Do Saproxylic Species Need Habitats, Connectivity, or Connected Habitats?

3

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Rosalia alpina on lying beech deadwood in an Austrian Natural Forest Reserve (Photo: BFW/ Janine Oettel)

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Abstract

The importance of saproxylic species within forest ecosystems cannot be overstated, as they span a wide range of taxa contributing to the recycling of dying and dead woody material. Originally defined as invertebrates reliant on decaying wood, wood-inhabiting fungi, or other saproxylics, the group has been expanded to include species involved in or dependent on moribund trees and wood decay processes. Since centuries, their habitat has faced loss and fragmentation from intensive forest management practices and land use changes, underscoring the urgency of conservation efforts. While habitat connectivity is crucial for species dispersal and colonization, evidence supporting its significance for saproxylic species conservation remains unclear. Dispersal abilities vary considerably across taxa, highlighting the importance of understanding these differences for effective forest management aiming at saproxylics conservation. Specialized species such as fungus-dwelling beetle *Bolitophagus reticulatus* demonstrate limited dispersal but robust recolonization capabilities facilitated by the availability of habitat, in this case, *Fomes fomentarius*. Similarly, saproxylic fungi with a broad dispersal ability such as *Fomitopsis rosea* rely on habitat amount for successful colonization. Efforts to increase the amount of deadwood at the landscape scale thus benefit species (re)colonization efforts. Prioritizing the preservation of large populations and distributing habitat patches are key strategies for supporting saproxylic biodiversity in forest ecosystems. Aggregating patches around dispersal sources can attract species of conservation concern, although identifying these sources remains challenging. Conversely, evenly distributed habitat patches throughout the forest landscape promote higher species diversity. A balanced approach combining both aggregation and distribution of habitats seems therefore essential for effective conservation efforts. However, scientific evidence tends to prioritize habitat quantity over habitat connectivity for the conservation of saproxylic species.

Keywords

Dispersal · Colonization · Habitat amount · Deadwood · Biodiversity conservation · Forest management

Saproxylic Species and Their Role in Forests

Saproxylics are a functional group of species that are perhaps more than any other reliant on trees and forest ecosystems, as they inhabit and thrive in dead and decaying trees. As a result, the significance of deadwood for biodiversity conservation cannot be overstated, as it provides essential habitats for thousands of species. Within forest ecosystems, the decay of wood is one of the major ecological processes alongside primary production. This process not only facilitates the recycling of deadwood but also ensures the long-term availability of essential nutrients.

Originally, saproxylic organisms have been defined as invertebrates that, at least during some part of their life cycle, rely on the deceased or decaying wood of dying or dead trees—whether standing or fallen—or on wood-inhabiting fungi, or on the presence of other saproxylic species (Speight 1989). This definition underwent revision by Alexander (2008), who shifted the focus toward the ecological functions of saproxylic organisms and defined them as species intricately involved in or dependent on the process of fungal decay of wood, or on the byproducts of decay. Moreover, saproxylics are associated with both living and dead woody material, including not only wood but also bark and sap at any stages of decay.

Saproxylic organisms represent a considerable share of forest biodiversity, encompassing a large range of species groups ranging from arthropods (such as insects, especially beetles) to birds (such as woodpeckers) and fungi (such as basidiomycetes). The estimated global number of saproxylic species ranges from 0.4 to 1 million. In well-explored Northern Europe, they represent up to 25% of all forest species, predominantly comprising mainly fungi and invertebrates (Stokland et al. 2012). Among these, insects and fungi are the two largest taxonomic groups, contributing between 30% and over 50% of the total saproxylic diversity in forests. This represents an important reason to address biodiversity in deadwood. Another reason is the alarming threat posed to this diversity by habitat loss in managed forests because of harvesting activities, as well as by loss and fragmentation of forested areas at the landscape level for centuries. Consequently, saproxylic species are of considerable conservation concern, as they exhibit high sensitivity to forest management practices that can alter their habitats by reducing the quantity and quality of deadwood habitats (Gossner et al. 2013a; Grove 2002; Müller et al. 2015; Seibold et al. 2017).

Gossner et al. (2013a) demonstrated a positive effect of deadwood enrichment initiatives in managed forests, where the presence and variety of saproxylic beetles are typically limited. The authors determined an immediate increase in species richness and a shift in guild composition upon increasing the deadwood amount, with the effect being even more pronounced in the tree canopy compared to the forest floor. Müller et al. (2015) showed that regional tree species composition influences the habitat preferences of early colonizing saproxylic beetle communities, showcasing local variations in their choice of host trees. With an increase in deadwood amount in European beech forests, Gossner et al. (2013b) observed a noticeable shift in assemblage composition, with larger species and those favoring deadwood of greater diameter and advanced decay stages becoming dominant. Plots with a mean deadwood amount ranging from 20 to 60 m^3ha^{-1} accommodated most species. Consequently, the authors recommend increasing the deadwood amount to more than 20 m^3ha^{-1}, refraining from the removal of large-diameter deadwood (>50 cm), facilitating the development of more deadwood in advanced decay stages, and establishing strict forest reserves characterized by exceptionally high deadwood amounts. These findings support the ecological thresholds reviewed by Müller and Bütler (2010). The authors highlighted deadwood amounts necessary for the conservation of saproxylic species with values ranging between 10 and 150 m^3ha^{-1} and

peak values between 20 and 50 m^3ha^{-1} for the survival of most species, depending on the forest type.

Most saproxylic species are associated with specific habitat quality in terms of, e.g., decay stage (fresh to soft powdery dead wood), dimension (small branches to large logs), position (lying or standing deadwood), microclimate, and tree species or genus (Lachat et al. 2013; Lettenmaier et al. 2022; Vogel et al. 2020). As deadwood habitats are steadily evolving, saproxylic organisms face the challenge of compensating for local extinctions due to the loss of their habitat through wood decay. To maintain populations, they must colonize new deadwood structures that are adapted to their ecological requirements both local and across landscapes (Jonsson and Siitonen 2012). Their dispersal strategies are affected by numerous driving forces, including the spatial and temporal variability of habitat within the landscape, feeding strategy, resource competition, and avoidance of inbreeding (Feldhaar and Schauer 2018). The significance of each factor in shaping dispersal strategy varies among species, contingent upon their unique life histories, and interactions with the environment, such as longevity of deadwood habitat. This habitat turnover has to be considered in conservation measures for this functional group as well as in integrative and segregative approaches (Bollmann and Braunisch 2013; Doerfler et al. 2018).

Habitat Amount vs. Habitat Connectivity

In the course of reduction of natural habitats through human activities, local habitats get more and more fragmented. Such a fragmented landscape affects local populations in two ways. First, the distance between patches increases (pure isolation effect), second the total amount of habitat in a landscape decreases and thereby the population size of a species in the landscape (Fahrig 2013). While in most landscapes nowadays, both habitat amount and spatial connectivity of resource patches are correlated, it is important to disentangle both mechanisms, particularly for restoration.

In response to the habitat deficit for saproxylic species resulting from forest management practices, the conservation of this functional group has become a priority in landscapes dominated by managed forests. In this context, different measures to improve habitat availability and amount at the landscape scale can be implemented, including setting aside natural forest reserves, establishment of (smaller) stepping stones of old-growth forest patches, or the retention of habitat trees and deadwood within managed forests (Bütler and Lachat 2009; Komonen and Müller 2018). The latter involves preserving trees in managed forests until they decay entirely. The underlying concept of these conservation measures is to create a network of habitats capable of supporting saproxylic species that would otherwise struggle to persist in managed forests due to insufficient deadwood resources (see Fig. 3.1).

This concept draws on the theory of island biogeography proposed by MacArthur and Wilson (1963, 1967), which posits that smaller and more isolated habitats tend to harbor fewer species compared to larger and less isolated ones. This theory has prompted conservationists to prioritize the establishment of singular large areas as

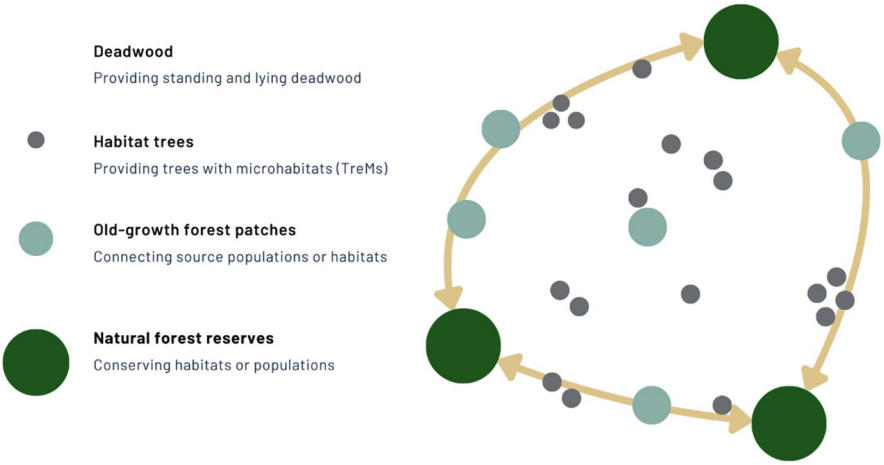

Fig. 3.1 Concept of habitat connectivity for the conservation of saproxylic species at the landscape level based on four different conservation measures: Natural forest reserves, old-growth forest patches, habitat trees, and deadwood, the last two distributed in a matrix of managed forests (adapted from Lachat and Bütler 2009)

the optimal conservation strategy for supporting biodiversity rather than implementing multiple smaller areas (Diamond 1975). In 1980, the IUCN developed a global conservation strategy emphasizing the importance of large contiguous areas in real-world conservation efforts (World Conservation Strategy).

Testing the validity of the "single large over several small" (SLOSS) theory, Simberloff and Abele (1982) conducted a comparative analysis of empirical data on species richness. They found that "not a single case" demonstrated superior species richness in single large habitats compared to several smaller ones covering the same total area. Conversely, most studies demonstrate that the same amount of habitat in a landscape with multiple small areas harbored more species than a single large one. Similar studies focusing on various species, such as Fahrig (2017), have echoed these findings, consistently indicating that species richness is higher in multiple small areas than in a single large one. The mechanisms behind this pattern range from increased habitat heterogeneity provided by more patches to ecological drift (Fahrig et al. 2022; Hovestadt et al. 2024).

Although scientific evidence consistently supports the superiority of several small protected habitats over a single large one, discussions among ecologists persist in part due to sampling biases in many SLOSS studies, where sampling intensity is not proportional to habitat size. Fahrig's (2020) research on species extinction challenges the assumption that larger habitats inherently support greater species richness because species depending on larger habitats for survival may become extinct in smaller habitats over time (process of selective extinction). However, even in studies with unbiased sampling efforts, several small areas exhibited higher species richness. This trend persisted when examining extinction rates in small areas, even within low-quality or hostile matrices, and held true for specialist species as

well. These findings suggest that species richness may be driven more by individual species' minimum habitat requirements than by minimum area size requirements, as emphasized by the Habitat Amount Hypothesis (Fahrig 2013). This hypothesis advocates for considering the overall amount of available habitat in an area rather than the size of the area to estimate species richness. For example, a large managed forest may provide a lower amount of deadwood than a smaller area of primeval forest.

The fragmentation of forest landscapes inevitably leads to reduced deadwood habitat availability and increased distances between dead trees, which can be termed isolated or connected depending on perspective (Lachat and Müller 2018). However, for forest management and conservation, the spatial distribution of restoration efforts such as retention of habitat trees or establishment of old-growth-forest patches or natural forest reserves significantly influence timber production and ecosystem services depending on their location. Conservation measures often prioritize either the creation of new suitable habitats within a forest area or the enhancement of connectivity to reduce habitat isolation. These differing concepts entail significant planning and financial implications, which can vary considerably depending on the initial conditions of the forest area. A comprehensive understanding of these factors is therefore crucial for successful restoration efforts.

Spatial Arrangement of Conservation Measures

Although concepts for habitat connectivity are widely accepted and integrated into many regional or national conservation strategies (see Chap. 22), there exists limited scientific evidence supporting the need for connectivity regarding the conservation of saproxylic species. Dispersal abilities vary greatly across taxa, with only a few species' abilities well understood. Nevertheless, understanding these abilities is crucial and can greatly improve forest management and conservation efforts, particularly in terms of the required spatial and temporal distribution of suitable habitats to enhance species persistence (Oettel et al. 2023).

The distribution of habitat within a landscape, whether aggregated or evenly dispersed, can influence the ability to maintain biodiversity across the landscape. While direct comparisons between areas with aggregated and distributed habitats are lacking, studies focusing on habitat patches within different landscape contexts have shed light on this issue. These studies assess whether aggregated landscapes host greater species richness compared to dispersed ones. Their findings indicate that distributing conservation efforts evenly across smaller patches covers greater landscape heterogeneity, potentially resulting in higher species richness (Fahrig et al. 2022; Haeler et al. 2024; Müller and Goßner 2010; Rubene et al. 2015).

Examples of Saproxylic Beetles

Saproxylic beetles are excellent ecological indicators for the quantity and quality of their habitat (e.g. Lachat et al. 2013) and therefore well adapted for testing hypotheses on habitat amount and connectivity in forest ecosystems. Each piece of deadwood—including logs, snags, and other saproxylic habitats like tree hollows or dead branches—undergoes constant evolution. Throughout the decay processes, the biotic and abiotic conditions of deadwood habitats constantly alter, thus influencing species assemblages. Schmidl and Bussler (2004) have categorized them into different guilds, spanning from initial colonizers of fresh deadwood to inhabitants of aged, decayed wood, including species developing in the mold of rot-holes. Saproxylic species have evolved as a group capable of continuously seeking out new habitats adapted to their specific requirements, as individuals must relocate when deadwood decays further. This raises the fundamental question of how far saproxylic beetles are able to disperse once they have to relocate following changes in their habitats that render them unsuitable for their development.

The empirical evidence regarding the dispersal ability of saproxylic species and the importance of connectivity to them is mainly indirect. It relies on comparisons of species presence/absence or richness in forest stands with varying degrees of spatiotemporal isolation or in landscapes exhibiting different levels of fragmentation (Sverdrup-Thygeson et al. 2014). Although such occupancy studies can offer valuable insights into the importance of dispersal and connectivity, few have been able to differentiate between habitat connectivity and habitat amount (or between dispersal limitation and habitat limitation) at scales relevant to management (Fahrig 2013). An experiment by Seibold et al. (2017) with different amounts of local deadwood habitat in landscapes with different amounts of dead trees, found no evidence for isolation effects but for habitat amount effects on saproxylic beetle diversity. Taking together the current evidence on the importance of isolation and resource amount, the conservation efforts for saproxylic beetles should prioritize increasing the amount of deadwood wherever possible.

Peltis grossa, a specialist beetle of primeval forests, breeds in standing stems with brown-rotted wood of different coniferous tree species (Palm 1951; Saalas 1917). This species gets locally extinct because of the lack of suitable breeding substrate in managed forests (Weslien et al. 2011). Initially considered regionally extinct in Bavaria National Park, its return was triggered by forest dieback caused by windstorms and bark beetle invasion (Busse et al. 2022). In Sweden, initial findings on *P. grossa* reveal an increase in colonization rate and a decrease in extinction risk with higher connectivity (100–200 m) (Djupström et al. 2012, 2024). However, this association was only evident when using connectivity-based information on species abundance. Structural measures of connectivity, such as the number of snags, failed to show any significant relationship. Despite generally optimal habitat conditions in Bavaria National Park, including a substantial increase in deadwood until the 1990s, *P. grossa* was absent. This may be attributable to irregularly distributed amounts of deadwood, with a less pronounced increase in deadwood in the refuge area of a smaller source population in the south. Bark beetle invasion in

subsequent years led to a population explosion of *P. grossa*, resulting in rare long-distance dispersal events and eventual colonization of the national park. By reconstructing the recolonization in Bavaria National Park, Busse et al. (2022) determined dispersal distances of up to 10–40 km, above which colonization rates significantly decreased. This indicates that the source population in the south before the bark beetle invasion was insufficient to fully recolonize the new habitats within the national park.

The rare hermit beetle *Osmoderma* spp. is associated with hollow trees, where its larvae develop in mold. For this rare species, different methods yielded similar dispersal distances (see Fig. 3.2), even though dispersal rates and distances seemed smaller for Swedish populations compared to those in more southern European regions. Populations of *O. barnabita* exhibited positive kinship up to 10 km, indicating a limit to their dispersal at this scale. The estimated average dispersal distance is much larger than the results for *Osmoderma* spp. using other methods (Oleksa et al. 2013). A study on the colonization-extinction dynamics of *O. eremita* over 25 years (Lindman et al. 2020) showed that colonization rates increased with connectivity at a 60-m scale and with tree characteristics indicative of early successional stages, leading to higher occurrence frequencies per tree. Conversely, extinction rates increased with larger tree diameter, indicating late succession stages. Most *O. eremita* individuals stay in the same hollow tree throughout their lifetime, with dispersal typically occurring between trees at distances of less than 250 m from one another (Dodelin et al. 2017). Although long-distance dispersals are rare, this does not mean that the species cannot fly further. These findings underscore the importance of connectivity, as *O. eremita* is more likely to colonize or recolonize habitats within about 200 m. However, these initial observations regarding its flight capabilities have been revised with subsequent studies, indicating that *O. eremita* is indeed capable of flights spanning several kilometers (Fig. 3.1).

Tenebrio opacus is known to inhabit hollow oak trees in pastures (Ranius and Fahrig 2006). A notable threshold regarding the frequency of presence per tree emerges in small areas with fewer than 10 hollow trees, where less than 5%

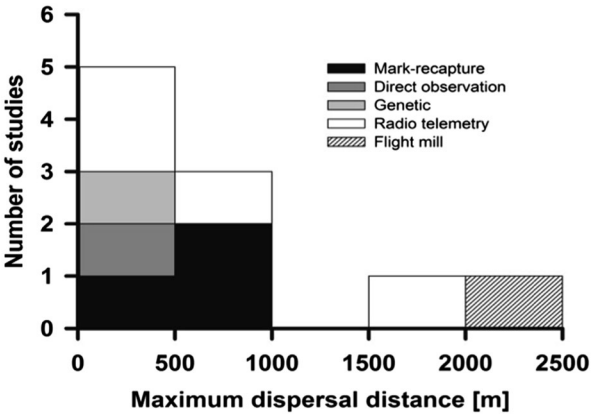

Fig. 3.2 Documented maximum flight distances in studies of the hermit beetle *Osmoderma eremita and O. barnabita* with different methods (n = 10 studies). Direct observation refers to dispersing individuals followed by foot. In the genetic study, the distance is average, not maximum. (Source: Komonen and Müller 2018)

occupancy is observed. However, this threshold significantly increases to over 40% occupancy per tree in areas with 11 or more hollow trees. This phenomenon is closely linked to the persistence of habitat over time. Highly specialized species like *T. opacus* may have developed strategies to thrive in long-lasting habitats such as hollow trees over generations. However, the spatial scale for measuring habitat amount involved oak trees located less than 250 m apart, indicating a sensitivity to habitat fragmentation (Ranius 2002).

Examples of Saproxylic Fungi

Wood-inhabiting fungi produce billions of minuscule spores daily with deposition rates ranging from 10 to 1000 spores per m^2 per day (Edman et al. 2004a). Notably, some old-growth forest species, like Fomitopsis rosea, can deposit even higher amounts, exceeding 5000 spores per m2 daily. F. rosea also exhibits a considerable dispersal ability. Even in landscapes with low proportions of old-growth forests, this species has been found to have spores present in sufficient quantities, suggesting potential for long-distance dispersal (Edman et al. 2004b). Despite this figure appears substantial, the precise threshold required for successful colonization is unknown (Edman et al. 2004a). Moreover, colonization of deadwood appeared to rely on neighboring occurrences of the species (Edman et al. 2004b; Jönsson et al. 2008).

Edman et al. (2004b) discovered that sites rich in deadwood generally harbor greater species richness, with several species being abundant due to high spore deposition from the local species pool. For instance, species like *Asterodon ferruginosus, Phellinus ferrugineofuscus, P. viticola, and Phlebia centrifuga* exhibited a preference for colonizing deadwood near previously occupied pieces. Jönsson et al. (2008) demonstrated the significant influence of both local deadwood characteristics within patches and connectivity between patches in an old-growth boreal Norway spruce forest on fungi species dynamics. According to the authors, substrate decay and resource disappearance are the main causes of local extinctions. This is in line with findings by Norros et al. (2012), showing a higher colonization probability on logs within a distance of up to 60 m from sporocarps. However, fungi still distribute spores beyond this distance, suggesting low or no dispersal limitations extending over several kilometers.

The duration of persistence on one resource depends on the specific habitat requirements of fungal species. Early successional species like *P. ferrugineofuscus* and *Stereum sanguinolentum* display high annual extinction rates, whereas late successional species like *Phellinus nigrolimitatus* exhibit lower rates. Jonsson (2012) summarizes time windows of up to 20 years for occurrences of deadwood-inhabiting fungi, with typical durations of less than 8 years. However, persistence time analyses for wood-inhabiting fungi are still scarce.

Biotic Interactions of Fungi and Beetles

Successful colonization requires both dispersal and establishment. Establishment relies on the availability of suitable habitat (substrate). The suitability of a substrate is determined by its characteristics, biotic competitive interactions, and abiotic conditions (Jonsson 2012). Characteristics encompass aspects like tree species, decay stage, genesis history, moisture content, chemical composition of deadwood, and temperature. Furthermore, the establishment of some species of fungi relies on biotic interactions. Indeed, some fungi species utilize specific vectors for establishment; for instance, *Amylostereum areolatum* depends on *Sirex* wood wasps for the transfer to suitable substrates. Other examples include blue-stain fungi and bark beetles inducing establishment through vector interactions. Sequencing fungi from saproxylic beetles revealed a high diversity of fungi transported by beetles (Seibold et al. 2019). Experiments have shown that the presence of saproxylic insects can affect the community of fungi (Jacobsen et al. 2018; Zou et al. 2023). Nonetheless, the relative importance of insects under natural conditions remains unclear (Sverdrup-Thygeson et al. 2014).

Zytynska et al. (2018) examined the fungus-dwelling beetle *Bolitophagus reticulatus* breeding on *Fomes fomentarius* in a broadleaf forest of southern Germany. The study revealed that the population genetic structuring is largely influenced by forest management history. Nevertheless, low isolation-by-distance and limited relatedness among beetles collected from the same trees or fungus occurrences suggest robust dispersal enabling recolonization across considerable distances. It is expected that genetic structuring will continue to decrease in the future, emphasizing that the increase of deadwood amount—regardless of its spatial arrangement—can foster species recolonization. As long as relic populations persist, the increase of deadwood amount and diversity can support to increase population sizes sufficient for the dispersal and recolonization of habitats.

Komonen and Müller (2018) gathered evidence demonstrating species-specific dispersal limitations for saproxylic insects and fungi at different spatial scales ranging from local (<50 m) to continental (>500 km) scale. Adult beetles disperse primarily through active flight, while fungi rely mainly on wind dispersal over longer distances (anemochory), making them more effective dispersers. Based on this review, insects show a majority of dispersal limitations at larger scales such as regional and continental scales, whereas even rare fungal species hardly exhibited any dispersal constraints. The authors concluded that while systematic and species-specific differences exist, most saproxylic species face colonization and establishment limitations in terms of finding suitable habitats rather than true dispersal limitations at management-relevant scales (see Fig. 3.3).

Implications for the Conservation of Saproxylic Species

Saproxylic species exhibit significant variations in their dispersal abilities and habitat requirements. For instance, species associated with ephemeral habitats like fresh deadwood, such as early successional bark beetles (Scolytinae), can disperse over

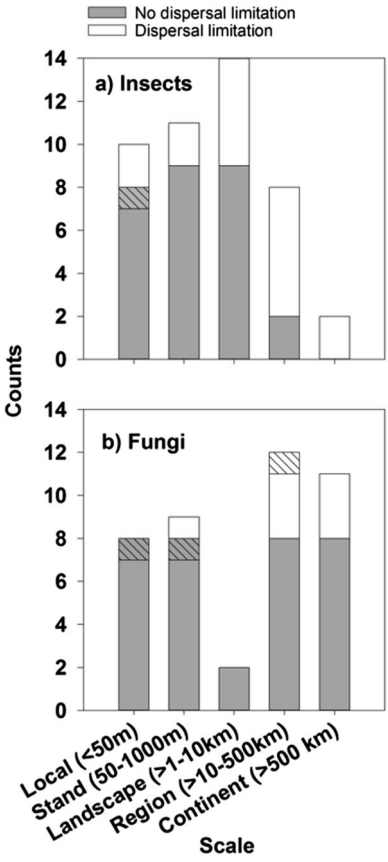

Fig. 3.3 Documented maximum flight distances of saproxylic (**a**) insects and (**b**) fungi in experimental and genetic studies ($n = 25$). 'Counts' indicate the number of studies. (Source: Komonen and Müller 2018)

large distances and swiftly locate and colonize new habitats. Additionally, these species are characterized by high reproductive rates (r-strategies) and can produce up to four generations per year (Perny et al. 2008; Steyrer et al. 2020). In contrast, species linked with long-lived habitats, such as hollow trees with mold, are less mobile and have lower reproduction rates (k-strategies). Such long-lasting habitats can harbor populations over multiple generations spanning decades, resulting in reduced dispersal necessity and limited individual mobility. However, dispersal is often underestimated. New research frequently reveals higher dispersal rates and distances than previously anticipated. Nevertheless, dispersal limitations exist among saproxylic beetles beyond 10 km. Other insect species in deadwood as some syrphids show similar dispersal abilities as beetles up to many kilometers. For fungi, which together with beetles represent the most diverse saproxylic group, the situation is even less critical. The production of huge quantities of spores highlights the importance of suitable habitat rather than the necessity of connectivity for the conservation of this group.

Accumulated knowledge for both species groups—beetles and fungi—suggests that the availability of habitat amount in the landscape is by far more critical than habitat connectivity. This holds true for the spatial scale at which forest managers operate. It is important to note that an increase in habitat amount can also enhance connectivity by enhancing population sizes, thereby increasing the number of dispersing individuals or serving as the most important component for dispersal. Moreover, it contributes to a reduction in spatial distances between deadwood objects. As more effective and better grounded by ecological studies, current knowledge suggests a focus on habitat amount management rather than on spatial distances in deadwood management.

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