

An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region

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Abstract. The habitat-amount hypothesis challenges traditional concepts that explain species richness within habitats, such as the habitat-patch hypothesis, where species number is a function of patch size and patch isolation. It posits that effects of patch size and patch isolation are driven by effects of sample area, and thus that the number of species at a site is basically a function of the total habitat amount surrounding this site. We tested the habitat-amount hypothesis for saproxylic beetles and their habitat of dead wood by using an experiment comprising 190 plots with manipulated patch sizes situated in a forested region with a high variation in habitat amount (i.e., density of dead trees in the surrounding landscape). Although dead wood is a spatio-temporally dynamic habitat, saproxylic insects have life cycles shorter than the time needed for habitat turnover and they closely track their resource. Patch size was manipulated by adding various amounts of downed dead wood to the plots (~800 m³ in total); dead trees in the surrounding landscape (~240 km²) were identified using airborne laser scanning (light detection and ranging). Over 3 yr, 477 saproxylic species (101,416 individuals) were recorded. Considering 20–1,000 m radii around the patches, local landscapes were identified as having a radius of 40–120 m. Both patch size and habitat amount in the local landscapes independently affected species numbers without a significant interaction effect, hence refuting the island effect. Species accumulation curves relative to cumulative patch size were not consistent with either the habitat-patch hypothesis or the habitat-amount hypothesis: several small dead-wood patches held more species than a single large patch with an amount of dead wood equal to the sum of that of the small patches. Our results indicate that conservation of saproxylic beetles in forested regions should primarily focus on increasing the overall amount of dead wood without considering its spatial arrangement. This means dead wood should be added wherever possible including in local landscapes with low or high dead-wood amounts. For species that have disappeared from most forests owing to anthropogenic habitat degradation, this should, however, be complemented by specific conservation measures pursued within their extant distributional ranges.

Key words: dead-wood enrichment; forest restoration; fragmentation; habitat loss; habitat-amount hypothesis; island effect; light detection and ranging (LiDAR); saproxylic beetles; single large > several small (SLOSS); woody debris.

INTRODUCTION

Patches of a particular habitat in terrestrial ecosystems are often thought to resemble islands in an “ocean”

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of non-habitat matrix (Hanski 1994, Warren et al. 2015). Based on island-biogeography theory, the habitat-patch hypothesis assumes that populations of species are more or less restricted to single patches, and that colonizations and extinctions of populations in patches and thus the number of species within patches depend on patch size and patch isolation (island effect; MacArthur and Wilson 1967, Hanski 1994). Some authors have challenged the analogy between oceanic islands and

habitat patches, particularly the assumption that patch boundaries delimit populations (Gilber 1980, Bowne and Bowers 2004, Tschardt et al. 2012, Mendenhall et al. 2014) and question whether patch size and patch isolation have independent effects on species number (Ewers and Didham 2006, Lindenmayer and Fischer 2007, Tschardt et al. 2012, Fahrig 2013, Villard and Metzger 2014, Hanski 2015). This is not just a question of academic interest but also of high practical importance for the conservation of biodiversity because it determines whether conservation strategies should focus only on habitat amount or also on its spatial configuration (Lindenmayer and Fischer 2007).

As an alternative to the habitat-patch hypothesis, Fahrig (2013) proposed the habitat-amount hypothesis, which provides a simpler view of the relationship between habitat distribution and species number. She hypothesized that in most terrestrial ecosystems, the effects of both patch size and patch isolation are driven by the sample area effect, as follows. The total number of individuals in a given habitat type within a landscape increases with increasing amount of that habitat in the landscape. This increase in the number of individuals represents a larger sample of the species in the regional species pool for that habitat; therefore, the number of species in the landscape also increases with increasing habitat in the landscape. Higher species numbers in a landscape then lead to higher species numbers on a plot sampled within the landscape because there are more species available to immigrate to the plot in a landscape with higher habitat amount. In other words, a sample of individuals from a landscape containing more habitat should contain more species than a sample of the same number of individuals from a landscape containing less habitat. As patch size and patch isolation are both elements of habitat amount (see figs. 6 and 7 in Fahrig 2003, and fig. 6 in Fahrig 2013), the habitat-amount hypothesis proposes that their effects are explained by the sample area effect.

To test the habitat-amount hypothesis, Fahrig (2013) proposed a comparison of the slopes of the relationship between species number and patch size in areas with different amounts of habitat. According to the habitat-amount hypothesis, the relationship between number of species and patch size should be lower for a set of patches surrounded by less habitat in their "local landscapes" (i.e., the area around a patch from which immigrants can reach it) than for a set of patches with more habitat in their local landscapes. However, the slopes of these two relationships should be the same (Fig. 1). By contrast, according to the habitat-patch hypothesis, the island effect should lead to a steeper slope of the relationship between species number and patch size in areas with less habitat than in areas with more habitat (Fig. 1; MacArthur and Wilson 1967). Such a difference between slopes, as indicated by a significant negative interaction between patch size and habitat amount in the local landscape, would refute the habitat-amount hypothesis.

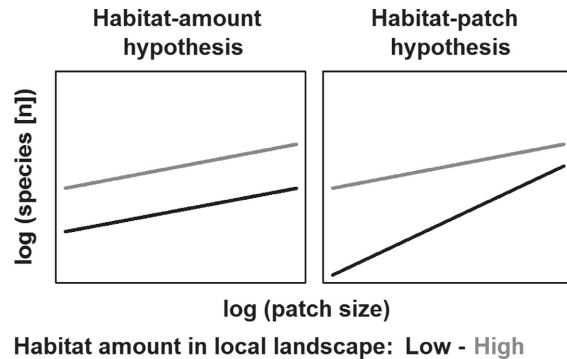


FIG. 1. Possible relationships between the number of species at a sample site and patch size in areas with low (black) and high (gray) habitat amount in local landscapes around the sites. According to the habitat-amount hypothesis, the slope of these relationships should be similar in local landscapes with low and high habitat amount. By contrast, the habitat-patch hypothesis predicts a steeper slope in areas with low habitat amount than in areas with high habitat amount in local landscapes and thus, a negative interaction between patch size and habitat amount in the local landscape.

Another way to compare the habitat-patch hypothesis to the habitat-amount hypothesis is to compare cumulative species-habitat area curves with patches added in order of increasing or decreasing patch size (Fahrig 2013). The habitat-amount hypothesis predicts similar curves irrespective of the order of accumulation of the patches, while the habitat-patch hypothesis predicts more species in a single large patch than in several small patches of the same total area (i.e., single large > several small: SLOSS).

We tested these predictions of the habitat-amount hypothesis and the habitat-patch hypothesis experimentally, using experimental patches of varying sizes situated in local landscapes with varying amounts of habitat (Fig. 2). By experimentally separating patch size from habitat amount in the local landscape, we could test for an interaction effect between the two. For this experiment, we sampled saproxylic beetles (i.e., species that depend on dying or dead trees) over 3 yr. Saproxylic beetles are suitable for testing these hypotheses because they are a large group of species specialized on a discrete type of habitat. Local patch size was manipulated by adding varying amounts of dead wood to the sample plots, and airborne light detection and ranging (LiDAR) was used to measure amounts of dead wood in the local landscapes surrounding the plots.

Despite the advantages noted herein, a potential drawback of using saproxylic beetles for these tests is that the habitat-patch hypothesis, based on island biogeography theory, assumes a dynamic equilibrium between species extinctions and colonizations on the patches. The spatial distribution of habitat must be established for long enough to approach this equilibrium. Although dead wood is a spatio-temporally dynamic resource (Saint-Germain et al. 2007, Jönsson et al. 2008, Caruso et al. 2010), we argue that it is relatively stable in comparison

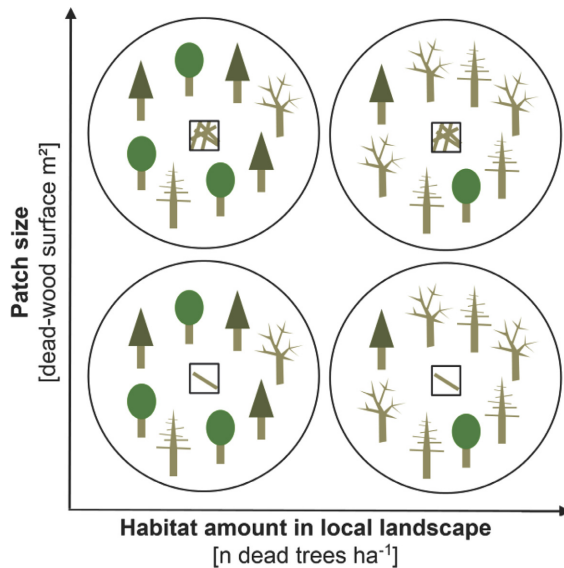


Fig. 2. Illustration of the study design. Experimental plots (square in the center of each large circle; 190 plots) were selected within local landscapes (large circles) varying widely in the number of dead trees. Plots were then cleared of dead wood, and fresh dead wood was added in various amounts to create different patch sizes. The design allowed the estimation of independent and interaction effects of patch size (dead-wood surface on plot; m^2) and habitat amount (number of dead trees/ha) in the local landscapes on species richness of saproxylic beetles. [Color figure can be viewed at wileyonlinelibrary.com]

to the life cycle of saproxylic beetles. Most species of the early-decay stage (~ 3 yr in Central Europe) complete their larval development within a few weeks (e.g., many scolytids) and some need up to maximally 2 yr (e.g., the larger cerambycids; Pfeffer 1995, Klausnitzer and Klausnitzer 2015). Therefore, most species can colonize a dead-wood object and become extinct several times for stochastic reasons within this first successional phase. Thus, we suggest that the saproxylic beetle system is appropriate for comparing the habitat-patch hypothesis and the habitat-amount hypothesis. Moreover, an issue under debate is whether conservation strategies for saproxylic species, such as dead-wood enrichment or dead-wood retention (Müller and Bütler 2010, Riffell et al. 2011, Halme et al. 2013, Seibold et al. 2015a), should focus only on dead-wood amount or also on its spatial configuration (Edman et al. 2004, Ranius et al. 2011, Nordén et al. 2013, Janssen et al. 2016). Testing the importance of the habitat-amount hypothesis for saproxylic species is thus crucial for designing conservation strategies for this species group.

METHODS

Study area

The study was conducted in the Bavarian Forest National Park, covering an area of about 240 km^2 in

southeastern Germany. The area is characterized by $\sim 97\%$ forest cover, mostly of anthropogenic origin, with European Beech *Fagus sylvatica*, Silver Fir *Abies alba*, and Norway Spruce *Picea abies* as the naturally dominant tree species. The fungus *Fomes fomentarius* and natural disturbances by the bark beetle *Ips typographus* have created high amounts of dead wood, but salvage logging is still conducted in some parts of the park (Müller et al. 2010). Thus, there is a gradient of dead-wood amount from the low amounts typical of European production forests to the extraordinarily high amounts created by forest disturbances (see Appendix S1: Fig. S1; Siitonen 2001, Müller et al. 2010). The area is a hotspot for saproxylic species in Central Europe because several rare saproxylic species with high habitat demands survived in small remnants of old-growth forest (Müller et al. 2010). From there, they colonized many formerly managed forest stands in the area.

Experimental design and manipulation of patch size

To test the habitat-amount hypothesis, we used an experiment initially designed to study the independent effects of amount and diversity of dead wood on saproxylic and non-saproxylic organisms (Seibold et al. 2016a, b). For this experiment, we used 190 0.1-ha plots grouped into five blocks (Appendix S1: Fig. S1). To create variation in patch size, we removed naturally occurring dead wood ($>2 \text{ cm}$; Appendix S1) from the plots and then added various amounts of freshly cut downed dead wood in fall of 2011. We created four patch sizes (Appendix S1: Fig. S1), characterized as the total surface area of all added dead wood: (1) 10 control plots (no dead wood); (2) 30 small patches (mean \pm SD: $1.7 \pm 0.72 \text{ m}^2$); (3) 90 medium patches ($23.1 \pm 4.92 \text{ m}^2$); and (4) 60 large patches ($163 \pm 28.1 \text{ m}^2$). All levels of patch size and dead-wood diversity (Appendix S1) were included in each of the five blocks in a randomized block design. To account for effects of microclimate, half of the plots in each block at each level were on clearings without canopy cover and the other half were under a closed canopy.

Mapping habitat amount in the local landscape with LiDAR

We used airborne LiDAR and the latest single-tree identification methods (Casas et al. 2016, Polewski et al. 2016) to identify all standing dead trees including snags (i.e., broken dead trees without crown) within the Bavarian Forest National Park in summer 2012 (Appendix S1). We then measured the habitat amount in the local landscape of each plot as the number of standing dead trees per hectare within a circle of a particular radius around the plots. The radius varied between 20 and 1,000 m in steps of 20 m (Appendix S1: Fig. S2). Although a more accurate measure of habitat amount would have been the total dead-wood surface area in the local landscape (Heilmann-Clausen and Christensen 2004), this cannot be estimated by LiDAR when tree crowns are partially or

completely missing. However, the number of dead trees has been shown to be a good surrogate for the total amount of dead wood (Appendix S1). Patch size and habitat amount in the local landscape did not co-vary across experimental plots (Appendix S1: Fig. S3), as required for testing the habitat-amount hypothesis (Fahrig 2013).

Beetle sampling

We installed two flight-interception traps and two pitfall traps on each plot. The traps were arranged in pairs; each pair consisted of one trap of each type, 5 m apart in the center of the plot (Seibold et al. 2016b, Appendix S1). Flight-interception traps were active May to September 2012, 2013, and 2014, and pitfall traps were operated May, July, and September in the same years. Trapped beetles were identified to the species level and classified as saproxylic according to Schmidl and Bußler (2004). We estimated the number of saproxylic beetle species per plot (including both trap types), pooled over 3 yr. As responses of species to habitat amount and pattern might be affected by species traits, such as rarity, body size, dispersal ability, and habitat specialization (Tschardt et al. 2002b, Ewers and Didham 2006), saproxylic beetle species were further separated into different subgroups according to their Red List status, body size, habitat guild, and host specialization (Seibold et al. 2015b; Appendix S1).

Statistical analyses

All statistical analyses were conducted in R 3.0.2 (www.R-project.org). First, we conducted a multi-scale analysis to determine the appropriate local landscape size (Fahrig 2013), for all saproxylic beetles, and for each subgroup, considering radii of 20–1,000 m (Appendix S2). These local landscape sizes were then used in all further analyses.

To test for an interaction effect between patch size and habitat amount in the local landscape, we fitted generalized additive models for count data with a negative binomial distribution (function `gam` in the add-on package `mgcv`; Wood 2006). Response variables were the observed number of species per plot of all saproxylic species and the observed per-plot number of species in subgroups. Predictor variables in all models included patch size (log surface area of added dead wood), habitat amount in the local landscape (log number of dead trees/ha), interaction of patch size and habitat amount, canopy cover (open or closed), plot dead-wood diversity (continuous variable 0–4; Appendix S1), and block (five levels) to account for the nested experimental design. A significant negative interaction of patch size and habitat amount in the local landscape would refute the habitat-amount hypothesis and support the habitat-patch hypothesis.

Because support for the habitat-amount hypothesis would be indicated by the lack of a negative interaction effect between patch size and amount of habitat in the

local landscape, it was important to evaluate if our study had sufficient power to detect such an interaction effect if it existed. We therefore conducted a simulation-based post-hoc power analysis (Onwuegbuzie and Leech 2004) by generating 3,000 synthetic replicates of the response and refitting the model for each of these replicates (Appendix S2). We repeated this for a grid of effect sizes, ranging from the observed effect size up to seven times the observed effect size.

For the SLOSS-type test, we made two species accumulation curves for all saproxylic beetle species, with plots ordered according to either increasing or decreasing patch size (surface area of dead wood). The habitat-patch hypothesis would be supported if the latter was higher than the former, while the habitat-amount hypothesis predicts no difference.

RESULTS

We trapped 283,243 individuals of 1,722 beetle species of which 101,416 individuals of 477 species were saproxylic. The correlation between the total number of species per plot and habitat amount surrounding the plots was highest at a radius of 40 m and decreased steadily with increasing radius (Appendix S2: Fig. S1). For the number of species in most subgroups, the highest correlation was also found at a radius of 40 m. Exceptions were red-listed (60 m), early-decay-stage (80 m), and medium-sized species (120 m; Appendix S2: Fig. S1).

Both patch size (surface area of added dead wood) and habitat amount in the local landscape (number of dead trees) positively affected the number of all saproxylic species (Fig. 3A, B, Table 1). Consistent with the habitat-amount hypothesis, the interaction between patch size and habitat amount in the local landscape was not significant ($P = 0.45$). The effects of patch size and habitat amount in the local landscape were approximately 30 and 10 times stronger, respectively, than the effect of their interaction. Moreover, the sign of the interaction term was positive and not negative as predicted by the habitat-patch hypothesis (Fig. 3C). Power analysis supported the low effect of the interaction term compared to the main effects of patch size and habitat amount in the local landscape. A four times stronger effect size of the interaction term was needed to identify it as significant (5% level) in 80% of the simulated replicates (Appendix S2: Fig. S2); significant effects of patch size and habitat amount in the local landscape were identified in 75.5% and 99.9% of the simulated replications already for the observed effect size.

Patch size had significant positive effects on the species number of all subgroups except late-decay-stage species, and habitat amount in the local landscape had positive effects on all subgroups except small species, species living in fungal fruiting bodies, and host generalists (Table 1). Consistent with the habitat-amount hypothesis, the interaction between patch size and habitat amount in the local landscape was not significant for any subgroup.

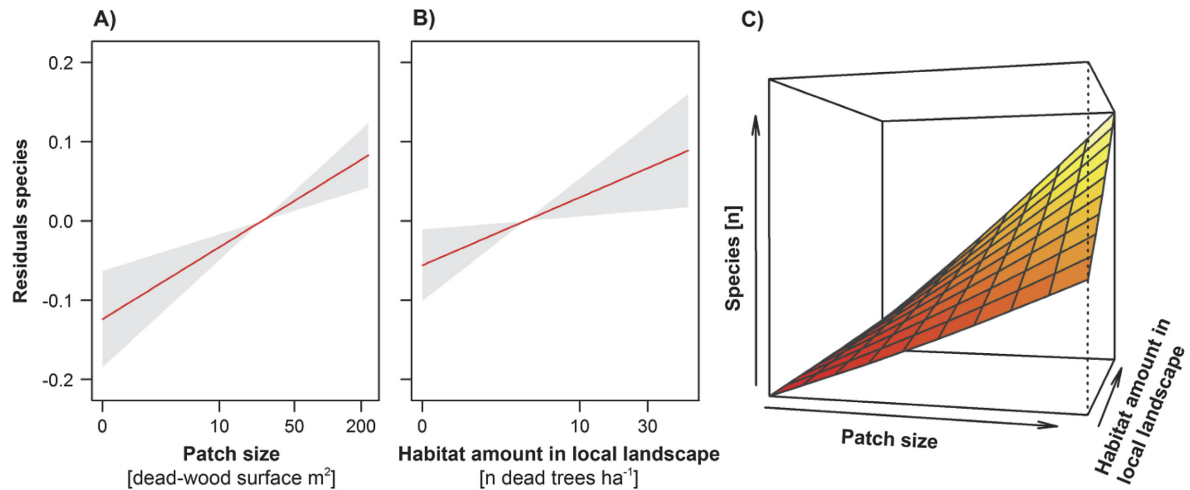


FIG. 3. Partial residual smoothed functions obtained from the generalized additive model showing independent positive effects of (A) patch size and (B) habitat amount in local landscapes on the total number of saproxylic beetle species. Note the logarithmic scales of the x -axes. (C) 3-D plot illustrating the relationship between species number and patch size as influenced by habitat amount in the local landscapes surrounding the plots. Note that although the effect of the interaction was weak and not significant, the increase in species number with local habitat amount tended to be stronger when the surrounding habitat amount was high (positive interaction); this pattern is opposite to that predicted by the island effect and is inconsistent with the habitat-patch hypothesis (see Fig. 1). [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1. Results of generalized additive models for the species number of all saproxylic beetles and specific subgroups.

Species group—response variable	Patch size (dead-wood surface area on plot)		Habitat amount in local landscape (number of dead trees/ha)		Patch size \times habitat amount in local landscape		R^2_{adj}
	<i>F</i> -value	<i>P</i> -value	<i>F</i> -value	<i>P</i> -value	<i>F</i> -value	<i>P</i> -value	
All species	15.5	<0.001	5.78	0.016	0.656	0.45	0.60
Red List status							
Red-listed	6.92	0.009	6.20	0.014	1.38	0.24	0.52
Not red-listed	15.3	<0.001	4.93	0.027	1.01	0.30	0.59
Body size							
Large species	6.13	0.013	6.53	0.056	1.04	0.35	0.85
Medium species	16.2	<0.001	5.02	0.025	0.807	0.37	0.37
Small species	10.2	0.001	0.488	0.49	2.45	0.12	0.36
Habitat guild							
Early-decay	21.9	<0.001	14.7	<0.001	0.219	0.82	0.38
Fungi	19.1	<0.001	0.438	0.51	2.60	0.11	0.49
Late-decay	1.16	0.28	4.64	0.031	0.022	0.93	0.82
Host specialization							
Generalist	6.13	0.013	1.76	0.19	2.01	0.37	0.75
Specialist	17.0	<0.001	6.51	0.015	0.866	0.35	0.51

Notes: Predictors included patch size (log-transformed surface area of downed dead wood added to experimental plots), habitat amount in the local landscape (log-transformed number of dead trees/ha) at the specific local landscape scale for each response, as well as the interaction between patch size and habitat amount in the local landscape. The habitat-patch hypothesis is supported by a negative interaction effect between patch size and habitat amount in the local landscape, while the lack of an interaction is consistent with the habitat-amount hypothesis. Significant results are indicated by boldface. All models included the factor block to account for the nested design and controlled for differences in dead-wood diversity and canopy cover.

The cumulative number of saproxylic beetle species increased with patch size more quickly when plots were ordered according to increasing patch size than when ordered according to decreasing patch size (Fig. 4). This result is not consistent with either the habitat-patch hypothesis or the habitat-amount hypothesis.

DISCUSSION

We tested the habitat-amount hypothesis vs. the habitat-patch hypothesis for beetles dependent on dead wood by combining experimental manipulation of patch size (dead wood added to sample plots) with remote-sensing

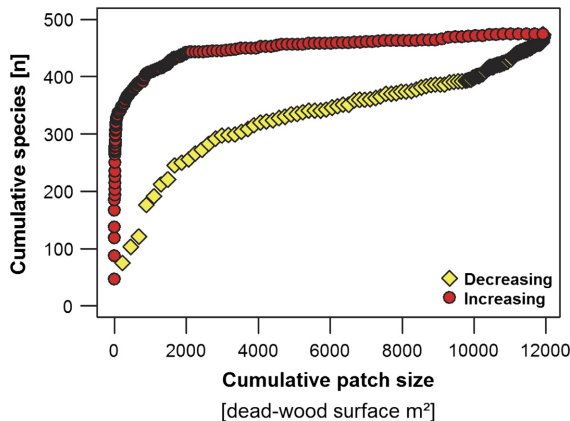


FIG. 4. Cumulative number of saproxylic beetle species relative to cumulative patch size either by beginning with the largest patch and adding plots in order of decreasing patch size (yellow diamonds, “decreasing”), or by beginning with the smallest patch and adding plots in order of increasing patch size (red circles, “increasing”). The observed pattern is inconsistent with both the habitat-patch hypothesis and the habitat-amount hypothesis. [Color figure can be viewed at wileyonlinelibrary.com]

estimation of the habitat amount (number of dead trees) in the local landscapes surrounding the plots. We found that the number of saproxylic beetle species was positively related to both patch size and amount of habitat in the local landscape, but not to their interaction. In other words, we did not find a stronger or weaker increase in species number with increasing patch size if the amount of dead wood surrounding a patch was higher. The lack of this interaction effect is not consistent with the island effect as predicted by the habitat-patch hypothesis but is consistent with the habitat-amount hypothesis. Differences between species accumulation curves in a SLOSS-type analysis, however, were inconsistent with both hypotheses.

While other studies have documented effects of local habitat amount (patch size; reviewed by Müller and Büttler 2010, Seibold et al. 2015a) or effects of landscape-scale habitat amount (Ranius et al. 2011, Nordén et al. 2013, Abrego et al. 2015, Buse et al. 2015) on diversity of saproxylic taxa, ours is the first to estimate the interaction effect of patch size and habitat amount in the local landscape. Ranius et al. (2011), for example, recorded increasing numbers of saproxylic insects on experimental dead-wood plots with increasing amount of dead wood in local landscapes (93 m radius). But as the same amount of dead wood was added to all plots, patch size did not vary, and hence, no interaction with amount of habitat in local landscapes could be tested. Thus, previous studies do not provide evidence for the occurrence or lack of occurrence of an island effect on saproxylic beetle richness. In one recent study of saproxylic beetles in Brazilian Atlantic forests, both local patch size and habitat amount in surrounding landscapes were measured, but the data have not yet been used to test the

habitat-amount hypothesis (Araujo et al. 2015). A lack of an island effect is supported by the finding that forests originating from afforestation of agricultural fields hold the same number of saproxylic beetle species as forests that have never been converted to a different land-use form as long as local dead-wood resources are high (Janssen et al. 2016). And also low genetic differentiation among populations of saproxylic insects even over hundreds of kilometers suggests that the dispersal capacity on the population level is strong and migratory barriers are weak, at least over several generations (Ranius and Douwes 2002, Oleksa 2014, Drag et al. 2015).

In our study, the local landscapes (i.e., the spatial extent within which surrounding habitat amount most strongly affects species numbers and beyond which additional habitat has only minor effects (Fahrig 2013) were estimated to be 40–120 m around sample plots. Theoretical work suggests that the radius of the local landscape is about 0.3–0.5 of the maximum dispersal range of an individual (Jackson and Fahrig 2012). Thus, our results suggest relatively short dispersal ranges for saproxylic beetle individuals in our study area. Other studies of saproxylic beetles have found spatial extents of landscape context effects on species numbers ranging from tens to thousands of meters (Rukke and Midtgaard 1998, Ranius et al. 2011, Bergman et al. 2012, Jacobsen et al. 2015). The sizes of local landscapes in our study were thus at the lower end of this range, similar to those of another study in an area with high forest cover (Ranius et al. 2011). The very large scales have been found, for example, for the number of species occurring on hollow oaks scattered across a region dominated by coniferous forest and arable fields, but even in that situation, some individual species showed scales of effect smaller than 100 m (Bergman et al. 2012). While flight-mill experiments indicate that some saproxylic beetle species are able to fly for 2–120 km (Jonsson 2003, Dubois et al. 2010, David et al. 2014), mark-recapture and radio-telemetry approaches have shown that dispersal ranges of the same or closely related species are regularly only 50–180 m in their natural environment (Shibata 1986, Starzomski and Bondrup-Nielsen 2002, Hedin et al. 2008). This suggests that dispersing saproxylic beetles tend to fly shorter distances if suitable new habitat is present. We speculate that new dead wood in ecosystems with a continuous forest cover is produced continuously over time in a relatively even spatial distribution, allowing dispersing beetles to reach new suitable resources within a shorter distance than in regions where trees are more sparse and typical dead-wood habitats, such as tree hollows, develop slowly.

Based on the habitat-amount hypothesis, species accumulation curves relative to cumulative patch area should be the same irrespective of the order of added plots (Fahrig 2013). In contrast to this prediction, and also in contrast to the prediction of the habitat-patch hypothesis, we found that species accumulated faster when plots were ordered according to increasing patch size than

when ordered according to decreasing patch size. This result is very similar to results of typical SLOSS analyses, which consistently report that several small habitat patches contain more species than a single large patch with an area equal to the sum of the areas of the small patches (Tschardt et al. 2002a, Hokkanen et al. 2009, Rösch et al. 2015). These studies regularly attribute this pattern to higher habitat heterogeneity represented by several small patches than a single large patch. Habitat heterogeneity with regard to, e.g., diameter of dead wood or microclimatic conditions, is an important driver of the diversity of saproxylic beetles (Seibold et al. 2016b) and beta-diversity of saproxylic beetle communities between forest stands is high (Müller and Gofner 2010). Thus, increasing habitat heterogeneity likely explains why we found that several small patches hosted more saproxylic beetle species than a single large patch (Fig. 4).

As mentioned earlier, a possible criticism of our test of the habitat-patch hypothesis is that the habitat in our system—dead wood—is dynamic, while the theory underpinning the habitat-patch hypothesis assumes a static habitat distribution that allows an equilibrium between species extinctions and colonizations. We evaluated whether our study duration of 3 yr was sufficient to observe an equilibrium between local colonizations and local extinctions. In our experimental system, we observed an increase in species number from year one to year two, which indicated initially more local colonizations than local extinctions. However, species number decreased from year two to year three (Appendix S2: Fig. S3), which suggested that local extinctions exceeded colonizations by the second year. This suggests that extinction and colonization rates were similar during the middle period of our study, and thus, that the assemblages were at equilibrium at least for a certain period. To evaluate the influence of a potential lack of equilibrium on our conclusions, we repeated our analyses for each year separately. These analyses produced results (not shown) similar to those of our analysis for the assemblages pooled over the 3 yr. The fact that the results were similar even in the second year when the system was at or about equilibrium reinforces the lack of support in our data for the island effect. Although we are confident that our study system is suitable for testing the habitat-patch hypothesis, it would be interesting to see whether a less dynamic habitat system would result in stronger support for the habitat-patch hypothesis.

When the habitat-amount hypothesis was first proposed, Hanski (2015) suggested that it might be valid only in small areas with a large total habitat amount. Our plots varied widely in the amount of dead wood in the local landscapes (Appendix S1: Fig. S3), covering the complete range of observed amounts in temperate European forests (Müller et al. 2010). Therefore, the range in habitat amounts in our study did not limit our ability to detect an island effect. Regarding the size of the study area, Hanski (2015) did not specify how large an area would be necessary to disprove the habitat-amount

hypothesis. Our study spanned 22 km, but the relevant scale for estimating habitat amount was very small (i.e., a circular area of 40–120 m radius around the sample plots). It is therefore possible that the habitat-amount hypothesis will be disproved in a different system in which the size of the relevant local landscape is much larger. This remains to be tested.

Hanski (2015) also suggested that multispecies analyses of island effects might be misleading, as species differ in their habitat requirements and in their sensitivities to habitat isolation. We therefore divided the saproxylic species into subgroups based on species traits assumed to affect the vulnerability of the species to habitat isolation (Tschardt et al. 2002b, Ewers and Didham 2006). However, none of the evaluated subgroups showed a significant interaction between local and landscape habitat amount (Table 1). Thus, the habitat-amount hypothesis was also supported when we focused on ecologically homogeneous species groups. Similarly to Hanski's (2015) concern about multispecies analyses, the use of flight-interception and pitfall traps, which do not differentiate between transient species not associated with the exposed dead wood and species colonizing it or emerging from it (Appendix S1), might have reduced our ability to find an island effect. However, we adjusted for this by analyzing the data separately for species associated with different decay stages. Early-decay species are most strongly associated with the exposed dead wood in our experiment, and their response was similar to that of all saproxylic species combined (Table 1). This indicates that the inclusion of potential transient species did not affect our conclusions. As expected, late-decay-stage species did not respond to added downed dead wood (Table 1) at an early stage of decay.

Island effects might depend on the type of matrix surrounding the habitat (Tschardt et al. 2012), and saproxylic species might not only be affected by loss of dead wood but also by loss of forest area. Therefore, it is possible that an island effect would be detected in a region where not only the amount of dead wood varies but also the amount of forest. On the other hand, local extinctions of saproxylic species owing to reduced dead-wood amount have been observed in areas with stable forest area (Speight 1989, Müller et al. 2010). This suggests that dead-wood amount is the more meaningful habitat variable (Hottola et al. 2009). In addition, colonization by saproxylic beetles of experimentally exposed fungal fruiting bodies in agricultural fields indicates that non-forest habitat may not inhibit colonization of these species (Jonsell et al. 1999). Nevertheless, it remains to be seen whether island effects appear when dead trees are distributed within other landscape contexts, such as agricultural or urban regions.

Conservation, for instance on a national level, usually aims at maintaining viable populations of all native species, particularly threatened species. But resources available for conservation are limited. Consideration of the spatial arrangement of conservation measures is both

labor and time intensive and restricts the area available for conservation. The spatial arrangement of conservation measures should thus only be considered on scales, in ecosystems and for species groups for which we have clear evidence that the spatial arrangement of habitat matters. A conservation strategy to promote and maintain viable populations of saproxylic beetle species, pursued for example in Germany, is to increase dead-wood amounts in many forest stands throughout the country (Neft 2006, BMUB 2007) because the distribution of most species is only roughly known. In particular, it targets timber production forests which comprise the vast majority of forests in Central Europe and aims at restoring dead-wood amounts similar to natural forests. It includes financial incentives for private forest owners and management goals for public forests. Our results show that the number of saproxylic beetle species increases locally in proportion to the amount of added dead wood independent of the amount of dead wood already present within local landscapes and thus irrespective of the spatial arrangement of dead-wood additions. This indicates that forest managers should increase dead-wood amounts wherever and whenever possible including in local landscapes with low or high dead-wood amounts. Dead wood amount can be increased by for example intentional creation of dead wood, retention of woody residuals during logging operations and retention of dead trees created by natural disturbances. Moreover, our results suggest that many smaller patches with dead wood should promote higher total species numbers than a single large patch equal in amount to the sum of the smaller patches, likely by providing higher habitat heterogeneity. Such a strategy will be faster and cheaper in reaching the minimum amount of dead wood needed to maintain viable populations of all extant saproxylic beetle species than a detailed consideration of spatial patterns.

However, some saproxylic species have disappeared from most production forests because they require a continuous supply of high dead-wood amounts and are nowadays restricted to a few—often protected—forest stands with sufficient habitat (Müller et al. 2005). To protect these demanding species, there is no doubt that conservation measures, such as promoting veteran trees or high quality dead wood, have to be spatially explicit, meaning that they have to be applied within their extant distributional ranges, to allow colonization. Combining a strategy to increase dead-wood amounts in production forests without consideration of its spatial arrangement and some spatially explicit conservation measures for species that survived only in a few restricted populations is probably the most efficient strategy to maintain viable populations of all saproxylic beetle species.

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