater ferrugineus
Eucnemis capucina
Exocentrus lusitanus
Gnorimus nobilis
Gnorimus variabilis
Hallomenus axillaris
Hypulus bifasciatus
Hypulus quercinus
Ischnodes sanguinicollis
Judolia sexmaculata
Leptura aethiops
Melandrya barbata
Melandrya dubia
Melasis buprestoides
Mycetochara axillaris
Neomida haemorrhoidalis
Oberea linearis
Oberea oculata
Oplosia cinerea
Orchesia fasciata
Orchesia luteipalpis
Osmoderma eremita

Osphya bipunctata
Pedostrangalia revestita
Pentaphyllus testaceus
Phymatodes alni
Pogonocherus decoratus
Prostomis mandibularis
Pyrrhidium sanguineum
Sinodendron cylindricum
Stenostola ferrea
Stenurella nigra
Strangalia attenuata
Tenebrio opacus
Tetratoma desmarestii
Tetratoma ancora
Tetrops starkii
Xylophilus corticalis
Xylotrechus rusticus

Saproxylic fungi
Anomoporia myceliosa
Antrodia heteromorpha
Antrodia malicola
Aurantiporus alborubescens
Aurantiporus croceus
Buglossoporus quercinus
Ceriporiapurpurea
Ceriporiopsis gilvescens
Ceriporiopsis pannocincta
Cerrena unicolor
Climacocystis borealis
Dentipellis fragilis
Fomitiporia robusta
Ganoderma adspersum
Ganoderma pfeifferi
Ganoderma resinaceum
Gloeophyllum trabeum
Hericium cirrhatum
Hericium coralloides
Hericium erinaceus
Inonotus dryadeus
Inonotus hispidus
Inonotus ulmicola
Irpex lacteus
Ischnoderma resinosum
Pachykytospora tuberculosa
Perenniporia fraxinea
Phellinus laevigatus
Phellinus tremulae
Porodaedalea pini
Pycnoporellus fulgens
Spongipellis delectans
Spongipellis fissilis
Trametes suaveolens
Tyromyces wynnei

Butterflies
Argynnis adippe
Argynnis paphia
Boloria euphrosyne
Carterocephalus silvicola
Coenonympha arcania
Leptidea juvernica
Leptidea sinapsis
Limenitis Camilla

Appendix A. (*continued*)

Melitaea athalia
Satyrium ilicis
Satyrium w-album
Thecla betulae

Vascular plants
Carex flava
Carex pendula
Cephalanthera damasonium
Cephalanthera longifolia
Cephalanthera rubra
Chimaphila umbellata
Circaea alpine
Corallorhiza trifida
Cypripedium calceolus
Cystopteris fragilis
Draba muralis
Epipactis atrorubens
Epipactis leptochila
Epipogium aphyllum
Laserpitium latifolium
Lunaria rediviva
Ophrys insectifera
Orchis purpurea
Phyllitis scolopendrium
Platanthera bifolia
Poa remota
Polystichum aculeatum
Ulmus laevis
Vicia dumetorum
Viola mirabilis

Mammals
Barbastelle barbastellus
Martes martes
Muscardinus avellanarius
Myotis brandtii
Myotis dasycneme
Myotis mystacinus
Myotis nattereri

Appendix B. Division of soil types

Clayey soils
- Freshwater clay
- Delta clay
- Saltwater clay
- Icelake clay
- Meltwater clay
- Moraine clay
- Eocene moler clay
- Oligocene/Miocene/Pliocene mica clay
- Eocene clay, plastic clay
- Eocene Røsnæs clay
- Selandien clay

Sandy soils
- Freshwater sand
- Delta sand
- Saltwater sand
- Dune sand
- Shifting sand
- Icelake sand

- Meltwater sand
- Moraine sand
- Oligocene/Miocene/Pliocene mica sand
- Miocene quartz sand
- Selandien sand
- Sand

Gravel soil
- Freshwater gravel
- Delta gravel
- Saltwater gravel
- Icelake gravel
- Meltwater gravel
- Moraine gravel
- Gravel/sand and gravel

Calcareous soil
- Spring-, marsh- and lake limestone
- Limemoraine gravel
- Limemoraine sand
- Danian bryozoan limestone, coral limestone
- Chalk and limestone
- Campanien-maastrichtien chalk
- Eocene Søvind marl
- Danian limestone and flint
- Saltwater gyttja
- Freshwater gyttja
- Saltwater shell gravel

Peat soils
- Freshwater peat
- Saltwater peat
- Alternating thin freshwater layers
- Alternating thin saltwater layers, marsh
- Oligocene/Miocene/Pliocene lignite

Appendix C. Additional tables

See Tables C.1–C.4.

Table C.1
Summary of maximum, mean and median values for forest area in the 10×10 km grid cells for the 15 forest variables, based on 487 cells.

Variable set	Variable	Maximum area (km^2)	Mean (km^2)	Median (km^2)
Simple forest areas	Current forest	56.1	11.1	9
	- 30×30 km radius	275.3	81.7	74.3
	- 50×50 km radius	542	193.8	170.6
	Historic forest area	56.2	5.5	1.5
	- 30×30 km radius	209.7	41.4	28.9
	- 50×50 km radius	418.8	99.8	80.3
Complex forest area	Coniferous forest	42	5.5	3
	New deciduous forest	11.6	1.5	0.6
	Lost deciduous forest	29.4	2	0
	Continuous deciduous forest	26.8	3.5	1.3
Forest area divided on soil types	Forest on gravel	25.5	0.6	0.1
	Forest on lime	4.8	0.2	0.1
	Forest on clay	29.3	2.9	1
	Forest on sand	40.1	5.2	2.3
	Forest on peat	10.9	0.8	0.3

Table C.2
Kendall's Tau Rank Correlation matrix for the eight organism groups. Values highlighted (bold) are significant at α = 0.05.

	Hydnoid thelephoroid mycorrhizal fungi	Other mycorrhizal fungi	Soil saprotrophic fungi	Saproxylic beetles	Saproxylic fungi	Butterflies	Vascular plants	Mammals
Hydnoid thelephoroid mycorrhizal fungi	1.00							
Other mycorrhizal fungi	**0.18**	1.00						
Soil saprotrophic fungi	**0.12**	**0.36**	1.00					
Saproxylic beetles	0.03	**0.27**	**0.29**	1.00				
Saproxylic fungi	0.07	**0.42**	**0.41**	**0.34**	1.00			
Butterflies	**0.15**	**0.31**	**0.29**	**0.27**	**0.39**	1.00		
Vascular plants	**0.20**	**0.27**	**0.27**	**0.19**	**0.30**	**0.34**	1.00	
Mammals	**0.14**	**0.22**	**0.18**	**0.24**	**0.21**	**0.25**	**0.22**	1.00

Table C.3
Pearson's correlation coefficients for explanatory variables. Significant values highlighted (bold) at p-value < 0.01.

|	Historic forest	Historic forest 30 × 30	Historic forest 50 × 50	Current forest	Current forest 30 × 30	Current forest 50 × 50	Coniferous	New deciduous	Lost deciduous	Continuous deciduous	Rainfall	Temperature	Distance to coast	Forest on gravel	Forest on lime	Forest on clay	Forest on sand	Forest on peat
Historic forest	1.00																	
Historic forest 30 × 30	**0.74**	1.00																
Historic forest 50 × 50	**0.64**	**0.93**	1.00															
Current forest	**0.45**	**0.26**	**0.18**	1.00														
Current forest 30 × 30	**0.29**	**0.39**	**0.32**	**0.67**	1.00													
Current forest 50 × 50	**0.21**	**0.32**	**0.33**	**0.57**	**0.93**	1.00												
Coniferous	0.10	−0.05	**−0.12**	**0.90**	**0.63**	**0.55**	1.00											
New deciduous	**−0.38**	**−0.30**	**−0.30**	**0.40**	**0.22**	**0.21**	**0.50**	1.00										
Lost deciduous	**0.92**	**0.63**	**0.53**	**0.33**	**0.23**	**0.16**	0.07	**−0.33**	1.00									
Continuous deciduous	**0.92**	**0.72**	**0.65**	**0.50**	**0.30**	**0.23**	0.11	**−0.37**	**0.70**	1.00								
Rainfall	−0.08	**−0.16**	**−0.25**	**0.35**	**0.45**	**0.44**	**0.47**	**0.30**	−0.01	**−0.14**	1.00							
Temperature	−0.05	−0.03	0.02	**−0.48**	**−0.68**	**−0.72**	**−0.49**	**−0.31**	−0.02	−0.08	**−0.50**	1.00						
Distance to coast	0.02	0.06	0.08	**0.38**	**0.62**	**0.73**	**0.42**	**0.24**	0.03	0.00	**0.51**	**−0.55**	1.00					
Forest on gravel	**0.39**	**0.28**	**0.20**	**0.42**	**0.26**	**0.20**	**0.30**	0.07	**0.35**	**0.36**	0.06	**−0.14**	0.09	1.00				
Forest on lime	**0.33**	**0.23**	**0.18**	**0.32**	**0.13**	0.05	**0.15**	0.04	**0.21**	**0.40**	−0.02	−0.02	−0.03	0.04	1.00			
Forest on clay	**0.76**	**0.64**	**0.61**	**0.33**	**0.19**	0.14	−0.02	**−0.27**	**0.59**	**0.80**	**−0.14**	0.07	−0.01	0.09	**0.42**	1.00		
Forest on sand	−0.05	**−0.17**	**−0.22**	**0.73**	**0.51**	**0.43**	**0.87**	**0.51**	−0.05	−0.04	**0.51**	**−0.44**	**0.34**	0.18	0.05	**−0.16**	1.00	
Forest on peat	**0.55**	**0.47**	**0.40**	**0.43**	**0.29**	0.20	**0.19**	−0.03	0.44	**0.58**	−0.02	**−0.13**	0.00	**0.59**	0.14	**0.33**	0.10	1.00

Table C.4

Table showing results for Moran's I p-value under 0.05 indicate spatial autocorrelation in the distribution data.

	p-value
Hydnoid thelephoroid mycorrhizal fungi	0.15
Other mycorrhizal fungi	0.12
Soil saprotrophic fungi	<0.05
Saproxylic beetles	<0.05
Saproxylic fungi	<0.001
Butterflies	<0.001
Vascular plants	<0.001
Mammals	<0.001

Appendix D. Moran's I correlograms

Moran's I correlograms for six out of the eight organism groups. Unfortunately R wouldn't cooperate to produce the final two correlograms, but these provide an idea of the change in spatial autocorrelation with distance. Red points indicate significant values (p < 0.05).
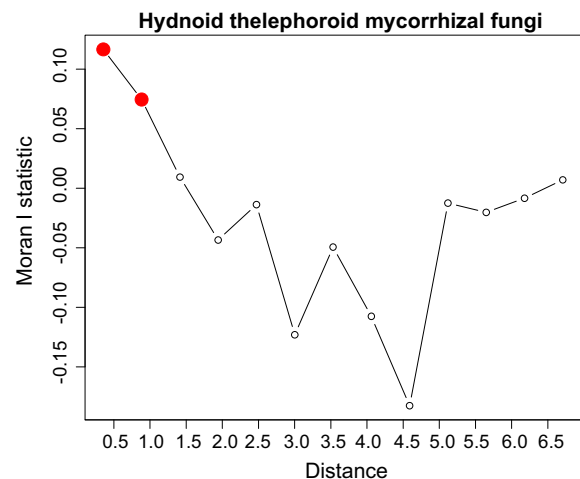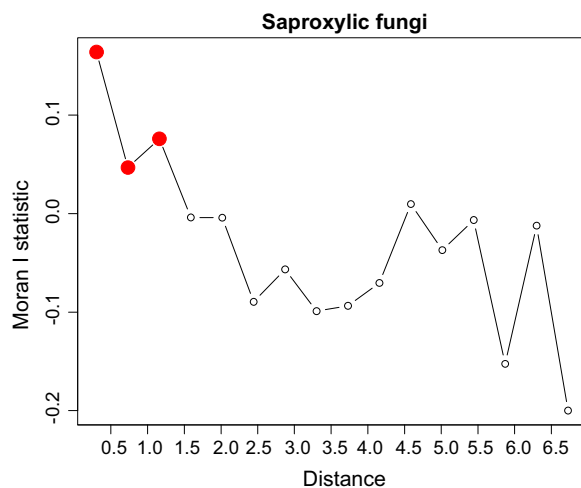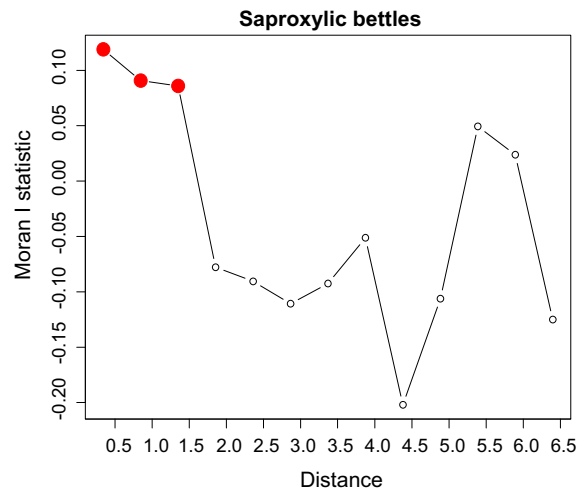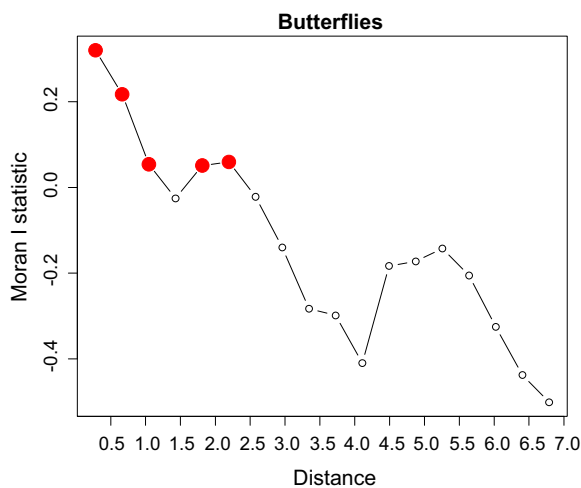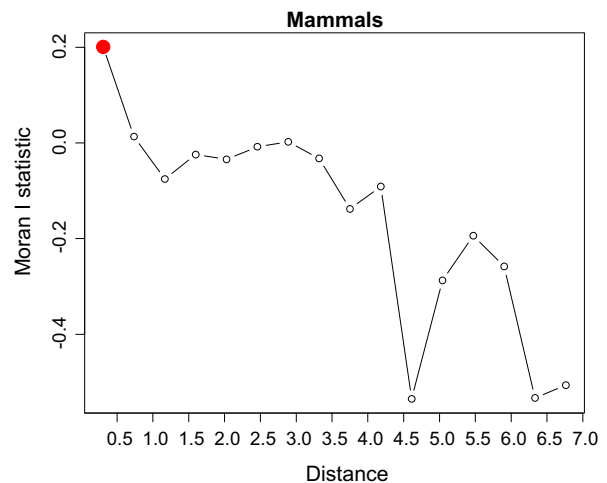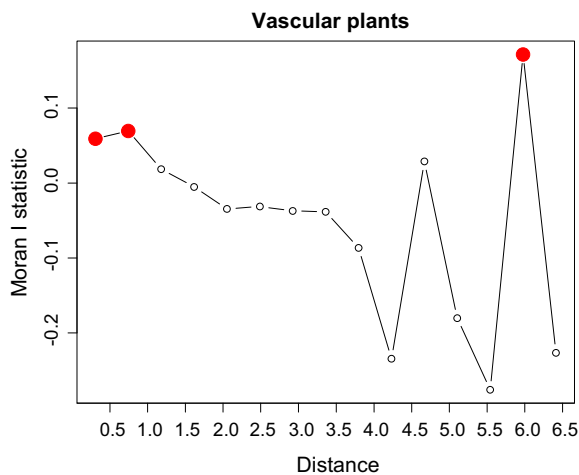
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