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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-