



Value of a broken umbrella: abandoned nest sites of the black stork (*Ciconia nigra*) host rich biodiversity

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Abstract

Protecting habitats for charismatic vertebrates can provide an ‘umbrella’ for less conspicuous organisms, especially when these are threatened by the same processes. However, such a conservation scheme is vulnerable to the extirpation of the focal species. We studied wider biodiversity values in long protected black stork (*Ciconia nigra*) nest sites, which were abandoned by the bird and thus legally subject to de-listing. In 20 abandoned nest sites in Estonia, we (i) mapped breeding birds within 600 m from the stork nest, and (ii) carried out time-limited surveys of lichens, polypore fungi, vascular plants and bryophytes in 2-ha plots. The breeding bird assemblages (64 species recorded) included 19 red-listed species, and showed no clear aggregation to the immediate surroundings of the stork nest. We recorded 740 plant and fungal species, of which 134 (18%) were of conservation concern (nationally protected, red-listed or extremely rare). Across the 2-ha plots, the numbers of the species of conservation concern varied more than three-fold (maximum 42 species), being affected notably by dead wood accumulation over time and presence of nemoral broad-leaved trees. The results demonstrate that many abandoned nest sites of the black stork have broader biodiversity significance, both due to the bird’s habitat requirements and the natural development during the protection. Expanding the umbrella function to sites abandoned by a focal species, but intact from anthropogenic degradation, can thus be a cost-effective conservation approach due to its low additional administrative burden. In most jurisdictions, the assessment procedure for such situations should be formalized, however.

Keywords Biodiversity · Conservation dilemma · Cost-effectiveness · Forest protection · Passive restoration · Umbrella species

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Introduction

For cultural and historical reasons, better studied taxon groups and iconic (flagship) species receive disproportionately much attention and funding for their habitat protection (Simberloff 1998; Seddon et al. 2005; McCarthy et al. 2012; Davies et al. 2018). Because the opportunity costs of biologically rich land are high, the set-asides established for such species can reduce future options for protecting additional areas for other species. Yet, simply allocating resources from iconic species to inconspicuous poorly known biodiversity may also fail due to a lack of social acceptance. A cost-effective solution could be reached through careful evaluation of set-aside habitats for socially valued species for wider representation of biodiversity (McGowan et al. 2020). Such a perspective is particularly needed for the cases when a species-based habitat protection system has been already implemented in areas or ecosystems that are exposed to heavy anthropogenic pressure.

The scientific *concept* to plan reserve networks based on selected species to provide reasonable protection (an ‘umbrella’) for full biodiversity emerged more than 30 years ago (Wilcox 1984), and has been heavily debated since then. The debate has focused on the ecological, distributional and cultural features of umbrella species; the effectiveness of this approach compared to the alternatives; and on combining sets of species for a conservation system (e.g., Roberge and Angelstam 2004; Caro 2010; Branton and Richardson 2011). However, the *practice* of creating reserves for priority species is much older, often legally and politically well established, and has continued in parallel. There are multiple reasons for why such practices evolved, including their historical selected-species roots in game management (e.g., Löhmus et al. 2017) and in the casewise building up of the environmental law (e.g., Brooks et al. 2002). Thus, in most regions with long and diverse nature conservation traditions, conservation managers are facing practical questions of how to manage existing set-asides that originally were not planned for broader biodiversity representation.

The existing networks protected for single (target) species can be substantial and carry significant opportunity costs in some regions, such as in temperate forests. For example, the 1994 Northwest Forest Plan in the U.S. reorganized a large share of 10 million ha of federal forests in the Pacific Northwest as late-successional reserves to protect the northern spotted owl (*Strix occidentalis caurina*) and marbled murrelet (*Brachyramphus marmoratus*), and a related network of riparian reserves as salmonid habitat (Spies et al. 2019). In the Baltic countries, more than 1% of all forest land is protected for a single species, the western capercaillie (*Tetrao urogallus*) (Löhmus et al. 2017). Altogether, the sites protected solely for birds of conservation concern comprise ca. 15% of the Natura 2000 network area of the European Union (EEA 2020).

Single-species reserves have straightforward management goals as long as they serve the target species. However, managers may face a *conservation dilemma* when the target species is lost, and they have to decide about continuing the protection of abandoned localities. The abandonment may result from an overall population decline of the target species, creating obvious problems when their protected localities hold a prominent position in the conservation system and the broader biodiversity is poorly known (Simberloff 1998). Similar dilemmas can occur due to spatio-temporal dynamics in species distributions when the reserves are small (Tingstad et al. 2020), or when the target species loses its protection status while the other (less known) species in the ecosystem remain threatened. Such dilemmas refer to a risk that repealing the protection status can create new conservation problems by: (i) eliminating the sites needed for the recovery of the target species (Camaclang

et al. 2015); (ii) degrading sites of a broader biodiversity value; and (iii) by undermining the public funds and social credibility spent for the establishing the reserve system. A key question for addressing all those risks is the habitat quality of the sites.

In the current study, we focus on the risk of losing broader biodiversity values in so-far protected, but abandoned, black stork (*Ciconia nigra*) nest sites at the northern margin of the species' European distribution range. In this region, the stork sparsely inhabits large forest landscapes with access to streams for foraging (Lõhmus et al. 2005; Treinys et al. 2009). Since it can occupy a nest stand for several decades in undisturbed conditions, several countries have practised establishing micro-reserves of at least 10–30 ha in size around the nests to buffer these against forestry impacts (Rosenvald and Lõhmus 2003; Strazds 2003; Zieliński et al. 2011). Despite such practices, the northern populations of the black stork have declined markedly (Konovalov et al. 2019); thus, hundreds of protected nest sites in this region have been abandoned and have unclear perspectives of re-occupancy.

We sampled the black stork nest sites abandoned in Estonia for five taxon groups (breeding birds, vascular plants, bryophytes, lichens, and polypore fungi), focusing on species of conservation concern and biodiversity variation among the nest sites (cf Lelli et al. 2019 for general relevance of such approach). Our broad study questions were: (1) Has the strict protection status provided a long-term umbrella for old-forest assemblages to develop? (2) Are those assemblages distinct also due to the habitat preferences of the black stork (as established in a comparison with reference datasets from non-stork sites)? (3) Which stand structural characteristics explain the variation among the nest sites in their conservation values?

Material and methods

The study system

The study system comprised 20 abandoned black stork nest sites distributed across the Estonian mainland where a large population decline has taken place since the 1980s (Sellis 2018). The study region is situated in the European hemiboreal vegetation zone (Ahti et al. 1968). The mean air temperature is 17 °C in July and –4 °C in January; the average precipitation is 600–700 mm year⁻¹. The topography is mostly flat and of glacial origin: uplands and plateau-like areas alternate with lowlands, depressions and large valley-like forms. Forests cover half of the land area, of which ca. 40% are wet forests; peatlands (both open and wooded) cover ca. 24%. As of 2019, the Estonian black stork population is red-listed as Critically Endangered (EELIS 2021) and it is subjected to national monitoring. The Estonian Nature Conservation Act prescribes strict protection within at least 250 m radius for every known black stork nest in the country; if the site is abandoned, removal of the legal protection requires special assessment for the potential of re-occupancy.

The 20 sites were selected from a total of 106 abandoned nests recorded in the Estonian Nature Information System in April 2014, excluding the sites degraded by forest cutting. Since our aim was to explore site variation, we first distinguished 63 abandoned nest sites in four common forest site-types, for which there was sufficient reference information on natural biodiversity and forest structure. For each site type, five replicate sites were selected in mainland Estonia to represent a stand age gradient from 70 to 85 years to the oldest available (131–176 years; Fig. 1; Online Resource 1). The site types were (sensu Lõhmus 1984): (i) *Oxalis-Myrtillus* mixed conifer forests with variable share of Norway

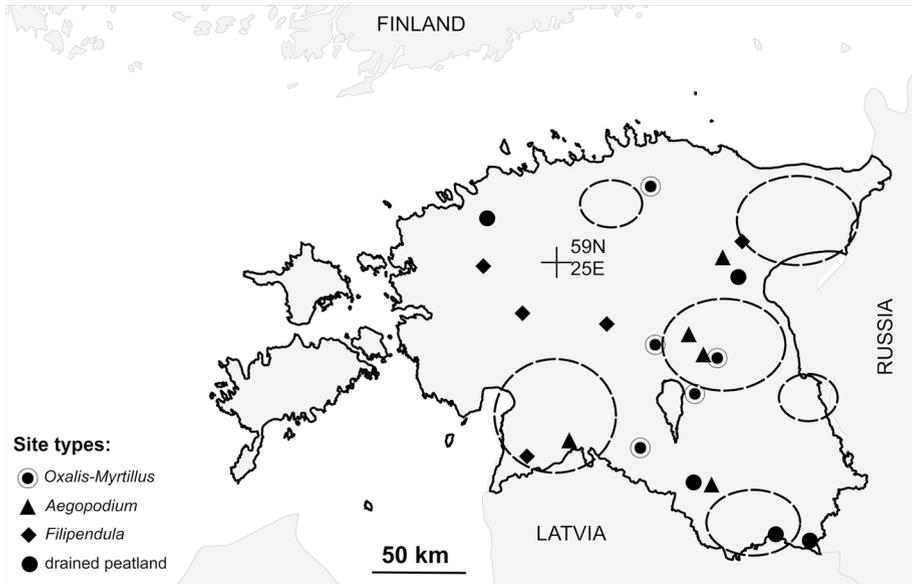


Fig. 1 Locations of the studied nest sites in Estonia (symbols indicate the site types). The dashed ovals mark the regions where reference datasets for comparison have been collected

spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) on Gleyic Podzols; (ii) eutrophic boreo-nemoral mixedwood of *Aegopodium* type, comprising spruce, silver birch (*Betula pendula*) and European aspen (*Populus tremula*) on Gleyic Cambisols and Gleyic Luvisols; (iii) mixedwood of the *Filipendula ulmaria* type on Gleysols, and (iv) spruce-dominated drained peatland forests (decayed-peatland site types).

Of the 20 nest sites, six had been found in the 2000s, seven in the 1990s, and seven were protected already earlier. Most stands could be confirmed to have developed without human intervention for at least 30 years or (in three sites) during the whole current stand development (Online Resource 1). The actual periods without timber cutting were apparently even longer in several cases, as judged by the present structure of the stand. The reasons for that include both the selection of (undisturbed) sites by the stork (Lõhmus et al. 2005) and the protection established after finding the nest. At the time of the study, one nest site was situated on private land and the rest were in state-owned forests, but all the sites were similarly under strict protection (13 in sites specifically protected for the species; seven incorporated into multi-purpose reserves).

Data collection

The field sampling was carried out in 2014 and 2016, using two types of plots. The bird census areas (23–76 ha in size, mean 46 ha) comprised the whole forest area that was strictly protected around each nest site. For sessile organisms, a homogeneous 2-ha plot was delineated around each nest tree. In the latter, we also sampled forest structure using four 50-m straight, spaced-out sampling lines according to the procedure described by Lõhmus and Kraut (2010). Live trees of ≥ 10 cm in diameter at breast height (DBH) were

measured within 2 m, and standing dead trees ≥ 1.0 m height and ≥ 10 cm DBH (or top diameter) within 5 m at both sides of these lines. The plot level volume of live tree trunks (including bark) was estimated according to species-specific diameter functions used in practical silviculture in Estonia (Padari 2004). The volume of coarse and fine fallen dead wood (diameter ≥ 10 cm and 0.3–9.9 cm, respectively) was estimated by measuring the diameter of each item at its crossing point with a transect line, and assuming circular cross-sections (Van Wagner 1968). A five-point scale was used for wood decay stage (Löhmus and Kraut 2010); the stages III–V are here termed as ‘well decayed’.

Experienced ornithologists mapped birds on two surveys in each area in spring 2014 (first mapping 9–26 May; second mapping 5–23 June). Each area was covered by walking slowly at tracks no more than 50–75 m apart in the morning, mapping all bird individuals heard or seen that could be breeders. The locations of the observations were digitalized in a GIS and interpreted as nesting territories by the same person (the author R.N.). The main criteria for the interpretation were (i) simultaneous observations of adjacent territorial birds or pairs, and (ii) distances between the locations depending on species biology (e.g., > 100 m observations of singing males of many small passerines were considered distinct territories). In the Estonian conditions, the numbers of nesting territories obtained with such methods probably form 60 to 90% (depending on species) of those estimated with thorough 10-time surveys (Leito et al. 2008). The underestimates are most likely for early breeders and non-passerines difficult to detect during few top-season surveys (Löhmus 2020), and for highly mobile species (e.g., corvids, thrushes, *Spinus spinus*) for which mostly the criterion (i) was used.

We surveyed four sessile species groups (vascular plants; bryophytes; lichens and allied fungi; polypore fungi—each by one field expert) in 2-ha plots following a standardised fixed-area-fixed-effort protocol (Löhmus et al. 2018a). In each plot, the full assemblage of each species group was inventoried for four hours in a suitable season (vascular plants in June–August; bryophytes and lichens in July–October; polypores in September–October). All types of suitable substrates up to 2 m height from the forest floor were checked, with the primary aim of finding as many species as possible. According to field estimates, this approach usually reveals $> 70\%$ of all species present in the 2-ha plot, ranging from ca. 50% in lichens and polypores in the most diverse forests to $> 90\%$ in vascular plants (Löhmus et al. 2018a). For each detected species, we categorized its abundance on an approximately logarithmic scale. For bryophytes, lichens, and polypores, a five-point scale was used (1, one record; 2, 2–5 records; 3, 6–15 records; 4, 16–100 records; 5, > 100 records). For vascular plants, a ten-point scale was used, ranging from one shoot (score 1), 2–3 scattered shoots or a clone (score 2) to local dominance (score 8) or total dominance (score 9 for $> 50\%$ total cover; score 10 for $> 90\%$ cover) (see Löhmus and Remm 2017 for % cover estimates related to this scale). Where necessary, specimens that could not be identified in the field were collected and examined in the lab using microscope, thin-layer chromatography method to detect lichen compounds or, in the case of polypores, sequencing for rDNA ITS region for comparisons with references. The nomenclature follows PlutoF database (PlutoF 2017) for vascular plants, Vellak et al. (2015) for bryophytes, Randlane et al. (2019) for lichens, and Runnel et al. (2021) for polypores. Vouchers of species of particular interest have been deposited in the collections of the University of Tartu Natural History Museum (TUF) and the Estonian University of Life Sciences (TAA).

For comparison, we used our reference datasets of the sessile species groups, which have been collected between 2006 and 2009 in mature managed and old-growth stands of mainland Estonia using the same survey protocol (Löhmus et al. 2018a). Here, we use the data from the site types comparable to those around the stork nests; notable exceptions

being that: the reference match for the *Filipendula* type had a similar tree composition but wetter soil (swamp); bryophytes lacked reference datasets for the *Aegopodium*-type, and polypores for the drained peatland type. There were six plots per forest type and age combination (except five sites for the swamp type). Thus, we included a total of 23 mature managed and 23 old growth reference sites for vascular plants and lichens, and 17 mature managed and 17 old-growth reference sites for bryophytes and polypores. See, e.g., Löhmus and Kraut (2010), Remm et al. (2013), Runnel and Löhmus (2017), Löhmus and Löhmus (2019) for analyses of the reference data.

Data analyses

Our analyses describe the biodiversity values and their linkages with the protection provided by the stork nest. A major focus was on species of conservation concern (SPEC), distinguished as species being nationally red-listed as threatened or Near Threatened, or legally protected or used as indicators for woodland key habitats (Anonymous 2017). The national red lists used followed the 2017–2021 assessments (EELIS 2021).

The analyses of birds specifically addressed the scale of the potential umbrella effect provided by the stork. For that, we distinguished distance zones of 100 m intervals from the historical nests. We expected that if the effect of protection was mainly the reduction of forestry disturbance, the bird assemblage parameters would be rather similar across the distance zones. Alternatively, if the stork would select distinct locations at a smaller scale, there could be differences or a gradient across the distance zones. The surveyed areas were sufficient to analyze areas up to 600 m from the nest; this analysis eventually included a total of 801 ha surveyed (23–62 ha per site; Online Resource 1).

We tested the differences in vascular plant, bryophyte, lichen and polypore assemblages in the stork plots and the two age classes of reference plots using multi-response permutation procedures (MRPP). MRPPs test whether Sørensen (Bray–Curtis) distances between predefined classes exceed those resulting from random assignment of the sample. The species matrix for each species group comprised species abundance class in each plot; the species recorded only in 1–2 plots were omitted. Were also excluded the site types for which reference data were unavailable (in bryophytes—*Aegopodium* type; in polypores—drained peatland type). We then carried out indicator species analyses (Dufrêne and Legendre 1997) to test for characteristic species in the stork plots. Finally, to visualise the differences between species assemblages, we used non-metric multidimensional scaling (NMS) based on the Sørensen (Bray–Curtis) distances. We used the medium autopilot mode (up to six axes; 200 runs with real data and 200 with randomized data; stability criterion 0.00001), and accepted the recommended three-dimensional solutions based on the mean stress value with real data (12.4–18.7). In the environmental matrix, thirteen potentially important structural variables (Online Resources 1–2) were included to explore their correlations with the formed ordination axes. All these analyses were carried out in PC-ORD vers. 6.07 (McCune and Mefford 2011).

To explore how the number of SPECs per plot may have developed during the protection, we built generalized linear models (GLM; Type III; Poisson distribution; log link) separately for each taxonomic group, and cryptogams pooled (since these three groups covaried, see "Results" sect.). Factor significance was estimated based on likelihood-ratio tests. The key factor of interest was the stand age (continuous variable), when accounting for forest type (two categories based on SPEC frequencies: conifer forests of the *Oxalis-Myrtillus* or drained peatland types vs. the mixedwood of the *Aegopodium* or *Filipendula*

types). First, we only documented their main effects. Then, we added the volume of coarse fallen wood (CWD) to test for independent contributions of stand structural development vs. the remaining stand-age effect. (Note that both stand age and dead wood abundance are also operational for management decisions.) Finally, we explored factor interactions in the model indicating the largest impact of the protected status. The analyses were performed using glm function in R-core package (R version 4.0.2).

Results

Biodiversity in the black stork nest sites

In total, 3850 pairs or territorial birds of 64 species were recorded in the protected forest areas within 600 m of abandoned black stork nests ($n=20$). We could not detect statistically significant gradients in the main bird assemblage characteristics. The fact that somewhat less dense and less diverse assemblages were recorded at distances > 500 m (Table 1) was attributable to the fact that the protected zones were smaller in more productive sites (the 501–600 m zone was absent in five such sites sampled). When standardizing the bird densities in all zones to the value observed in the closest (0–100 m) zone, the variation among the zones was convincingly non-significant (ANOVA: $F_{4,90}=0.85$; $P=0.50$).

The bird assemblages in the protected zones included 19 red-listed species (14 threatened; 5 Near Threatened). Some Vulnerable species that are generally sparsely distributed in Estonia, but regularly occurred around the nest sites, included: *Tetrastes bonasia* (4.1 territories km^{-2}), *Picoides tridactylus* (1.9), *Tetrao urogallus* (0.9) and *Columba oenas* (0.6). The densities of two putative old-forest passerines, *Ficedula parva* and *Phylloscopus trochiloides*, were 8.7 and 3.6 territories km^{-2} , respectively. Raptors and owls were present at a total density 1.0 territories km^{-2} (five species: *Buteo buteo* and *Strix uralensis* 3 pairs each; *Accipiter gentilis*, *Aquila pomarina* and *Pernis apivorus* 1 pair each).

In the 2-ha plots in the black stork nest stands, we recorded a total of 266 species of vascular plants, 133 species of bryophytes (additionally, unidentified *Sphagnum* spp.), 229 species of lichenized and allied fungi, and 112 species of polypore fungi (Table 2; Online Resource 3). According to the NMS ordination, the assemblage structure varied along with

Table 1 Mean breeding bird community characteristics (\pm SE) in the protected forests surrounding 20 abandoned black stork nests in Estonia

Variable	Distance from the nest (m)					
	0–100	101–200	201–300	301–400	401–500	501–600
No. of pairs ha^{-1}	5.6 \pm 0.3	5.3 \pm 0.4	4.7 \pm 0.3	5.1 \pm 0.5	5.5 \pm 0.6	4.2 \pm 0.4
Red-listed species (%)	12 \pm 2	9 \pm 1	13 \pm 2	14 \pm 2	9 \pm 1	12 \pm 2
Dominant passerines (%) ^a	48 \pm 3	48 \pm 2	48 \pm 2	53 \pm 2	52 \pm 3	52 \pm 4
Non-passerines (%)	4 \pm 1	7 \pm 1	5 \pm 1	5 \pm 1	4 \pm 1	5 \pm 1
Shannon species diversity	3.10	3.10	3.12	3.06	3.04	2.92
N (no. of pairs)	325	836	931	867	597	294
No. of species	41	49	56	48	45	33

^aFive most abundant species: *Fringilla coelebs*, *Phylloscopus sibilatrix*, *P. trochilus*, *Erithacus rubecula*, *Regulus regulus*

Table 2 The numbers of plant and fungal species (mean \pm SD, totals in brackets), and those of conservation concern (SPEC), and those of conservation concern (SPEC) found per 2-ha plots in the nest sites of the black stork

Taxon group	All sites (n = 20)	Forest site type		
		<i>Oxalis-Myrtillus</i> (n = 5)	<i>Aegopodium</i> (n = 5)	<i>Filipendula</i> (n = 5)
All species				
Vascular	98 \pm 24 (266)	107 \pm 15 (203)	106 \pm 16 (174)	101 \pm 14 (176)
Bryophytes	66 \pm 8 (134)	65 \pm 6 (106)	69 \pm 8 (104)	65 \pm 8 (104)
Lichens	74 \pm 11 (112)	71 \pm 8 (142)	82 \pm 12 (164)	78 \pm 6 (148)
Polypores	37 \pm 6 (112)	36 \pm 4 (77)	43 \pm 5 (80)	37 \pm 6 (76)
Total	275 \pm 37 (741)	279 \pm 20 (528)	299 \pm 31 (522)	282 \pm 9 (504)
SPEC				
Vascular	4 \pm 2 (21)	3 \pm 1 (11)	4 \pm 2 (11)	4 \pm 2 (11)
Bryophytes	8 \pm 2 (21)	8 \pm 1 (14)	10 \pm 2 (15)	8 \pm 4 (14)
Lichens	9 \pm 5 (63)	8 \pm 3 (23)	12 \pm 5 (39)	12 \pm 7 (34)
Polypores	5 \pm 3 (29)	4 \pm 2 (12)	7 \pm 2 (17)	5 \pm 4 (16)
Total SPEC	26 \pm 9 (134)	23 \pm 4 (60)	33 \pm 9 (82)	29 \pm 12 (75)
				Drained peatland (n = 5)
				77 \pm 36 (167)
				63 \pm 10 (103)
				66 \pm 10 (135)
				32 \pm 4 (65)
				238 \pm 53 (470)

several stand characteristics (Online Resource 2); notably: (i) the density of large live trees was a major factor for vascular plant and bryophyte assemblages (Fig. 2a, b), while (ii) the tree species composition and dead-wood variables were major factors for lichen and polypore assemblages (Fig. 2c, d); (iii) stand age had the largest effect on the assemblages of polypore fungi.

In three of the four groups (except vascular plants), the assemblages in the stork plots differed significantly from those in the reference sites (Fig. 2; MRPP test: $P < 0.001$ for all three comparisons). The nest sites were most distinct for lichens, and in drained peatland sites (Fig. 2a–c; the latter not studied in polypores). Additionally, the indicator species analyses revealed that several bryophyte species were more likely to occur around the nest sites: six of seven species with high (> 50) and significant indicator values were bryophytes. These species included three hepatics of conservation concern that primarily inhabit well decayed downed wood (*Crossocalyx hellerianus*, *Nowellia curvifolia* and *Riccardia latifrons*).

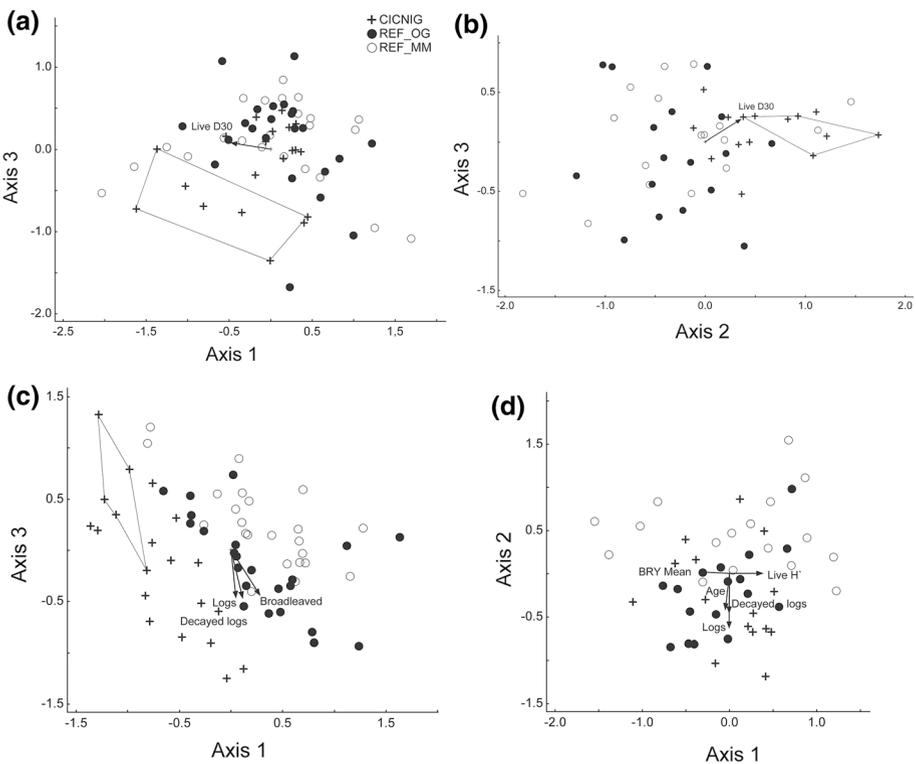


Fig. 2 Nonmetric multidimensional scaling ordination graphs of the assemblages of vascular plants (a), bryophytes (b), lichens (c), and polypore fungi (d) in the abandoned nest sites of the black stork (CICNIG) compared to reference sites in old growth (REF_OG) and mature managed forests (REF_MM) of the same site types. The arrows denote stand variables correlated with the axes ($r^2 \geq 0.2$; see also Online Resource 2): “Live D30”—density of live trees with diameter at breast height ≥ 30 cm, “Broadleaved”—density of overstorey nemoral hardwoods (*Acer*, *Fraxinus*, *Quercus*, *Tilia*, *Ulmus*); “Logs”—volume of all fallen trunks ≥ 10 cm in diameter; “Decayed logs”—volume of fallen trunks in the decay stages III–V; “BRY mean”—mean ground cover of bryophytes, “Live H”—Shannon diversity of live trees; “Age”—mean age of overstorey trees. The nest sites in drained peatlands are delineated with polygon lines

Plants and fungi of conservation concern in the nest sites

The recorded assemblages of the four sessile groups included 134 (18%) species of conservation concern (SPEC; Online Resource 3). Their share in the species pool was distinctly smaller in the conifer dominated *Oxalis-Myrtillus* and drained sites (11%) than in the eutrophic mixedwood of *Aegopodium* and *Filipendula* types (15–16%; Table 2). The numbers of all sessile species recorded per 2-ha plot varied less than two-fold (range 174–334), while the numbers of SPECs varied more than three-fold (range 13–42), again with clear differences between the site types (Table 2). The minimum set containing all SPECs found was 18 plots, which was entirely due to each of these plots hosting at least one species found in no other plot.

Both in terms of all species, and of the SPECs recorded, the three cryptogam groups co-varied across the plots, while the numbers of vascular plant species varied independently (Table 3). Within taxon groups, the correlations between the numbers of SPECs and all species were moderate to strong in cryptogams ($r=0.52\text{--}0.77$; $P<0.05$; $n=20$), while such correlation was absent in vascular plants ($r=0.37$; $P>0.1$; $n=20$).

Four groups of SPECs could be distinguished based on their practical value (Online Resource 3):

- (i) *Nationally protected species* (37 species in total) were present in every plot, and five plots had ≥ 10 such species. The species of European significance included, for example, the grass *Cinna latifolia* (in two plots) and the wood-inhabiting polypore *Skeletocutis odora* (in four plots). The iconic macrolichen, *Lobaria pulmonaria*, was also recorded in four plots.
- (ii) 92 species found were *nationally red-listed* (4 Critically Endangered, 16 Endangered, 33 Vulnerable, 37 Near Threatened), including 66 species that lacked legal protection. No plot had fewer than four, and seven plots had ≥ 10 red-listed species. Major ecological groups (> 10 species each) were: lichens inhabiting aspen and nemoral broad-leaved trees; the species (mostly polypores) inhabiting coarse woody debris; and thirteen calicioid fungal species (six lichenized) that inhabit specific microhabitats. Windthrow mounds—a substrate abundant in these naturally developing stands—hosted a small group of specialized red-listed species (*Chaenothecopsis nigra*, *Micarea myriocarpa*, *Microcalicium arenarium*, *Psilolechia lucida*).
- (iii) A subset of (ii) were *very rare taxa* whose localities have a wider regional significance. These included, for example, three macrolichens of the genus *Cetrelia* (distinguished based on lichen substances); a calicioid microlichen *Sclerophora amabilis* (one of two records in Estonia); and four of the less than 10 locations of the polypore

Table 3 Cross-taxon covariance (Pearson correlation coefficients) in the total numbers of species (above the diagonal) and in the numbers of species of conservation concern (below the diagonal) recorded in the 2-ha plots ($n=20$)

Taxon group	Vascular plants	Bryophytes	Lichens	Polypores
Vascular plants		0.36	0.35	0.25
Bryophytes	– 0.14		0.65*	0.67**
Lichens	– 0.07	0.73***		0.76***
Polypores	0.34	0.47*	0.50*	

P-values are indicated as: * <0.05 , ** <0.01 , *** <0.001

Junghuhnia autumnale known in Estonia so far. Some of such species are also poorly known, e.g., lichens *Biatora vernalis* and *Megaspora verrucosa*.

- (iv) The 51 official *indicator species of woodland key habitats* found included 13 bryophytes, 8 lichens, and 10 polypores that are neither protected nor red-listed. Several of those species have a threatened status elsewhere in North Europe. Individual plots had 6–22 indicator species (mean: 14 ± 5 SD).

The general linear modelling showed that per-plot numbers of SPECs among lichens, polypores, and cryptogams pooled were highest in the mixedwood sites and increased along with the stand age (Table 4: upper panel). Adding CWD volume to the model revealed its positive independent effect on SPECs of bryophytes, lichens, and cryptogams pooled, while all significant stand age effects became non-significant (Table 4, lower panel).

Exploring Stand age \times Site type interactions for the model with the clearest effects (cryptogams pooled) indicated similar site-type specific increases both in the numbers of SPECs and CWD volumes (Fig. 3). The interactions indicating significantly steeper increases in the mixedwood types were significant in both cases ($P=0.038$ for SPECs; $P=0.045$ for CWD). The mean (\pm SD) observed CWD volume in conifer-dominated and eutrophic mixedwood stands was 48.5 ± 30.3 and 93.5 ± 53.6 m³/ha, respectively, and the mean volume of medium to well decayed CWD (decay stage III–V) was 25.0 ± 18.9 and 42.2 ± 30.2 m³/ha, respectively (Online Resource 1).

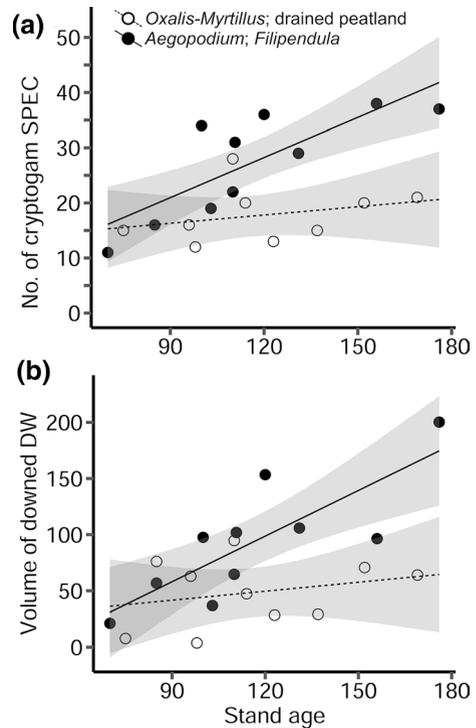
Table 4 Generalized linear models (Type III; Poisson distribution; log link) of the stand age and site type effects (upper panel), and the additional effect of downed coarse woody debris (CWD) (lower panel) on the number of species of conservation concern in black stork nest sites ($n=20$ 2-ha plots)

Taxon group	Stand age effect		Site type effect		CWD (m ³ /ha) effect	
	estimate \pm SE	<i>P</i>	estimate \pm SE ^a	<i>P</i>	estimate \pm SE	<i>P</i>
Two-factor models						
Vascular	-0.004 ± 0.004	0.374	-0.084 ± 0.118	0.478		
Bryophyte	0.004 ± 0.003	0.244	-0.098 ± 0.079	0.212		
Lichen	0.009 ± 0.002	<0.001	-0.327 ± 0.078	<0.001		
Polypore	0.006 ± 0.003	0.061	-0.217 ± 0.101	0.030		
Cryptogam	0.006 ± 0.002	<0.001	-0.217 ± 0.048	<0.001		
Three-factor models						
Vascular	-0.003 ± 0.005	0.547	-0.096 ± 0.140	0.492	-0.001 ± 0.004	0.871
Bryophyte	-0.001 ± 0.003	0.756	0.010 ± 0.096	0.918	0.005 ± 0.002	0.048
Lichen	0.005 ± 0.004	0.147	-0.208 ± 0.096	0.029	0.004 ± 0.002	0.037
Polypore	0.002 ± 0.004	0.665	-0.106 ± 0.125	0.392	0.004 ± 0.003	0.127
Cryptogam	0.002 ± 0.002	0.345	-0.101 ± 0.060	0.088	0.005 ± 0.001	<0.001

Each row presents a separate model; P-values refer to likelihood-ratio tests (values <0.05 in **Bold**)

^aRefers to conifer forests (*Oxalis-Myrtilus* and drained peatland types) as compared with mixedwood (*Aegopodium*, *Filipendula* type)

Fig. 3 Stand age effects in 2-ha plots around the black stork nests on: **a** the number of cryptogam (lichens, bryophytes, polypores) species of conservation concern (SPEC), and **b** the volume of downed coarse woody debris. The symbols distinguish 10 conifer-dominated (*Oxalis-Myrtillus*, drained peatland) and 10 mixedwood (*Aegopodium*, *Filipendula*) forests; the shaded areas are 95% confidence intervals for the regressions



Discussion

The conservation literature on the potential use of umbrella species for protecting wider biodiversity has mainly focused on species co-occurrence patterns (Roberge and Angelstam 2004; Caro 2010). In forests, there is much evidence to date that cross-taxon congruence can be weak, particularly at local scales that are relevant for management decisions (e.g., Similä et al. 2006; Burrascano et al. 2018; Jokela et al. 2018). However, as pointed out by Caro (2010, p. 119), there seems to be a mismatch between the spatial incongruence problems highlighted and the apparent success in several realized schemes of reserve establishment for selected species. A likely reason for such difference is that the reserves, once established and properly protected, can *become* biodiversity hotspots along with the impoverishment of the surrounding landscape and, perhaps, also local biodiversity gains in time. Documentation on such long-term outcomes of realized protection for selected species remains rare, and their specific role for diverse set-aside systems has not been assessed.

Our results support the view that many historical nest sites of the black stork in Estonia have broader biodiversity significance, due to a combination of the bird's nest-site requirements and natural development under the protection. In terms of total bird densities (Table 1), these protected forests were intermediate between typical production forest landscapes (ca. 3 pairs ha⁻¹; Ellermaa 2005; Löhmus 2020) and old-growth stands (6–12 pairs ha⁻¹ depending on site type; Rosenvald et al. 2011). Nevertheless, some old-forest bird species of productive site types were well present, notably *Phylloscopus trochiloides*, which is so rare in Estonia that it has generally been missed in plot-based studies (Väli

and Vaan 2020). Furthermore, across all taxon groups, all the nest stands hosted nationally protected species, and the minimum set hosting all cryptogam species of conservation concern was 18 sites of the 20 sites studied. This indicates that a reasonable precautionary approach would be to assume a high conservation value for any protected black stork site unless shown otherwise.

The ecological key factors involved were best revealed by the comparative surveys of full cryptogam assemblages in the nest stands (cf. Nitare 2000; Paillet et al. 2010). Those factors acted in concert (see below), ultimately shaping hotspots of bryophyte, lichen and polypore species of conservation concern among the sample of nest sites (Table 3). In contrast, the assemblage patterns for vascular plants remained independent and unrelated to the stand structural and stand age factors of interest. An apparent reason for that was that the main environmental gradients for vascular plants were either standardized (soil-based site types) or varied little (light and disturbance regimes; management history; landscape connectivity) in our study system (cf. Pärtel et al. 2005; Reier et al. 2005; Palo et al. 2013). While vascular plants may be informative for some forest conservation planning goals (e.g., Kati et al. 2004; Lelli et al. 2019), they are apparently less informative for assessing conservation perspectives for small undisturbed old-forest set-asides in large forests.

Of the major factors affecting the conservation value in our study system, the contribution of CWD to forest biodiversity is perhaps the best documented (Gao et al. 2015), including the evidence of cross-taxon benefits from dead wood management for target bird species (Bell et al. 2015). A new insight from our study was an interplay of the CWD pool, stand age, and the protection status. Specifically, the mean CWD amounts observed in the youngest nest stands (Fig. 3) were close to those in production forests in Estonia (Lõhmus and Kraut 2010), while the fact that stand age lost its significance in the models containing CWD (Table 4) is best explained by wood accumulation along with the natural stand development.

We have shown elsewhere that CWD accumulations can have an impact on wood-inhabiting species independent of old growth conditions (Runnel and Lõhmus 2017). However, since the protected stands were developing naturally, the CWD variable in our models probably co-varied with, and revealed, multiple successional changes in stand structure and substrate qualities. Additionally, finding of several regionally rare species in the protected nest stands supports the view that a set-aside may retain rarities also due to a lack of severe disturbance, not only due to specific habitat conditions provided (Lõhmus and Lõhmus 2019). Overall, such combined effects may explain the strong and ubiquitous effects of the CWD and stand age variables. Also, the site-type specific effects of the stand age (Fig. 3) confirm that eutrophic forests start providing old-growth habitats sooner and, when impoverished, can recover more readily without restoration intervention (Lõhmus et al. 2020).

For lichens, a distinct assemblage factor present in many stork sites was the share of nemoral broad-leaved trees; this effect has been explicitly documented based on our reference dataset (Lõhmus and Lõhmus 2019). These tree species are generally disfavoured in the Estonian production forests and their lack in overstoreys is a major limiting factor for epiphytes in most reserves that have a production-forest history (Lõhmus et al. 2020). In a long perspective, natural tree species composition can recover, but the process is sporadic and slow (Palo and Gimbutas 2017). Small set-asides with such trees outside the main reserve system would thus help to sustain a pool of specialized forest species in the coming decades.

Importantly, the hotspots studied by us had developed largely due the cultural position of an iconic species. In our study region, the black stork is well known to the wider public (Sellis 2000), its nest sites have been protected in several countries (Kurlavičius et al. 2004;

Banaś et al. 2019), and it has been listed as a landscape-scale umbrella species for forest conservation (Angelstam et al. 2004). Thus, our data reveal that many abandoned, but protected, nest stands of the Black stork are functioning similarly to woodland key habitats, which are identified based on multiple ‘indicator’ species and structural proxies (Timonen et al. 2010). For some rare species, such as the poorly known polypore *Junghuhnia autumnale*, the stork’s nest site protection is even the only explicit conservation approach identified in this region (Löhmus et al. 2018b). Furthermore, our bird surveys suggested that the habitat qualities can extend to areas at least 500 m away, if protected. Hence, (i) priorities for preservation are large areas that have been long protected and contain nemoral broad-leaved trees in the overstorey, but (ii) also somewhat degraded forest sites can passively recover under the cultural ‘umbrella’ of the black stork in the surroundings.

Using the regulations present for the existing set-asides and their status as “last sites” of an extirpated iconic species might thus provide a rapid and, perhaps, attractive tool to protect and develop forest biodiversity hotspots. Similar shifts to biodiversity targets can be observed, for example, in many rural parks that have initially been protected for their cultural virtues but have developed high habitat values in time (Löhmus and Liira 2013). Also, habitats of some target species might provide additional non-timber benefits, such as the potential of bilberry-picking in capercaillie lekking sites later in the season (Remm et al. 2018). However, for legitimate switching from one protection goal to another, a special habitat assessment procedure for abandoned sites is necessary.

Wider applicability of such an approach is affected by the role of habitat degradation in the abandonment of the site. If it happened due to other reasons (e.g. human disturbance), the protection perspectives are obvious, particularly in key locations on landscapes and in those successional stages (such as maturing forests) that can passively recover. Such sites could be recolonized if maintained intact. However, we argue that, even when sites are abandoned due to habitat change, it may still not affect all coexisting non-target species of conservation concern. Furthermore, the sites can be subjected to habitat restoration, which is a priority option for the sites protected for priority species listed in the EU Habitats and Birds Directives.

Practical conclusions

- (1) Forest set-asides that have historically targeted specific species are very likely of wider biodiversity significance. In production forest landscapes, such sites can become irreplaceable biodiversity hotspots depending on their size, forest type, and time since protection.
- (2) In the Baltic region, the main conservation values in the abandoned, but historically protected black stork nest sites are related to the natural development of the stands. A precautionary approach would be to continue with the same protection status and spatial extent, unless a biodiversity assessment in the specific case suggests otherwise.
- (3) Multi-taxon surveys are crucial for understanding overall biodiversity values in forests. Given the laboriousness of such surveys, a cost-effective survey strategy in the case of long-protected sites would be to prioritize those sites that are suspected to have a reduced value (i.e., where changing of the conservation status would be most realistic).

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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