



Habitat connectivity affects specialist species richness more than generalists in veteran trees



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ABSTRACT

Intensified human land use continues to increase habitat loss and fragmentation, and leads to a homogenization of biodiversity. Specialized species with narrow niches seem to be declining more rapidly than generalist species. Veteran trees offer an excellent model system for testing the responses of habitat specialists vs. generalists in a changing environment, as they host a rich fauna of associated insects, with different degrees of strict habitat affinity.

In this study, we use an extensive dataset of more than 22 000 wood-living beetles collected from 62 veteran oaks across Southern Norway, combined with a full-cover map predicting the occurrence of similar oaks in the surrounding landscape. We calculate three different connectivity measures, at eight different scales up to 25 km radius, and compare the response to patch size and patch connectivity for the specialist beetles in the veteran oak community, with that of the remaining beetle species in the community. We investigate these responses in oaks in two different surroundings; forests and parks. Our overall aim is to test whether habitat specialists and generalists respond differently to habitat patch connectivity, and if so, if differences in species traits or close surroundings can explain the response.

We found that the specialists showed a positive response to habitat amount on a small scale (0.5 km), and this effect of small-scale connectivity was the only common factor explaining a high species richness of specialists in all models, independent of park or forest surroundings. For generalists, there was no or only a weak response to connectivity, and only at the largest scale (25 km) tested.

The differences in response to habitat connectivity between specialists and generalists in veteran oaks can partly be explained by differences in traits, as the specialists were found to have larger body sizes, and feed on larger and more decayed dead wood material. These are all traits that have been related to increased sensitivity to forest fragmentation in earlier studies. The size and vitality of the oak, as well as the openness around it, also influenced the species richness, with different patterns between specialists and generalists and between the two types of oak surroundings.

We conclude that increasing biotic homogenization is likely to take place with further fragmentation and loss of veteran trees, and specialist species will be the major group affected.

1. Introduction

Understanding how biotic communities respond to spatial landscape structures is critically important for conservation management (Miller et al., 2015). At present, human land use and the resulting habitat fragmentation is one of the greatest threats to global biodiversity (Dirzo et al., 2014; Newbold et al., 2015), but the loss of biodiversity is not occurring at random: Mounting evidence suggests an ongoing

homogenization of biodiversity (Solar et al., 2015; Wang and Loreau, 2016), with specialist species across taxa declining more rapidly than its wide-niched counterparts (reviewed in Devictor et al., 2008).

The disproportional loss of biodiversity among specialists might reflect unfavorable life history traits within this group, relative to present habitat fragmentation. Previous reviews support that traits reflecting high habitat affinity can make species more sensitive to fragmentation (Henle et al., 2004; Keinath et al., 2017), because habitat

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specialists adapted to a specific resource are likely to be affected more from loss or fragmentation of this resource than habitat generalists occupying the same resource (Miller et al., 2015).

Veteran trees represent a patchy habitat well known for its rich and specialized biodiversity, including a high number of rare and endangered species (Siitonen and Ranius, 2015). The trees have distinctive characteristics and microhabitats such as cavities with nutrient-rich wood mould, cracked, thick bark, and complex canopy structures including dead branches (Lindenmayer and Laurance, 2016). Oaks in this stage are known to host a suite of highly specialized invertebrates that are dependent on specific microhabitats for their development (Ranius and Jansson, 2000; Ohsawa, 2007; Sirami et al., 2008; Sverdrup-Thygeson et al., 2010). At the same time, the trees also provide habitat for large groups of wood-living invertebrates with wider ecological niche breadth; species that may also complete their life cycle in dead oak wood of smaller and younger trees, or even in other tree species.

The veteran oaks represent a stable habitat, which can remain suitable for the specialized invertebrate fauna for hundreds of years (Ranius et al., 2009; Sverdrup-Thygeson et al., 2010). In recent time, the density of old and senescent trees in European forest has been drastically reduced from its reference state in old-growth forest (Hannah et al., 1995). The prevalence of veteran oaks is on average very low, but highly variable geographically (Skarpaas et al., in press). Based on the vulnerability of specialized species to habitat fragmentation, one would therefore expect the amount of suitable habitat patches (veteran oaks) in the surroundings to be of much larger importance for specialists than generalists in this system. Veteran oaks thus provide an excellent model system for testing the responses of habitat specialists vs. generalists to the amount and connectivity of habitat.

Scaling is a major limitation in many studies of habitat fragmentation. In a recent review, Jackson and Fahrig (2015) concluded that most ecological studies fail to identify the appropriate scale for their study. Investigating a wide range of scales around the focal patch will improve the chance of detecting meaningful relationships between ecological phenomena and landscape (Jackson and Fahrig, 2015). Therefore, habitat data should be collected at multiple scales, including large scales. In reality practical concerns often limit the spatial extent of fragmentation and connectivity studies.

Beside scaling, the quality of the surrounding matrix has been recognized as a strong modifier of habitat fragmentation effects (Franklin and Lindenmayer, 2009). The theory of island biogeography was developed for a favorable habitat (e.g. true islands) embedded in a matrix of hostile habitat (ocean), with island size and isolation as the most important determinants of species richness (MacArthur and Wilson, 1967). In terrestrial environments, however, these contrasts are not common, and many species may breed and find resources outside what is assumed to be their optimal patch (Prugh et al., 2008). As the ability to find resources in the matrix might differ between species with different degree of habitat affinity, one might expect surroundings to affect specialist and generalist species differently.

Habitat connectivity has been studied for a range of organisms, and while it has proven to be of high importance for species richness in some studies (e.g. for plants in grasslands (Münzbergova et al., 2013; Evju and Sverdrup-Thygeson, 2016) and for wood-living fungi in forest (Nordén et al., 2013)), other studies have found no such effect (Krauss et al., 2004; Bisteau and Mahy, 2005). Previous studies on beetles living in oaks in Sweden indicate responses to connectivity on a range of scales, depending on the species. Ranius et al. (2011) found that the connectivity measure that generated the best fit varied between 135 and 2857 m in radius, with longer distances for more threatened species. Bergman et al. (2012) found relationships with oak density at scales ranging from 52 m to more than 5200 m, with a characteristic scale of response at 2284 m.

In this study, we seek to quantify the effect of connectivity while taking scaling and matrix quality into account. We use an extensive and

large-scale dataset of beetles in 62 veteran trees across Southern Norway, and combine it with a full-cover map of the probability of veteran oak occurrence in the surrounding landscape (Skarpaas et al., in press). This permits the calculation of patch connectivity at different scales. In addition, the study is carried out in two different habitat types; forests and parks, representing contrasting small-scale matrixes.

We compare the response of the specialist beetles in the veteran oak, and the remaining oak-associated wood-living beetle community, to patch size and patch connectivity. The veteran trees represent local habitat patches, which are also described by their size (circumference) and quality (openness and tree vitality) in the analysis.

To understand the response of narrow-niched specialists and broad-niched generalist species to landscape structures, in these diverse beetle assemblages, we address the following questions:

- Do habitat specialists and generalists respond differently to habitat connectivity, if so at what scales? Does the effect of habitat connectivity change with different connectivity measures, or when considering oaks in different surroundings?
- Can trait information help explain the responses to connectivity?

We expect that specialists will be more strongly affected by low or high habitat connectivity than the generalists. Specialists may also react at smaller scales, as required resources are more sparsely distributed. In fragmented landscapes specialist species will then reach their extinction threshold before the generalists (Nordén, 2013 #7931). Such differences in the responses of habitat specialists and generalists may be related to differences in traits that characterize vulnerable species in dead wood ecosystems; body size, trophic level and preferences for large tree diameter and late-stage wood decay (Seibold et al., 2014; Bouget et al., 2015). We therefore test for such differences, and expect that the specialists on veteran oaks will be larger and depend on coarser and more decayed wood, than the generalists.

2. Material and methods

2.1. Study area and beetle sampling

The study was carried out in Southern Norway, covering the main distribution of oak (*Quercus* sp.) in Norway. The data set used in this study is a part of a long-term study of veteran oaks, as part of the National Program for Surveying and Monitoring Biodiversity in Norway (ARKO, 2011). It includes data from 62 oak trees at 29 sites, where a hollow oak was defined as a tree of at least 95 cm circumference with a visible cavity in the trunk, as per the Regulation on Selected Habitats 2011 (Lovdata, 2011).

Each oak tree was sampled for beetles in one to seven years between 2004 and 2011 (20 trees sampled for 1 year, 27 trees for 4 years and 15 trees for 5 years). The unequal number of trapping years is adjusted for in analyses, see below). Two flight interception traps (20 cm × 40 cm windows, traps with ethylene glycol and detergent) were used per tree, one directly in front of the cavity opening and one in the canopy. Traps were emptied once a month between May and August. The sampling process is described in detail in Sverdrup-Thygeson et al. (2010). Species counts were summed per tree for each year.

All beetles were identified to the species level following the taxonomy of The Norwegian Biodiversity Information Centre (<http://doi.org/10.15468/4dd3tf>). We used existing literature to classify wood-living beetle species as:

- (1) Species dependent on old veteran oaks. Primarily cavity dwellers, but also species with other niche requirements associated with veteran oaks (Bergman et al., 2012; Agency, 2012), hereafter called “specialists” (48 species, see Supplementary), and
- (2) Remaining species in the oak-associated wood-living beetle community (517 species, see Supplementary). This group contains oak-

associated beetle species with various degrees of oak affinity that can make use of old oaks but are not dependent on this specific resource. Therefore, with respect to veteran trees, we call them “generalists” in the context of this paper.

For trait analyses, we chose traits that are known to be associated with stenotopic or eurytopic saproxylic beetles (Holt et al., 1999; Seibold et al., 2014; Brin et al., 2016); body size, wood-diameter niche and decay niche. Data on the mean body sizes (mm) were collated from Gillespie et al. (2017) (data for 99% of the included species), while the remaining trait data were compiled from Seibold et al. (2014) (data for 76% of the included species). For calculation of the dimensionless wood-diameter niche and decay niche, see Appendix 1 in Seibold et al. (2014). Species without available trait data were excluded from the trait analyses.

2.2. Patch, surrounding habitat type, and connectivity

We assessed veteran oaks in two habitat matrices, depending on the dominating habitat in the closest surroundings (~50 m radius): 39 oaks were located in forests, mostly managed forest that contained a diversity of other tree species and some decaying wood. The remaining 23 oaks were located in either parks or agricultural landscapes, surrounded by fields or gardens with low amounts of dead wood.

Each oak represents a habitat patch, and we used oak circumferences to reflect patch size. Patch quality was represented by two habitat variables shown to be important in several oak-beetle studies (Ranius, 2002; Vodka et al., 2009; Sverdrup-Thygeson et al., 2010); the vitality of the oak and openness (Table 1). The method for field measurements is described in more detail in Sverdrup-Thygeson et al. (2013).

We calculated connectivity based on a prediction model of veteran oak occurrence based on a mixture of ecological and anthropogenic factors. Our model produced a 10 × 10 m raster map of probability of veteran oak occurrence (Skarpaas et al., in press). Based on this map, we calculated three different connectivity measures, for each of eight different buffer distances from each focal oak. As a previous study of oak beetles found the characteristic scale of response for species richness of oak specialist species to be 2284 m (Bergman et al., 2012), while Ranius et al. (Ranius et al., 2011) found that the best fit for threatened species was generated for radii of a few kilometers, we chose to use buffer distances of 0.5 km, 1 km, 2 km, 3 km, 4 km, 5 km, 10 km and 25 km.

All connectivity measures were based on the summed predicted

Table 1
Description of variables used in the study. More detailed descriptions can be found in Sverdrup-Thygeson et al. (2013).

Variable	Type	Measurement
Circumference	Continuous	In cm
Surroundings	Categorical, 2 levels	Park: Oak situated in parks, agricultural landscapes or similar surroundings Forest: Oak situated in forested surroundings
Vitality	Categorical, 3 levels	Low: less than 20% of canopy alive and vital Medium: 20–50% of canopy alive and vital High: more than 50% of canopy alive and vital
Regrowth	Categorical: 3 levels	Open: No regrowth around oak Scrubs: Regrowth by low vegetation; scrubs, small trees Trees: Regrowth of a height similar to the oak itself
Connectivity	Categorical, 8 levels	0.5 km, 1 km, 2 km, 3 km, 4 km, 5 km, 10 km and 25 km

occurrence probabilities for all pixels within the given radii, but with three different adjustments for spatial configuration:

- (1) No adjustment
- (2) Linear down-weighting with increasing distance from the focal tree with a weighting factor between 1 at the focal oak and 0 at current buffer distance.
- (3) Exponentially down-weighting with increasing distance from the focal tree with a weighting factor between 1 at the focal oak and almost 0 at current buffer distance (the weighting factor was determined by the following formula: $\exp(-3.25 * ((10.0^d - 4.75) * (d * 100000.0/b)))$), where d is the distance of a particular pixel in the prediction model and b represents the current buffer distance. The values were chosen to consistently achieve a weighting-factor value close to zero at the buffer distances).

2.3. Statistical analyses

First, we used ANOVA to analyze trait differences between specialists and generalists. We then investigated the strength of the relationship between species richness and connectivity at different spatial scales. To identify the spatial scale(s) where the relationship between species richness and habitat amount was the strongest (‘scale of effects’, sensu Holland et al., 2004; Fahrig, 2013), we calculated Pearson’s correlation coefficient r for each spatial scale.

Using the connectivity value of scale(s) thus found, as well as the environmental variables, we constructed regression models for generalists and specialists, respectively. None of these variables were strongly collinear ($R^2 > 0.7$). We used generalized linear mixed-effects model (GLMM) for the Poisson family and included site, tree and sampling year as random factors, to adjust for the unequal sampling effort between sites, repeated sampling of trees and year-to-year variation. We centered and scaled all predictor variables by one standard deviation, to facilitate the interpretation of the relative importance of the predictors (Nakagawa and Cuthill, 2007). We checked for overdispersion of the residuals in the global model for each species group, and inspected model validation plots to ensure normal distribution of residuals and homoscedasticity. The initial analysis revealed an extreme outlier in the dataset; a tree about to die in the year of our trapping, attracting a very high number of species. Although this is an ecologically relevant pattern, the inclusion of this tree prevented construction of meaningful models and we therefore chose to exclude it.

Spatial analyses were conducted with GRASS GIS 7.0.4 (GRASS GIS Development team 2016), and statistical analyses were performed in R version 3.2.2 (R Core Team 2015) using the packages nlme (Pinheiro et al., 2013) and lme4 (Bates et al., 2014).

3. Results

Our dataset contained 28 762 individuals (842 species) of beetles. Of these, 22 699 individuals (322 species) were wood-living species associated with oak and included in the analyses. A total of 10 223 individuals, belonging to 48 species, were defined as specialists on old, hollow, veteran oaks, while the remaining individuals were defined as generalists (12 476 individuals, 274 species). Two specialist species were numerous and accounted for 88% of the specialist individuals; *Euglenes oculatus* (6814 individuals) and *Dorcatoma chrysomelina* (1827 individuals), while 27 specialist species occurred with 10 or fewer individuals.

3.1. Comparing traits for specialists and generalist

ANOVAs comparing the mean trait values for specialists versus generalists showed that specialists were larger than the generalists (mean size: specialists: 5.33 mm [95% CI 4.34–6.32 mm], generalists: 4.15 mm [95% CI 3.84–4.46 mm], $p = 0.03$). Specialists were also

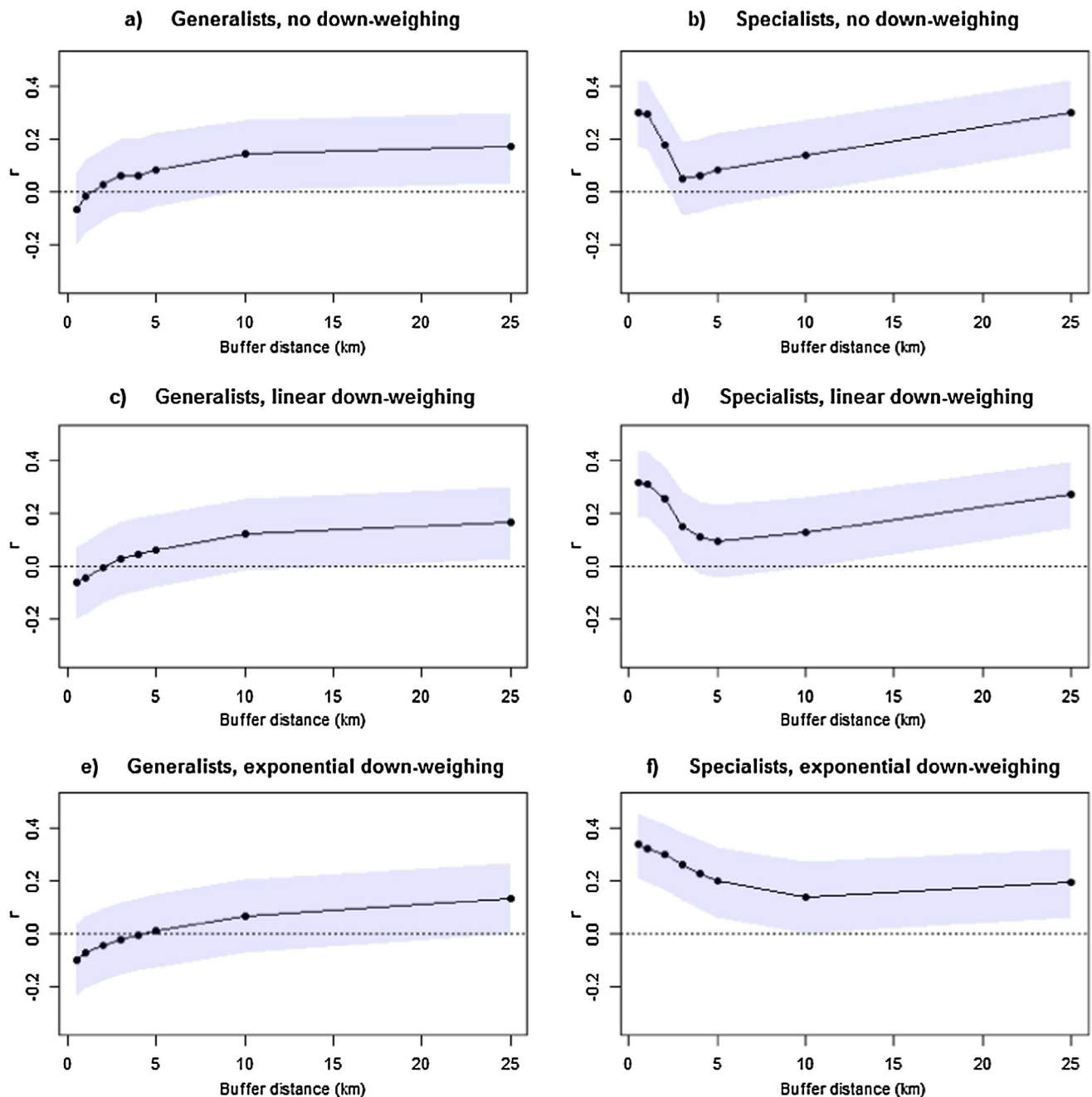


Fig. 1. Plot of correlation coefficient (Pearson's r , with confidence intervals (gray shading)) between species richness of generalists (a, b, c) and specialists (d, e, f) and three different measurements of connectivity, across eight spatial scales from 0.5 km to 25 km.

associated with larger and more decayed wood (mean diameter niche (dimensionless): specialists 3.22 [95%CI 3.00–3.44], generalists: 2.33 [95% CI 2.26–2.41], $p < 0.001$); mean decay niche (dimensionless): specialists 3.67 [95% CI 3.46–3.89], generalists: 2.98 [95% CI 2.89–3.07], $p < 0.001$).

3.2. Modelling species richness and connectivity

The correlation between species richness and connectivity on different scales showed contrasting patterns for generalists and specialists at all three connectivity measurements (Fig. 1).

For the generalist species, the correlations were mainly negative, but increased with scale. All correlations were rather weak, and had confidence intervals including zero for almost all scales. The highest absolute value of the correlation coefficient was found at the largest

scale, 25 km, for all connectivity measurements.

For the specialists, the correlations showed a u-shaped relationship with scale: they were highest at the smallest scale, 0.5 km, decreased for intermediate scales (with confidence intervals including zero) and increased again up to the largest scale included, 25 km radius.

Down-weighting the probability scores with increasing distance (either linearly or exponentially, Fig. 1 e and f) dampened these differences, but the broad patterns were similar. As the model without down-weighting is easier to understand and has been shown in comparisons for similar datasets to give good predictions (Ranius et al., 2010), we decided to use that connectivity measure in the regression models.

Based on the correlation between species richness and the buffer measurement, we identified 25 km as the “scale of effect” (sensu Holland et al., 2005; Fahrig, 2013), i.e. the scale with the highest

Table 2

Results of full models of species richness of specialists and generalists, for pooled data and for forest and park oaks separately (generalized linear mixed models, Poisson distribution, log link). Significant relationships in bold. All continuous variables are scaled (see text). The number of variables varies between models, as the variable Surrounding is not a relevant variable in the models for only park or only forest oaks, the categorical variables Vitality cannot be included in park oak models as too few park trees belong to the lowest level, and for the categorical variable Regrowth, the level Regrowth (Trees) does not exist in parks.

Variable	Estimate	Std. error	z-value	p-value
<i>Response: Generalists, pooled</i>				
(Intercept)	2.530	0.108	23.456	< 0.001
Circumference	-0.071	0.031	-2.255	0.024
Surrounding (Park)	-0.303	0.081	-3.754	< 0.001
Vitality (Low)	0.096	0.086	1.118	0.264
Regrowth (Scrubs)	0.232	0.105	2.214	0.027
Regrowth (Trees)	0.010	0.081	0.123	0.902
Connectivity (25 km)	0.017	0.030	0.574	0.566
<i>Response: Generalists, forest</i>				
(Intercept)	3.009	0.095	31.730	< 0.001
Circumference	-0.127	0.032	-3.980	< 0.001
Vitality (Low)	0.107	0.099	1.080	0.278
Regrowth (Scrubs)	0.325	0.110	2.950	0.003
Regrowth (Trees)	0.186	0.078	2.400	0.017
Connectivity (25 km)	0.076	0.036	2.130	0.033
<i>Response: Generalists, parks</i>				
(Intercept)	2.775	0.162	17.174	< 0.001
Circumference	-0.016	0.046	-0.342	0.732
Regrowth (Scrubs)	0.608	0.235	2.593	0.010
Connectivity (25 km)	0.019	0.095	0.205	0.837
<i>Response: Specialist species, pooled</i>				
(Intercept)	1.189	0.173	6.859	< 0.001
Circumference	0.163	0.063	2.612	0.009
Surrounding (Park)	-0.436	0.215	-2.032	0.042
Vitality (Low)	0.541	0.194	2.783	0.005
Regrowth (Scrubs)	-0.147	0.210	-0.699	0.484
Regrowth (Trees)	-0.799	0.256	-3.127	0.002
Connectivity (25 km)	-0.094	0.094	-1.006	0.314
Connectivity (0.5 km)	0.376	0.096	3.906	< 0.001
<i>Response: Specialists, forests</i>				
(Intercept)	1.006	0.211	4.774	< 0.001
Circumference	0.004	0.089	0.051	0.960
Vitality (Low)	0.409	0.162	2.521	0.012
Regrowth (Scrubs)	-0.078	0.227	-0.343	0.731
Regrowth (Trees)	-0.612	0.302	-2.025	0.043
Connectivity (25 km)	-0.088	0.144	-0.611	0.541
Connectivity (0.5 km)	0.393	0.152	2.593	0.010
<i>Response: Specialists, parks</i>				
(Intercept)	0.762	0.094	8.137	< 0.001
Circumference	0.331	0.069	4.833	< 0.001
Regrowth (Scrubs)	-0.362	0.344	-1.051	0.293
Connectivity (25 km)	-0.080	0.084	-0.947	0.343
Connectivity (0.5 km)	0.254	0.076	3.341	< 0.001

absolute value of the correlation coefficient), for generalist species (Fig. 1a–c). The buffer connectivity measurements on the 25 km scale were therefore included in the subsequent analyses of generalist species richness.

For the specialist species, no obvious single scale of effect could be identified, as the relationship strength was very similar for 0.5 km and 25 km (and both with confidence intervals not including zero) (Fig. 1d–f). The connectivity measurements for 0.5 km and 25 km were also not highly correlated (Pearson correlation coefficient = 0.54). We therefore included the buffer connectivity measurements for both 0.5 km and 25 km scales in the further analyses of specialist species richness.

3.3. Effect of connectivity and surroundings on generalist species richness

The overall species richness of generalists was highest in small trees in forest surroundings and could be partly explained by local patch

quality linked to openness (lack of regrowth). However, habitat connectivity did not significantly affect the species richness (Table 2).

When we repeated the analysis of species richness for forest oaks and park oaks separately, the results in the forest were similar to the overall results: Most species occurred in small trees surrounded by a field layer of either scrubs or trees. However, high connectivity on the 25 km scale also increased species richness in the forest (Table 2). In the parks, the only significant variable explaining generalist beetle species richness was scrubs in the field layer surrounding the oaks (Table 2).

3.4. Effect of connectivity and surroundings on specialist species richness

The species richness of specialists increased significantly with increasing habitat connectivity at the 0.5 km scale, in all analyses independent of surroundings (Table 2). As opposed to the generalists species richness described above, the species richness of specialists increased as the trees got larger, and regrowth by surrounding trees had a rather large, negative effect on species richness in the overall analyses. These analyses also revealed a large, positive effect of reduced oak vitality.

In addition to the increase in species richness with connectivity at the 0.5 km scale, the number of specialists increased with openness (lack of regrowth) around the oaks and low tree vitality in forest, whereas tree size had a large effect in parks.

4. Discussion

The unique biodiversity of beetles in veteran trees responded in accordance with our hypotheses: Specialist species showed a positive response to habitat amount at a smaller scale than generalist species. The small-scale (0.5 km) connectivity effect was retained when including predictors describing oak size and quality in the models. The scale of effect for the generalists, on the other hand, was much larger (25 km) and the effect of connectivity was unclear and only partly retained in the full models.

The size and vitality of the oak, as well as the openness around it, also influenced the species richness, with important differences between specialists and generalists and the two types of surroundings.

4.1. Connectivity on small scales most important for specialists

Our findings partly concur with a recent study of beetles in oak by Buse et al. (2016), who studied abundance responses of different trophic levels to small-scale connectivity. They found that species abundance in higher trophic levels (predators) increased with increasing patch connectivity, but lower trophic levels were unaffected or even decreased with increasing patch connectivity. Although we did not focus on trophic levels, we know that several of our specialist species are predators. On the other hand, Ranius et al. (2011), in their study of a range of buffer distances, found that the more threatened beetles (partly similar to our group of specialist species) responded at larger scales than less threatened beetles, which is opposite of our results.

One important explanation for different results could be that landscapes differ in their amount and configuration of patches, as well as patterns of occupancy, and this may influence the detected patterns. This might also explain why Bergman et al. (2012), in their study of 35 beetle species associated with old oaks, found the maximum correlation between species richness of oak specialist species and oak density to be four times the distance found in this study (500 m vs 2284 m).

That connectivity influenced species richness of specialists on a small scale in all our models, is consistent with ecological theory. Natural selection induces more or less specialized strategies among species. There is an evolutionary tradeoff between specializing to perform well in strictly defined habitat conditions, versus generalizing to perform fairly across a range of conditions (Devictor et al., 2008). In an unfragmented natural environment, specialists might persist because

they have a higher fitness in the habitat they are adapted to, than a generalist utilizing the same habitat (HilleRisLambers et al., 2012; Buchi and Vuilleumier, 2014). However, in a human-altered landscape, where fragmentation has increased the distance between the unique habitats required by the specialists, these adaptations might be maladaptive and increase the likelihood of extinction.

Nordén et al. (2013) argued that suitable resources for specialists – like veteran trees – will be more sparsely distributed than resources required by generalists, so even with similar dispersal abilities, specialists are expected to be the first ones to fall below their extinction threshold in a fragmented landscape. This could generate a positive relationship with connectivity at a small scale like we see for the specialized species in this study.

4.2. Does it matter how we measure connectivity?

In this study, we tested three different connectivity measures, with no, linear, or exponential down-weighting of distant patches, and found only small differences. This could be because the effect of distant patches was insufficient to make down-weighting matter. It could also be due to a larger variation in connectivity at large scales being lower than at smaller scales, making it difficult to detect any differences.

Our results concur with a modelling study of beetles in hollow oaks in Sweden, where Ranius et al. (2010) compared six different connectivity measures for eight oak-associated beetles. They found that the simple buffer measure of available habitat within a radius, comparable to our first connectivity measure, performed better for most species than more complex measures (Ranius et al., 2010). They hypothesize that down-weighting distant patches does not improve connectivity models as beetle dispersal is an active process that is less limited by distance than passive dispersal of seeds and fungal spores at the scales tested.

4.3. Surroundings modulate responses

We tested our hypotheses in two different surroundings and found substantial differences in the response to connectivity for generalists, in addition to large effects of other predictors for both generalists and specialists. This was expected, as the habitats around patches are known to be a strong determinant of fragmentation effects. This is because of its effects on regulating dispersal, providing resource subsidies and influencing micro-climatic edge effects (Ewers and Didham, 2006).

While connectivity restricted species richness of specialists independently of their surroundings, species with a wider niche show different responses according to the surroundings. Most likely, the responses of generalists are related to more habitat available in the forest correlating with the hollow oak occurrence.

In parks, the species richness of specialists is further related to oak size, whereas in forests, the negative effect of regrowth is more important. The shading effect of regrowth probably reduces the ambient temperature in the oak microhabitats, and the negative effects of regrowth around the oak is in line with other studies of specialized oak beetles (Ranius and Jansson, 2000; Widerberg et al., 2012; Gough et al., 2014). Generalists, on the other hand, respond positively to regrowth in both parks and forests. Wood-living generalists are probably less sensitive to temperature than the specialists are (Gough et al., 2015). Regrowth might also indicate more supplementary dead wood resources, as indicated above, and explain the positive effect for the generalists.

A competitive advantage of specialists in their optimal habitat can be thought of as a prerequisite for their survival, and has been shown in other systems (Futuyma and Moreno, 1988). Thus, if specialists are better competitors in high-quality patches (larger trees), this might simultaneously reduce generalist species richness. Such a mechanism might explain the decrease of specialist richness in the forest with decreasing oak size as well as the increase of specialist richness with tree size in parks. Why this pattern is not present in both parks and forests,

for both specialists and generalists, is unknown. Possibly, competition could be more dependent on specialist abundance in the forest.

4.4. Specialists are characterized by different set of traits than generalists

The specialists found in our study were larger than the oak-associated generalists, and the specialists also occurred on dead wood of larger dimensions and later stages of decomposition. Species adapted to similar conditions generally share several life history traits due to similar trade-offs and evolutionary history, and trait-based approaches have been suggested as a useful method to evaluate impacts of habitat fragmentation and connectivity for a range of taxa (Öckinger et al., 2010; Nordén et al., 2013; Evju et al., 2014; Sverdrup-Thygeson et al., 2014; Villemey et al., 2015; Keinath et al., 2017).

Large wood-living beetles are sensitive to extinction and are absent from forest areas with short continuity (Davies et al., 2000; Seibold et al., 2014; Brin et al., 2016). This corresponds well with our specialists that live in trees of large-diameter trunks and coarse branches as well as cavities with highly decomposed wood mould – resources not commonly found elsewhere in a managed forest. Other studies have confirmed the importance of sites with large-diameter deadwood both for such sensitive beetles (Brin et al., 2011; Gossner et al., 2013) and specialized fungi (reviewed in Junninen and Komonen, 2011). Thus, the differences we found in response to habitat connectivity between specialists and generalists in veteran oaks can at least partly be explained by differences in traits.

5. Conclusions

To understand responses of narrow and broad-niched species to landscape structures in communities with exceptionally high diversity, we investigated species richness of beetles in veteran oaks across a range of habitat connectivity and in two different types of surroundings. Based on our results, increasing biotic homogenization is likely to take place with further fragmentation and habitat loss, and specialist species will be the major affected group. Local patches of high veteran tree densities (i.e. within 0.5 km) are of particular importance to maintain high biodiversity, although habitat continuity is also of importance at larger scales in the forests.

The grouping of species into specialists and generalists revealed important patterns of habitat connectivity that would have been overlooked if analyzing total species richness instead. Differences in surrounding habitat interacted with connectivity as well as with habitat patch (tree) size and quality. This further stresses the importance of a broad approach when establishing community effects of landscape structures. As our specialists share life history traits with other vulnerable and threatened species in the dead wood ecosystems, our study also emphasizes the overall importance of connectivity of dead wood in large dimensions and advanced stages of decay to preserve biodiversity in forests.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.08.003>.

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