Ecological Indicators 66 (2016) 275–280

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Habitat indicators for cavity-nesters: The polypore *Phellinus pini* in pine forests

Asko Lõhmus

Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, EE-51014 Tartu, Estonia

ARTICLE INFO

Article history:
Received 10 August 2015
Received in revised form 27 January 2016
Accepted 1 February 2016
Available online 13 February 2016

Keywords:
Heart decay fungi
Hole-nesting passerines
Pinus sylvestris
Snag
Tree cavity
Woodpecker

ABSTRACT

Foresters and arborists have long used fruit-bodies of heart-rot fungi as signs of advanced live-tree decay, but such usage has not been elaborated for forest conservation. I analysed relationships between a heart-rot fungus, tree-cavity supply, and cavity-nesting bird assemblage in wet hemiboreal Scots pine (*Pinus sylvestris*) forests in Estonia. The focal species, *Phellinus pini*, is the main heartwood decayer of live pines; it typically forms fruit-bodies at the stage of advanced decay on old trees. I found that the pine wetlands had few tree-cavities (mostly in snags) and cavity-nesting birds (woodpeckers being almost absent) despite abundant snag supply. Only one fruit-body of *P. pini* was found on cavity-tree but stand-scale abundance of the fruit-bodies correlated well with cavity-nester densities. Multifactor models indicated that cavity formation, not tree death, was the limiting process for secondary cavity-nesters, and *P. pini* could indeed be used (in combination with old-pine abundance) for assessing their habitat quality. This fungus could also serve as an educational flagship species to bridge conservation biology and forest pathology, and its fruit-bodies can signal trees to be retained at harvesting in pine forests. The conclusion is that there is hope for developing practical indicators to manage for the hidden decay processes that govern tree-cavity development.

1. Introduction

Foresters and arborists have long been interested in assessing the extent of internal decay processes in live trees and considered visible fruit-bodies of heart-rot fungi as warnings of timber losses and hazard for humans (e.g., Boyce and Wagg, 1953; Wagener, 1963). The implication of such assessments has been to fell the trees or forest stands 'in right time'. Such practices have dramatically reduced the incidence of heart-rots and hollow trees in landscapes, and several heart-rot fungi have even become threatened (Vasaitis, 2013). A wider, accompanying conservation problem is that the rich biota inhabiting tree cavities (i.e., tree hollows with external opening) has suffered globally (Gibbons and Lindenmayer, 2002; Cockle et al., 2011; Remm and Lõhmus, 2011). The conservation concern has thus motivated an opposite movement to detect, protect and sustain cavity development in impoverished forests; however, with most research performed on cavity-excavating animals (primary cavity nesters), not tree decay (Bednarz et al., 2004). Communication between conservation biologists, forest pathologists, and arborists on heart-rot processes seems to have much unused potential for ecological research and planning of sustainable land use.

The current paper explores relationships between a heart-rot fungus, tree-cavity supply, and cavity-nesting bird assemblage in wet pine forests. Wide global distribution of pine (*Pinus* spp.) forests, combined with their relatively species-poor tree layer and (often) poor soils, makes such ecosystems attractive test grounds for describing functional links in the 'tree-cavity networks' (sensu Cockle et al., 2012). In simple ecosystems, it is easier to assess slow background processes rapidly by using comparative observational methods. Some pine ecosystems, such as the ponderosa pine (*Pinus ponderosa*) forests in the U.S. (Chambers and Mast, 2014), have outstandingly rich cavity-nesting wildlife. On the other hand, slow development and long natural persistence of cavities in pines (e.g., Rudolph and Conner, 1991; Wesołowski, 2011) make their dependent biota vulnerable to cavity-tree removal. For hole-nesting birds, the resulting cavity limitation can be so dominant that no additional benefits of old-growth structure are observable (Remm et al., 2008). A specific management issue in pine wetlands is their widespread artificial draining for timber production (Paavilainen and Päivänen, 1995), with undocumented impacts on cavity supply.

My broad question is whether a specialized heart-rot fungus, the polypore *Phellinus (Porodaedalea) pini*, indicates habitat quality for cavity-nesting birds. *P. pini* (Brot.) Bondartsev & Singer refers

E-mail address: asko.lohmus@ut.ee

http://dx.doi.org/10.1016/j.ecolind.2016.02.003
1470-160X/

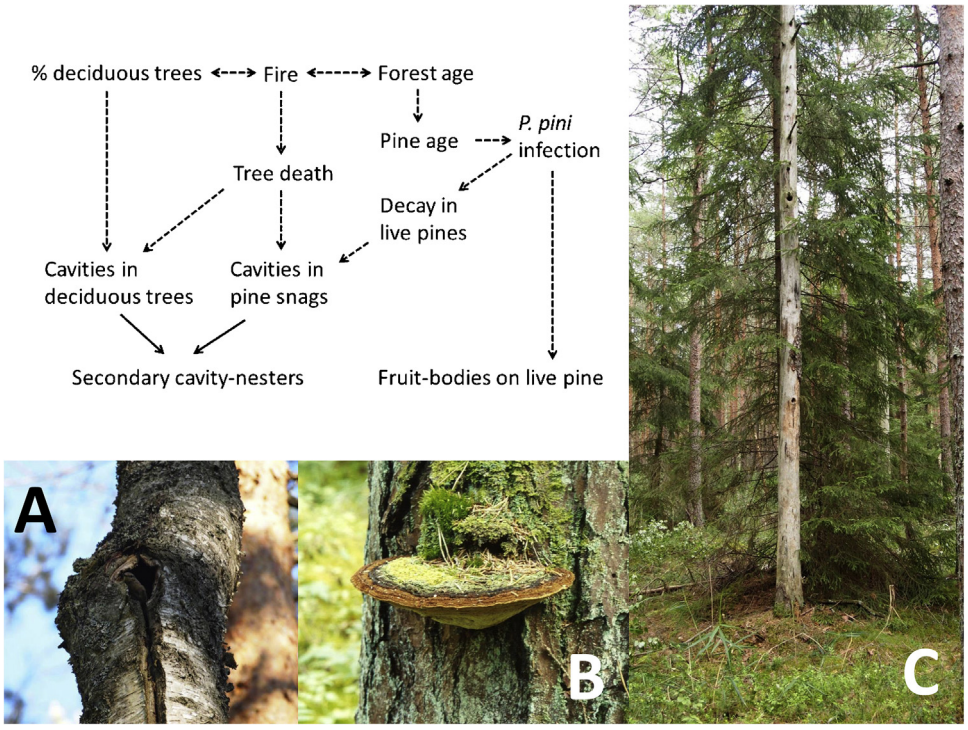

Fig. 1. Stand-scale features and processes in tree-cavity network in pine wetland. Secondary cavity nesters can benefit from the presence of decay-prone deciduous trees (A: *Phoenicurus phoenicurus* at a decay-cavity entrance in birch), while cavity development in dominant pines requires both advanced heart-rot (indicated by *Phellinus pini* fruit bodies; B) and woodpecker excavation after tree death (C). Tree death can be promoted by low-severity fires, which do not eliminate old live pines from the stand (the stand on Photo C burned in the mid-1970s).
Photos by A. Lõhmus.

to several geographically and ecologically segregated lineages (Brazee and Lindner, 2013), which are dominant heartwood decayers in several conifers, including northern pines (e.g., Scharpf and Coheen, 1993). The process from infection to hollow development takes many decades, and advanced decay and fungal fruit-bodies ('conks') may not develop until the tree is at least 50–150 years old, depending on climate and pine species (Boyce, 1961; Conner et al., 1994; Nitare, 2000; Minkevich and Ezhov, 2001; Marmolejo et al., 2011). The resulting hollow or soft heartwood provides cues to excavators, such as woodpeckers and some tits (Paridae), for completing the cavities, particularly after the tree death (Rudolph and Conner, 1991; Jusino et al., 2015). Because there are rarely other fruit-bodies on live pine trunks than those of *P. pini*, this single species could predict habitat suitability for cavity-nesting assemblages in pine forests. Moreover, its long-living fruit-bodies are observable year-round, while many northern cavity-nesters are migratory birds or bats that can only be censused during a short season. The age record of a fruit-body on pine is 100 years and 40–50 year-old fruit-bodies are frequent (Minkevich and Ezhov, 2001). Since the fruit-bodies appear mostly on old trees, they have been also proposed to indicate valuable pine-forest assemblages of less conspicuous fungi, insects, and bryophytes (Nitare, 2000; Unterseher et al., 2012). In terms of the surrogate species schemes of conservation biology (Caro, 2010), *P. pini* could thus serve as an 'ecological engineer' (a subtype of functionally important keystone species), a 'biodiversity indicator' in pine forests, an educational 'flagship species' for stimulating conservation awareness on tree-cavity networks, or a combination of these qualities.

The conceptual setup of the current study (Fig. 1) includes three sets of processes, each linked with wood decay in pine wetlands: cavity formation in live pines; in pine snags; and in the deciduous trees present. My goal was to measure, at the stand scale, the indirect relationship between *P. pini* and cavity-nester abundance, and to describe the functional links producing or confounding that relationship. I expected that, regarding cavity supply, (i) the presence of *P. pini* is more informative than simple tree-layer data (such as stand age and pine abundance), while (ii) its performance can be further modified by abundant deciduous trees and impacts of past fires. I also checked whether surveying *P. pini* fruit-bodies might be efficient due to better precision than tree cavity surveys at given study effort. I am not aware of other quantitative stand-scale analyses that link fungi and cavity-nesters; thus, this study supplements tree-scale studies on cavity networks (e.g., Conner et al., 1994; Cockle et al., 2012) with a broader indicator and management perspective.

2. Materials and methods

The approximately 70-km^2 study area (58°20′ N; 25°00′ E) was situated in the sparsely inhabited Soomaa forest-wetland complex in southwestern Estonia. The area belongs to the European hemiboreal vegetation zone. The climate is humid temperate, with mean temperatures +17 °C in July and −5.5 °C in January, and ca. 750 mm annual precipitation. Most forests are on peat soils, heavily drained for forestry, and dominated by Scots pine (*Pinus sylvestris*) and downy birch (*Betula pubescens*). The study system comprised 18 relatively homogeneous plots of drained pine wetlands (9.8–30.1 ha each; 305.5 ha in total), where the forest cover had at least partly developed secondarily after the draining in the 1960s (11 plots) or in 1980 (7 plots). One plot had pre-draining clearcut origin (67 years old at the time of the study). According to the State Forest Registry, the mean age of the overstorey (hereafter: stand age) varied between 50 and 110 years (grand mean: 78 years); the proportion of Scots pine in the overstorey – between 71% and 97% (86%); and the proportion of Scots pines >100 years old (hereafter: old pines) – between 0% and 72% (16%). The 100-year limit is highlighted here

because it is a typical minimum tree age for the appearance of *P. pini* fruit-bodies in northern Europe (Nitare, 2000; Minkevich and Ezhov, 2001).

The plots were originally established for planned hydrological restoration (as the largest contiguous patches of drained pine wetland) and the data presented here represent thorough pre-restoration surveys of biodiversity and forest structure. Collectively, these surveys covered comprehensively the components of tree-cavity network and also enabled to confirm historical wildfire occurrence and scarcity of recent tree harvesting. Fire incidence was recorded by snags or stumps with burnt bases (up to three items ha^{-1} found in six plots). Local foresters reported the fires to date back to the 1970s (E. Ilmet, pers. comm.). Half of one plot had been commercially thinned in the 1990s, but there were only a very few heavily decayed stumps of old thinnings in some other plots (usually none).

I censused birds in one spring in each plot (either in 2013 or 2014), using a previously tested two-visit survey approach (Remm et al., 2008; Rosenvald et al., 2011). Each visit (one in mid-May, the other between 25 May and 10 June) included a conventional morning mapping (between sunrise and 11:00 a.m., in good weather) and additional surveys in the evening of the same or preceding day to find previously undetected pairs, nests, etc. The position of singing males, nests or (in the absence of these) any other observations referring to nesting were recorded on a topographic map. The abundance of each species in each site was determined as the maximum count plus probable or confirmed nestings in clearly different locations during the other visit. Territorial birds moving across site borders as well as adult individuals of species with large home range or unstable pairs were counted as 0.5 territories.

I mapped tree cavities and trees with *Phellinus pini* fruit-bodies routinely both during the bird surveys and a total of ca. 250 field hours spent on plant and fungal surveys (see Runnel et al., 2015, for the latter). In those ground-based surveys, I only recorded cavities that appeared suitable for vertebrates (entrance diameter at least 2 cm) and I carefully attempted to exclude shallow cone-shaped holes. These data were supplemented with intensive studies of forest structure on a total of 305 straight 50-m strip transects. Here, I include the transect data on standing dead trees and broken-top snags (hereafter collectively 'snags'), which were at least 15 cm in diameter at breast height (DBH) and at least 1.5 m tall (minima for the snags that contained cavities in the area). Snags were mapped on 5 + 5 m strips to both sides of the transect line, on 9–30 transects (0.45–1.5 ha) per plot depending on plot area. In the youngest plot, I supplemented the transect approach with searching all over the area to confirm snag absence.

Apart from descriptive statistics, the data analyses included two approaches: (i) linear regression for testing the hypothesized simple relationships between densities of cavity-nesters, cavity-trees, snags, and the trees with *P. pini* fruit-bodies; and (ii) multi-factor general linear modelling based on a wider set of stand factors (see Appendix A) – snags, *P. pini* fruit-bodies, and those stand features reported above (mean age; % Scots pine; % old pine; fire incidence). Considering causality, I included cavity-tree densities only in cavity-nester models. All models included intercept. In each case, I started with the list of AICc values for the full set of possible models, distinguishing top-ranked models based on $\Delta AICc < 2$ compared with the best model (Burnham and Anderson, 2002). I then manually inspected factor contributions in each top-ranked model and distinguished the best model(s) as those having all factors at least marginally significant ($P < 0.1$; Type III approach to sums of squares). Finally, I checked for non-linearity by adding square terms to the model. The analyses were run using STATISTICA 7.1 software (StatSoft Inc., 2005).

3. Results

The plots hosted a sparse nesting assemblage of six species of secondary cavity-nesters with a total of 61.5 nesting territories (17.5 *Ficedula hypoleuca*; 8.5 *F. parva*; 14.5 *Muscicapa striata*; 11 *Parus major*; 9 *Phoenicurus phoenicurus*; 1 *Periparus ater*). Their mean pooled density was 0.22 ± 0.08 (95% CI) territories ha^{-1} (maximum 0.72) in the 18 plots. Additionally, there were on average 0.11 ± 0.03 territories of primary cavity-nesters, mostly resident tits *Lophophanes cristatus* (15.5 territories) and *Parus montanus* (14). Three species of woodpeckers were observed and winter feeding tracks of *Dendrocopos major* (spruce cones under 'anvils') were regular. However, no active woodpecker nests were found and only two nesting territories extended to the plots (0.5 *Dryocopus martius*; 0.5 *Dendrocopos major*). *Dendrocopos minor* was only seen foraging. Pooled nesting densities of secondary cavity-nesters varied significantly more than those of primary cavity-nesters among plots (coefficients of variation, CV = 81% and 59%, respectively; Levene's test: $F_{1,34} = 6.8$, $P = 0.013$).

Tree cavities and fruit-bodies of *Phellinus pini* were scarce (Table 1), while snags were abundant. The mean density of cavity-trees (62 found in total) was 0.24 ± 0.12 trees ha^{-1}, varying considerably among plots (CV = 112%). Those trees contained a total of 82 cavities (1.3 per tree) – typically as a single cavity (45 trees, including all eight non-excavated side-cavities) or two woodpecker holes per tree (9 trees). Additionally, there were three trees with three side-cavities each, three trees with only a top cavity, one with both a side-cavity and a top-cavity, and one tree with five side-cavities. All trees with more than one cavity were pine snags. *Dendrocopos major* had a double role: it had originally excavated most cavities (typically for roosting) but, as a major nest predator, it also damaged many cavities where passerines were breeding. As a result, 11 recorded cavities were semi-open at the time of the survey and many were classified as unsuitable (not counted). All top-cavities had probably formed due to trunk breakage at excavated cavity; this was the only cavity type where passerine nesting was not confirmed during the study.

Most of the 88 records of *P. pini* fruit-bodies were on old live pines (Table 1); its fruit-bodies on snags were typically old and, often, dying (as judged by the colour of the hymenophore). Among cavity trees, only one pine snag beared a fruit-body of this polypore. The total densities were on average 0.34 ± 0.21 trees with *P. pini* fruit-bodies ha^{-1}, with high variation among plots (CV = 132%).

Table 1
Types and sizes of trees with *Phellinus pini* fruit-bodies and tree cavities found. 'Snags' include all standing dead trees; DBH – diameter at breast height.

Tree type	No. of records (%)			Tree DBH range	
	P. pini	Side-cavities	Top-cavities	*P. pini*	Cavities
Live Scots pine	74 (84%)	1 (2%)	–	13–45	35
Scots pine snag	14 (16%)	42 (71%)	2 (67%)	14–36	16–31
Live birch	–	5 (8%)	–	–	13–24
Birch snag	–	10 (17%)	1 (33%)	–	17–25
Spruce snag	–	1 (2%)	–	–	18
n	88	59	3		

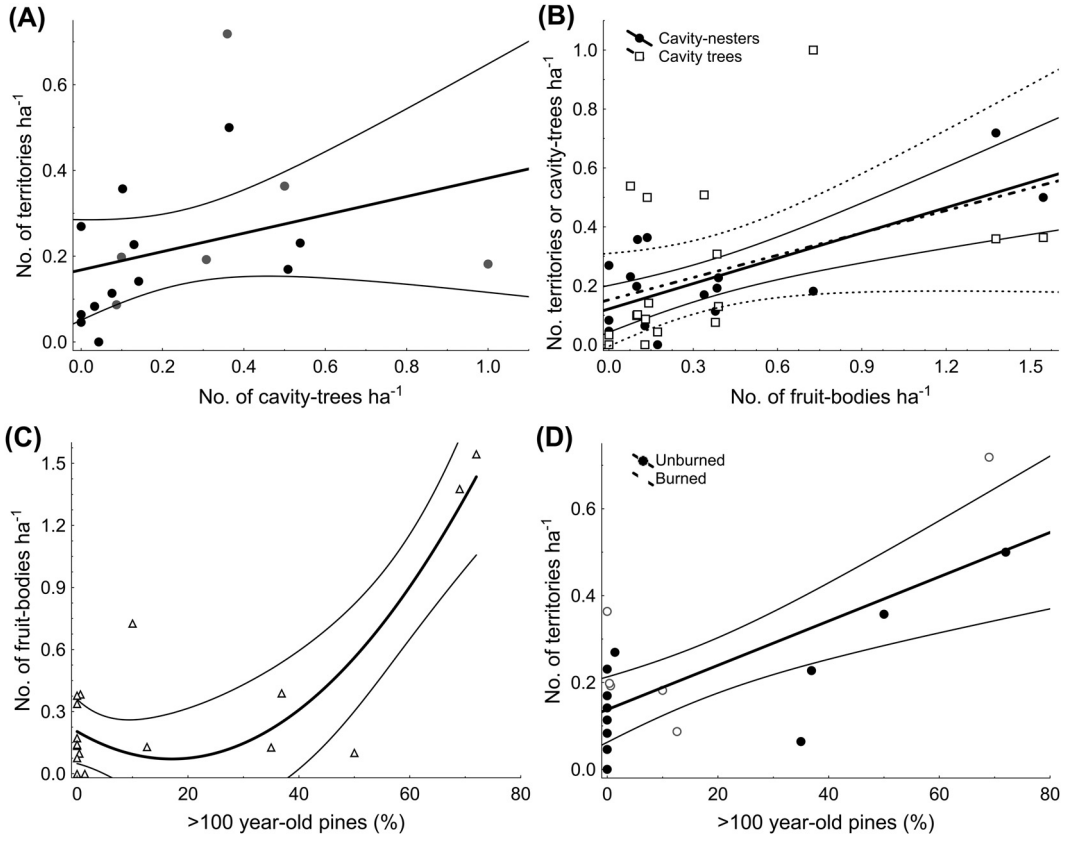

Fig. 2. The main relationships explored in the tree-cavity network of pine wetlands ($n = 18$ plots; linear regressions, except the quadratic regression in C). (A) Loose dependence of secondary cavity-nester densities on recorded cavity-tree densities (slope: $P = 0.192$; $R^2 = 0.10$). (B) Indicator properties of *P. pini* fruit-bodies: similar slopes but smaller variation and more consistent regression for secondary cavity-nesters ($P < 0.001$; $R^2 = 0.53$) than for cavity-trees ($P = 0.079$; $R^2 = 0.18$). (C) Non-linear dependence of *P. pini* on the abundance of old pines ($R^2 = 0.74$). (D) Secondary cavity-nester densities in relation to the abundance of old pines and fire incidence ($R^2 = 0.62$). See Table 2 for the parameters of models C and D.

In contrast, snags large-enough for cavities were consistently abundant (44.5 ± 10.8 snags ha^{-1}; CV = 52%). The 622 snags sampled included 76% pines, 21% birch and 2% spruce. Comparison of the snag and cavity-tree densities indicates that <1% of snags contained cavities.

Stand-scale correlations between the key variables confirmed indicative value of *Phellinus pini* fruit-bodies. Importantly, I did not detect simple dependence of secondary cavity-nester densities on cavity-tree abundance (Fig. 2A), while *P. pini* abundance was well related to cavity-nester densities and marginally also to cavity trees (Fig. 2B). Moreover, no other measured stand characteristic (cavity-trees; snags; stand age; % of all pines and of old pines) significantly improved the relationship between the cavity-nester and *P. pini* densities. However, multifactor models expaining the densities of *P. pini*, tree cavities, snags, and cavity-nesters indicated distinct environmental determinants (Table 2):

Table 2
The best general linear models explaining the abundance of tree-cavity network components in pine wetlands ($n = 18$ plots; $P < 0.001$ for all models). See also Fig. 2.

Model and factors	Factor contribution			
	Coefficient ± SE	df	*F*	*P*
No. of *Phellinus pini* fruit-bodies ha^{-1} ($R^2 = 0.74$)				
% of old pines in overstorey	−0.015 ± 0.009	1; 15	2.9	0.108
(% of old pines in overstorey)^{2} [a]	0.0005 ± 0.0001	1; 15	10.8	0.005
Intercept	0.203 ± 0.073	1; 15	7.9	0.013
No. of cavity-trees ha^{-1} ($R^2 = 0.81$)				
Stand age (years)	0.020 ± 0.004	1; 12	24.2	<0.001
% of pines in overstorey	−0.009 ± 0.005	1; 12	4.0	0.067
% of old pines in overstorey	−0.020 ± 0.004	1; 12	27.7	<0.001
No. of *Phellinus pini* fruit-bodies ha^{-1}	0.575 ± 0.132	1; 12	18.9	<0.001
Fire incidence (1; 0)	0.090 ± 0.037	1; 12	5.9	0.032
Intercept	0.373 ± 0.320	1; 12	1.4	0.267
No. of secondary cavity-nester territories ha^{-1} ($R^2 = 0.62$)				
% of old pines in overstorey	0.005 ± 0.001	1; 15	20.7	<0.001
Fire incidence (0; 1)	0.056 ± 0.029	1; 15	3.6	0.076
Intercept	0.155 ± 0.034	1; 15	20.6	<0.001

'Old pines' refer to trees >100 years old.
[a] Square term.

(i) The single best model for *P. pini* included only the proportion of old pines (positive effect: $P < 0.001$; $R^2 = 0.52$). This variable was present in all five top-ranked *P. pini* models and none of the other factors appeared statistically significant in any combination (all positive effects: proportion of pine – 3 models; fire incidence – 2 models; stand age – 1 model). Furthermore, the old-pine effect was non-linear: the square term added was highly significant and further improved the model (Fig. 2C; Table 2).

(ii) In contrast, the top-ranked models for cavity trees were necessarily multifactorial (no factor had significant univariate effect). AICc combined with factor significance criteria distinguished one best model ($R^2 = 0.81$), which combined positive effects of stand age, fire incidence and *P. pini* abundance with negative effects of the proportion of old pines and (marginally) of all pines.

(iii) Snag abundance had no strong models with the variables measured: only three alternative, marginal ($P = 0.061$-0.072; $R^2 = 0.20$-0.21) positive univariate relationships with stand age, proportion of old pines, and the abundance of *P. pini*.

(iv) AICc distinguished a total of 18 top-ranked models for secondary cavity-nesters, but only one model had all factors statistically significant: an increase with the proportion of old pines combined with fire incidence (Fig. 2D). The abundance of *P. pini* was not significant in any of the seven top-ranked models where it was included (together with 1–4 other factors).

4. Discussion

In many conifer forests worldwide, cavity-nesters are limited by tree cavities (e.g., Newton, 1994) and snags constitute a critical resource as a favoured substrate for primary cavity nesters (Bunnell, 2013). In the Estonian pine wetlands, however, snag abundance did not correlate with cavity-nester abundance, although most cavities occurred in snags. An obvious reason was the very low cavity incidence (<1%) despite abundant snag supply, which can be partly due to the near-absence of nesting woodpeckers. A similar pattern is known from undrained pine wetlands, with slightly lower snag and higher cavity abundances (40 snags of ≥10 cm DBH and 0.45 cavity trees ha^{-1}; Lõhmus et al., 2005).

Cavity formation, not tree death, thus emerged as a limiting process for cavity nesters in pine wetlands but, supporting the motivation of this study, cavity supply was difficult to predict and measure. A large measurement error of the ground-based surveys (see also Koch, 2008) could explain why I failed to detect a relationship between cavity-tree and secondary cavity nester abundances despite the low and variable densities of cavities. Both the cavity-tree and cavity-nester densities were roughly 7–10 times smaller compared with natural conifer forests on mineral soils in Estonia (Remm et al., 2008; Rosenvald et al., 2011). Prediction problems were illustrated by the complex environmental effects on cavity abundances despite the relatively homogeneous study system. The effects of stand age and pine proportion probably reflected generally slow hollow development in aging, preferably deciduous trees, while the three other factors might describe *Phellinus pini* decay. I suggest that the "negative effect" of old pines should be interpreted together with the positive effect of *P. pini* as these structures are causally related. Specifically, the scarcity of *P. pini* in certain old-pine-rich stands was accompanied with the lack of cavities, which may refer to local decay suppression. The positive effect of historical fires is attributable to infections through fire wounds in live trees (Minkevich and Ezhov, 2001) and accelerated cavity formation in those fire-killed trees that had heart-rot before their death (Basham, 1957).

In contrast to cavities, stand-scale occurrence of *P. pini* fruit-bodies was determined by one major factor – the abundance of old live pines, its main substrate. This pattern corresponded to a chronic infectious disease: (i) exponential dependence on host density (Fig. 2C; cf. Burdon and Chilvers, 1982; Gilbert et al., 2002), which is supported by the data from old-growth pine stands (typically 2–8 trees ha^{-1} with fruit-bodies; A. Lõhmus and K. Runnel, unpublished data); (ii) declining condition of fruit-bodies on snags, which suggests that *P. pini* is outcompeted by invading decomposer taxa after tree death. In 20 downed pine trunks inspected with high-throughput sequencing in the same plots, the DNA of *P. pini* was indeed not recorded (Runnel et al., 2015). These observations are in line with the knowledge that *P. pini* fruit-bodies indicate advanced heart-rot (Boyce and Wagg, 1953) and with other facts supporting rare occurrence of such heart-rot in the studied forests. Thus, I only found one cavity in a live pine, and no decayed heartwood was encountered in 35 randomly selected large trees (cored at breast-height; A. Almik, pers. comm.). Hence, the relationship between *P. pini* fruit-body records and cavity-nesters was only partly functional, but followed the conceptual scheme (Fig. 1): "cavity initiations" by *P. pini* were completed by woodpeckers, tits and, apparently, many deadwood-inhabiting fungi only after tree death.

In pine wetlands, a question for practical use of *P. pini* is whether the proportion of old pines might not represent an even simpler stand-scale indicator. I argue that these two features (and additionally, fire incidence where known) should be combined: forestry data usually allows coarse filtering of stands and landscape-scale analyses based on tree variables (e.g., Virkkala et al., 1994), while there is seldom comprehensive information on heart-rots. However, the absence of *P. pini* from old stands distinguished cavity-poor sites, which might inform habitat quality assessments or management decisions in the field. The usefulness of heart-rot indicators for the conservation of threatened cavity-nesters remains to be tested, since the current study system was not suitable for such specific assessment.

Since the hidden heart-rot phase precedes actual cavity formation into snags, *P. pini* also indicates cavity-forming potential. Thus, its generally rare occurrence in live pines was probably related to cavity shortage in snags in my study. A dominant primary cavity-nester, *Lophophanes cristatus*, can excavate cavities also into decayed sapwood of pine snags with intact heartwood, but this requires large snags (Summers, 2004) that are rare in wetlands. A management implication is that, in mid-successional forests where trunk decay is rare, fruit-bodies on live pines could distinguish trees or parts of stands to be retained at harvesting. Such simple retention criteria are much needed (Perhans et al., 2014), and the suggested one should be cost-effective both in terms of current timber and future biodiversity. Even when suitable cavities will not form, hollow trees are more prone to trunk breakage (Kane et al., 2001), which effectively creates diverse dead wood (Runnel et al., 2013). Casual snag retention, in contrast, may have little value for hole-nesters, although it may support other organisms, such as lichens and insects.

My broad conclusion is that there is hope for developing practical indicators of the hidden decay processes that govern tree-cavity development. Even preliminary indicators, which are established based on correlational patterns (like in this study), can add opportunities for reversing the loss of cavity-using communities in managed forests (Cockle et al., 2011). The fungi treated in traditional silviculture as 'disease agents' that cause 'damage' (e.g., Boyce, 1961; Tainter and Baker, 1996) could serve as powerful educational flagship species for explaining sustainable forest management and conservation. Because pine forests are widely distributed and heavily managed, *P. pini* is a suitable specialist species to draw the attention of forest managers and forest owners

to habitat provisioning services of tree pathogens. Broader awareness might also enhance public acceptance of intensive restoration techniques, such as fungal inoculation of live trees in impoverished forests (Bednarz et al., 2013).

Acknowledgements

I am grateful to Kadri Runnel for several field records and commenting on the manuscript; and to all the field assistants who participated in the transect counts of stand structures. Anu Almik and Elor Ilmet provided some important details on the studied forests. Panu Halme and an anonymous reviewer constructively commented on the manuscript. The study was supported by the Estonian Research Council (projects IUT34-7 and ETF5091) and the State Forest Management Centre.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2016.02.003.

References

Basham, J.T., 1957. The deterioration by fungi of jack, red, and white pine killed by fire in Ontario. Can. J. Bot. 35, 155–172.
Bednarz, J.C., Ripper, D., Radley, P.M., 2004. Emerging concepts and research directions in the study of cavity-nesting birds: keystone ecological processes. Condor 106, 1–4.
Bednarz, J.C., Huss, M.J., Benson, T.J., Varland, D.E., 2013. The efficacy of fungal inoculation of live trees to create wood decay and wildlife-use trees in managed forests of western Washington, USA. For. Ecol. Manag. 307, 186–195, http://dx.doi.org/10.1016/j.foreco.2013.06.041.
Boyce, J.S., 1961. Forest Pathology. McGraw-Hill, New York.
Boyce, J.S., Wagg, J.W.B., 1953. Conk rot of old-growth Douglas-fir in western Oregon. Oregon For. Prod. Lab. Bull. 4.
Brazee, N.J., Lindner, D.L., 2013. Unravelling the *Phellinus pini s.l.* complex in North America: a multilocus phylogeny and differentiation analysis of *Porodaedalea*. For. Pathol. 43, 132–143, http://dx.doi.org/10.1111/efp.12008.
Bunnell, F.L., 2013. Sustaining cavity-using species: patterns of cavity use and implications to forest management. ISRN For., 457698, http://dx.doi.org/10.1155/2013/457698.
Burdon, J.J., Chilvers, G.A., 1982. Host density as a factor in plant disease ecology. Annu. Rev. Phytopathol. 20, 143–166, http://dx.doi.org/10.1146/annurev.py.20.090182.001043.
Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer.
Caro, T., 2010. Conservation by Proxy: Indicator, Umbrella, Keystone, Flagship, and Other Surrogate Species. Island Press, Washington, DC.
Chambers, C.L., Mast, J.N., 2014. Snag dynamics and cavity excavation after bark beetle outbreaks in southwestern ponderosa pine forests. For. Sci. 60, 713–723.
Cockle, K.L., Martin, K., Wesołowski, T., 2011. Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. Front. Ecol. Environ. 9, 377–382, http://dx.doi.org/10.1890/110013.
Cockle, K.L., Martin, K., Robledo, G., 2012. Linking fungi, trees, and hole-using birds in a Neotropical tree-cavity network: pathways of cavity production and implications for conservation. For. Ecol. Manag. 264, 210–219, http://dx.doi.org/10.1016/j.foreco.2011.10.015.
Conner, R.N., Rudolph, D.C., Saenz, D., Schaefer, R.R., 1994. Heartwood, sapwood, and fungal decay associated with red-cockaded woodpecker cavity trees. J. Wildl. Manage. 58, 728–734, http://dx.doi.org/10.2307/3809687.
Gibbons, P., Lindenmayer, D., 2002. Tree Hollows and Wildlife Conservation in Australia. CSIRO Publishing, Collingwood.
Gilbert, G.S., Ferrer, A., Carranza, J., 2002. Polypore fungal diversity and host density in a moist tropical forest. Biodivers. Conserv. 11, 947–957, http://dx.doi.org/10.1023/A:1015896204113.
Jusino, M.A., Lindner, D.L., Banik, M.T., Walters, J.R., 2015. Heart rot hotel: fungal communities in red cockaded woodpecker excavations. Fungal Ecol. 14, 33–43, http://dx.doi.org/10.1016/j.funeco.2014.11.002.
Kane, B., Ryan, D., Bloniarz, D.V., 2001. Comparing formulae that assess strength loss due to decay in trees. J. Arboric. 27, 78–87.
Koch, A.J., 2008. Errors associated with two methods of assessing tree hollow occurrence and abundance in *Eucalyptus obliqua* forest, Tasmania. For. Ecol. Manag. 255, 674–685, http://dx.doi.org/10.1016/j.foreco.2007.09.042.
Lõhmus, A., Lõhmus, P., Remm, J., Vellak, K., 2005. Old-growth structural elements in a strict reserve and commercial forest landscape in Estonia. For. Ecol. Manag. 216, 201–215, http://dx.doi.org/10.1016/j.foreco.2005.05.031.
Marmolejo, J.G., Méndez Cortés, H., Cantú, C.A., 2011. Impact of *Phellinus pini* (Brot.) Bondartsev & Singer in *Pinus greggii* Engelm. forests of Nuevo León state. Rev. Mex. Cienc. For. 2, 85–94.
Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biol. Conserv. 70, 265–276, http://dx.doi.org/10.1016/0006-3207(94)90172-4.
Minkevich, I.I., Ezhov, O.N., 2001. Spreading and morphological diversity of fruit bodies of the pine fungus in the forests of the European North of Russia. Lesnoy Zhurnal 3, 42–46 (in Russian).
Nitare, J. (Ed.), 2000. Indicator Species for Assessing the Nature Conservation Value of Woodlands Sites – A Flora of Selected Cryptogams. Skogsstyrelsen, Jönköping, Sweden.
Paavilainen, E., Päivänen, J., 1995. Peatland Forestry: Ecology and Principles. Springer, Berlin/Heidelberg.
Perhans, K., Haight, R.G., Gustafsson, L., 2014. The value of information in conservation planning: selecting retention trees for lichen conservation. For. Ecol. Manag. 318, 175–182, http://dx.doi.org/10.1016/j.foreco.2014.01.020.
Remm, J., Lõhmus, A., 2011. Tree cavities in forests – the broad distribution pattern of a keystone structure for biodiversity. For. Ecol. Manag. 262, 579–585, http://dx.doi.org/10.1016/j.foreco.2011.04.028.
Remm, J., Lõhmus, A., Rosenvald, R., 2008. Density and diversity of hole-nesting passerines: dependence on the characteristics of cavities. Acta Ornithol. 43, 83–91, http://dx.doi.org/10.3161/000164508X345365.
Rosenvald, R., Lõhmus, A., Kraut, A., Remm, L., 2011. Bird communities in hemiboreal old-growth forests: the roles of food supply, stand structure, and site type. For. Ecol. Manag. 262, 1541–1550, http://dx.doi.org/10.1016/j.foreco.2011.07.002.
Rudolph, D.C., Conner, R.N., 1991. Cavity tree selection by red-cockaded woodpeckers in relation to tree age. Wilson Bull. 103, 458–467.
Runnel, K., Rosenvald, R., Lõhmus, A., 2013. The dying legacy of green-tree retention: different habitat values for polypores and wood-inhabiting lichens. Biol. Conserv. 159, 187–196, http://dx.doi.org/10.1016/j.biocon.2012.11.029.
Runnel, K., Tamm, H., Lõhmus, A., 2015. Surveying wood-inhabiting fungi: most molecularly detected polypore species form fruit-bodies within short distances. Fungal Ecol. 18, 93–99, http://dx.doi.org/10.1016/j.funeco.2015.08.008.
Scharpf, R.F., Coheen, D., 1993. Heart rots, in: Scharpf, R.F. (Tech. Coord.), Diseases of Pacific Coast Conifers. Agric. Handb. 521. U.S. Dept. Agric., For. Serv., Washington, DC, pp. 150–180.
Summers, R.W., 2004. Use of pine snags by birds in different stand types of Scots pine *Pinus sylvestris*. Bird Study 51, 212–221, http://dx.doi.org/10.1080/00063650409461356.
Tainter, F.H., Baker, F.A., 1996. Principles of Forest Pathology. John Wiley and Sons.
Unterseher, M., Westphal, B., Amelang, N., Jansen, F., 2012. 3,000 species and no end – species richness and community pattern of woodland macrofungi in Mecklenburg-Western Pomerania, Germany. Mycol. Progr. 11, 543–554, http://dx.doi.org/10.1007/s11557-011-0769-7.
Vasaitis, R., 2013. Heart rots, sap rots and canker rots. In: Gonthier, P., Nicolotti, G. (Eds.), Infectious Forest Diseases. CAB International, Wallingford, pp. 197–229.
Virkkala, R., Rajasärkkä, A., Väisänen, R.A., Vickholm, M., Virolainen, E., 1994. Conservation value of nature reserves: do hole-nesting birds prefer protected forests in southern Finland? Ann. Zool. Fenn. 31, 173–181.
Wagener, W.W., 1963. Judging Hazard from Native Trees in California Recreational Areas – A Guide for Professional Foresters. U.S. For. Serv. Res. Paper PSW-P1, Berkeley, CA.
Wesołowski, T., 2011. Lifespan of woodpecker-made holes in a primeval temperate forest: a thirty year study. For. Ecol. Manag. 262, 1846–1852, http://dx.doi.org/10.1016/j.foreco.2011.08.001.