

## **Importance of spatial configuration of deadwood habitats in species conservation**

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Running head: Deadwood habitat

Keywords: beetles, connectivity, colonization, extinction threshold, fungi, landscape

Article impact statement: Use occurrence patterns and spatial population dynamics of  
deadwood-dependent organisms to evaluate importance of spatial habitat configuration.

This is the peer reviewed version of the following article:

Ranius, Thomas; Snäll, Tord; Nordén, Jenni.

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## Introduction

Komonen and Müller (2018) aimed to inform connectivity conservation of saproxylic (deadwood-dependent) organisms. Out of the many different definitions of *connectivity*, they focus on structural connectivity and relate it to dispersal ability, concluding that spatial configuration of habitat is of little importance in conservation of saproxylic organisms.

Komonen and Müller also point out it would be better to measure connectivity as dispersal success or search time, but they did not include such studies in their review, probably because of the small number of studies in which these measures are compared between landscapes.

Their focus on dispersal ability and the measures they used to quantify this ability strongly limits the conclusions that can be drawn about the importance of spatial configuration of habitat to population persistence. We think it is vital to include a broader range of relevant knowledge when drawing general conclusions about the importance of spatial configuration of habitat on the outcome of conservation strategies. Therefore, we considered the effect of spatial configuration of habitat on colonization, extinction, and occupancy, which are major factors in nature conservation because they affect long-term persistence.

Komonen and Müller reviewed only studies on dispersal ability and spatial variation in genetic patterning and ignored literature on occurrence patterns and colonization-extinction dynamics of species. We agree dispersal studies are important, but because spatial population dynamics are affected by more processes than just dispersal, studies of dispersal ability provide only part of the information needed to understand effects of the spatial configuration of habitat. Observations of colonizations, extinctions, and occurrence patterns instead reveal the sum of processes taking place. Genetic differentiation patterns and species occurrence

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patterns both reflect the effects of current and historical population dynamics, including dispersal. However, it is usually easier to assess and interpret patterns of occurrence than patterns of genetic variation. Consequently, one should expect such studies to occur in larger numbers and thus be overall more important for development of conservation strategies than studies of genetic patterns.

Komonen and Müller focused more on maximum observed dispersal distances (reflecting dispersal ability) than was the case in the papers they cited. Their cited papers also considered, for instance, the rate of individuals leaving a local habitat patch, dispersal mortality, ability to reach habitat, and shape of the dispersal probability-distance curve. The concept behind the dispersal probability-distance curves is that a wide range of dispersal distances are possible, but the probability differs and can be very low, especially at longer distances. With that concept in mind it becomes clear that the observed maximum dispersal distance will increase as sample size increases and that it cannot be used to predict the probability of colonization of habitat patches with different spatial configurations.

Regarding occupancy studies, Komonen and Müller wrote, “these studies have been at very small substrate scales, have entailed vague proxies for dispersal limitation, or have been conducted in continuous forest landscapes.” They used single, nonrepresentative examples from the literature to support this statement. However, many studies have tested the importance of the spatial configuration of habitats for biodiversity by observing the effects of configuration on colonization-extinction dynamics and patterns of species’ occurrence – which, if many species are considered, result in patterns of species richness. We thus sought

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to give a more balanced view by describing 4 types of such studies that were not mentioned by Komonen and Müller.

### **Tests of extinction-threshold hypothesis by estimating species richness in standardized samples**

According to the proportional area hypothesis, population densities in an area do not change with habitat amount, whereas according to the extinction threshold hypothesis, population densities decrease as amount of habitat decreases (Fahrig 2003). If the proportional area hypothesis is true, the spatial distribution of habitat is not important, but if there are extinction thresholds (Müller & Bütler 2010), an uneven spatial distribution of habitat is better because it makes the habitat amount exceed the threshold in at least some areas. These contrasting hypotheses have been tested for saproxylic organisms by taking standardized samples in deadwood items and using species occupancy as a proxy for abundance (Ranius 2002; Sahlin & Schroeder 2010). Deadwood items in large patches turn out to have higher occupancy and consequently higher species richness than similar deadwood items in small patches. Thus, the outcome supports the extinction threshold hypothesis, which means that concentrating deadwood items makes them used by more species.

### **Tests of effect of connectivity on patch-level species occupancy or species richness**

Several studies of saproxylic organisms report a positive effect of connectivity on species occupancy or species richness (e.g., Penttilä et al. 2006; Nordén et al. 2013, 2018; Abrego et al. 2015). *Connectivity* here refers to commonly used patch connectivity measures that aim to reflect the immigration rate by summing the amount of surrounding dispersal sources, in most

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cases combined with decreasing weights for more distant patches (Ranius et al. 2010). Thus, the effects of habitat amount and isolation are not disentangled, but disentanglement is not necessary for drawing conclusions about the spatial configuration of habitat relevant for nature conservation. For instance, Ranius et al. (2010) show that a hollow tree located in a local landscape (within a radius of 200–2500 m) with many hollow trees has higher biodiversity value (measured as the probability of specialized species using the tree) than a hollow tree with the same characteristics that is isolated from other hollow trees (i.e., situated in a local landscape with few hollow trees). Moreover, even in a study in which habitat amount is controlled for, isolation has a negative effect on species richness (Mestre et al. 2018).

### **Tests of effect of connectivity on colonization-extinction dynamics**

Komonen and Müller's claim that "many saproxylic beetles and fungi have persisted for decades and centuries in reserves and in isolated fragments" is supported by a study on flightless beetles (Buse 2012). However, the other references cited to support this statement seem to be an interpretation of anecdotal notes about species findings. However, the colonization-extinction patterns can be assessed systematically by repeated surveys. Such studies provide data for modeling rates of colonizations and extinctions, including testing whether these processes are explained by connectivity. For example, such models have been used to estimate how species with different dispersal traits vary in their extinction risk depending on the density and rate of disappearance of host trees (Fedrowitz et al. 2012).

Studies on saproxylic insects and fungi suggest populations of these organisms can be highly

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dynamic; local colonizations and extinctions occur frequently (Ranius et al. 2014; Mair et al. 2017; Kärvelo et al. 2016).

### **Tests of interactions between local and landscape-level habitat amount**

In a study of saproxylic beetles, Seibold et al. (2017) did not find interactions between habitat amount in the landscape and response of local biodiversity to local habitat amount, indicating that it does not matter where local conservation efforts are conducted. In contrast, Rubene et al. (2017) found such interactions, which indicates that a local increase in deadwood generates greater increases in beetle species richness if the increase is in landscapes with a lot of deadwood. Nordén et al. (2018) also found a strong interaction between large-scale (100 km), old-growth forest patch connectivity and the local amount of deadwood for red-listed fungi. These 3 studies were conducted at different spatial scales; thus, they focused on different parts of the dispersal range. Local patches (forest stands) in Rubene et al. (2017) and Nordén et al. (2018) were larger than the landscapes identified in Seibold et al. (2017). Another difference was that Seibold et al.'s (2017) study was conducted in a national park, whereas the other 2 were in forest landscapes with either small or highly varying amounts of unmanaged forest.

The scientific literature describes how occurrence patterns and spatial colonization-extinction dynamics are affected by the interaction between dispersal biology and the spatial distribution of habitat, which is relevant when making decisions about conservation measures. Several studies suggest habitat aggregation means that each deadwood item is used to a greater extent by saproxylic species of conservation concern. This was not mentioned by Komonen and Müller, but it is important to be aware of because it means forestry policies that tend to level

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out differences in forestry intensity and conservation measures between areas are probably not optimal for biodiversity. Instead, zoning approaches may be better options (Ranius & Roberge 2011). Because empirical studies have been restricted to certain ecological groups, more studies, with a variety of approaches, are needed on a wider range of taxa. These studies should focus on species occurrence, colonization, and extinction patterns and on the dispersal biology behind these patterns. To understand the consequences of different conservation strategies, single-species studies and studies of local species richness are not sufficient, and more information is needed on the representativeness and complementarity of communities of saproxylic species to better understand the value of small and isolated habitat patches (Wintle et al. 2019).

### **Acknowledgments**

L. Fahrig gave valuable comments on an earlier draft of this article.

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