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SHORT COMMUNICATION

Fragmentation effects on dead wood-dependent species associated with disturbed forest habitats: implications for stump harvesting

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ABSTRACT

Stump harvesting after clear-felling may be detrimental for species' landscape-scale persistence. Sensitivity to it is most likely due to reductions in habitat density, resulting in a non-linear relationship between population size and total habitat amount (i.e. fragmentation effects). Here we summarize theoretical expectations and empirical findings on fragmentation effects in stumps and other types of dead wood in disturbed forest habitats and draw conclusions about the consequences of stump harvesting. Within disturbed patches, some negative fragmentation effects have been observed for beetles and lichens, but most studies have found a linear relationship between habitat amount and population size. At landscape scale, evidence of fragmentation effects in disturbed forest habitats has been detected in some published investigations, but none of them focused on stumps. Thus, although organisms associated with disturbed forest habitats are assumed to be strong dispersers, they may still be sensitive to habitat fragmentation. We conclude that stump harvesting at a moderate level is not likely to increase risks for landscape-scale species extinctions markedly, despite clearly negative local effects. However, due to large uncertainties, adaptive management with monitoring of dead wood-dependent species should be applied wherever stump harvesting is more extensive.

Introduction

An important goal of the EU's energy policy is to mitigate climate change by replacing fossil fuels with renewable energy sources. In Sweden, biomass from forests is already extensively used, but according to governmental goals its use should be further increased (Regeringskansliet 2009). This raises environmental risks, including risks for loss of biodiversity. Biofuel is mainly harvested after clear-felling, and may involve extraction of stumps in addition to tops and branches (Ranius et al. 2014a). Stump extraction is a common practice in Finland, and is being experimentally trialled in several other countries. In Sweden, stump extraction is currently limited to 1–2% of all clear-cuts due to uncertainties regarding environmental risks (Swedish Forest Agency 2014).

The Swedish government has formulated a goal that viable populations of all native species should be maintained (Bill [Proposition] 1992/93:226, p. 27). Such a goal is meaningful not only at a national level, but also at regional and landscape levels. However, at the forest stand scale it is rarely crucial to maintain species currently present. This is because forest dynamics continuously change the conditions, and also because many species have small population sizes, so they continually face some risk of local extinction. In accordance with metapopulation theory (Hanski 1998), species colonize stands when they become suitable while disappearing from others (Ranius et al. 2014b). Consequently, populations may go extinct at a stand level, but if there are enough compensatory colonizations, the species will remain viable at a landscape

level. Thus, knowledge of landscape-scale processes is required to evaluate the potential to maintain viable populations, but most studies of consequences of stump harvesting (Walmsley & Godbold 2010) and other forest management practices (e.g. Fedrowitz et al. 2014) are at stand scale.

The aim of this paper is to bridge the gap between empirical knowledge of effects of stump harvesting on biodiversity in Sweden and the need to predict its consequences for the viability of populations, based on the following three premises. (i) Even if a significant proportion of stumps is harvested, there will still be a huge total number of stumps in Sweden. Thus, (ii) if species are sensitive to stump harvesting, this should be due to fragmentation effects (i.e. because the density of the resource becomes too low) rather than too small total amounts of stumps. Furthermore, (iii) the most sensitive species are likely specialists that require large-diameter, sun-exposed dead wood, since more generalistic species are less affected by stump harvesting. The latter arguments are consistent with a theoretically based suggestion that stump harvesting may have negative effects, even at moderate levels, on the persistence of strongly dispersal-limited and specialized species (Johansson et al. 2016). Here we first summarize theories on the relationship between species' dispersal and occurrence patterns in fragmented habitats. Then we review the scientific literature on occurrence patterns (including multi-species analyses) of species on stumps and in other disturbed forest habitats. Finally, we discuss the risks associated with large-scale stump harvesting and how knowledge uncertainties can be handled.

Species in stumps and other disturbed forest habitats

Biofuel harvesting has potentially large consequences for biodiversity because many species are associated with dead wood, and modern forestry has decreased the amount of dead wood to only a small proportion of what occurs in unmanaged forest (Siitonen 2001). Accordingly, extensive recent research suggests that biofuel harvesting may have substantial effects on saproxylic organisms, by reducing amounts of their habitats (Bouget et al. 2012). In managed forest landscapes in Sweden, it has been estimated that stumps constitute a major part of the coarse woody debris (Dahlberg et al. 2011). This is reflected in comparisons of species' occurrences on stumps and other dead wood types showing that stumps harbour > 50% of the landscape-level populations of some dead wood-dependent beetles (Jonsell & Schroeder 2014) and lichens (Svensson et al. 2016). Stump harvesting is likely to have the most severe consequences for these species, which occur more frequently in stumps and similar substrates in comparison to other types of dead wood, while smaller proportions of landscape-level populations of more generalist species rely on stumps.

Stumps created at clear-felling have similarities to dead wood formed by stand-replacing disturbances such as storms, wildfires, and insect outbreaks. Many organisms are associated with early-successional stages following such disturbances, since they require sun-exposed habitats, burned substrates, or large amounts of dead wood (Swanson et al. 2010). Durations of these stages are usually short relative to the intervals between disturbances. A key adaptation to early-successional stages is an ability to colonize new habitats efficiently and rapidly. Thus species associated with such conditions are likely to be less affected by habitat fragmentation than species adapted to old forest.

When harvesting stumps, around 25% are retained for practical reasons or conservation concerns (Victorsson & Jonsell 2013). With no fragmentation effects (i.e. supporting the "proportional area hypothesis", *sensu* Fahrig 2003; Figure 1(a)), theoretically there should be a linear relationship between population size and habitat amounts at both local and landscape scales. Under such conditions, stump harvesting would probably not affect species' persistence at a larger spatial scale since so many stumps would still be retained. However, if present (i.e. supporting the "extinction threshold hypothesis", *sensu* Fahrig 2003), fragmentation effects could increase risks for species' extinction (Figure 1(a)). At a local level, a fragmentation effect can be detected as a correlation between species' population densities (usually measured as frequencies of presence/absence per dead wood item) and the amount of habitat per clear-cut (i.e. the population density–patch size pattern; Figure 1(b)). At a landscape scale, a fragmentation effect can be observed as a correlation between species' presence/absence per clear-cut and connectivity (a measure reflecting colonization probability) with surrounding dispersal sources. The pattern at a larger scale reflects colonization–extinction processes directly affecting extinction risks. However, local fragmentation effects are also interesting, since they indicate limitations in species' ability to colonize individual stumps, which will also probably
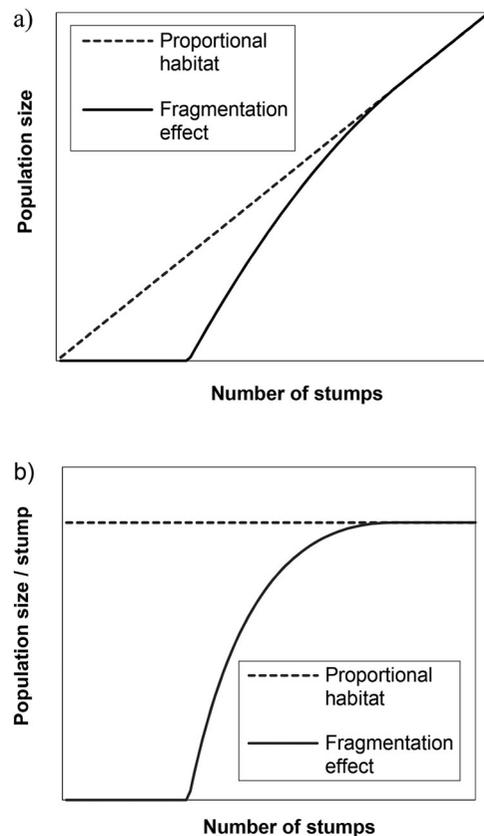
Figure 1. Theoretical relationship between population size of inhabiting species and the amount of habitat at a local (clear-cut) level (a). The fragmentation effect is possible to observe in the field by estimating population size of presence/absence per stump (b).

generate a fragmentation effect at landscape level, at least if the level of fragmentation is high and enough time has elapsed since the habitat was fragmented.

Theoretical background: species occurrence – connectivity patterns

The effect of connectivity on species occurrence has been particularly studied in metapopulation ecology contexts (Hanski 1998). Metapopulation theory assumes dispersal limitation, that is, that species may be absent from suitable habitat patches because there has been no successful colonization. The probability of colonization increases with connectivity. The connectivity measure most frequently used in metapopulation studies is positively related to numbers and sizes of populations in the surrounding landscape, inversely weighted by distance (Hanski 1998). Furthermore, the probability of local extinction decreases with increasing habitat patch size. The probability of occurrence reflects both colonization and extinction probabilities, and is thus expected to increase with increasing connectivity and patch size (Hanski 1998). It is important to consider habitat dynamics, since metapopulation dynamics are often driven by the formation, successional change and loss of habitat patches (Thomas 1994). If so, the probability of occurrence should increase with patch age until an equilibrium is reached between colonization and extinction events. In conclusion, according to metapopulation

theory, large-scale stump harvesting could have negative effects on species presence per clear-cut by reducing patch sizes, thereby raising local extinction risks, and connectivity, since there will be fewer and smaller surrounding populations.

Theoretical background: population density–patch size patterns

If the stumps on a clear-cut are seen as a habitat patch, stump harvesting will reduce the concentration of resources in the patch, which for many organisms corresponds to a reduction in patch size. Several reviews have shown that relationships between patch size and population density cover the whole gamut of possibilities, even within groups of similar species (Bowers & Matter 1997; Bender et al. 1998; Connor et al. 2000; Otway et al. 2005; Figure 2). Theoretical models have been built to predict how migration rates affect density/patch size relationships by incorporating dispersal behaviour and sensory orientation mode as traits that determine how organisms detect patch edges (Bowman et al. 2002; Englund & Hambäck 2007). This is relevant when comparing disturbed forest patches differing in area. In a newly formed habitat patch, immigration, but not emigration or population growth, governs population densities. At that stage, propagules of passively dispersing organisms, such as plants and fungi, have the same probability of landing anywhere in patches, regardless of their boundaries or resource concentration, so population density is independent of patch size (Hambäck & Englund 2005). This also holds for stumps; the number of spores landing on a stump is independent of the number of stumps on the same clear-cut, until the stumps on the clear-cut are old enough to constitute dispersal sources. However, the behaviour (and associated relationships) of animals may vary substantially. For instance, attraction to vegetation patches mediated by odours of hosts in them promotes a negative population density/patch size relationship (Bukovinszky et al. 2005; Andersson et al. 2013a, 2013b). Similarly, we expect that stump harvesting reduces stump odour emissions which decreases the total number of attracted individuals, but not sufficiently to offset increases in numbers of attracted individuals per stump due to a crowding effect. By contrast, positive density/patch size relationships have been observed for species in other habitats, possibly because they have mechanisms of conspecific attraction based on aggregation pheromones (Hambäck & Englund 2005; Jackson et al. 2013).

For habitat patches older than the time required for inhabiting species to complete one generation cycle, emigration and population growth will modulate the initial density/patch size relationship (Hambäck & Englund 2005; Hambäck et al. 2007). Patch size determines whether migration rates or demographic parameters influence the density/patch size relationship most strongly, migration being more important in small patches and population growth rate in large patches (Hambäck & Englund 2005). When demographic parameters and emigration are important, species' population densities are positively correlated to patch size (Connor et al. 2000; Bowman et al. 2002). For stump-inhabiting species this is because increases in the density of stumps

will result in a larger proportion of propagules dispersed from a stump reaching another stump in the same patch. This small-scaled colonization–extinction process on stumps within a single clear-cut can be described as metapopulation dynamics, with each stump being a local habitat patch potentially hosting a local population (Caruso et al. 2010). However, since only one published study has applied such a small-scale approach, we do not use that terminology here, although we acknowledge that such processes occur within clear-cuts.
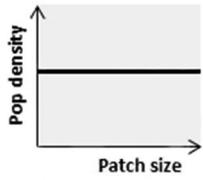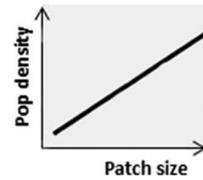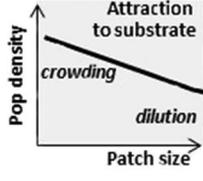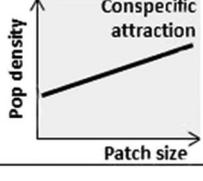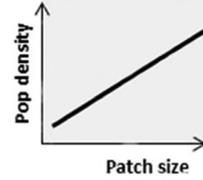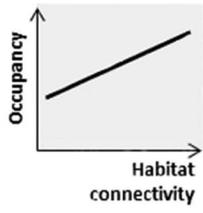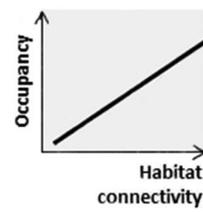
In conclusion, we do not expect stump harvesting to have any immediate effect on the frequency of occurrence per stump for passive dispersers such as air-dispersing fungi and lichens, but it may have negative effects in following generations due to demographic factors. For animals that actively search for stumps, stump harvesting may initially cause changes in population density in any direction, but there will be increasingly negative effects after reproduction in a clear-cut with a reduced number of stumps. Thus, we expect outcomes to vary depending on both time since the disturbance and dispersal behaviour of the species.

Literature survey

In databases, we searched for scientific studies on the effect of patch size on population densities and effects of connectivity (measured as the amount of disturbed forest habitats in the surrounding landscape) on species' abundance and presence/absence of dead wood-dependent organisms in (i) stumps and (ii) other forest habitats formed by disturbance. Studies of species richness were included, since species richness reflects the additive presence/absence of many species. If a paper indicated that certain species were associated with disturbed forest habitats (either as preferential habitats or as dispersal sources), we only retrieved information on those species. Regarding patch-scale data, we compiled estimates connected to defined pieces of habitat. We assumed it is impossible to estimate population densities per unit habitat amount using devices for sampling flying organisms, for instance, flight-interception or Lindgren traps. In the surveyed studies, such estimations had rarely been made based on sampling with such traps, and if they had the outcome would have been unreliable. Regarding landscape-scale data, we included studies that used species' presence–absence (in accordance with metapopulation theory) or abundance per patch as response variables. We included the study by Boulanger et al. (2010), although it was conducted in a mosaic landscape with a less patchy structure than focal landscapes in the other studies. However, studies of landscapes where the disturbed forest habitat was even more continuous were discarded.

Empirical studies: connectivity effects at the landscape level

The effect of connectivity of stump habitats on species' presence or abundance per clear-cut has not been specifically addressed in any of the studies we considered. However, we found nine studies that have addressed connectivity effects on insects in other disturbed forest habitats. Five detected

Figure 2. Possible effects of stump harvesting on inhabiting species according to general ecological theories (the effect of conspecific attraction is however not formulated in any theory, but only discussed). The graphs show the direction of the relationship, while the shape of the curves may differ from the linear. For an explanation, see section "Theoretical background: population density–patch size patterns".

some positive effects of connectivity, and one detected negative effects for one species (Table 1). However, potential effects of colonization–extinction dynamics can only be observed if presence/absence per stand is used as a response variable, and none of the three studies that did so detected any significant effect. A comparison at a larger, regional level of fire-associated beetle species revealed differences in the species pool affecting colonization rates (Kouki et al. 2012).

Empirical studies: patch size effects on population densities

We found three studies on effects of stump-habitat patch size on population densities, and five on effects of patch sizes of other disturbed forest habitats (Table 2). There was some evidence of negative fragmentation effects (i.e. a positive relationship between population density and patch size) in stump habitats. However, the negative effect reported in one of the studies (Victorsson & Jonsell 2013) may have resulted from stumps being larger in non-harvested clear-cuts, according to Work et al. (2016). If so, the only dead wood-dependent species found to be affected by stump density within stands to date is a single lichen species.

However, lower abundances of millipedes and centipedes per stump have also been found in stumps remaining after stump harvesting than in stumps in unharvested clear-cuts, but these species are not confined to dead wood (Taylor & Victorsson 2016).

In accordance with theoretical expectations, a negative effect of patch size was only detected for a species using a given storm-felled tree for a single generation (*Ips typographus*), while all reported positive effects were on species that may use the habitat patches over several years, and generations (Table 2). It has been suggested that the dispersion effect also results in negative effects in fire-dependent species (Länsstyrelsen Norrbotten 2009), but we found no scientific study supporting this hypothesis (see, for instance, Appendix).

Implications for stump harvesting

Although species associated with disturbed forest habitats are assumed to be strong dispersers, fragmentation effects are sometimes present both within stands and at landscape scale. However, little is known about effects of stump harvesting. From theory we expect fragmentation effects to be stronger for species associated with rarer habitats, which are more

Table 1. Studies addressing the relationship between abundance or occurrence of dead wood-dependent species and the connectivity of disturbed forest habitat patches (measured as the total sum (or with nearby sites upweighted) of patch area or substrate amount in surrounding landscapes).

Reference	Tree species	Country	Patch origin	Connectivity measure	Sampling method	Years after disturbance	Response variable	Species	Effect of connectivity[a]
Studies in stumps									
None									
Studies in other disturbed forest habitats									
Response variable: occupancy per stand									
Rubene et al. (2014)	*Betula* spp.	Sweden	Clear-cutting	Volume of birch DWR weighted based on distance	Bark inspection (larvae)	3–20	Occupancy per clear-cut	*Upis ceramboides, Platysoma minus* (beetles)	no
Ranius et al. (2014b)	*Pinus sylvestris*	Sweden	Fire	Number of suitable trees within 30 km	Bark inspection (galleries)	2–15	Occupancy and colonisation per burn	*Stephanopachys linearis* (beetle)	no
Rubene et al. (2015)	*Picea abietis, Pinus sylvestris*	Sweden	Clear-cutting	Early-successional area within 2 km	Window traps, pan traps	3–5	Species richness per clear-cut	dead wood nesting bees and wasps	no
Response variable: species abundance									
Bouget (2005)	*Quercus, Carpinus*	France	Storm	Clear-cut area within 500 m	Window trap	1–2	No. ind./trap	*Rutpela maculata, Aspidiphorus orbicularis, Cerylon* sp. (beetles)	pos.
Bouget (2005)	*Quercus, Carpinus*	France	Storm	Clear-cut area within 500 m	Window trap	1–2	No. ind./trap	20 beelte species	no
Bouget and Noblecourt (2005)	*Quercus, Carpinus*	France	Storm	Clear-cut area within 500 m	Window trap	1–2	No. ind./trap	*Xyleborus saxesenii, X. cryptographus, Platypus cylindrus* (beetles)	no
Schroeder et al. (2006)	*Picea abietis, Pinus sylvestris*	Sweden	Clear-cutting	Clear-cut area within 1000 m	Bark sieving	3–9	Occupancy per high stump	*Hadreule elongatula* (beetle)	pos.
Boulanger et al. (2010)	*Picea mariana, Pinus banksiana*	Canada	Fire	Distance from earlier fire	Trunk-window trap	<1	No. ind./trap	*Corticaria dentigera* (beetle)	pos.
Boulanger et al. (2010)	*Picea mariana, Pinus banksiana*	Canada	Fire	Distance from earlier fire	Trunk-window trap	<1	No. ind./trap	*Sphaeriestes virescens* (beetle)	neg.
Boulanger et al. (2010)	*Picea mariana, Pinus banksiana*	Canada	Fire	Distance from earlier fire	Trunk-window trap	<1	No. ind./trap	*Monochamus scutellatus, Clypastraea fusca, Sphaeriestes virescens, Sericoda obsoleta* (beetles)	no
Boulanger et al. (2013)	*Picea mariana, Pinus banksiana*	Canada	Fire	Distance from earlier fire	Trunk-window trap	<1	No. adults/trap	*Acmaeops proteus, Monochamus scutellatus* (beetles)	pos.
Boulanger et al. (2013)	*Picea mariana, Pinus banksiana*	Canada	Fire	Distance from earlier fire	Trunk-window trap	<1	No. adults/trap	*Acmaeops pratensis* (beetle)	no
Boulanger et al. (2013)	*Picea mariana, Pinus banksiana*	Canada	Fire	Distance from earlier fire	Rearing from bole sections	<1	No. adults/bole	*Acmaeops proteus, A. pratensis, Monochamus scutellatus* (beetles)	no
Schroeder (2013)	*Picea abies*	Sweden	Clear-cutting	Clear-cut area within radii between 0.5 and 4 km	Pheromone traps	<1	No. ind. /trap	*Pityogenes chalcographus* (beetle)	no
This paper (Appendix)	*Pinus sylvestris*	Sweden	Fire	Negative exponential function	Bark inspection (galleries)	2–15	Occupancy per burned pine	*Stephanopachys linearis* (beetle)	pos.

[a]Sign of connectivity effect, that is, a positive effect of an isolation measure (such as distance to dispersal source) is reported as a negative connectivity effect. If $p > .05$, it is reported as no effect.

Table 2. Studies addressing the relationship between population densities of dead wood-dependent species associated with disturbed forest habitat and the size of the disturbed forest habitat patches (measured as patch area or substrate amount). The sampling was inspection or emergence trapping of individual dead wood items.

Reference	Tree species	Country	Patch origin	Patch size measure	Years after disturbance	Response variable	Species	Effect of patch size[a]
Studies in stumps								
Caruso et al. (2010)	*Picea abies*	Sweden	Clear-felling	No. occupied stumps	4–21	Colonization rate per stump	*Cladonia botrytes* (lichen)	pos.
Caruso et al. (2010)	*Picea abies*	Sweden	Clear-felling	No. occupied stumps	4–21	Colonization rate per stump	*Xylographa parallela*, *Lecidea turgidula* (lichens)	no
Victorsson and Jonsell (2013)	*Picea abies*	Sweden	Clear-felling	Stump harvest/no harvest	2	Species richness per stump	Beetles (totally and functional groups)	pos. (but no effect on some groups)
Work et al. (2016)	*Picea abies*	Sweden	Clear-felling	Stump harvest/no harvest	2–4	Species richness per stump	Beetles (totally)	no
Studies in other disturbed forest habitats								
Eriksson et al. (2005)	*Picea abies*	Finland	Storm	No. downed trees	1–2	Occupancy per down tree	*Ips typographus* (beetle)	no
Eriksson et al. (2006)	*Picea abies*	Finland	Clear-cutting	No. downed trees	1–2	Occupancy per down tree, No. galleries/m^2	*Ips typographus* (beetle)	neg.
Schroeder (2010)	*Picea abies*	Sweden	Storm	No. of down trees	<1	Occupancy per down tree	*Ips typographus* (beetle)	no
Rubene et al. (2014)	*Betula* spp.	Sweden	Clear-cutting with DWR	Amount of birch dead wood	3–20	Occupancy per dead wood item	*Upis ceramboides*, *Platysoma minus* (beetles)	pos.
This paper (Appendix)	*Pinus sylvestris*	Sweden	Fire	No. of burned trees	2–15	Occupancy per burned tree	*Stephanopachys linearis* (beetle)	no

[a]If $p > .05$, it is reported as no effect.

fragmented (Fahrig 1998). Thus, there should be less fragmentation effects in stumps than in other studied habitats, but there is too little relevant information to test this hypothesis.

In conservation biology, often only stand-level populations and factors are considered. For instance, frequently cited reviews on effects of retention forestry (Fedrowitz et al. 2014), stump harvesting (Walmsley & Godbold 2010), and dead wood amounts (Müller & Bütler 2010) have adopted purely stand-level perspectives. From such a perspective, our conclusion would simply be that stump harvesting has negative effects on biodiversity, since it reduces local species richness (Work et al. 2016). However, we are convinced that larger spatial scales are more relevant, because many populations are adapted to transient successional stages, so their persistence is based on dynamics at a larger scale. From a species' persistence perspective, relevant spatial scales span areas in which the amount of habitat is relatively constant over time. Thus, since forest stands change over time, many stands with asynchronous rotations are required. From policy perspective even larger spatial scales may be most important (Stevens et al. 2007).

A synthesis commissioned by the Swedish Energy Agency (de Jong et al. 2012) suggested that stump harvesting would substantially compromise biodiversity goals if practiced at ≥20% (but not ≤10%) of all clear-cuts. The basis of these estimates was not reported. Since field data indicate that there are fragmentation effects, we agree that species would be at risk if stumps were harvested from every clear-cut. However, we also believe that harvesting stumps in 10–20% of clear-cuts could have minor effects, if appropriate sites (in forest stands and landscapes with low conservation values) are selected. This is because it is generally more important for biodiversity to maintain some landscapes with sufficient amounts of each habitat than for all habitats to be present everywhere (Hanski 2011).

More field studies on fragmentation effects could increase our understanding of processes affecting communities on clear-cuts, which would be useful for developing and evaluating conservation strategies. However, we see no possibility to determine how much stump harvesting would increase risks for landscape-level biodiversity losses with a reasonably amount of time and efforts spent. This is due both to the practical difficulties of empirically assessing such losses over relevant spatial and temporal scales, and uncertainties arising from up-scaling interpretation from smaller scale studies (cf. Underwood et al. 2005). Under such conditions, it has been suggested that instead of collecting more data of the same kind, it would be more important to develop strategies for communicating and handling the unavoidable uncertainties (Uggla et al. 2016). One such strategy may be to maintain structured dialogue with key stakeholders, which may facilitate the development of widely accepted policies that may include new solutions and research directions (cf. Mårald et al. 2015).

We suggest that if large-scale stump harvesting is introduced in Sweden, there should be variation in its extension among landscapes and adaptive forest management applied (Rist et al. 2016), with monitoring of biodiversity. From recent studies we can identify suitable species for

such purposes, with populations that can provide useful indications of more general effects of treatments or factors on biodiversity (Jonsell & Schroeder 2014; Svensson et al. 2016). Theoretical modelling (Johansson et al. 2016) indicates that possible population density reductions may be visible after about two decades, while landscape-level extinctions may occur several decades later. Therefore, sufficient time would be available to stop harvesting and apply compensatory measures (cf. Ranius et al. 2014a) if necessary to avoid extinctions following possible declines in population densities.

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Appendix

We analysed the population density/patch size relationship for a beetle, *Stephanopachys linearis*, which is confined to burned forest sites. For the analysis we used a dataset from 128 sites which have been used for analysing colonizations, extinctions and presence/absence (Ranius et al. 2014b). In the analysis we only included the 78 patches where the species was present. Forest fires occurred 2–15 years before the survey, and the number of suitable trees per patch varied from 5 to 30,000. The population density was measured as the proportion of surveyed trees where the species was found (larvae or remains showing that the species had used the tree; arcsin-transformed). Twenty suitable trees per site were sampled (or all trees, if less than 20 were available). We analysed population density in relation to patch size (measured as the number of suitable trees, log-transformed), time since fire, connectivity (measured as the occupied patches within 30 km, weighed according to their distance and estimated population size), and the interaction between time since fire and the other factors. We constructed statistical models with all combinations of predictor variables, and searched for the combination with the lowest AIC value. This resulted in a model with only one predictor variable: intercept, 0.614***; connectivity, 0.00171** (estimates and statistical significance: ***$p < .001$; **$p < .01$, in the negative exponential function $a = 1/6764$ m). This means that the immigration rate had a clear effect on the population density, since connectivity to dispersal sources was an important factor explaining population density, but patch size had no effect.