

Contrasting long-term effects of transient anthropogenic edges and forest fragment size on generalist and specialist deadwood-dwelling fungi

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Summary

1. Forests are becoming increasingly fragmented world-wide, creating forest patches with reduced area and greater exposure to human land uses along fragment edges. In this study, we predict the future impacts of anthropogenic edges and fragment size on the future occupancy of deadwood-dwelling fungi in boreal old-growth forest fragments.
2. We used Bayesian models fitted to empirical data to predict 40 years of occupancy dynamics of logs by a group of old-growth forest indicator fungi and two common fungi under different scenarios of clear-cutting in adjacent forest (0%, 25%, 50% and 100%) and fragment sizes (1–20 ha).
3. Small fragment size (1–3.14 ha) and intensified forestry with 50–100% clear-cutting of forest around old-growth forest fragments lead to lower predicted occupancy of old-growth indicator fungi while common generalist species like *Fomitopsis pinicola* increased.
4. There was a trade-off between fragment size and management, where increasing fragment size buffered the negative long-term effects from increased adjacent clear-cutting. These changes in fungal occupancy at the edge should be accounted for when working towards conservation targets for protected areas, such as the Aichi target 11.
5. *Synthesis and applications.* Preserve what is left – but buffer for change. Small forest fragments often represent the last vestiges of high habitat quality (i.e. species, structures) in managed forest landscapes. As effective area-based conservation measures for the long-term occupancy of old-growth fungi, small fragments need to be managed to protect species from degrading transient edge effects. Management should focus on increasing the size of conservation areas with permanent buffer zones. Alternatively, non-simultaneous adjacent clear-cutting in a way that reduces the edge effect over time (i.e. dynamic buffers) may increase the effective area and improve performance of set-asides in protecting species of special concern for conservation.

Key-words: boreal forests, common and indicator species, core : edge ratio, deadwood, edge effect, fragment size, projection scenarios, protected areas, set-asides

Introduction

Setting aside land as protected areas has been the foundation of global efforts to conserve biodiversity (Rodrigues *et al.* 2004). In the light of the proposed Aichi biodiversity target 11 to protect '17% of terrestrial areas of particular importance for biodiversity and ecosystem services' (CBD 2010), additional area-based conservation measures are needed to fulfil this target (Butchart *et al.* 2015). In regions

with a long forest management history, the effort is often focused on preserving the last vestiges of small and isolated old-growth forest fragments independent of their current area (Gascon, Williamson & da Fonseca 2000). For example, old-growth forests currently represent <2% of European forests, excluding Russia (Parviainen *et al.* 2000). Degrading the effects of fragmentation are typically most influential in small and isolated forest remnants (Laurance & Yensen 1991; Magura, Tóthmérész & Molnár 2001; Berglund & Jonsson 2008; Ruete, Snäll & Jönsson 2016), and these effects magnify with the passage of time (Haddad

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et al. 2015). A recent review suggests that anthropogenic edges do not have as strong, extensive or persistent influence on vegetation in boreal ecosystems, as in tropical or temperate forest ecosystems (Harper *et al.* 2015). Nevertheless, notable differences between forest structure and the response of several organism groups (Harper *et al.* 2015) to natural and anthropogenic edges raise concerns about biodiversity implications of extensive creation of anthropogenic edges. For example, it is unclear if small protected areas and other set-asides that are heavily affected by edges can sustain forest-dwelling species over time (Gascon, Williamson & da Fonseca 2000; Timonen *et al.* 2011). Half-way towards the 2020 Aichi Targets, a key question is whether very small forest fragments (typically about 1–3 ha) should be included as ‘effective area-based conservation measures’ in target 11? If so, how can they be effectively managed to sustain species over time?

Since conservation areas are typically embedded in a matrix of productive forest, the fragment size and shape determine the core area of effective forest-interior conditions (Laurance & Yensen 1991). Therefore, in a landscape where the norm is small remnants of old-growth forest, edge effects play a critical role in determining what proportion of the fragment retains forest-interior conditions (Aune, Jonsson & Moen 2005). Species show varying responses to edges (e.g., positive, negative and neutral responses) depending on edge-to-interior gradients of resources and microclimatic conditions (Ries & Sisk 2004; Ries *et al.* 2004; Ewers & Didham 2006; Laurance *et al.* 2011). For many sessile forest species, edge influence may be even more detrimental than the effects of habitat loss and isolation (Moen & Jonsson 2003). Declines in abundance of old-growth forests species due to changes in substrate quality and exposure in close proximity to younger clear-cut edges can be expected (Stokland & Kausrud 2004; Ruete, Snäll & Jönsson 2016). At the same time, edge effects can result in an influx of generalist species or species adapted to specific conditions found at the interface between two environments (Duelli *et al.* 1990; Magura, Tóthmérész & Molnár 2001; Laurance *et al.* 2011; Ruete, Snäll & Jönsson 2016). Hence, as the fragment core : edge ratio declines with decreasing fragment size, the ratio of generalist to specialist species is likely to increase (Humphreys & Kitchener 1982; Magura, Tóthmérész & Molnár 2001; Matthews, Cottee-Jones & Whittaker 2014). Therefore, the ‘preserve what is left’ policy leaves open the question if edge effects will prevent small forest areas from functioning as refuges for forest-interior specialist species (Aune, Jonsson & Moen 2005; Rybicki & Hanski 2013). A recent systematic review highlighted that evidence remains limited concerning the management regimes under which protected areas succeed or fail to deliver conservation outcomes (Geldmann *et al.* 2013). In the light of edge-effect theory, the implementation of buffer zones as a standard practice around fragments has been strongly recommended (Laurance & Yensen 1991), assuming that they are completely surrounded by hard edges (i.e. clear-cuts in the case

of forests). However, this is often not the case. In the Swedish boreal forest, it is estimated that 20–25% of the perimeter of any random old-growth forest fragment is adjacent to a recent clear-cut (<20 years) or a mature stand subjected to imminent clear-cut (>90 and ≤110 years), given typical forest stand sizes and current forest rotation times (Reese *et al.* 2003). Hence, management strategies aiming to mitigate edge effects needs to be based on a varied set of edge conditions, which should also be transient in time and dependent on fragment size. Forecast studies of ecological dynamics are increasingly important tools for identifying effective conservation strategies (Mouquet *et al.* 2015). However, there are no simulation studies investigating the future, possibly transient, characteristics of edge effects under different management scenarios. Such simulations could help identify levels of anthropogenic edge creation around small old-growth forest fragments that would not jeopardize future biodiversity values.

Deadwood-dwelling fungi are ubiquitous and functionally important organisms within forest ecosystems worldwide, but with a substantial fraction of species red-listed due to old-growth forest habitat loss and isolation (e.g. ArtDatabanken 2015). Generalist and specialist wood fungi are known to respond differently to old-growth forest amount and isolation (Nordén *et al.* 2013), but little is known about their response to edge effects (Snäll & Jonsson 2001; Junninen & Komonen 2011; Crockatt 2012; Abrego & Salcedo 2014; Ruete, Snäll & Jönsson 2016). However, through a recent study we do know that anthropogenic edges create transient edge-to-interior gradients that at least temporally (within a time window of 40 years) reduces the occupancy of indicator fungi while increasing the occupancy of common fungi (Ruete, Snäll & Jönsson 2016). These new insights on the spatio-temporal role of edges on deadwood-dwelling fungi allowed us to parameterize models for the dynamic impact of anthropogenic edges surrounding forest fragments of different sizes on the number and occupancy of logs by fungi, at time-scales relevant from a forest management perspective.

We aim to determine if forest fragments 1–20 ha in size set aside for conservation can sustain deadwood-dwelling fungi under current forest management policies. We project the long-term (40 years) future occupancy dynamics of logs by a group of old-growth indicator species and two common species, using simulations fitted to empirical data (Ruete, Snäll & Jönsson 2016). The empirical data on fungal occurrence and deadwood dynamics were obtained through a transect-based re-inventory of 31 old-growth forest stands dominated by Norway spruce (*Picea abies*). We ran 16 scenarios combining four sizes of old-growth forest fragment under 4% of the fragment’s perimeter that is adjacent to clear-cuts. This allowed us to quantify how the future deadwood availability and occupancy of logs by deadwood-dwelling fungi may be influenced by fragment size and edge creation as two intertwined factors. We hypothesize that trade-offs between size and edge creation may influence the future occupancy levels of the focal

species. Spatially explicit projections of fungal occupancy of logs allowed us to better understand the long-term effectiveness of small area-based conservation measures within a managed and fragmented boreal forest landscape.

Materials and methods

THE STUDY REALM

The study realm covers forests in the middle and south boreal regions (*sensu* Ahti, Hämet-Ahti & Jalas 1968) in central Sweden. The forest landscape in the region is strongly influenced by modern forestry and characterized by even-aged monocultures of conifers, few old trees, and low amounts of deadwood. Old-growth forest remnants are typically few and small, occurring isolated in a matrix of managed forests and representing only a few percent of the landscape. About 87 000 small (median size 1.4 ha) and isolated 'woodland key habitats' (WKHs) have been identified and set aside from forest management in Sweden because of their high conservation values and potential to host and mitigate the decline of nationally red-listed forest-dwelling species (Timonen *et al.* 2011). We applied recently published models of occupancy probability of logs by deadwood-dwelling fungi derived from re-inventories of boreal old-growth forest fragments dominated by Norway spruce (*P. abies*) (Ruete, Snäll & Jönsson 2016; further details of the model below).

MODELS TO SIMULATE LOGS AND FUNGAL OCCUPANCY DYNAMICS

The models in Ruete, Snäll & Jönsson (2016) predict the occupancy probability of 12 deadwood-dwelling fungal species (Table 1) in old-growth forest fragments in relation to distance from clear-cut forest edges and natural edges (e.g., mires, lakes). The species grow chiefly on Norway spruce logs and the models applied predict the dynamics of logs in relation to edges. Two species (*Fomitopsis pinicola* and *Trichaptum abietinum*) are non-fragmentation-sensitive and generalist species in terms of deadwood substrate resource and forest type (Nordén *et al.* 2013), common in the managed forest landscape, and have a large influence on spruce deadwood dynamics (Ottosson *et al.* 2014). The remaining 10 are indicator species for high nature conservation values such as long-term continuity of deadwood and high naturalness (Nitare 2000; Niemelä 2005). They are highly fragmentation-sensitive and generally specialized on natural logs, large-diameter dead trees, a particular tree species (spruce or pine) and stage of decay, and mainly occur in closed forests (Nordén *et al.* 2013). We studied indicator species as a group because there is no single deadwood-dwelling fungal species that alone would be a good indicator for all deadwood-dwelling fungi (Halme *et al.* 2009; Junninen & Komonen 2011) and because their individual frequencies were generally too low to model them individually. In the analysis, we refer to the species as indicator species, *F. pinicola* and *T. abietinum*. Focusing our inventory on species with relatively large and long-lived fruit bodies, we minimized sampling bias in mycelia presence and temporal fruiting patterns. Molecular studies have shown that such species with high mycelia abundance typically also have a high fruiting rate (Ovaskainen *et al.* 2013) and low temporal bias in fruiting (e.g. Abrego *et al.* 2016).

To simulate the impact of anthropogenic edges on old-growth forest substrate availability and species occupancy over space and

Table 1. Key ecological characteristics of the studied indicator and common species. Red-list status according to Artdatabanken (2015)

Scientific name	Red-list status	Rot type	Fruiting body life span
<i>Asterodon ferruginosus</i>	NT	White	Annual
<i>Climacocystis borealis</i>	LC	White	Annual
<i>Cystostereum murrayi</i>	NT	White	Perennial
<i>Fomitopsis pinicola</i> *	LC	Brown	Perennial
<i>Fomitopsis rosea</i>	NT	Brown	Perennial
<i>Leptoporus mollis</i>	NT	Brown	Annual
<i>Phellinus chrysoloma</i>	NT	White	Perennial
<i>Phellinus ferrugineofuscus</i>	NT	White	Perennial
<i>Phellinus nigrolimitatus</i>	NT	White	Perennial
<i>Phellinus viticola</i>	LC	White	Perennial
<i>Trichaptum abietinum</i> *	LC	White	Perennial
<i>Trichaptum laricinum</i>	NT	White	Perennial

*Common species. Else, indicator species following Nitare (2000).

time, we used Bayesian hierarchical generalized linear models accounting for the spatio-temporal effect of different edge types and edge ages (Ruete, Snäll & Jönsson 2016). The original models were parameterized using data from 1381 transect segments of 140 m² (hereafter referred to as sample units) from 31 boreal old-growth forest fragments in central Sweden (Table S1, Supporting Information). A first set of models estimated the effect of edges on the number of logs per sample unit and the change in number of logs per sample unit between decades. These models show a transient increment in the number of fallen trees close to young clear-cut edges. However, the rate of change in the number of logs after a decade was not affected by distance to the edge but by the initial number of logs, as well as their volume and decay class. Another set of models estimated the effect of distance to edge, edge type (i.e. clear-cut vs. natural), and edge age on the occupancy of logs by indicator and common species, accounting for variation in the number of logs per sample unit. The probability of an indicator and common species occurring on a log in a particular sample unit (i.e. log occupancy) was based on binary presence-absence data and the number of logs per sample unit, assuming a Binomial distribution. These models captured contrasting responses to clear-cut edges by indicator and common species. Indicator species were negatively affected by proximity to young clear-cut edges, while common species were positively affected (*F. pinicola*) or unaffected (*T. abietinum*). Anthropogenic edge effects were transient for indicator species (reduced over time), but time-independent for the common species. The among-fragment variability and the change over time in fragment-level mean log occupancy were retained in the models used for simulations although no clear change was detected over a decade, i.e. the fungal populations seemed to be stable. See Appendix S1 and Ruete, Snäll & Jönsson (2016) for detailed descriptions of the model.

FRAGMENT SIZES AND MANAGEMENT SCENARIOS SIMULATED

Spatially explicit simulations were run on 140 m² hexagonal grid cells (i.e. the same area as the surveyed sample units) covering the closest approximation to circular forest stands (Fig. 1) of

sizes 1, 3.14, 10 and 20 ha (i.e. 56, 100, 178 and 252 m in radius, respectively). Selected stand sizes represent a range of potential old-growth forest stands found in the landscape, specifically including stands with radius equal to the maximum depth of edge influence (DEI = 100 m) assumed in the model fitting process (Ruete, Snäll & Jönsson 2016). Initial conditions for the number and quality of logs and logs occupancy by fungi within grid cells followed the probability distributions estimated for the forest interior in Ruete, Snäll & Jönsson (2016). Subsequent inter-decadal dynamics also followed the dynamics estimated for the forest interior, unless the grid cell centroids were within the maximum DEI of 100 m (Fig. 1) where the fitted distance-to-edge models were used. The simulated number of logs per cell excludes further log inputs than those predicted after the edge creation and applies the rate of deadwood decomposition observed in the field. These are reasonable assumptions based on the knowledge that it is during the initial exposure of surrounding clear-cutting that the majority of old-growth Norway spruce trees are killed (e.g. Jönsson *et al.* 2007). Simulations were run for five time steps at decadal intervals (i.e. 0, 10, 20, 30 and 40 years), allowing sufficient time for forest re-growth in adjacent clear-cuts. Forty years is also the average log decomposition time in central Sweden (Kruys, Jonsson & Ståhl 2002). Four realistic scenarios of adjacent forest management were used:

1 Reference: 0% of the surrounding forest is clear-cut; i.e. all cells in the forest stand are simulated as forest interior.

2 Current: 25% of the surrounding forest is clear-cut at $t = 0$. This scenario represents the estimated edge proportion of any random old-growth forest fragment adjacent to a clear-cut, given current forest rotation times and forest stand sizes in the study region. We inferred from data published by the Swedish National Forest Inventory (Reese *et al.* 2003) that 25% of all forest stands

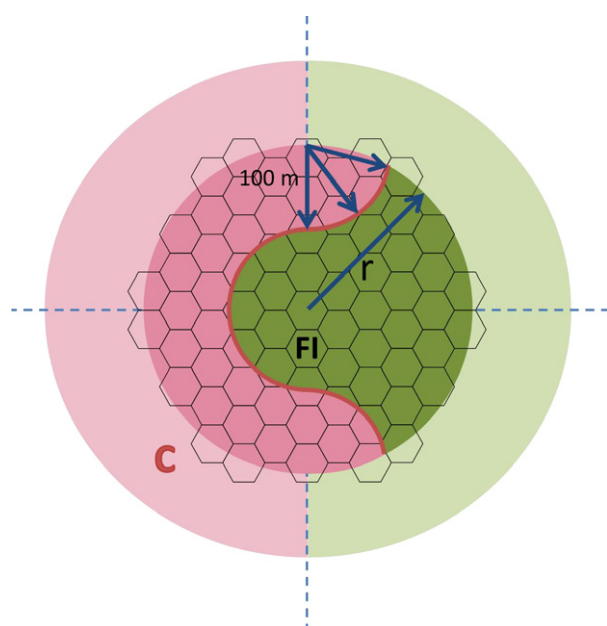


Fig. 1. Schematic representation of the spatially explicit simulation setup of edge effects on forest fragments. r , radius; FI, forest interior; C, clear-cut. Each hexagonal cell is a study unit of 140 m² (out of scale). Edge habitat models were applied for pink hexagons, and forest-interior models were applied for green hexagons.

in the study region have recently been clear-cut (<20 years) or may imminently be clear-cut (>90 and ≤110 years). The edge was simulated as a single continuous section of the stands' perimeter.

3 Intensive: 50% of the surrounding forest is clear-cut at $t = 0$. This scenario represents an hypothetical situation where rotation times are significantly shortened, which is possible given current trends towards more intensive forestry and increased extraction of forest biomass in the future (Strengbom *et al.* 2011). The edge was simulated as a single continuous section of the stands' perimeter.

4 Extreme: 100% of the surrounding forest is clear-cut at $t = 0$. This scenario represents an extreme case that can happen in particular locations.

Simulations were run in R 3.1 (R Development Core Team 2014). For each combination of forest stand sizes and forestry scenarios, we ran 10 000 simulation replicates each using a particular set of parameters from the full parameter posterior distributions (Ruete, Snäll & Jönsson 2016). In this way, we obtained a probability distribution for the response variable for each sample unit (i.e. hexagonal grid cell; Fig. S1).

Results

EDGE EFFECTS AND FOREST FRAGMENT SIZE

In fragments smaller than 3.14 ha (≤100 m radius), more than 60% of the area was influenced by the edge when 25% of the fragment's edge was adjacent to a clear-cut (Table S2). Extreme deadwood inputs occurred on cells closer to clear-cut edges within the first decade after clear-cutting (Fig. 2). Log numbers were highest in small fragments and decreased over time (Fig. 3a). There were clear opposite spatial edge-to-interior gradients between the log occupancy probabilities by indicator species and by *F. pinicola* (Fig. 2). The occupancy probability of indicator species was negatively affected by decreasing distance from the edge, while the opposite pattern was projected for *F. pinicola*. The species *T. abietinum* was unaffected by distance from the edge, but there was a marginal difference in mean occupancy levels between the edge habitat (i.e. forest within 100 m from the edge) and the forest interior (i.e. forest beyond 100 m from the edge) (Fig. 2).

The mean occupancy of logs by indicator species was higher in large fragments and was projected to increase marginally or remain stable in the future (Fig. 3b). The mean occupancy of logs by *F. pinicola* was initially lower in larger fragments, but was projected to increase to levels similar to smaller fragments over time (Fig. 3c). The mean occupancy of logs by *T. abietinum* was lower in larger fragments and decreased marginally over time (Fig. 3d). These trends in the reference scenario (0% clear-cut scenario and only forest-interior conditions) show the projected decadal change in mean stand occupancy estimated with the original model assuming forest-interior conditions (Fig. 3). Differences from this reference scenario (Fig. 4 showing differences compared to the reference scenario, over time) were driven by the transient character of

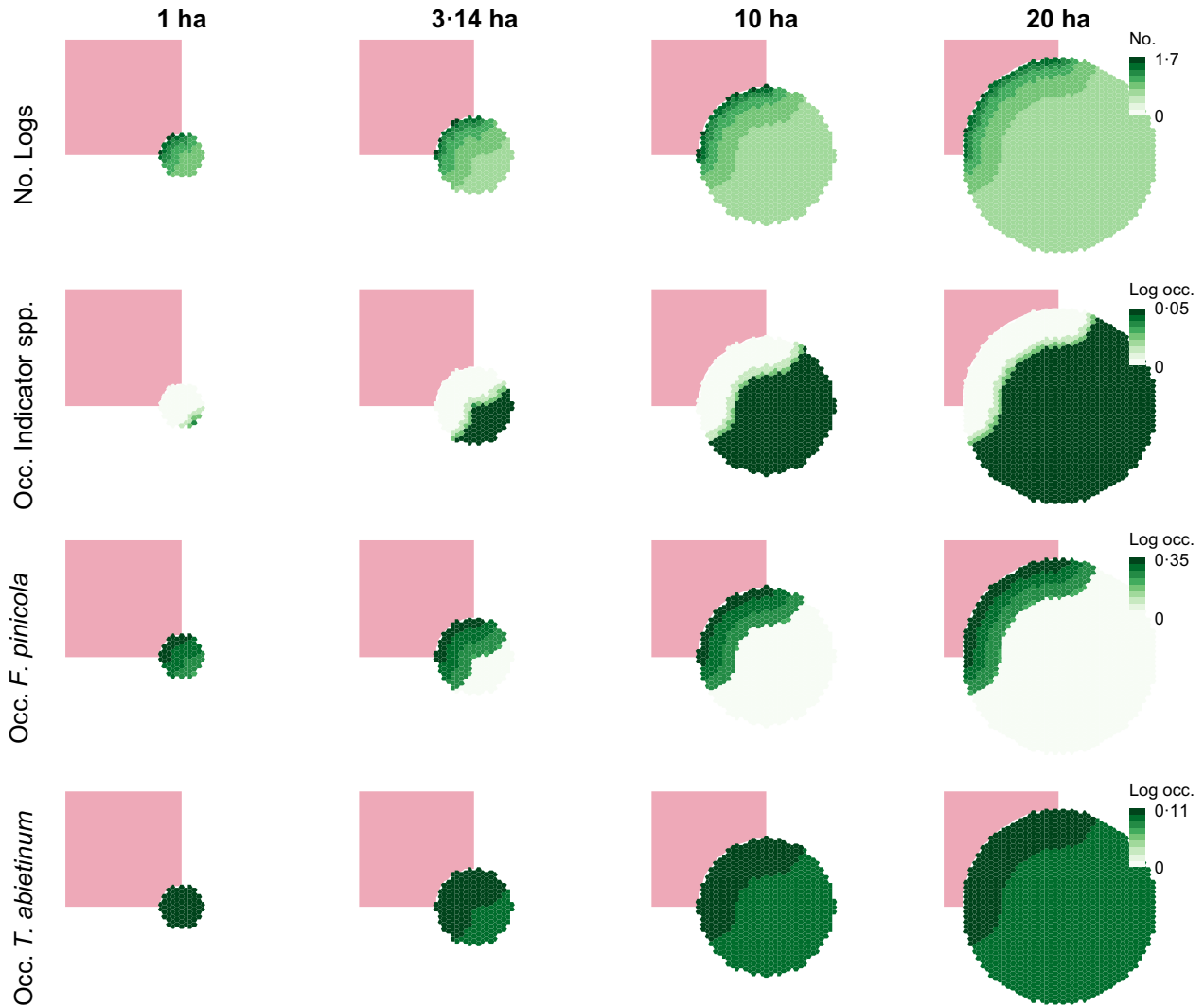


Fig. 2. Starting conditions predicted by models at $t < 10$ years under current forestry management conditions; that is 25% of the forest fragment edge adjacent to a clear-cut (pink square). The colour scale of each cell (140 m^2 sample units) shows the median value of the posterior distribution of the number of logs (no. logs) or occupancy of logs (Occ.) by indicator species, *Fomitopsis pinicola* and *Trichaptum abietinum*.

the edge effect and the implicit forest regrowth on the adjacent clear-cut. The future number of logs (Fig. 4a) and occupancy of logs by common species (Fig. 4c,d) tend to converge to the reference scenario after 40 years of exposure in both large and small fragments (note varying scales on Fig. 4). The exceptions were indicator species, for which occupancy of logs will decrease due to exposure to anthropogenic edges. While occupancy levels are stable in the future for the largest forest fragments, they continue decreasing in smaller forest fragments (Fig. 4b).

EDGE EFFECTS AND FOREST MANAGEMENT SCENARIOS

Mean log numbers was higher in fragments exposed to a greater proportion of adjacent clear-cutting (Fig. 3a), but

was projected to converge to the reference scenario after 40 years (Fig. 4a). The mean occupancy of logs by indicator species was higher in management scenarios with lower proportions of adjacent clear-cutting and was projected to increase marginally or remain stable over time (Fig. 3b). The mean occupancy of logs by *F. pinicola* was initially lower under reference and current scenarios, but increased to levels similar to intensive and extreme scenarios over time (Fig. 3c). The mean occupancy of logs by *T. abietinum* was lower in scenarios with less adjacent clear-cutting, and decreased marginally over time (Fig. 3d). Projections of the occupancy of logs by common species tend to converge to the reference scenario after 40 years of exposure under all management scenarios (Fig. 4c,d). In contrast, the future mean occupancy of logs by indicator species was projected to remain lower than the reference levels under any management scenario (Fig. 4b).

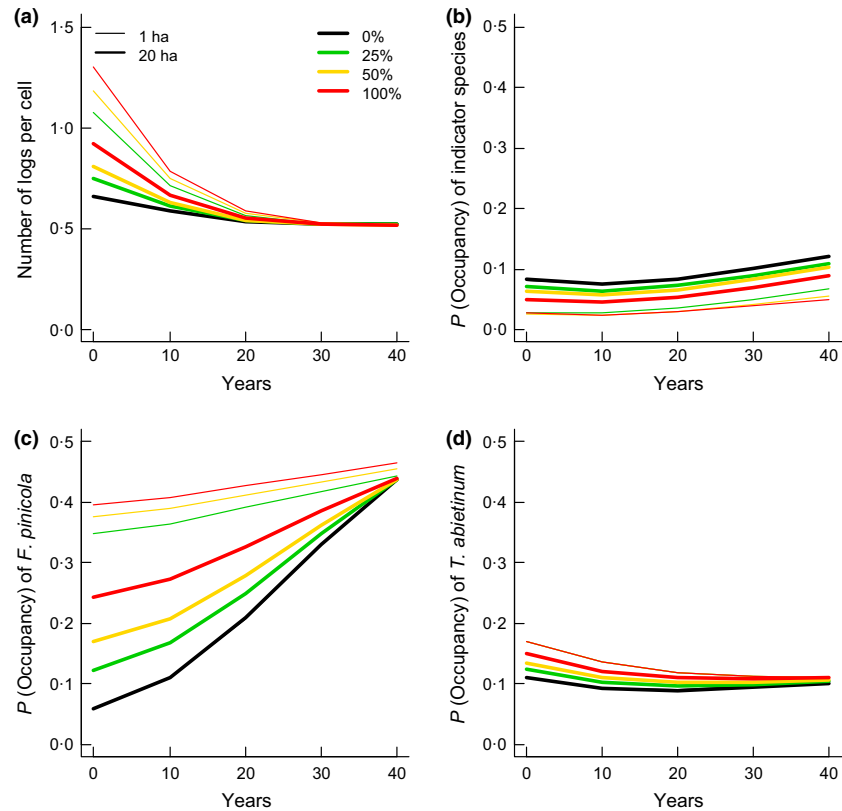


Fig. 3. Projections of the future mean values for (a) the number of logs per cell and occupancy probability of logs by (b) indicator species, (c) *Fomitopsis pinicola* and (d) *Trichaptum abietinum* in cells of old-growth forest fragments over time. Projections are shown only for the smallest and largest forest fragment sizes. Line colours indicate management scenarios, where 0% is the reference (forest interior) scenario with no adjacent clear-cut, 25% is the current scenario with a quarter of the surrounding forest clear-cut, 50% is the intensive scenario with half of the surrounding forest clear-cut and 100% is the extreme scenario with all of the surrounding forest clear-cut. Note the varying scale between the panels. (d) The lines for the smallest forest fragments (25–100% clear-cutting) overlap.

TRADE-OFFS BETWEEN FOREST FRAGMENT SIZE AND MANAGEMENT SCENARIOS

Especially for indicator species, both fragment size and the extent of clear-cutting in the adjacent forest were important to sustain future stable occupancy levels. Figure 5 illustrates the trade-off effects between all fragment sizes and management scenarios, compared to the reference scenario, at two time points ($t < 10$ years; $t = 40$ years). We found largest departures from the reference scenario under the intensive and extreme management scenarios (i.e. 50% and 100% clear-cut), although the differences between management regimes were lower in the smallest 1 ha forest fragment (Fig. 5b). The increase in number of logs and in occupancy of logs by common species after adjacent clear-cutting was transient and independent of the fragment size or management regime (Fig. 5a,c,d). However, the negative edge effects observed for the occupancy of indicator species seem to range from almost stable to declining in the future for the two smallest fragments with more than 50% of its perimeter facing clear-cuts (Fig. 5b).

An interesting result was that all species groups had similar future occupancy levels in 100-m-radius fragments (3.14 ha) with a quarter of its perimeter exposed to clear-cuts as in 252-m-radius fragments (20 ha) with its entire perimeter exposed to clear-cuts (Fig. 5b–d). Hence, the forest fragment size was a major variable in regulating the future impact of the different forest management scenarios.

Discussion

Understanding the future responses of species to fragmentation and edge creation is essential when developing and implementing cost-effective management actions to mitigate further species losses. This study is the first projection that investigates the dynamic edge effects of different forest fragment sizes and clear-cutting management scenarios on the future occupancy of logs by deadwood-dwelling fungi.

Our results showed that the effectiveness of area-based conservation strategies, such as WKHs, depend on both fragment size and the management of the surrounding productive forest. We projected that future intensified forestry with extensive creation of anthropogenic edges around old-growth forest fragments will lead to declining occupancy of old-growth specialist deadwood-dwelling fungi while some common generalist species such as *F. pinicola* may increase. Two important results were derived. First, as expected, larger forest fragments were more resistant to negative impacts on occupancy levels of indicator species in the future. In the smallest 1-ha fragments, occupancy levels of indicator species, relative to the reference scenario, were projected to continue to decline in the future. Relative occupancy levels in fragments ≥ 3.14 ha, however, were projected to remain stable in the future at levels below the reference scenario (interior forest conditions), at least under current and intensive management scenarios. Occupancy levels of the common species *F. pinicola* were instead lower in larger fragments, but were projected to increase in the future. Second, even in larger fragments (up to 20 ha) with

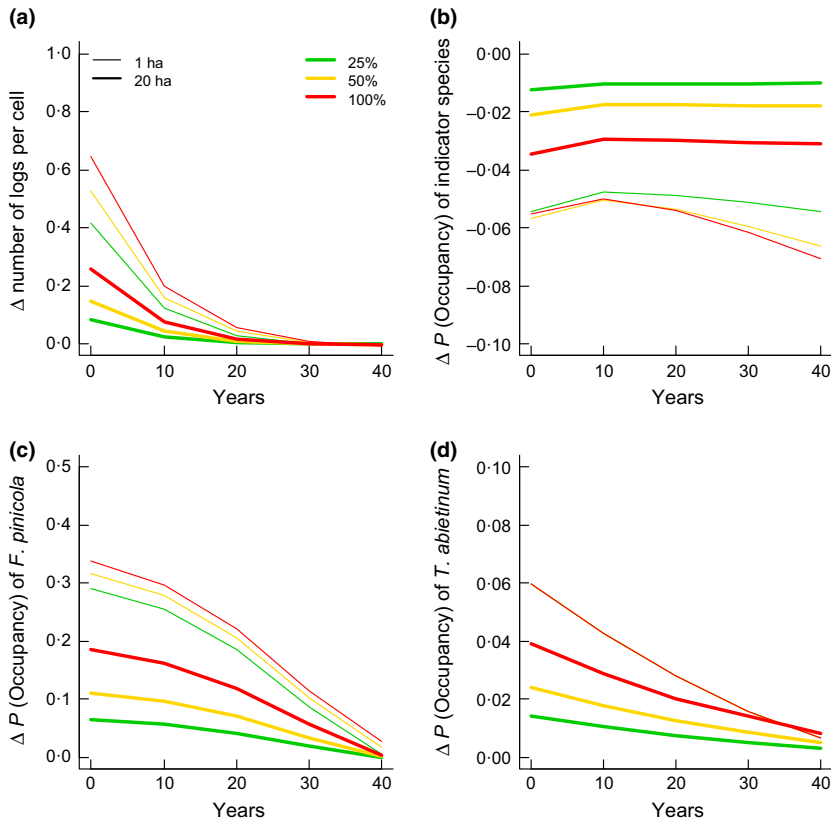


Fig. 4. Projections of the differences in future mean values for (a) the number of logs per cell and occupancy of logs by (b) indicator species (note negative scale), (c) *Fomitopsis pinicola* and (d) *Trichaptum abietinum* in cells of old-growth forest fragments over time compared to the projected levels for the reference scenario (i.e. 0% clear-cut). Projections are shown only for the smallest and largest forest fragment sizes. Line colours indicate management scenarios, where 0% is the reference (forest interior) scenario with no adjacent clear-cut, 25% is the current scenario with a quarter of the surrounding forest clear-cut, 50% is the intensive scenario with half of the surrounding forest clear-cut and 100% is the extreme scenario with all of the surrounding forest clear-cut. Note the varying scale between the panels. In (d), the lines for the smallest forest fragments (25–100% clear-cutting) overlap.

a substantial interior core area, intensive clear-cutting (50–100%) around the fragment would compromise the long-term persistence of old-growth forest indicator species. There are some precautionary principles to be aware of when applying our results to particular forest management cases. These simulations are optimistic because they handle only the optimal stand shape (i.e. a circle having the lowest possible shape index). Increased shape index will certainly reduce the core : edge ratio, significantly reducing the area with forest-interior conditions (Fig. S2; Laurance & Yensen 1991; Aune, Jonsson & Moen 2005). We may also underestimate the impact of adjacent suboptimal older productive forest. We assume that adjacent forests that are not clear-cut are forest interior, while the most likely situation is that these forests are dominated by middle-aged to mature productive forest. Climate change effects are likely to become more influential in the future, possibly also influencing future fungal responses at the forest edge. There is evidence for changes in fungal fruiting patterns over time with changing climate for some fungal groups (e.g. Kauserud *et al.* 2010), but for deadwood-dwelling species with a northern geographical distribution, knowledge is lacking. Therefore, while the forecast of fungal responses under climate change is in its infancy, we cannot wait for it to develop in order to simulate and manage nature the best way we can given current knowledge (Urban *et al.* 2016).

In agreement with our simulations of future fungal occupancy, declines in the occurrence of old-growth indicator species have been shown to take place already in a few decades in small (generally <10 ha) forest fragments

(Berglund & Jonsson 2005, 2008), but more evident after c. 50 or more years (Gu, Heikkilä & Hanski 2002; Sverdrup-Thygeson & Lindenmayer 2003; Paltto *et al.* 2006; Penttilä *et al.* 2006; Ranius *et al.* 2008). Increasing occupancy of common species such as *F. pinicola* in edge environments of small conservation areas has not been reported earlier. Between the two common generalist species, the stronger buffering potential of *F. pinicola* against clear-cut edges and microclimatic changes compared to *T. abietinum* could be a result of the former species larger and more long-lived fruit bodies and mycelia. Also, the mycelia of *F. pinicola* occur in the heartwood, whereas the mycelia of *T. abietinum* concentrate in the sapwood and may thus be more affected by drying and microclimatic conditions at the edge (Ryvarden & Melo 2014). However, the overall role of different ecological traits in regulating fungal responses to forest edge environments needs further research. One recent forest management simulation study incorporated snapshot occupancy data of deadwood-dwelling fungi to project the future polypore diversity based on deadwood dynamics in managed and natural Norway spruce forests (Peltoniemi, Penttilä & Mäkipää 2013). They projected that increased deadwood stocks and qualities were required to elevate fungal diversity of spruce stands to levels in natural-like stands. They also concluded that managed forests are unlikely to reach the deadwood volumes and naturalness needed to conserve many old-growth specialist fungi, and for these species, a functional network of forest conservation areas seems to be the best way to ensure viable populations.

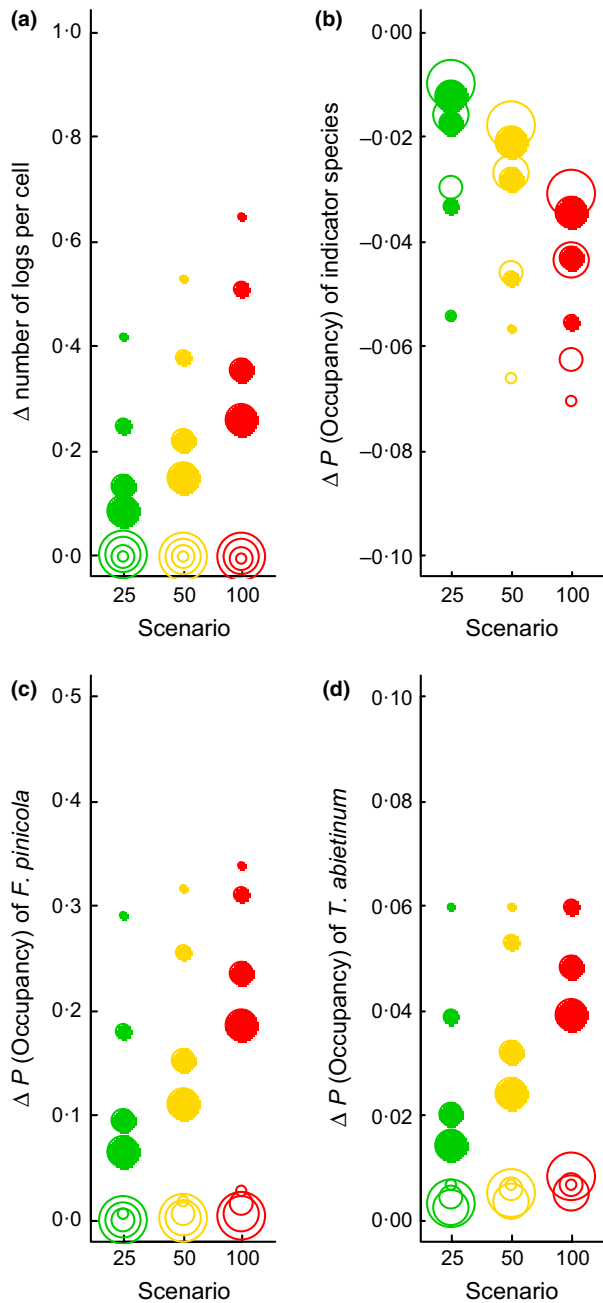


Fig. 5. Projections of the differences in future mean values for (a) the number of logs per cell and occupancy of logs by (b) indicator species (note negative scale), (c) *Fomitopsis pinicola* and (d) *Trichaptum abietinum* in cells of old-growth forest fragments at two time points $t < 10$ (filled circles) and at $t = 40$ years (empty circles) compared to the projected levels for the reference scenario (0% clear-cut). Circle size represents forest fragment size (i.e. 1, 3–14, 10 and 20 ha). Colours of circles and the x-axis indicate management scenarios, where green is the current scenario with a quarter of the surrounding forest clear-cut, yellow is the intensive scenario with half of the surrounding forest clear-cut, and red is the extreme scenario with all of the surrounding forest clear-cut. Note the varying scale between the panels.

Our study highlights that transient anthropogenic edge effects and fragment size need to be considered if conservation areas within such a network are to be functional

for the future conservation of fungi. Simulation studies that examine how area and edge effects influence local biodiversity in the future are relatively few (but see Ries & Sisk 2004; Didham & Ewers 2012), especially for lesser studied organisms like sessile cryptogams (but see Roberge *et al.* 2011; Fedrowitz, Kuusinen & Snäll 2012). For wood fungi, we do know that edge effect is one of the variables explaining lower occupancies in small fragments (Snäll & Jonsson 2001; Siitonen, Lehtinen & Siitonen 2005; Abrego & Salcedo 2014). Our study extends this knowledge by showing that smaller fragments with lower occupancy levels of indicator fungi are also more likely to experience declining populations in the future and that such declines will be dependent on the extent of the adjacent clear-cut creation. These future declines are partly linked to the altered substrate dynamics in the edge environment (Söderström 1988; Snäll, Ribeiro & Rydin 2003; Roberge *et al.* 2011; Ruete, Snäll & Jönsson 2016), but may also be linked to altered microclimate conditions.

The contrasting future development between forest-interior specialists and common fungi is likely explained by the specialists' greater vulnerability to changes in forest stand characteristics, effects of logging and habitat fragmentation (e.g. Junninen & Komonen 2011; Stokland, Siitonen & Jonsson 2012; Nordén *et al.* 2013). A high temporal variability in the occupancy of logs even in core areas suggests that indicator species are particularly vulnerable to future environmental and demographic stochasticity (Boyce, Haridas & Lee 2006; Ruete, Wiklund & Snäll 2012; Shriver, Cutler & Doak 2012). The future increased occupancy of common fungi is likely also due to commonly altered forest landscapes dominated by man-made deadwood substrate types (Nordén *et al.* 2013; Komonen *et al.* 2014). These substrate types favour common species such as *F. pinicola*, whose increased establishment, fruiting and spore deposition (i.e. a so-called bulk effect) may disfavour interior specialist species (Nordén *et al.* 2013).

PRESERVE WHAT IS LEFT, BUT BUFFER FOR CHANGES

The trade-off between fragment size and the extent of anthropogenic edge creation has clear implications for forest management policies and actions. Forest fragment size was a major variable regulating the future impact of adjacent forest management. The larger the forest fragment, the more room for achieving positive management results and for trade-offs in each particular case. For example, the same future occupancy levels of logs by indicator species was obtained in a 20 ha forest fragment where 100% of the surrounding forest was clear-cut as in a 3 ha forest fragment where only 25% was clear-cut. Identifying such trade-offs and management options is highly relevant for forest management policies, enabling managers of forest ecosystems to understand and balance the pros and cons of different management scenarios. A mixture of approaches might be the best way to improve the viability of forest-dwelling species at the landscape

scale (e.g. Peltoniemi, Penttilä & Mäkipää 2013). However, given that 50% of the old-growth forest remnants in Sweden are small fragments of 1–4 ha or less (Swedish Forestry Agency 2013), the general situation is towards the worst-case scenario for indicator species. This limits management options and calls for stronger national scale policies promoting larger set-asides and buffer zones.

The Swedish FSC standard for forest certification states that ‘Managers shall demarcate as care-demanding patches (i) small habitats with specific biodiversity values and (ii) any buffer zones required adjacent to habitats with specific biodiversity values’ (Forest Stewardship Council 2010). In order to maintain the long-term conservation capacity, or effective size, of small conservation areas, we advocate that buffer zones of productive forest are left uncut around these habitats. It is important to preserve the high-quality fragments that are left in the managed forest landscape regardless of their size, but equally important to buffer for anticipated future change in relation to the effective fragment size. If small old-growth forest fragments are to be included as effective area measures in the Aichi target 11, surrounding forests need to be managed to protect species in such fragments from degrading temporal edge effects. The Swedish FSC does not provide any specific recommendations for buffer zone widths, likely because buffer zones are highly context dependent in relation to aspect, forest type and the taxonomic group considered. Nonetheless, buffer zones between 25 and 100 m are likely relevant for reducing edge effects for many specialized deadwood-dwelling fungi (Snäll & Jonsson 2001; Ruete, Snäll & Jönsson 2016). Our results highlight the importance of longer rotation times adjacent to small protected areas and forest set-asides as previously suggested by Dettki & Esseen (2003), Siitonen, Lehtinen & Siitonen (2005), and Berglund & Jonsson (2008). Longer rotation times may increase the chances of indicator species recolonizing the restored once-edge forest habitat. As an alternative to permanent buffer zones, non-simultaneous clear-cuts of surrounding productive forest in a way that reduces the edge effect over time (i.e. dynamic buffers) may increase the core area of small old-growth forest fragments and improve their performance in protecting species of special concern for conservation.

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Data accessibility

R script for simulations and shape files are available in Figshare <https://dx.doi.org/10.6084/m9.figshare.4129821.v1> (Ruete 2016).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Survey of the focal forest fragments.

Table S1. Characteristics of the forest stands surveyed.

Table S2. Affected area given combination of fragment sizes and proportion of edge.

Fig. S1. Expected variability among sample units.

Fig. S2. Effects of shape index and depth of edge influence on core area affected.