Metapopulation dynamics and future persistence of epiphytic cyanolichens in a European boreal forest ecosystem

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Summary

1. One approach to biodiversity conservation is to set aside small woodland key habitats (WKHs) in intensively managed landscapes. The aim is to support species, such as epiphytes, which often depend on old trees and are negatively affected by intensive forestry. However, it is not known whether the number of host trees within these areas can sustain species in the long term.

2. We studied metapopulation dynamics and assessed the future persistence of epiphytes assuming host tree numbers similar to those observed in large north European WKHs. The study species were seven cyanolichens confined to *Populus tremula* in the boreal study area. Colonizations and extinctions were recorded in 2008 on trees that had been surveyed 13 years earlier. We applied generalized (non)linear models to test the importance of environmental conditions, facilitation and spatial connectivity on the metapopulation dynamics. We also simulated the effects of tree numbers and tree fall rates on future species persistence.

3. Metapopulation dynamics were explained by tree quality, size or tree fall. In one species, colonizations increased with increasing connectivity, and in a second species it increased if other lichens sharing the photobiont with the focal species were present, suggesting facilitation. Both stochastic extinctions from standing trees and deterministic extinctions caused by tree fall should be accounted for in projecting epiphyte metapopulation dynamics.

4. One to three infrequent, sexually dispersed study species face a significant extinction risk within 50 years, especially in areas with low tree numbers.

5. *Synthesis and applications.* During the coming decades, infrequent, sexually dispersed, epiphytic lichens are likely to be lost from small woodland habitat set asides in intensively managed landscapes. Local extinction will be a consequence of low colonization rates and tree fall. Low colonization rates can be prevented by retaining large trees on which lichen species colonization rates are the highest and by assuring a high density of occupied trees. The negative effect of tree fall should be compensated for by assuring continuous availability of old trees. This can be achieved by decreasing the populations of large browsers, or by retaining trees with high conservation value during management operations.

Key-words: aspen, colonization, dynamic landscape, extinction, forestry, habitat quality, lichens, woodland key habitat

Introduction

The intensification of forestry during the last century has influenced biodiversity in forest biomes worldwide. The European

boreal forest represents a case in which forestry operations have transformed a large proportion of the land. It is now characterized by even-aged, fragmented forests with shorter rotation periods, less dead-wood, and a reduced amount of old-growth forests (Esseen *et al.* 1997; Östlund, Zackrisson & Axelsson 1997). Worldwide, Sweden and Finland were the second and sixth, respectively, largest exporter of pulp, paper and sawn timber in 2009, totalling more than that of the largest exporter, Canada (Swedish Forest Industries Federation 2011).

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For many species, this intense utilization represents a shift from suitable to unsuitable environments. This is the case for species confined to old-growth forest structures, such as old trees. Many of these species have experienced decreased population sizes (Hanski 2000), which can be assumed to be followed by declines in diaspore availability, dispersal and population colonization rates. This change moves populations closer to the threshold where colonizations no longer compensate for extinctions, and where species will eventually go extinct (Hanski 1999).

Epiphytes are a large group of species that are negatively affected by land-use change (Zotz & Bader 2009). Few studies have investigated the probability of their future persistence although a lack of host tree recruitment or edge effects has been identified as potential threats (Snäll *et al.* 2005; Roberge *et al.* 2011). However, the basic question of long-term persistence in areas with low host tree numbers has not been investigated.

Different strategies have been suggested to counteract biodiversity losses in intensively utilized forest ecosystems, for example, the establishment of large reserves, buffer zones adjacent to aquatic systems or small protected areas (Lindenmayer, Franklin & Fischer 2006). One widely implemented approach in northern Europe is the set-aside of small, stand-sized, woodland key habitats (WKHs henceforth) from forestry operations (Timonen *et al.* 2011). WKHs support a high diversity of species (Timonen *et al.* 2011), but their capacity to preserve species in the long run is largely unknown.

Metapopulation models can help managers to understand and project the spatial population dynamics of species that are confined to discrete patches in the landscape. They are therefore useful tools in conservation (e.g. Akçakaya & Sjögren-Gulve 2000). However, reliable predictions of metapopulation dynamics require an understanding of how environmental conditions affect colonizations and extinctions.

According to theory, colonizations of unoccupied patches are explained by the distance to surrounding occupied patches (Hanski 1999). There is also increasing evidence for the effects of local conditions on colonizations, including habitat patch quality and habitat patch size (e.g. Moilanen, Smith & Hanski 1998; Fleishman *et al.* 2002; Snäll, Ehrlén & Rydin 2005; Jönsson, Edman & Jonsson 2008; Caruso, Thor & Snäll 2010). For epiphytes, tree size often explains occurrence (Riiali, Penttinen & Kuusinen 2001; Snäll *et al.* 2004b), but colonization studies are rare as they require repeated surveys. For example, Laube & Zotz (2007) found higher colonization rates of tropical vascular epiphytes on large than on small trees. Local environmental conditions may also explain epiphyte colonizations (Snäll, Ehrlén & Rydin 2005; Lohmus & Lohmus 2010). In epiphytic cyanolichens, which we use as model organisms, facilitation may also explain colonizations, because lichens require a suitable photobiont partner for lichenization if they disperse by fungal spores (sexually). Hence, lichens dispersing symbiotically (mycobiont and photobiont together) may facilitate the establishment of other, sexually dispersed lichens by distributing commonly used photobionts (Rikkinen, Oksanen & Lohtander 2002).

Metapopulation theory predicts that local extinctions occur because of demographic or environmental stochasticity (Hanski 1999). The extinction risk decreases with increasing patch area, which is assumed to be positively correlated with population size (Hanski 1999). Extinctions caused by deterministic patch destruction are usually neglected, as the basic theory is based on organisms with colonization-extinction rates that are much higher than the patch turnover rate. However, for many species, the rates of creation and destruction of their habitat patches are higher than their colonization-extinction rates (Thomas 1994). For these species, the patch dynamics also need to be accounted for to predict the species dynamics ('habitat-tracking metapopulations', Thomas 1994; Thomas & Hanski 1997). Habitat-tracking metapopulation dynamics have been found for several organisms (e.g. Sjögren Gulve 1994; Laube & Zotz 2007; Burns & Neufeld 2009; Caruso, Thor & Snäll 2010; Öckinger & Nilsson 2010). Other species essentially do not go extinct until their patches disappear ('patch-tracking metapopulations', Snäll, Ribeiro & Rydin 2003), whereby stochastic extinctions can be ignored in predicting the metapopulation dynamics (Snäll, Ehrlén & Rydin 2005; Jönsson, Edman & Jonsson 2008). Accurate predictions of metapopulation dynamics and persistence require a proper understanding of the relative importance of stochastic and deterministic extinctions.

In boreal landscapes that are dominated by coniferous trees, deciduous trees, especially aspen *Populus tremula* L., are key components for biodiversity (Esseen *et al.* 1997). In northern Europe, aspen hosts about 150 obligate species (Kouki, Arnold & Martikainen 2004). Despite their conservation value, large aspens have declined in northern Europe as a result of fire suppression, intensive forestry and increased moose *Alces alces* populations (Kouki, Arnold & Martikainen 2004; Latva-Karjanmaa, Penttilä & Siitonen 2007; Edenius *et al.* 2011). This may lead to future declines of its associated species (Kouki, Arnold & Martikainen 2004; Latva-Karjanmaa, Penttilä & Siitonen 2007), including epiphytes (Kuusinen 1996).

Lichens are major components of boreal forest biodiversity (Esseen *et al.* 1997). Large epiphytic species provide shelter and food for invertebrates, and nesting material for birds. Our model species, cyanolichens, even have the ability to fix atmospheric nitrogen and therefore supply the ecosystem with nutrients as they decompose or through leaching of the thallus (Richardson & Cameron 2004). Finally, many cyanolichens are red-listed and several are used as indicators of old-growth forest conditions (Kuusinen 1996; Rassi *et al.* 2010).

The aims of this study were to (i) increase our understanding of which factors explain the metapopulation dynamics of epiphytic cyanolichens in order to be able to (ii) assess their future persistence in areas with different host tree numbers and tree fall rates. Using data from two surveys of cyanolichens and their host trees, we first tested which variables explained colonizations and extinctions. We then examined how host tree numbers and tree fall rates affected epiphyte persistence and species numbers using simulations. The tree numbers used are comparable with aspen numbers in a nature reserve and in

large northern European WKHs (see Table S1, Supporting Information).

Materials and methods

STUDY AREA AND STUDY SPECIES

The 25 ha study area is situated in the old-growth Kotinen nature reserve forest (61°14'N, 25°04'E) in the southern boreal zone, Finland (Ahti, Hämet-Ahti & Jalas 1968). Because the study area is part of a larger protected forest, the observed host tree and epiphyte dynamics are not influenced by edge effects. The forest is dominated by 80–150-years old Norway spruce *Picea abies* (L.) Karst. with interspersed birch *Betula* spp., aspen *P. tremula* and Scots pine *Pinus sylvestris* (L.).

We studied the epiphytic macrolichens with cyanobacterial photobionts that are confined to aspen in the study region. We also included *Protopannaria pezizoides*, which may grow on soil or detritus, because it was confined to aspen in the study area. *Leptogium saturninum*, however, was excluded because it often occurred high up in the trees and is not easy to detect with binoculars. This resulted in seven study species (Table 1), all except *Nephroma parile* red-listed in Finland (Rassi *et al.* 2010). Three species disperse mainly asexually, that is, both symbiotic partners together. They may also disperse sexually by fungal spores, but we found no apothecia, which are rare in the region. The other four species disperse mainly sexually by fungal spores. All species have cyanobacterial *Nostoc* spp., either as main photobionts, or, in the case of *Lobaria pulmonaria*, as additional photobiont located in internal cephalodia. All except *P. pezizoides* and *L. pulmonaria* belong to the *Nephroma* guild, a group in which the same or very similar *Nostoc* strains occur (Rikkinen, Oksanen & Lohtander 2002). Nomenclature and photobiont information follow Ahti *et al.* (2007).

EMPIRICAL DATA

In 1994, we mapped all 456 aspens that were ≥11 cm in diameter at breast height (1.3 m, d.b.h. henceforth). In 2008, we noted which trees had fallen and searched for new trees that had become ≥11 cm.

During 1994–1996, and in 2008, we recorded the occurrence of the study species on each tree. For simplicity, we refer to the first survey years as 1995. We started searching for the species at the tree base, then searched upwards, and above 2 m we used a pair of binoculars. Most species mainly occur on the lower part of the stem (Koskinen 1955) or are easily observed with binoculars.

The following binary response variables (1/0) were compiled for each species. Local colonization of a standing tree (1) was defined as species absent in 1995 and present in 2008; non-colonization (0) as species absent in 1995 and 2008. Local extinction from a standing tree (1) was defined as species present in 1995 but absent in 2008; non-extinction (0) as species present in both 1995 and 2008. Extinctions were further divided into (i) stochastic from live trees, (ii) stochastic from standing dead trees with at least some bark and (iii) deterministic, whereby the tree occupied in 1995 had fallen or had no bark in 2008.

For each tree, we recorded the following explanatory variables in 2008: d.b.h. (11–72 cm; median = 35 cm) and depth of bark crevices (mm) at breast height, percentage of corticated trunk (bark cover henceforth), tree inclination and whether the tree was alive (0) or dead (1). We estimated the degree of shade on a four-level ordinal scale (Snäll, Ribeiro & Rydin 2003). We recorded whether a spruce twig touched the host tree, because rainwater percolating through coniferous tree branches may affect host tree bark chemistry and epiphytes of the *Lobaria* community are absent on acidic bark (Gauslaa 1985). We estimated the soil moisture for a 2-m radius zone around each host tree on a four-level ordinal scale (Appendix S1, Supporting Information). Additionally, we recorded the bryophyte cover up to 2 m height hypothesizing that bryophytes hinder lichen growth. We also hypothesized that cyanolichens facilitate the establishment of other cyanolichens (Rikkinen, Oksanen & Lohtander 2002). In the colonization model of *Nephroma bellum*, we therefore included the variable 'species of the *Nephroma* guild occurred (1) or not (0) on the tree in 1995', 'guild' henceforth. The other spore-dispersed species were not analysed statistically because of lack of data.

STATISTICAL ANALYSIS

We modelled colonization and extinction probabilities using generalized (non)linear models with logit link function (logistic regression) (GLM, McCullagh & Nelder 1989). For each species, we built the models based on Akaike's Information Criterion (AIC, Akaike 1974) and on knowledge of the biological system studied (Burnham & Anderson 2002). We first assessed the predictive power of each explanatory variable based on AIC and on the significance of the associated regression parameters. Next, we fitted a multiple model containing the retained explanatory variables, biologically reasonable squared terms and interactions. After having removed variables not improving the model, we tested whether adding connectivity (S_p , see below), which corresponds to fitting

Table 1. Study species, their occupancy and observed rates of colonization, extinction and tree fall 1995–2008

Aspen and epiphyte species	Main reproductive strategy	Occupancy 1995 (%)	Total 1995	Alive trees 1995	Dead trees 1995	Occupancy 2008 (%)	Total 2008	Colonization rate	Stochastic extinction rate	Tree fall rate
<i>Populus tremula</i>			456	367	89		456			0.107
<i>Lobaria pulmonaria</i>	Asexual*	23	105	84	21	19	85	0.07	0.31	
<i>Nephroma parile</i>	Asexual†	19	86	71	15	17	78	0.08	0.31	
<i>Nephroma bellum</i>	Sexual†	10	44	34	10	10	44	0.05	0.24	
<i>Parmeliella triptophylla</i>	Asexual†	6	28	24	4	8	34	0.04	0.20	
<i>Nephroma laevigatum</i>	Sexual†	2	9	7	2	1	4	0	0.20	
<i>Protopannaria pezizoides</i>	Sexual†	1	5	4	1	1	3	0	0.50	
<i>Nephroma resupinatum</i>	Sexual†	1	4	4	0	1	5	0.01	0	

*Photobiont green algae or green algae and cyanobacteria.

†Photobiont cyanobacteria.

the dispersal kernel for the species (Hanski 1999), improved the model.

In the following, we describe the general colonization model, and the same principle holds for the extinction model. The full start model including connectivity was

$$\text{logit}(C_i) = \beta_0 + \sum \beta_m x_{im} + \phi \underbrace{\sum_{j \neq i} p_j \exp\{-\alpha[\ln(d_{ij})]^2\} \text{d.b.h.}_j^\gamma}_{S_i},$$

where, for the i th tree, C_i is colonization probability, β_0 is an 'intercept' parameter, x_{im} is the i th value of the m th local variable assumed to affect C_i , and β_m is the associated 'effect size' parameter. The third term, connectivity S_i with the 'effect size' parameter ϕ , accounts for the relationship between C_i and the occurrence of the focal epiphyte on the surrounding source trees j . The indicator variable $p_j = 1$ if the species occurred on tree j in 1995, otherwise $p_j = 0$. The influence of the surrounding trees (j) is quantified by the one-parameter log-normal function with distance d_{ij} in metres between the trees i and j . The parameter α controls for the rate of decay with distance. The d.b.h. of j -trees was included as a proxy for the local population size on these trees. The parameter γ scales the relationship between d.b.h. and rate of emigration. The values of S_i computed for trees near the edges of the area were potentially biased because we did not have data on species occurrences outside the study area. We therefore only included in S_i neighbouring aspen (j) within a radius of 150 m, thus max d_{ij} was 150 m. Moreover, trees i were always > 150 m from the edge of the study area. Exact P -values were not calculated for the spatial variable as this would have required computer-intensive bootstrap estimation (Snäll, Ribeiro & Rydin 2003). However, the 0.05-limit of a likelihood-ratio test lies between $\chi^2_{0.05,1} = 3.84$ and $\chi^2_{0.05,2} = 5.99$. We estimated the confidence limits for α and γ based on the likelihood profile (Hudson 1971).

SIMULATIONS

We simulated four scenarios to investigate the effects of tree numbers and tree fall rate on future metapopulation sizes and species numbers. The scenarios differed in initial number of host trees and in whether host trees fell or not. In all scenarios, we assumed fixed empirical epiphyte colonization and extinction rates (Table 1). We thus used the raw rates instead of the fitted colonization and extinction models with significant explanatory variables because the models only explained a small proportion of the variation, and we did not have access to data on the rate of change for most explanatory variables (only d.b.h. was measured both in 1995 and 2008).

The first scenario (F1) was according to the empirical data in terms of number of host trees (395), of occupied trees (Table 1) and of tree fall rate (0.107). The second scenario (F2) assumed the same rates, but initially one-fifth of the tree numbers (79). The number of occupied trees was also one-fifth. For species that occurred on less than one-fifth of the trees, we started with one occupied tree. The tree numbers of this scenario are comparable with aspen numbers in a large northern European WKH (see Table S1, Supporting Information). The third (F3) and fourth (F4) scenarios were included to investigate the importance of tree fall on future species dynamics. They were equal to F1 and F2 except that the tree fall rate was 0. For each time step, we simulated tree fall, colonization of

unoccupied trees and extinction of extant local populations in the order described. We simulated four 13-year time steps corresponding to 52 years. For each scenario, we ran 1000 replicates.

We used the statistics software R 2.11.0 (R Development Core Team 2010) with the add-on library `geoR` 1.6-23 (Ribeiro & Diggle 2001) for the GLMs. We wrote our own R code for fitting the GLM and for running the simulations.

Results

OBSERVED TREE AND EPIPHYTE METAPOPULATION DYNAMICS

Among the living trees, 16% had died but remained standing and 5% had fallen (Table 1). Among the trees that were dead in 1995, 33% had fallen. Ten percent of the dead trees had no bark in 2008 and were therefore excluded from the statistical analyses. Colonizations and stochastic extinctions were hence studied on 395 trees of which 73% were alive and 27% dead. No new aspen had reached 11 cm in d.b.h. in 2008.

The lichen colonization rates increased with increasing number of trees occupied in 1995 (Table 1, Fig. S1, Supporting Information). Most of the species with high colonization rates disperse asexually. Stochastic extinction rates from living and dead trees were relatively high, and also deterministic extinctions caused by tree fall occurred (Fig. S1, Supporting Information).

COLONIZATION MODELS

The number of colonizations observed allowed models to be developed for four species (Fig. 1a, Table S2, Supporting Information). All models explained a small proportion of the variation in probability (Fig. 1a). The colonization probability of *L. pulmonaria* was higher on living than on dead trees. For *N. parile*, it was lower on trees with spruce branches touching the stem if the focal tree had low d.b.h. For trees without spruce branches touching the stem, no effect of d.b.h. was found. Colonizations also increased with increasing connectivity to trees that were occupied in 1995. Colonized trees generally occurred in the near vicinity of trees occupied in 1995 ($\alpha = 0.21$; 95% CI: 0.12–0.52; Table S2, Supporting Information). The colonization probability of *N. bellum* tended to increase with increasing d.b.h., was lower on trees with spruce branches touching the stem, and decreased nonlinearly with increasing inclination. This probability was also higher on trees that were occupied than unoccupied by other species belonging to the *Nephroma* guild 13 years earlier. Finally, the colonization probability of *P. triptophylla* increased nonlinearly with increasing d.b.h.

EXTINCTION MODELS

The number of extinctions observed allowed us to develop models for four species (Fig. 1b, Table S3, Supporting Information). All models explain a small proportion of the variation

Fig. 1. Explanatory variables (x-axis) of the generalized (non)linear models for colonization (a) and extinction (b) probabilities. Black bars represent negative, grey bars positive estimates. The reduction in residual deviance, with its associated *P*-value, is given above the bar. *P*-values were not calculated for the connectivity variable (see explanation in Materials and Methods). Dead host tree = 'dead'; tree diameter = 'dbh'; spruce twigs touching host tree = 'spruce'; tree inclination = 'incl'; occurrence of *Nephroma* guild species on host tree in 1995 = 'guild'; connectivity to trees occupied by focal species in 1995 = 'connectivity'; '*' = interaction terms; '^2' = squared terms.

in probability (Fig. 1b). The extinction probability of *L. pulmonaria* decreased with increasing bark cover. The same was found for *N. parile*, and its extinction probability also decreased with increasing d.b.h. The extinction probability of *N. bellum* was higher on dead than on living trees, and for *P. triptophylla* it tended to decrease with increasing d.b.h.

METAPOPULATION VIABILITIES

All scenarios predicted viable metapopulations of the frequent species during the coming decades (Fig. 2). This group included all asexually and one sexually dispersed species. In contrast, two of the infrequent, sexually dispersed species, *N. laevigatum* and *P. pezizoides*, faced significant extinction risks in all scenarios. Moreover, in the scenario with low tree numbers and observed tree fall rate (F2, Figs 2 and S2, Supporting Information), all infrequent sexually dispersed species faced significant extinction risks. This additional species loss was the result of tree falls, because the loss did not occur in the scenario without tree falls (F4, Fig. 2). These metapopulation and tree fall dynamics are predicted to cause a loss of one to three of the seven study species during the coming 52 years (Fig. 3), with the higher losses in areas with low tree numbers and tree fall (F2).

Discussion

Our study of a lichen epiphyte community over a 13-year period showed that the metapopulation dynamics are explained by tree conditions, including tree size, connectivity to trees that were occupied 13 years ago, and maybe facilitation by photobiont sharing. It also showed that projections of future

epiphyte metapopulation dynamics should acknowledge both stochastic extinctions from standing trees and deterministic extinctions caused by tree fall. The simulations reveal significant extinction risks for one to three of the seven study species within the next decades, especially in areas with low tree numbers. This suggests that small set-asides, such as WKHs of the intensively utilized north European forest landscapes, may not be able to preserve species in the long term. Moreover, because low colonization rates characterize the species facing extinction risk in all scenarios, conservation strategies need to ensure that species colonization rates remain large enough to counteract local extinctions.

COLONIZATIONS

The colonization rates of different species generally increased with increasing number of occupied trees, showing the importance of maintaining high numbers of occupied trees. The more frequent, asexually dispersed species tended to have higher colonization rates than the infrequent, sexually dispersed species. It is likely that frequent species have more dispersal sources, leading to higher colonization rates, or that asexually dispersed species have more frequent dispersal events or higher establishment probabilities than sexually dispersed ones. The latter has been explained by greater metabolic reserves available in the larger asexual than sexual diaspores, or by a competitive advantage of large asexual diaspores against small sexual ones because of rapid germination and dense growth (Westoby, Jurado & Leishman 1992; Kimmerer 1994). In lichens, an explanation may also be that sexually dispersed species need to find a suitable photobiotic partner for lichenization after reaching a suitable patch.

Fig. 2. Projected number of aspens occupied, and extinction probabilities (proportion of replicates with metapopulation extinction) of epiphytic cyanolichens in simulations. Note different y-axis limits.

The effect of connectivity on the colonization probability of the species for which we had the most data, *N. parile*, is probably a consequence of efficient short-distance dispersal. The steep dispersal kernel is in agreement with other cryptogamic epiphyte dispersal studies based on observed colonizations (Snäll, Ehrlén & Rydin 2005), diaspore deposition patterns (Walser *et al.* 2001; Dettki & Esseen 2003), and spatial genetic structuring (Snäll *et al.* 2004a). Restricted dispersal range is the main explanation for low colonization rates and low species persistence and can be counteracted by

sufficient amounts of suitable habitat in the vicinity of the occupied patches.

It is increasingly acknowledged that local patch conditions explain colonizations by metapopulation species (Fleishman *et al.* 2002; Moilanen & Nieminen 2002). Lichen metapopulations are no exception: in one species, the colonization probability decreased with increasing tree inclination, that is, the more the tree leaned over. The same result was found for an epiphytic moss (Snäll, Ehrlén & Rydin 2005) and is probably explained by more unsuitable bark moisture and chemistry

Fig. 3. Projected numbers of cyanolichens in simulations that differ in terms of initial tree numbers and tree fall rates. Means and the upper and lower 2.5% quantile limits are shown.

because of the lower vitality of trees that lean over to a greater degree. Moreover, the colonization probability of two species was lower on trees where spruce branches touched the stem. In one species, this effect was only valid for small-diameter trees, where most of their bark surface is in the vicinity of spruce branches. This finding may reflect an alteration of the bark pH due to the proximity of acidic spruce needles, because epiphytes of the *Lobarion* community are absent on acidic bark (Gauslaa 1985).

Tree size is yet another local patch condition that is known to explain the occurrence pattern of epiphytes (e.g. Barkman 1958; Rose 1992) and is analogous to patch size in metapopulation theory (Hanski 1999). However, studies of species distribution patterns cannot disentangle the effect of tree size from that of tree age in explaining occurrences. We are only aware of two studies that have investigated the effect of tree size on colonization probability. Snäll, Ehrlén & Rydin (2005) did not find any effect of d.b.h. on colonizations of an epiphytic moss, while Laube & Zotz (2007) found an effect for certain tropical vascular plants. We found that the colonization probability of *P. triptophylla* increased with increasing d.b.h. This emphasizes the importance of retaining large trees in the forest landscape. Three main mechanisms may explain this finding. Firstly, a large surface is more likely to be hit by a diaspore; secondly, the suitability of the tree increases as the bark becomes rougher and develops higher spatial variation in chemistry and moisture; and thirdly, the risk of diaspore flush-off decreases with increasing bark roughness, which correlates with tree size.

Several studies have suggested that facilitation between species plays a key role in the colonization of different habi-

tats (Bruno, Stachowicz & Bertness 2003). This should include lichen communities where symbiotically dispersing species may provide photobionts for spore-dispersed species so that they can lichenize (Rikkinen, Oksanen & Lohtander 2002). We found support for this phenomenon because the colonization probability of the spore-dispersed *N. bellum* was higher on trees occupied by *Nephroma* guild species than on other trees. Genetic data on the photobionts are also supportive, except that the same photobiotic strain is only shared by some species of the *Nephroma* guild: *N. bellum*, *N. resupinatum* and *P. triptophylla* (Myllys *et al.* 2007; Fedrowitz, Kaasalainen & Rikkinen 2011). When excluding *N. parile* and *N. laevigatum* as *Nephroma* guild members from the colonization analysis of *N. bellum*, we still found a clear effect ($P = 0.03$). Nevertheless, these results may also reflect similar habitat requirements among the species (Myllys *et al.* 2007).

EXTINCTIONS

Stochastic extinctions generally increased with variables reflecting decreasing tree vitality, but they were as frequent as deterministic extinctions caused by tree fall. Hence, epiphytic lichens seem to show habitat-tracking metapopulation dynamics (Thomas 1994; Thomas & Hanski 1997), whereby not only stochastic extinctions but also the dynamics of the patches need to be accounted for in predicting metapopulation dynamics.

Extinction probabilities from living trees were explained by tree d.b.h. (= patch size) and tree vitality variables. This highlights the importance of retaining large, living trees in the

forest landscape. The assumed mechanism behind decreasing extinction risk with increasing patch area is that the area reflects the local population size (Hanski 1999). An increase in local species abundance with increasing tree size has indeed been shown for epiphytes (Snäll *et al.* 2004b; Öckinger & Nilsson 2010), but extinctions have, to our knowledge, previously not been explained by tree size in accordance with theory (Burns & Neufeld 2009; Caruso, Thor & Snäll 2010; Öckinger & Nilsson 2010). The likely explanation for the effects of tree vitality variables is tree deterioration, which precedes patch destruction and deterministic species extinction. Other possible causes of local extinctions include invertebrate grazing or local bark peeling (Löbel, Snäll & Rydin 2006; Gauslaa 2008).

METAPOPULATION VIABILITIES AND CONCLUSIONS FOR CONSERVATION

Our projections of future dynamics for areas with different host tree numbers reveal two important conservation messages. First, two infrequent sexually dispersed species face significant extinction risk in all projected scenarios. The explanation is their low colonization rates that do not compensate for their extinction rates resulting from stochastic extinctions and tree fall. Secondly, the observed tree fall rate increases epiphyte extinction risks, especially in areas with low tree numbers.

The results are supported by empirical observations of one of our study species, *L. pulmonaria*, which has gone extinct from several protected areas, especially where populations were small (Öckinger & Nilsson 2010). Moreover, all species that face significant extinction risk in our study are red-listed in Finland (Rassi *et al.* 2010). They may constitute parts of an extinction debt of the intensively utilized north European forest landscape (Hanski 2000).

Our results suggest that small set-asides, such as WKHs of the north European forest landscapes, will not be able to preserve species in the long term. The low tree numbers used in the simulations are comparable to those of large WKHs. A decline and significant extinction risk has previously been projected for a red-listed bryophyte when assuming the tree fall rate that was observed in a WKH near a clear-cut edge (Roberge *et al.* 2011). However, our study, which included several species, suggests losses even in areas with no edge effect, suggesting that the extinction risks may be even higher in small WKHs.

Conservation strategies need to ensure that species colonization rates remain large enough to counteract local extinctions, because low colonization rates characterize the species facing extinction risk in all scenarios. High colonization rates can be promoted by preventing populations from becoming so small that they produce and disperse insufficient numbers of diaspore. In addition, distances between habitat patches in the landscape must be kept low, especially for species with a restricted dispersal range (Hanski 1999). A continuous availability of old trees in protected areas needs to be assured, because tree fall was another reason for species loss. This can be accomplished by reducing the populations of large brows-

ers, and by retaining trees of high conservation value during management operations. It is important not to wait long to start promoting the development of old trees, as their old-growth properties take a long time to develop.

LIMITATIONS OF THE SIMULATIONS

Our simulations have limitations that are important to acknowledge. One limitation is that the same rates are used for the entire 50-year period. In reality, the colonization rates of declining species can be expected to decrease, because the number of dispersal sources will decrease and the average distance to these will increase. We do not believe that the stochastic extinction rates will increase. If anything, they will decrease because the local abundance on individual trees can be expected to increase (Öckinger & Nilsson 2010; Roberge *et al.* 2011). It is more difficult to assess how the rates of deterministic extinction caused by aspen fall will change. The current rate is high and will probably remain high for the next two or three decades. Thereafter, it may decrease because few large competitive aspen will remain. Our main findings are, however, relatively insensitive to this uncertainty because even the scenario that assumed no tree falls suggested significant epiphyte extinction risks and decreased species richness in the coming decades. A final limitation is that the estimated colonization and extinction rates used for the infrequent species are uncertain. This is difficult to overcome in studying many species. On the other hand, multiple-species studies have the advantage of bringing the variation in response by different species to light, and to allow wider generalizations than single-species studies. The infrequent, spore-dispersed cyanolichens are the ones most likely to be first lost from areas with low host tree numbers that are set aside from forestry.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Colonization and extinction rates.

Fig. S2. Projected number of aspens.

Table S1. Woodland key-habitat sizes and aspen densities.

Table S2. Parameter estimates of models for colonizations.

Table S3. Parameter estimates of models for extinctions.

Appendix S1. Scale for soil moisture.

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