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Edge creation and tree dieback influence the patch-tracking metapopulation dynamics of a red-listed epiphytic bryophyte

Jean-Michel Roberge[1,2 *], **Stina B.K. Bengtsson**[3], **Sören Wulff**[4], **Tord Snäll**[1]

[1] Department of Ecology, Swedish University of Agricultural Sciences (SLU), Box 7044, SE-75007 Uppsala, Sweden. E-mail (J.-M. Roberge): Jean-Michel.Roberge@slu.se. E-mail (T. Snäll): Tord.Snall@slu.se

[2] Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences (SLU), SE-90183 Umeå, Sweden.

[3] Department of Forest Mycology and Pathology, Swedish University of Agricultural Sciences (SLU), Box 7026, SE-75007 Uppsala, Sweden. E-mail (S.B.K. Bengtsson): Stina.Johansson@mykopat.slu.se

[4] Department of Forest Resource Management, Swedish University of Agricultural Sciences (SLU), SE-90183 Umeå, Sweden. E-mail (S. Wulff): Soren.Wulff@slu.se

[*] Correspondence author. Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences (SLU), SE-90183 Umeå, Sweden. Tel.: +46-90-7868359. Fax: +46-90-7868162. E-mail: Jean-Michel.Roberge@slu.se

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Summary

1. Edges in landscapes have an effect on the abundance of many species but the underlying ecological mechanisms are poorly known for most taxonomic groups. One way to gain insight into the mechanisms is to examine how key demographic or metapopulation parameters are affected by proximity to edge. The main objective of this study was to investigate the effects of edge creation through clearcutting on the dynamics of forest species' metapopulations.

2. We used the red-listed epiphytic moss *Neckera pennata* as a model species. Based on data from repeated surveys of a metapopulation and its host tree network in a hemiboreal forest, we tested the effect of edge creation on key metapopulation parameters: rates of local colonisation and extinction, local abundance growth, and patch destruction through the fall of host trees. We predicted the long-term consequences of the edge effects using simulations with Bayesian statistical models. We also explored the potential effects of the pathogen *Chalara fraxinea* causing ash dieback, a tree disease currently spreading in Europe.

3. The colonisation probability on host trees unoccupied by the moss increased with increasing connectivity to occupied trees. The growth of local populations on occupied trees decreased with increasing proximity to edge, and with initial local abundance. Stochastic extinctions of the epiphyte from standing trees were very rare and only occurred near the edge; most of the observed extinctions were deterministic due to tree fall. Tree fall decreased with increasing distance from the edge into the forest, and with increasing tree diameter.

4. Under edge conditions, simulations predicted decreases in the total number of host trees, number of occupied host trees, and in the total abundance of the epiphyte over a 30-year period. We suggest that ash dieback increases the tree fall rate and thereby the local extinction rate, leading to increased metapopulation extinction risk.

5. *Synthesis and applications*. The results show that small protected forest areas such as woodland key habitats may not allow long-term persistence of red-listed epiphytes if they are influenced by edge creation through clearcutting. Delineating uncut buffers of 50-100 m around the protected areas may alleviate such effects.

Keywords: Bayesian modelling, *Chalara fraxinea,* colonisation, edge effects, extinction, population growth, hemiboreal forests, *Neckera pennata*, windthrow, woodland key habitats.

Introduction

An edge is a more or less abrupt transition between two habitats. This commonly occurring landscape feature is known to result in ‘edge effects’, i.e. physical or biological processes originating from the edge and influencing processes on either side of it. Studying the effects of human-induced edges in forest landscapes has been a prominent area in ecology for several decades (Murcia 1995; Ries *et al.* 2004). This interest stems from the fact that the fragmentation of formerly continuous forest through human activities increases the prevalence of anthropogenic edges which differ from natural edges in several respects (Matlack & Litvaitis 1999). While some species are favoured by the new conditions following anthropogenic edge creation, others are affected negatively due to changed microclimate or altered species interactions (Murcia 1995).

Most studies of biotic edge effects in forest have focused on describing patterns of abundance in relation to distance from the edge into the forest interior. However, studies directly addressing the ecological mechanisms underlying edge effects are rare for most taxonomic groups (Murcia 1995; Honnay *et al.* 2005). One way to gain insight about ecological mechanisms is to examine how key demographic parameters such as recruitment, growth and mortality are affected by proximity to an edge. For vertebrate animals, a large body of literature addresses the effects of forest edges on recruitment (e.g. nest parasitism) and mortality (e.g. predation) (Ries *et al.* 2004). As regards plants, the great majority of studies addressing edge effects on demographic parameters deal with trees and other woody species (e.g. Chen, Franklin & Spies 1992; Laurance *et al.* 2006). In non-woody forest plants, focus on demographic parameters has been far less common, although a few studies of common species exist. For instance, negative effects of edge proximity on key parameters such as recruitment and growth have been found for field-layer herbaceous plants (e.g. Jules 1998) and some terricolous bryophytes (e.g. Hylander, Jonsson & Nilsson 2002), probably due to deviating microclimatic conditions near edges. Rare plant species have not been studied in that respect, however.

Epiphytes constitute a particularly interesting ecological group for studying edge effects, as their population dynamics are directly influenced by the availability of standing trees offering suitable growth conditions. In northern forests, epiphytic communities are dominated by lichens and bryophytes. Many such species are sensitive to desiccation, and can be assumed to be dependent on trees with suitable conditions including humidity. Many studies suggest that epiphytic lichens and bryophytes respond negatively to forest edges, as their abundance is generally lower near edges than in the forest interior (e.g. Esseen & Renhorn 1998). Regarding demographic parameters, past studies have been limited to lichens. Transplant experiments have shown varied effects of edge proximity on lichen growth (e.g. Sillett 1994; Renhorn *et al.* 1997; Stevenson & Coxson 2008). Moreover, Hilmo, Holien & Hytteborn (2005) found a lower colonisation rate near the edge.

An epiphyte may form a metapopulation where suitable trees represent individual habitat patches (Snäll, Ehrlen & Rydin 2005). The creation of an edge through clearcutting can be hypothesised to influence the metapopulation dynamics of epiphytes chiefly by altering the rate of local colonisation, population growth, or the rate of local extinction, the latter being caused either by stochastic population processes or deterministically through tree fall, which is often high near edges (e.g., Snäll & Jonsson 2001).

For classic metapopulations where the colonisation-extinction rates are much higher than the rate of patch turnover, the patch network can be assumed to be static when describing and predicting the metapopulation dynamics. However, for species with lower metapopulation turnover in relation to habitat patch longevity, the dynamics of the patches may need to be accounted for (Thomas 1994; Thomas & Hanski 1997; Snäll, Ribeiro & Rydin 2003). In some epiphytic mosses and lichens, local stochastic extinctions have even been found to be negligible whereby the rate of extinction is determined by the rate of tree fall (Snäll *et al.* 2005). Here, the presence of a sufficient number of suitable trees is expected to be more critical for metapopulation persistence than processes influencing local populations on individual standing trees.

The magnitude of edge effects can be expected to be influenced by other variables influencing the focal species' habitat, such as the occurrence of tree pathogens. Non-native pathogenic tree fungi may have important effects on forest ecosystems, such as observed for the chestnut blight fungus *Cryphonectria parasitica* Murr. in North America and the Dutch elm disease (*Ophiostoma* spp.) in Europe and North America (see Loo 2009 for a review). A potential new example is the increasing ash dieback in Europe. The disease was first reported in the early 1990s in Poland and Lithuania (Juodvalkis & Vasiliauskas 2002), and is currently spreading through Europe. It reached the Nordic countries around the beginning of the century, and has been considered widespread since 2004 within the area where the current study was conducted. The non-native ascomycete *Chalara fraxinea* (Kowalski) is regarded as the causal agent of the disease (Bakys *et al.* 2009). Pathogenicity tests (Kowalski & Holdenrieder 2009) have shown that the fungus causes seedling death. Moreover, the fungus has been shown to cause death of full-grown trees (Rimvis Vasaitis pers. comm. and personal observations). In Lithuania it is estimated that the ash *Fraxinus excelsior* L. population has declined by >60% since the early 1990s due to ash dieback (Vasiliauskas *et al.* 2006). The biology of the disease is just beginning to be described and its spread has been systematically documented only recently. Therefore, its impacts on ecosystem processes and biodiversity remain to be understood.

The main objective of this study was to investigate the effects of silvicultural edge creation on the metapopulation dynamics of forest species – particularly threatened epiphytes – using a red-listed (ECCB 1995, Gärdenfors 2010) moss, *Neckera pennata* (Hedw.), as the model species. Data from repeated surveys of the epiphyte and its host tree network were used to quantify the influence of edge creation on (1) the rates of local colonisation and extinction of the moss, (2) local population growth on trees occupied by the moss, and (3) host tree (i.e. patch) destruction. We then predict the long-term consequences of the edge effects using simulations with Bayesian models fitted to the empirical data. The simulated scenarios differ in terms of distance from edge, and whether the models are fitted to data collected during the whole survey period, or to data collected after the pathogenic fungus *C. fraxinea* had established in the study area.

Materials and methods

Model species and study system

The model species is the epiphytic feather moss, *Neckera pennata*, which grows attached to the bark of standing trees. It is autoicous and dispersed by spores from frequently occurring sporophytes, or by stoloniform branches. It mainly occurs on trees with high bark pH, in northern Europe mainly on European ash, elm *Ulmus glabra* Huds., Norway maple *Acer platanoides* L. and aspen *Populus tremula* L.. *Neckera pennata* is red-listed in Sweden (‘near threatened’; Gärdenfors 2010) and in Europe (‘vulnerable’; ECCB 1995). It is mostly encountered in old, moist forests, and considered to be a good indicator of the occurrence of other red-listed bryophytes and lichens (Nitare 2005). Previous studies have identified a number of variables influencing the occurrence, abundance and colonisation of *N. pennata* (see *Explanatory variables* below). Although we are not aware of any study directly addressing the effects of edge creation on metapopulations of *N. pennata*, two studies suggest that it may have decreased growth and colonisation near edges due to the reduced air moisture following edge creation. *Neckera pennata* exhibited greater growth at a mesic site compared to a xeric site (McGee & Kimmerer 2004) and dry conditions led to low germination and viability of spores (Wiklund & Rydin 2004a).

The study was performed in the hemiboreal zone (Ahti, Hämet-Ahti & Jalas 1968) in the province of Uppland, east-central Sweden. The study area (3-4 ha in size; 59^{o}52'4"N, 18^{o} 30'15"E) consists of old, mixed forest composed of Norway spruce *Picea abies* L., European ash, black alder *Alnus glutinosa* L., and other deciduous trees. We mapped all potential host trees with a diameter at breast height (dbh) ≥5 cm in 1997 (eastern part of the study area) and 1998 (western part). The host trees were clustered within a moist area stretching in a northwest-southeast direction and surrounded by spruce-dominated forest of similar height (Fig. 1). European ash was the most common host of *N. pennata* (88% of occupied trees). In

2000, a clearcut of approximately 30 ha was created southwest of the study site (Fig. 1). The clearcut was irregular in shape and some retention trees were left singly or as small groups.

Modelled response variables

We modelled the influence of a range of explanatory variables on: (1) the probability of colonisation of unoccupied trees by *N. pennata*, (2) the probability of local stochastic extinction from occupied trees, (3) the relative local abundance growth on occupied trees, and (4) the probability of host tree fall.

We obtained data on colonisations and stochastic extinctions by recording the presence or absence of *N. pennata* on each host tree in 1997/98, 1999, 2001, 2003, 2006, and 2008, but focus here on changes in *N. pennata* occurrence following edge creation, between 2001 (496 trees, 180 were occupied) and 2008. From 1999, we also recorded which host trees had fallen for each inter-survey period.

We obtained data on abundance growth (i.e. change in abundance) by measuring the total area covered (cm^2; hereafter 'local abundance') by all colonies on each stem in 1997/98 and 2006. The area was measured by gently pressing a plastic sheet with a grid of one-cm^2 squares against each *N. pennata* colony and then summing them to obtain the tree-specific local abundance. The measure of local abundance growth to be modelled assumed exponential relative growth, which has been found appropriate for describing the growth of individual colonies of *N. pennata* (Wiklund & Rydin 2004b). Specifically, we calculated a measure of relative abundance growth (or decrease) from the abundance data as:

$$G_i = \frac{\ln(A_{i,t}) - \ln(A_{i,0})}{t} \qquad \text{eqn 1}$$

where G_i is this relative abundance growth rate of a local population on tree i, $A_{i,0}$ is the initial abundance measured, $A_{i,t}$ is the abundance measured at t, the time length between the abundance measurements (i.e. $t = 9$ and $t = 8$ for trees where abundance was initially measured in 1997 and 1998, respectively). G was hence used as the third modelled response variable (see above).

Explanatory variables

For each host tree, we recorded the following explanatory variables in addition to distance (m) from clearcut edge: tree species, dbh (cm), stem inclination (degrees), depth of bark crevices (mm) at 50 cm above ground, and soil moisture (ordinal scale; see below). Additionally, we estimated connectivity (*sensu* Hanski 1999) to trees occupied in the 2001 survey as a variable (see Appendix S1 Supporting Information for details). These variables have been found to explain abundance, occurrence or colonisation of epiphytic bryophytes in previous studies (Snäll *et al*. 2005; Löbel, Snäll & Rydin 2006a; Löbel & Rydin 2010). When we modelled relative growth, the residual analysis suggested an effect of initial abundance, which was therefore also included as an explanatory variable in this model.

Soil moisture, or actually depth of ground water table, was assessed according to the methodology of the Swedish Soil Survey of the National Forest Inventory. The variable class assessment is based on topography, type of superficial deposit, assessment of what the ground wetness would be after heavy rain and after snow melting in the spring, presence of surface water on the ground and in hollows, tree pedestals, and occurrence of swamp bryophytes (for details, see Anonymous 1997; Snäll *et al*. 2003).

Statistical modelling

We used the Bayesian generalised linear modelling framework (Gelman *et al.* 2004) because it allows providing estimates of the uncertainty of the simulation results. These uncertainties reflect the uncertainty of the models used to make the simulations, which in turn reflect the natural variation and sampling uncertainty in the empirical data (see e.g. Drechsler *et al.* 2003 for further details on why the Bayesian approach is recommended for predictive simulations and metapopulation viability analysis). We built the models based on the Deviance Information Criterion (DIC; Spiegelhalter *et al.* 2002) and on knowledge of the biological system studied (Burnham & Anderson 2002): We first assessed the predictive power of each explanatory variable based on DIC and on the posterior distribution of the parameters. Next, we fitted a multiple model containing the retained explanatory variables, distance from edge and biologically reasonable squared terms, logged terms, and interactions, and finally we simplified this multiple model based on DIC and on knowledge of the biological system studied (as suggested by Burnham & Anderson 2002). The difference in DIC between the final models and the corresponding (null) model with intercept only, ΔDIC, is reported. For modelling the probability of colonisation by *N. pennata*, we used the complementary log-log link and assumed binomial errors. This link function follows from the assumption that the arrival of diaspores to trees follows a Poisson process (cf. Appendix S1). For modelling the probability of *N. pennata* extinction and tree fall, we used the logit link and assumed binomial errors, and for modelling the relative abundance growth we used the identity link and assumed normal errors.

Different tree fall rates 1997-2006 and 2006-2008

To describe trends in the observed temporal dynamics in host tree fall, we calculated the mean annual rate of tree fall, F, for the inter-survey periods from the empirical data as

$$F = 1 - (R/N_0)^{1/t} \qquad \text{eqn 2}$$

where R is the number of trees that remain standing at the end of the inter-survey period, N_0 is the number of trees standing in the beginning of the inter-survey period, and t is the length of the inter-survey period in years.

Field observations suggested increased tree fall rates after 2006. This coincides with the time when the pathogen *C. fraxinea* is assumed to have established in the study area. Therefore, in addition to calculating tree fall rates for each inter-survey period, we established that *C. fraxinea* was common in the stand through symptom assessment (Skovsgaard *et al.* 2010) and fungal isolations from seedlings and standing trees (method of Bakys *et al.* 2009). We also produced the first summaries of the data available on the variable “crown defoliation caused by fungus or unknown” for ashes in the Swedish National Forest Inventory 2003-2008, and on the variables “defoliation” and “damage to canopy, branches or tree top caused by fungus” for ashes in the Swedish National Forest Damage Inventory 1994-2006 (Wulff, Hansson & Witzell 2006).

Simulation models and simulated scenarios

We simulated three scenarios for investigating future metapopulation structure and extinction risk of *N. pennata*. First, we simulated two scenarios that assumed rates of metapopulation and tree fall dynamics according to the empirical data from the period 2001-2008 (1997/98-2006 for abundance). The rate of tree fall was found to be much higher after than prior to 2006, so we investigated an additional scenario that assumed tree fall rates according to the empirical data from the period 2006-2008.

We simulated 30 time steps (years). All simulations were started at the conditions prevailing in 2001 at our 3-4 ha study site (Fig. 1) in terms of number of host trees (patches), dbh and *N. pennata* occurrence. The size of the study site is typical of woodland key habitats that are delineated for the conservation of red-listed species and biodiversity in Sweden (Hansson 2001). Moreover, an overlay analysis of *N. pennata* observations reported to the Swedish Species Gateway together with woodland key habitats on private land using a GIS revealed that the median size of key habitats hosting *N. pennata* is 3.4 ha.

For each time step, we simulated tree fall, dbh growth and recruitment of new (randomly located) host trees in the order described. Next, local population and metapopulation dynamics were simulated: abundance growth on occupied trees, colonisation of unoccupied trees, and extinction of extant local populations. Two types of local extinctions occurred: stochastic extinctions from occupied trees and deterministic extinctions as occupied trees fell. The models used for the simulations are described in detail in Appendix S1. For each scenario, we ran 700 replicates using 700 draws from the posterior distribution of the parameters of the separate Bayesian models.

Scenario 1 (S1). The first scenario assumed interior forest conditions and rate of tree fall as observed during the whole study period: The simulation models for rate of tree fall and relative abundance growth were based on data recorded ≥100 m from the clearcut edge.

Scenario 2 (S2). In this scenario edge conditions were assumed to prevail throughout the forest patch regarding rate of tree fall and relative abundance growth. Specifically, the models for rate of tree fall and relative abundance growth were based on data recorded <100 m from the clearcut edge.

Scenario 3 (S3). S3 also assumed edge conditions, but differed from S2 in assuming a rate of tree fall corresponding to the higher rate observed after 2006. This tree fall rate is assumed to reflect the conditions that prevailed after ash dieback had spread in the study region.

Results

Metapopulation dynamics and local growth

Among the 184 host trees which were unoccupied in 2001 and still standing in 2008, the seven-year colonisation rate was 17% (32 trees). The final model for colonisation probability included connectivity only, with restricted dispersal distance. For parameter estimates, see Appendix S1.

From the 133 trees which were occupied in 2001 and still standing in 2008, we observed only two (1.5%) local stochastic extinctions. These took place 0 m and 10 m into forest. Moreover, 26% of the occupied trees fell, leading to deterministic local extinctions.

In 1997/98, the mean abundance of *N. pennata* on the 134 occupied trees which remained standing until 2006 was 661 ± 1452 (SD) cm^2 (median 47 cm^2). In 2006 the mean abundance on these trees had increased to 994 ± 1848 cm^2 (median 194 cm^2). The final model for relative growth of *N. pennata* (ΔDIC = 46.4, mean deviance [$\overline{D}$ henceforth] explained =32%, pD = 4.1, where pD is a measure of Bayesian model complexity, *cf.* Spiegelhalter *et al.* 2002, n = 132; see Appendix S2 Supporting Information for model details) showed that it increased with increasing distance into the forest interior – especially at short distances from the edge – but decreased with increasing initial abundance (Fig. 2). Closer than 30 m from the edge, the observed abundance generally decreased (negative growth) or increased only slightly, while all of the larger increases observed (>0.20) were at distances greater than ~35 m into the forest (cf. triangles in Fig. 2). The model predicted negative growth on 13 trees, all located <50 m from the edge (cf. upper-left corner of Fig. 2).

Tree fall rates and C. fraxinea *infection*

Thirty-six % (177 trees) of the host trees fell between 2001 and 2008. Fifty-one % of these (90 trees) fell during the first five years after edge creation (2001-2006), whereas almost as many, 49% (87 trees), fell during the last two years of the study (2006-2008). The rate of tree fall was much higher 2006-2008 than for any other inter-survey period (Fig. 3).

All of the ash trees examined in 2009 showed symptoms of infection by *C. fraxinea* and the fungus was identified in isolates. The 13-year time series on the proportion of defoliated trees and the proportion of trees with fungus-related crown damage collected in the Swedish National Forest Damage Inventory 1994-2006 showed the highest proportions of defoliated ash trees ever observed in 2005 and 2006 (Fig. 3). The six-year time series on ash crown defoliation from the National Forest Inventory 2003-2008 showed its highest values from 2006.

The final model for probability of tree fall included distance from edge, dbh, dbh squared, and the interaction between distance and dbh (ΔDIC = 79.4, $\overline{D}$ explained = 13%, pD = 4.9; see Appendix S3 Supporting Information for model details). Except for trees with small diameters, the probability of tree fall decreased with increasing distance from the edge (Fig. 4, x-axis). It also decreased with increasing tree diameter (Fig 4; y-axis).

Predicted future host tree and metapopulation dynamics

The scenario that assumed interior forest conditions (tree fall rates observed ≥100 m from clearcut edge) predicted increased number of occupied trees and a stable total abundance (Scenario 1; Fig. 5). The scenario assuming edge conditions (rates of tree fall and relative abundance growth observed <100 m from clearcut edge) instead predicted a decrease in the number of host trees, number of occupied trees, and in total abundance (Scenario 2; Fig. 5). When assuming the tree fall rates prevailing after the onset of accelerated tree fall in 2006, the predicted total number of trees and occupied trees were further reduced by approximately 50%, the metapopulation extinction risk was increased from 3 to 5%, and the total abundance was reduced by approximately 30% (Scenario 3; Fig 5).

Discussion

This study shows how key parameters of an epiphytic moss metapopulation are affected by edge creation in forest, and how these changed parameter values can affect future metapopulation dynamics and persistence. Near edge, growth of *N. pennata* was lower and local abundance was even predicted to decrease on trees with large initial abundances. The increased tree fall rate near edge increased the rate of deterministic local extinction of the epiphyte. The simulations showed that metapopulations experiencing edge conditions can be expected to decrease, while those experiencing interior forest conditions can be expected to increase. Finally, we found support for the hypothesis that invading diseases affecting host tree survival may increase the metapopulation extinction risk for forest-interior species. We are not aware of any other study directly addressing the effects of distance to edge on epiphyte or bryophyte metapopulation parameters in combination with predictions of future metapopulation development.

Observed metapopulation and local population dynamics

The colonisation rate by *N. pennata* for trees near the edge was not different from the rate in the forest interior. This deviates from findings for epiphytic lichens showing lower colonisation rate at the forest edge (Hilmo, Hytteborn & Holien 2005). The lack of effect of distance to edge on colonisation in the present study may be due to the sample size being too small. As previously found, colonisation was explained by connectivity to nearby dispersal sources; the estimate of the dispersal range (parameter α in eqn S1-3 in Appendix S1) is similar to that obtained by Snäll *et al.* (2005) who utilised data from two other forest areas and from the eastern cluster of trees in the present study area (Fig. 1). In an analysis of common terricolous bryophyte species assumed to be sensitive to clearcutting, Hylander (2009) did not find any effect of distance to potential propagule sources on re-colonisation of formerly clearcut forest stands. This is in contrast with our results at the tree scale, and with those of Zartman & Nascimento (2006), who found evidence that dispersal limitation affected the abundances of epiphyllous bryophytes in a tropical forest fragmentation experiment.

The relative abundance growth rate of *N. pennata* increased with increasing distance from the edge into the forest interior. This is in contrast with the results of Löbel, Snäll & Rydin (2006b) obtained at a larger scale in a fragmented landscape: using stand shape (edge length-stand size ratio) as a measure of edginess, they did not find any edge effect on the stand-scale abundance of this species. The local population declines (negative growth) of *N. pennata* are probably due to changes in microclimatic conditions close to the edge (Chen, Franklin & Spies 1995), including desiccation due to increased sun exposure or wind speed (e.g., Seel, Baker & Lee 1992; Pharo & Zartman 2007). In a study of bryophytes in forested buffer strips along streams, Hylander *et al.* (2005) showed that bryophyte species growing on convex substrate such as tree bases and bark (as is the case for *N. pennata*) were more affected by clearcutting than species growing on concave substrates (most ground-living species), probably because the former are more affected by extended desiccation. In the present study, colonies may also have been mechanically removed by neighbouring trees falling onto the stems of occupied trees. This may also explain the decreasing growth rate of *N. pennata* with increasing initial abundance: a falling tree is more likely to hit and damage a colony on a neighbouring tree if the occupying moss is abundant. Another explanation is that moss colonies on trees already harbouring a large local population cannot expand further due to limited area of suitable bark free from *N. pennata*, i.e. the growth would be density-dependent, or due to interference competition from other epiphytes. In any case, our results suggest that growth of local abundance on the whole tree deviates from the exponential model previously applied for modelling growth of individual *N. pennata* colonies (Wiklund & Rydin 2004b).

Decreasing distance to edge increased the rate of tree fall, and this was by far the most important cause of local extinctions in this species. The probability of local extinction from trees that remained standing was very low: only two local extinctions from standing trees occurred during the seven-year period after edge creation. This supports earlier findings showing that boreal epiphytes and other sessile tree-dependent organisms are relatively unaffected by local stochastic extinctions, and that their local extinction rate is largely determined by the rate of tree fall (Snäll *et al*. 2003; Pykälä 2004; Snäll *et al*. 2005; Jönsson, Edman & Jonsson 2008). In a study of epiphyte dynamics on retention trees 2–6 years after clearcutting, Lõhmus & Lõhmus (2010) also identified host tree loss as the main source of local epiphyte extinction. Note, however, that they included tree cutting as a cause of tree loss. As regards stochastic extinction and colonisation rates in bryophytes, they did not find any general differences between retention trees on clearcuts and trees standing in forest.

Our study suggests that the commonly found 50-m penetration depth of edge effects on plants (Murcia 1995; Ries *et al.* 2004) is an underestimate for epiphytes in northern forests. Effects on growth were suggested for depth <50 m by our abundance growth model and individual observations (Fig. 2). However, the penetration depth for tree fall reached 70-80 m for intermediate-sized trees, which means that small forest remnants may have increased tree fall rates across a large proportion of their area, with likely negative consequences for their associated species. It should be noted that in the present study, the edge was mostly facing southwest and south – the direction with the strongest edge effects at these latitudes (Hylander 2005). This may explain at least partly the relatively large depth of influence observed here.

Effects on future metapopulation size

Our simulation results corroborate the view that for sessile organisms dependent on suitable trees as substrate, wind-throw following edge creation is an important mechanism affecting metapopulation persistence: forest edge conditions predict decreased metapopulation size and significant extinction risk in the coming 30 years (Scenario 2; Fig. 5), while forest interior conditions predict a stable or increasing metapopulation size (Scenario 1; Fig. 5).

A limitation of the simulations is that the same models are used for the entire 30-year period. In reality, conditions will gradually change as vegetation grows on the clearcut area, leading to reduced tree fall rates in adjacent forest. However, the scenarios assuming edge conditions predict drastic decreases in the number of host trees and a non-negligible extinction risk already after 20 years, a time frame during which the clearcut land will remain relatively open. Also, the predicted negative metapopulation development under edge conditions can be assumed to be underestimated: First, the model does not account for the decrease in diaspore output (i.e. emigration) with decreasing local abundance under edge conditions. Secondly, we only observed local stochastic extinctions near the edge but in the simulations we assumed the same rates in forest interior and as near the edge.

Ash dieback involved in decreasing metapopulation persistence?

Many lines of evidence point toward *C. fraxinea* as the most probable underlying cause of elevated tree fall rate after 2006: (1) Field work in June 2009 for sampling *C. fraxinea*, less than one year after the 2008 survey, showed continued high tree fall rate (~0.10); (2) Symptoms of *C. fraxinea* were found on all examined ash trees in the study area in 2009; (3) Independent, large-scale monitoring data from the region show increasing *C. fraxinea* infection and decreased ash vitality during the same period; (4) *C. fraxinea* has been shown to cause death of ash seedlings (Bakys *et al.* 2009) and large trees (R. Vasaitis pers. comm. and personal observations). *C. fraxinea* infection makes the host more susceptible to infection by secondary pathogens such as root and butt rot fungi (Skovsgaard, Thomsen & Barklund 2009), which may accelerate tree fall. These lines of evidence suggest that the ongoing invasion by *C. fraxinea* increases the tree fall rate, leading to lower future metapopulation size and enhanced extinction risk for *N. pennata* – an epiphytic bryophyte vulnerable at the European level – over the simulated time span (Scenario 3; Fig. 5).

This study shows a potential negative effect of the ongoing European ash dieback on a red-listed species whose main host is ash. This calls for further studies aiming to increase our understanding of the epidemiology of this pathogen so that we can prevent it from causing the same continent-wide cascading ecosystem effects as caused by the chestnut blight fungus or the Dutch elm disease.

Implications for management

The forest stand area in the present study (3-4 ha) corresponds to the median size of woodland key habitats hosting *N. pennata* in hemiboreal forest landscapes. These set-asides support a high diversity of red-listed bryophytes and lichens (Perhans *et al.* 2007), and are part of a widely implemented conservation approach in north-European forests (Hansson 2001). However, little is known about their capacity to support threatened species in the long run. Our study suggests that if they are affected by edge-effects through clearcutting, most woodland key habitats risk being too small to allow long-term persistence of epiphytic bryophytes. This is further strengthened by the fact that the overall median size for Swedish woodland key habitats is only 1.5 ha (Skogsstyrelsen 2007). To alleviate negative edge effects on red-listed epiphytes, woodland key habitats and other small forest reserves should be protected from edge creation. This could be done by delineating a 50-100 m buffer which is exempt from clearcutting around these areas.

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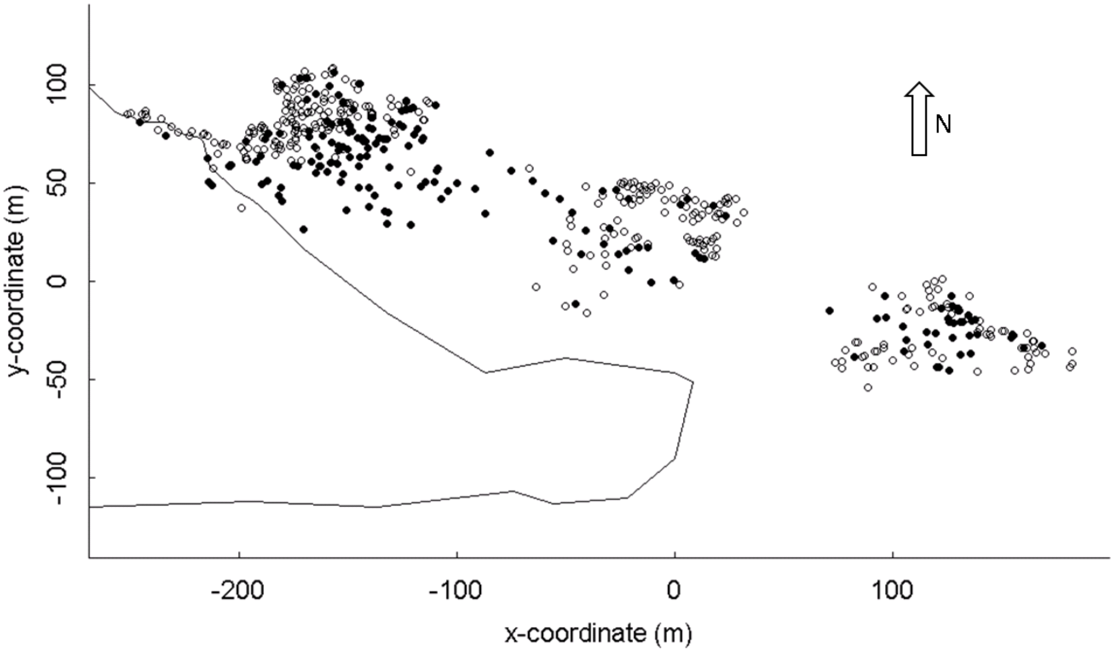

Fig. 1. Map of the study area with the clearcut-forest edge (line) and host trees occupied (filled circles) and unoccupied (empty circles) by *Neckera pennata* in 2001 (n = 496).

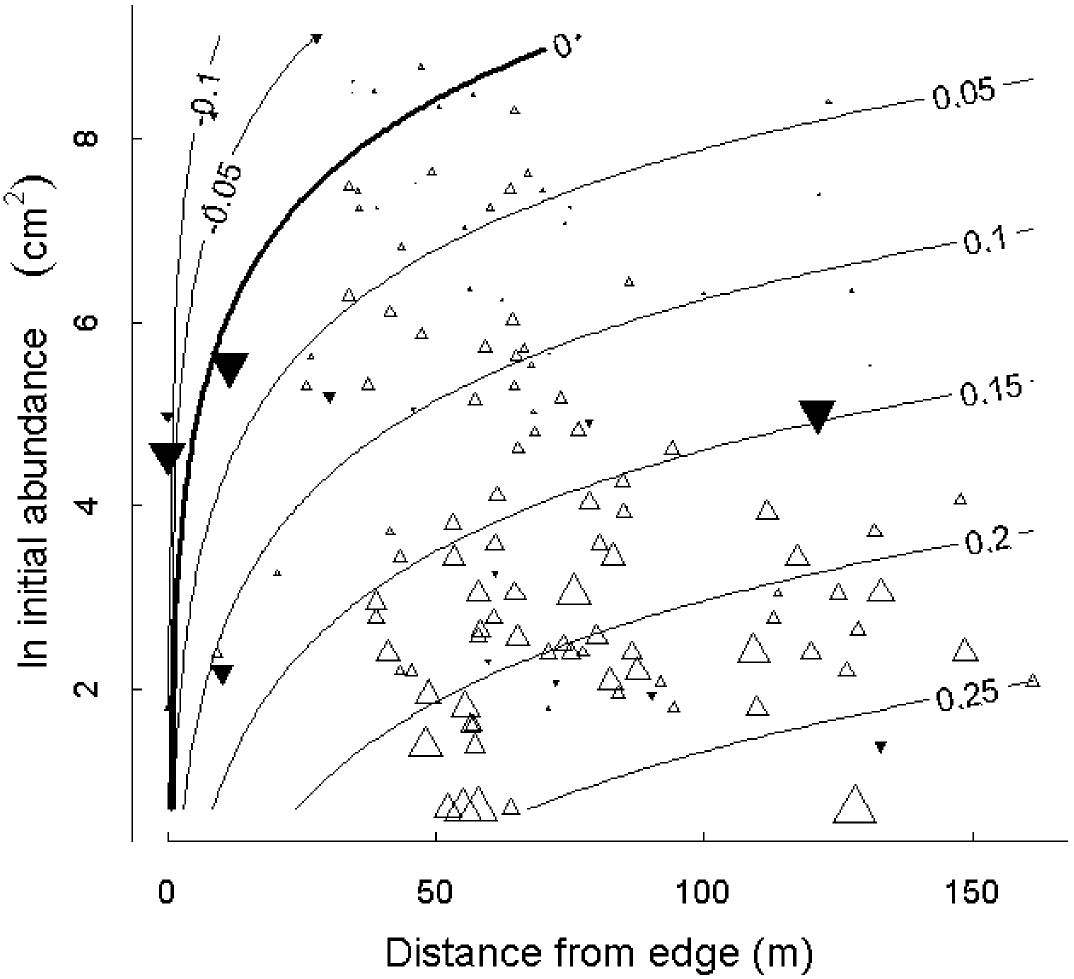

Fig. 2. Relative growth of *Neckera pennata* on individual trees in relation to initial abundance and distance from clearcut-forest edge. Contours depict the modelled relative growth rate. Up-pointing open triangles show observed positive growth and down-pointing filled triangles show observed negative growth. Triangle size reflects growth values.

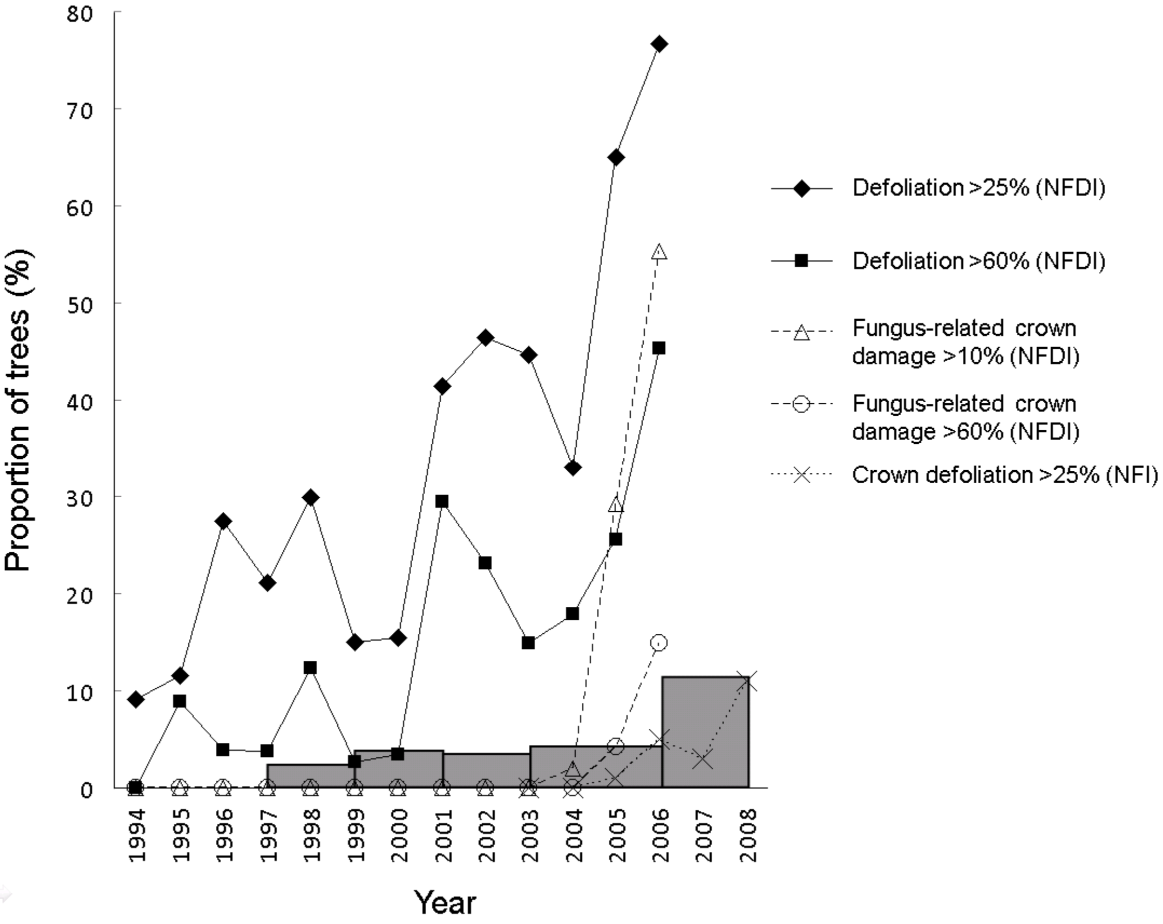

Fig. 3. Mean annual rate of tree fall in the study area for the different time intervals 1997-2008 (bars), and frequency of crown damage in European ash in Sweden 1994-2008 (lines) based on data from the National Forest Damage Inventory (NFDI; "defoliation and fungus-related crown damage") and the National Forest Inventory (NFI; "crown damage").

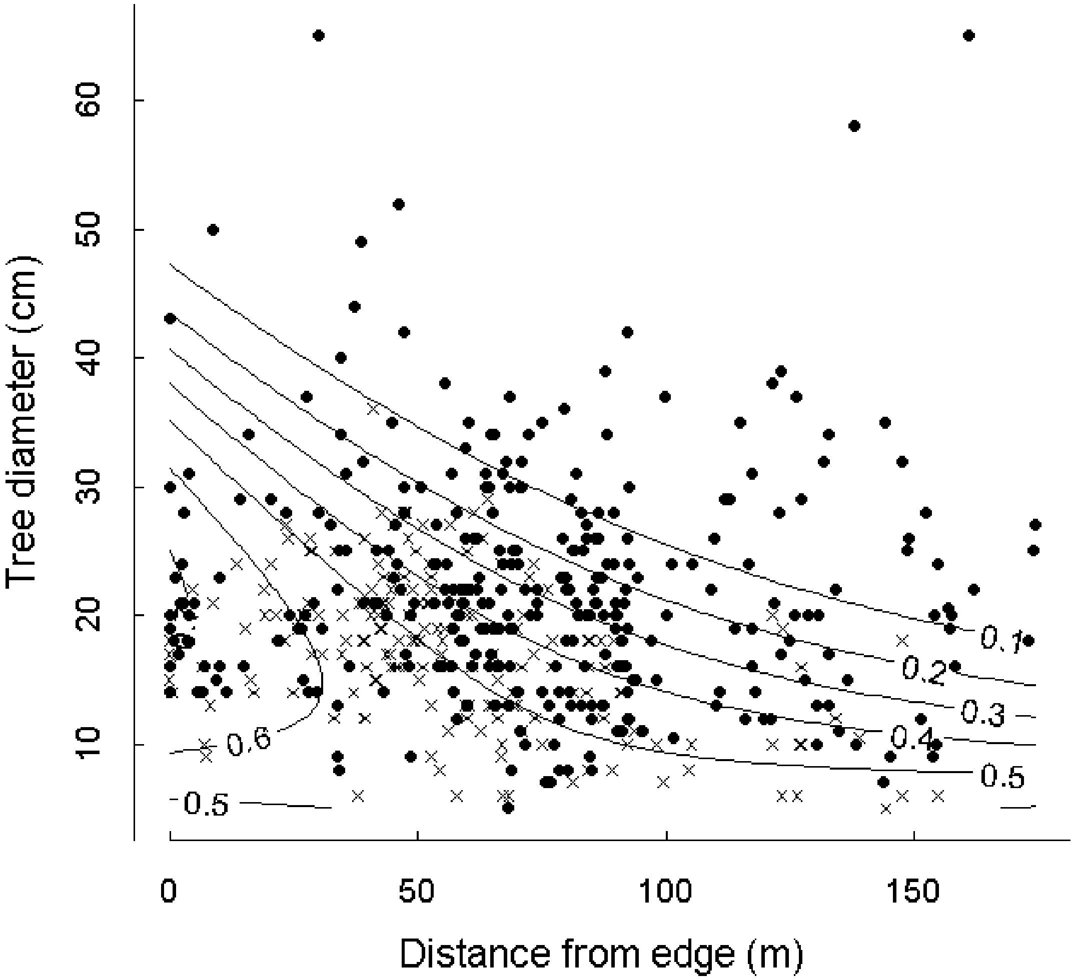

Fig. 4. Probability of fall of *Neckera pennata* host trees in relation to distance from the clearcut-forest edge and tree diameter (dbh). Contours depict the modelled probability of tree fall over a seven-year period. Xs depict observed tree fall events and filled circles depict trees that remained standing during 2001-2008.

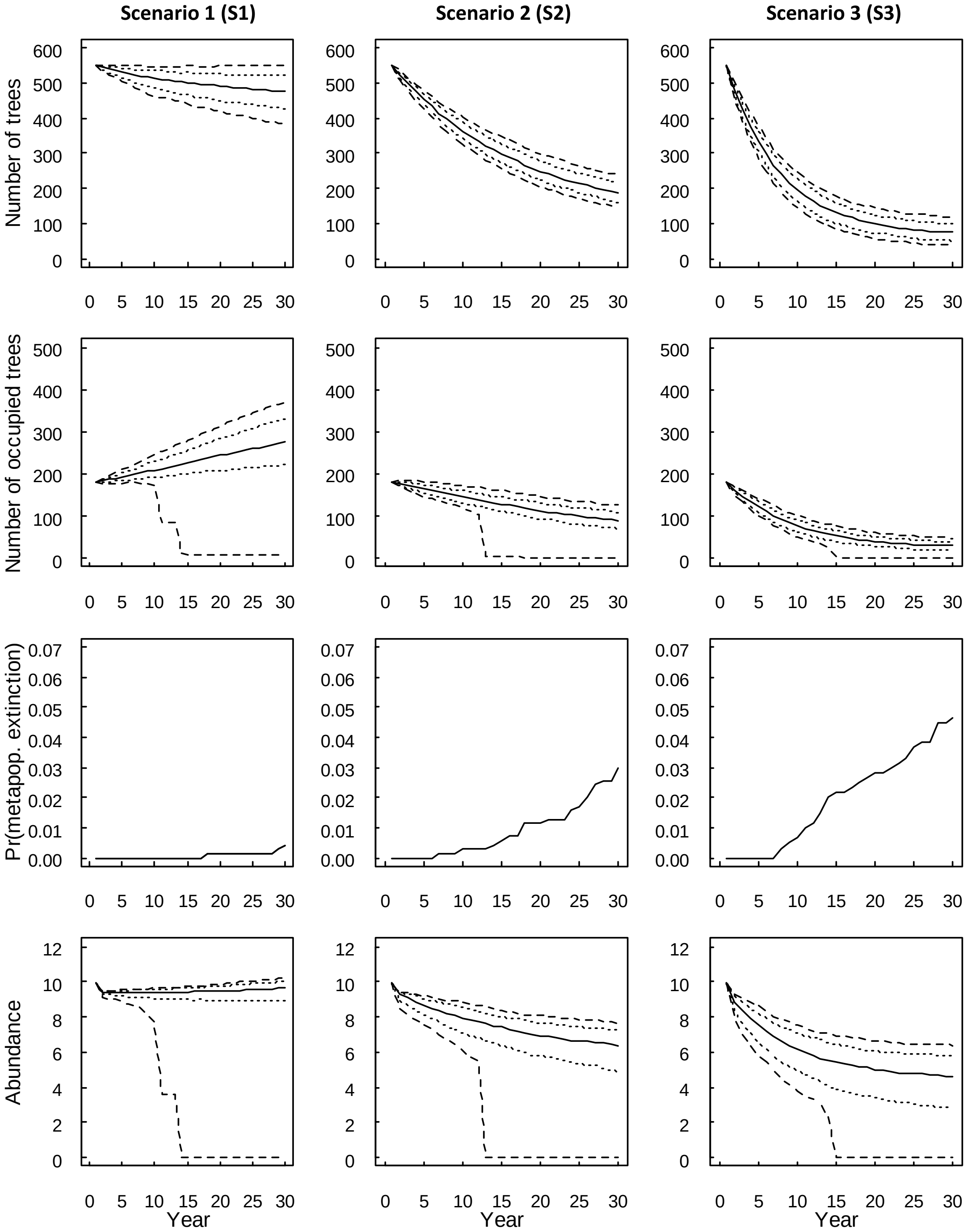

Fig. 5. Three projections of total number of potential host trees, number of trees occupied by the epiphytic moss *Neckera pennata*, probability of metapopulation extinction, and summed abundance (in m^2) for all trees. Medians, 95% and 75% quantiles are shown. S1. ≥100 m from

clearcut edge, tree fall rate observed 2001-2008; S2. <100 m from clearcut edge, tree fall rate observed 2001-2008; S3. <100 m from clearcut edge, tree fall rate observed 2006-2008.

Supporting information

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

Appendix S1. Detailed description of simulation models

Appendix S2. Model for relative growth of *Neckera pennata* on occupied trees

Appendix S3. Model for the probability of fall of *Neckera pennata* host trees

Appendix S1. Detailed description of simulation models

In the following we describe the models used for the simulations. This includes the model for probability of *N. pennata* colonisation (eqn S1-3 below) which is also presented in the Results. For this model, we did not find any effect of distance from edge (after accounting for connectivity), and hence the model did not need to be adapted for the different simulated scenarios assuming interior or edge conditions. The models for tree fall and abundance growth presented here, however, differ from the models presented in the Results: Here, distance to edge was not included as an explanatory variable. Instead, the effect of edge was addressed by fitting separate models for forest interior and forest edge conditions.

In Scenario 1 (S1; forest interior conditions), the simulation models were based on empirical data on the rate of tree fall collected ≥100 m from the clearcut edge during 2001-2008, and on data on relative abundance growth collected ≥100 m from the clearcut edge. In Scenario 2 (S2; forest edge conditions), models were fitted to data based on the rate of tree fall collected <100 m from the clearcut edge during 2001-2008, and to data on relative abundance growth collected <100 m from the clearcut edge. In Scenario 3 (S3; edge conditions and post-2006 tree fall rate), the tree fall model was fitted to data collected <100 from the clearcut edge 2006-2008. This tree fall rate is assumed to reflect the conditions that prevailed after ash dieback had spread in the study region.

We simulated tree fall using a logistic regression model. More specifically, the probability of tree *i* falling during the seven-year study period followed a Bernoulli distribution with probability F_i where

$$\mathrm{logit}(F_i) = \beta_0 + \beta_1\, dbh_i\,. \qquad \text{eqn S1-1}$$

In the simulations however, where each time step corresponded to only one year, we instead used $F_i^* = 1-(1-F_i)^{1/7}$. This correction was also applied in modelling colonisation and extinction (see below). For diagnostics and estimates of the parameters β_0 and β_1 for the different models used in the simulations, see Appendix Table S1.

Tree dbh growth was simulated using a linear regression model (ΔDIC = 43.1, mean deviance ($\overline{D}$ henceforth) explained = 26%, pD = 3.1, where pD is a measure of Bayesian model complexity, *cf.* Spiegelhalter *et al.* 2002). The model was based on data on diameter growth during the last 10 years obtained from tree cores collected at the study site and at another similar old-growth site (see Snäll, Ehrlen & Rydin 2005). These observations of ten-year growth data were divided by ten, and used as the response variable to fit the model used for yearly tree growth. Specifically, each tree *i* grew following a normal distribution with mean μ where

$$\mu_i = \omega_0 + \omega_1\,(dbh_i, - \overline{dbh}), \qquad \text{eqn S1-2}$$

and precision τ_D (=1/variance). ω_0 is an “intercept” parameter and ω_1 is a “slope” parameter. The posterior distribution of τ_D had a mode of 0.06 and a Bayesian 95% confidence interval of 0.05-0.08. Summaries of the parameter distributions are hereafter presented as vectors, in this case τ_D = [0.06, 0.05, 0.08]. ω_0 = [0.20, 0.19, 0.22] and ω_1 = [0.0043, 0.0031, 0.0054].

We subtracted $\overline{dbh}$ (23.9 cm) from each observation in order to reduce parameter correlations. As in Snäll *et al.* (2005), we assumed that trees with a dbh greater than the maximum observed among trees used for fitting the model (65 cm) grew at the same mean rate as the model prediction (eqn S1-2) for this largest tree ($\mu_i = 0.38$ cm per year) .

Host tree recruitment was simulated by drawing a value (number of trees recruited) from a Poisson distribution with a mean of 1.5. This rate was estimated based on counting all new trees in 2003 that had become >5 cm in dbh since the first mapping in 1997/98 (see Snäll *et al.* 2005).

N. pennata colonisation of an unoccupied tree was simulated using a complementary log-log link (cloglog) regression model (ΔDIC = 5.2, $\overline{D}$ explained = 5%, pD = 1.7). The model assumes that the number of diaspores arriving at a tree follows a Poisson distribution, so that the probability of at least one successful colonisation is $C_i = 1 - \exp(-\lambda_i)$, where λ_i is the rate of colonisation. Specifically, the yearly probability of colonisation followed a Bernoulli distribution with mean $C_i^* = 1\text{-}(1\text{-} C_i)^{1/7}$ where

$$\mathrm{cloglog}(C_i) = \log(\phi) + \log\Bigl(\sum_{i \neq j} \exp(-\alpha \log(D_{ij})^2)\, p_j\Bigr)\,, \qquad \text{eqn S1-3}$$

where $\log(\phi) = [-3.44, -5.63, -2.10]$ is a parameter that regulates the colonisation rate of the species, $\alpha = [0.25, 0.07, 0.43]$ is a parameter which regulates the decay of the one-parameter log-normal dispersal function used, D_{ij} is the distance in m from tree i to trees j that were present in the preceding time step, and is p_j an indicator variable which is coded 1 if tree j was occupied by *N. pennata* in the preceding time step, or 0 otherwise. The probability of colonisation was thereby a function of an index of connectivity (*sensu* Hanski 1999) to patches occupied in the preceding time step.

The relative abundance growth (or decrease) of *N. pennata* on individual trees – i.e. *G* as calculated using eqn 1 – was simulated using a linear regression model. Specifically, the relative change in abundance between time *t*-1 and *t* on a tree *i* that was occupied at both events followed a normal distribution with mean $\mu_{i,t}$ as

$$\mu_{i,t} = \gamma_0 + \gamma_1 \,(\log(A_{i,t-1}) - \overline{\log(A_{t-1})}\,), \qquad \text{eqn S1-4}$$

where $A_{i,t-1}$ is the abundance on tree *i* at the beginning of the time period, and precision τ_G (=1/variance). For diagnostics and estimates of the parameters γ_0 and γ_1 for the different models used in the simulations, see Appendix Table S1.

Local stochastic extinction from an occupied tree followed a Bernoulli distribution with mean $0.00216 = 1\text{-}(1\text{-} 2/133)^{1/7}$ (2 of the 133 trees that were occupied in 2001 were unoccupied in 2008). That is, the probability of extinction from an occupied tree in each simulation year was 0.00216. Local deterministic extinction occurred as an occupied tree fell.

For all Bayesian models fitted, we used a Normal distribution with a mean of 0 and a precision (=1/variance) of 0.001 as prior distribution for ‘regression parameters’. For precision parameters, e.g. τ_D (eqn S1-2), we used a gamma distribution with shape and scale equal to 0.001. For α (eqn S1-3) we used an exponential distribution with a mean of 0.001. The Bayesian models were fitted using OpenBUGS 3.0.3 (Thomas *et al.* 2006). We wrote our own R 2.7.2 code (R Development Core Team 2008) for running the simulations.

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See main article for references.

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Appendix Table S1. Summaries of estimates of parameters of Bayesian models for probability of tree fall, and for relative *N. pennata* abundance growth for three simulated scenarios (S1-S3). Modes and 95% confidence interval limits are shown. The same growth model was used in S2 and S3. Values of mean initial abundance used, $\overline{\log(A_{t-1})}$, are also shown.

Scenario	Tree fall (eqn S1-1)			Relative abundance growth (eqn S1-4)			
	β_0	β_1	β_2	τ_G	γ_0	γ_1	$\overline{\log(A_{t-1})}$
S1	0.66 (-1.99, 4.28)	-0.21 (-0.48, -0.04)		0.17 (0.12, 0.24)	0.16 (0.08,0.24)	-0.05 (-0.09, -0.01)	3.53
S2*	-1.66 (-3.73, 0.24)	0.14 (-0.04, 0.34)	-0.004 (-0.010, -0.0006)	0.14 (0.12, 0.15)	0.12 (0.09, 0.14)	-0.03 (-0.04, -0.02)	4.50
S3*,†	-4.11 (-6.94, -1.45)	0.34 (0.08, 0.59)	-0.008 (-0.014,-0.003)	0.14 (0.12, 0.15)	0.12 (0.09, 0.14)	-0.03 (-0.04, -0.02)	4.50

* The tree fall model also included dbh^2 with associated parameter β_2.

† The tree fall model was based on data collected 2006-2008, therefore $F_i^* = 1-(1-F_i)^{1/2}$ (see eqn S1-1).

Appendix S2. Model for relative growth of *Neckera pennata* on occupied trees

This model, in contrast to the models in Appendix S1, is based on the whole dataset including trees at all distances to edge. The relative change in abundance per year on an occupied tree *i* followed a Normal distribution with mean $\mu_{i,t}$ and standard deviation σ_G.

$$\mu_{i,t} = \gamma_0 + \gamma_1 (\log(A_{i,t-1}) - \overline{\log(A_{t-1})}) / \mathrm{sd}(\log(A_{t-1})) + \gamma_2 (\log(Dist_i+0.1) - \overline{\log(\mathrm{Dist}+0.1)}) / \mathrm{sd}(\log(Dist_i+0.1))$$

where $A_{i,t-1}$ is the abundance on tree *i* at the beginning of the time period and $Dist_i$ is its distance from the edge. $\overline{\log(A_{t-1})} = 4.34$; $\mathrm{sd}(\log(A_{t-1}) = 2.26$; $\overline{\log(\mathrm{Dist}+0.1)} = 3.97$; $\mathrm{sd}(\log(Dist_i+0.1)) = 1.11$.

Parameter estimates:

	Mode	**Lower limit of 95% confidence interval**	**Upper limit of 95% confidence interval**
γ_0	0.127	0.104	0.149
γ_1	-0.069	-0.092	-0.046
γ_2	0.054	0.032	0.077
σ_G	0.132	0.116	0.148
Deviance	-163.4	-165.3	-155.6

Appendix S3. Model for the probability of fall of *Neckera pennata* host trees

This model, in contrast to the models in Appendix S1, is based on the whole dataset including trees at all distances to edge. The probability of fall of tree *i* (F_i) was assumed to follow a Bernoulli distribution. More specifically,

$$F_i \sim \mathrm{dbern}(\mu_\mathrm{i}),$$

where

$$\mathrm{logit}(\mu_\mathrm{i}) = \beta_0 + \beta_1 Dist_\mathrm{i} + \beta_2 dbh_\mathrm{i} + \beta_3 dbh^2_\mathrm{i} + \beta_4 Dist_\mathrm{i} dbh_\mathrm{i},$$

where $Dist_\mathrm{i}$ is the distance from tree *i* from the edge, and dbh_i is its diameter at breast height.

Parameter estimates:

	Mode	**Lower limit of 95% confidence interval**	**Upper limit of 95% confidence interval**
β_0	-0.878	-3.23	1.545
β_1	1.11e-02	7.22e-03	3.11e-02
β_2	1.78e-01	-2.98e-02	0.374
β_3	-4.36e-03	-8.67e-03	-4.57e-04
β_4	-1.62e-03	-2.78e-03	-5.86e-04
Deviance	561.6	558.4	569.3