Chapter 15
Dispersal of Saproxylic Insects

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Abstract Dispersal is a key trait of species that is required to maintain gene flow between habitat patches. Furthermore, it allows the colonization of new habitats and thus affects population dynamics, extinction risk of populations, and species distributions. Dispersal enables species to persist in a changing environment. Saproxylic insects, depending on deadwood at some stage during their life cycle, must compensate local extinctions resulting from the decay of deadwood with colonizations of new deadwood structures locally and on the landscape scale. Their dispersal strategies are shaped by a suite of driving forces such as spatial and temporal variability of deadwood structures in the environment, feeding strategy, resource competition, kin competition, and inbreeding avoidance. The importance of each factor in selecting for a dispersal strategy will vary among species depending on their life history and interactions with the environment, such as the longevity of the deadwood habitat used. Species using a more transient habitat, such as freshly killed wood, have better dispersal abilities than those in more persistent habitats such as tree hollows that may exist for several decades. Dispersal abilities of only a few saproxylic insect species are known, and these comprise mostly pest species or flagship species of interest to conservation. Dispersal distances vary greatly from a few meters in passalids dispersing by walking to over 100 km in some flying bark beetles. Knowledge of dispersal abilities is of paramount importance though, as it can help to improve conservation strategies and forest management especially in terms of spatial distribution of suitable habitats to enhance species persistence. In this chapter we first review the factors driving dispersal ability and our current knowledge on dispersal distances of saproxylic insects. We provide an overview of different methods used to measure dispersal ability of saproxylic species. We discuss whether saproxylic species are rather dispersal or habitat limited and identify open questions in the study of dispersal of saproxylic insects.

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15.1 Introduction

Dispersal is defined as any movement of individuals or propagules with potential consequences for gene flow across space (Ronce 2007). Dispersal is a three-step process where individuals leave their birthplace and then cross a more or less hostile matrix before settling down in a new habitat patch to reproduce (Bonte et al. 2012). Most species live—at least to some degree—in spatially structured populations. Species with such a metapopulation structure are comprised of spatially discrete local populations in patches that are connected by the migration of individuals between local populations. Metapopulations are characterized by frequent extinction of local populations. For long-term persistence of a metapopulation, local extinctions and colonization through local dispersal need to be balanced (Hanski 1998). Dispersal ability (and propensity) is therefore an important life-history trait as it strongly impacts persistence of a species, especially in human-impacted landscapes. Anthropogenic habitat destruction often results in habitat fragmentation, reduced connectivity between suitable habitats, and a reduction in habitat size and quality. These transformations of ecosystems negatively impact many species, potentially driving them toward extinction. Therefore dispersal has received increasing attention by ecologists and conservationists.

As a result of habitat fragmentation, connectivity between suitable habitat patches is often reduced, and species with limited dispersal abilities may not be able to recolonize patches where they have become extinct or reach new habitat patches. In addition, smaller populations often release a smaller number of dispersing individuals, which may reduce not only demographic connectivity but also the genetic exchange between habitat patches even further. Additionally, the smaller the habitat patches, the smaller population sizes will be locally, which renders populations more prone to extinction by stochastic processes (Hanski et al. 1994). The strength of Allee effects (positive density dependence) may also become stronger in smaller populations, and, e.g., finding a mating partner may become more difficult, which may increase dispersal propensity of individuals (Kuussaari et al. 1996). Dispersal has consequences not only for the fitness of the respective individual moving from one habitat patch to another but also for population dynamics and genetic cohesion of species across their range (Bowler and Benton 2005). Spatially structured populations are largely dependent on dispersal for their long-term persistence. Immigrating individuals may rescue small populations by preventing local extinction events due to stochastic processes (Brown and Kodric-Brown 1977; Gotelli 1991) or enhance the fitness in small populations by genetic rescue (Whiteley et al. 2015). Empty habitat patches can only be (re-)colonized by dispersal (Fahrig and Merriam 1994; Hanski et al. 1994), and thus dispersal also determines the ability of populations to track favorable conditions or cope with habitat loss or fragmentation in a changing world (Travis et al. 2013).

Dead and decaying wood represents a spatially and temporally dynamic habitat for insects. Insects depending on deadwood structures at some point of their life cycle have been termed saproxylic insects (Speight 1989). Species depending on wood-decomposing fungi or other saproxylic species are also considered as saproxylic. These saproxylic insects constitute a large part of forest biodiversity and play a major role in nutrient cycling and ecosystem functioning (Stokland 2012; Ulyshen 2016), and diversity is driven by the range of decay stages and types of deadwood structures that provide habitat to different saproxylic insect assemblages (Grove 2002b; Schauer et al. 2018a; Ulyshen 2011; Ulyshen et al. 2004). Habitat patches for saproxylic insects can be as small as an individual deadwood structure, such as a tree, log, or fungal sporocarp, and can host several to many generations of a particular insect species. However, eventually the insect population will become extinct as the resource decomposes. Locally, new habitat patches will become available for colonization with the appearance of new deadwood structures. While forest management or natural disturbances alter patch dynamics and abundance locally, forest fragmentation determines connectivity and ecological continuity on the landscape level (Grove 2002b).

Saproxylic insects are adapted to their spatially and temporally dynamic habitat and have developed a range of dispersal strategies. In general, it is assumed that species inhabiting long-lived (e.g., specialists of tree hollows) or abundant habitat patches are poor dispersers (Nilsson and Baranowski 1997; Ranius and Hedin 2001) in comparison to those relying on more ephemeral or scarce habitat patches (e.g., scolytine beetles on wind- or fire-damaged trees) (Nilssen 1984; Saint-Germain et al. 2008).

Many saproxylic insect species can actively disperse on their wings, while others disperse passively by hitchhiking on dispersing animals (so-called phoresy). Phoresy as dispersal strategy is most often used by small-bodied and/or flightless saproxylic arthropods such as mites or pseudoscorpions (Karpinski et al. 2017; Katlav et al. 2014; Ranius and Douwes 2002; Zeh and Zeh 2013). As dispersal distances of phoretic saproxylic arthropods are determined by the dispersal abilities of the individual they hitchhike on, these often tiny arthropods may be able to disperse over relatively large distances (Ranius and Douwes 2002). Other flightless taxa reach new habitat patches actively by walking and are assumed to be strongly limited in their dispersal range in comparison to flying or phoretic saproxylic arthropods (Buse 2012; Horak et al. 2013; Janssen et al. 2016). A mixture of active and passive dispersal may be used by thrips. Saproxylic species may have rudimentary wings only (Kettunen et al. 2005). However, aside from active dispersal by walking, thrips as tiny insects may potentially sail with the wind and may thus cover larger dispersal distances passively without using energy for flight (Compton 2002).

Many saproxylic insect species are regarded as threatened worldwide due to fragmentation, loss of habitat, or degradation of forests resulting in reduced amounts of deadwood structures (Grove 2002a, b; Seibold et al. 2015; Siitonen 2001; Speight 1989). Aside from the absence of suitable habitat patches (habitat limitation), the entailing lower connectivity between those patches may result in dispersal limitation, i.e. the inability of a species to occupy all suitable patches in the environment or reach suitable habitat patches due to insufficient dispersal abilities. This is often invoked as a reason for the absence of a particular species within a habitat patch (Brin et al. 2016; Brunet and Isacsson 2009; Irmler et al. 2010; Schiegg 2000a, b).

Knowledge on dispersal biology of saproxylic insects is therefore of paramount importance to improve conservation strategies.

This chapter reviews the current knowledge of dispersal abilities of saproxylic insects (also in relation to habitat fragmentation). We first provide an overview of the factors influencing dispersal. As knowledge on dispersal abilities of saproxylic insects is based on different methods we will then compare the direct and indirect methods for measuring dispersal with advantages and drawbacks. We provide an overview of dispersal distances of various taxa. Lastly, we will discuss the role of potential dispersal limitation in population dynamics and colonization of new habitats by saproxylic insects.

15.2 Factors Influencing Dispersal Strategies: Why Disperse and How Far?

Dispersal strategies of organisms are shaped by a suite of driving forces such as environmental stochasticity, resource competition, kin competition, and inbreeding avoidance (Benton and Bowler 2012; Bonte et al. 2012; Bowler and Benton 2005; Matthysen 2012). The importance of each factor in selecting for a dispersal strategy will vary among species in accordance to their life-history traits and their interactions with the environment.

15.2.1 Longevity and Spatial Distribution of Habitats of Saproxylic Insects

Theory on dispersal suggests limited dispersal of species inhabiting long-lasting and stable habitats, while those inhabiting ephemeral habitats should have a higher dispersal propensity as suitable habitat is present for a short time only (Southwood 1962; Shaffer 1981; Roff 1994; Denno et al. 1996). The spatial distribution of suitable habitat should also have a strong influence on dispersal abilities. If habitat patches are rare and more isolated, then dispersal ability needs to be greater to colonize new habitat patches. Availability of habitat patches is also dependent on the range of habitats used per species. Habitat specialists potentially have fewer habitat patches available than species being able to use a broader range of habitats.

Habitats of saproxylic insects differ strongly in their persistence and spatial distribution. One habitat type with very short availability only is freshly burned wood. Pyrophilous insects, whose larvae require the nutritional conditions present in the very early decay stages, colonize it immediately after a forest fire (Hanks 1999; Heikkala et al. 2017). These specialists use the freshly burned wood as a habitat for a single to a few generations only before their populations decline again (Hanks 1999; Heikkala et al. 2017). In addition, burn sites are spatially and temporally unpredictable and may occur at relatively great distances from each other. Consequently, spatial separation and transience of the habitat should select for very good dispersal abilities of pyrophilous species. Indeed, pyrophilous species have been shown to colonize freshly burned forest stands quickly, and they do not seem to be dispersal limited if sufficient source populations are available on the landscape scale (Boulanger et al. 2010; Heikkala et al. 2017; Kouki et al. 2012; Ranius et al. 2014; Saint-Germain et al. 2013). Other early decay stages have also been shown to favor good dispersal abilities. For example, bark beetles colonizing stressed or freshly killed trees have excellent dispersal abilities (Forsse and Solbreck 1985).

Standing and downed dead trees or coarse woody debris are deadwood habitats of intermediate longevity. In contrast to early decay stages that are the result of forest fires or other stressors to trees, deadwood at intermediate and late decay stages is a resource that may have become available more gradually and continuously in comparison to the early decay stages (Nilsson and Baranowski 1997). In addition, these habitat types should be the most common within natural forests (Nordén et al. 2004), in contrast to the very early decay stages with limited temporal (and spatial) availability or hollows in living trees with a naturally patchy spatial distribution. Saproxylic insect species utilizing intermediate to late decay stages of deadwood should thus have more limited dispersal abilities in comparison to species utilizing ephemeral early decay stages. However, evidence for limited dispersal abilities of saproxylic species using deadwood structures of intermediate longevity is equivocal. Saint-Germain et al. (2013) did not find an effect of isolation in colonization patterns of burned forest sites by pyrophilous vs. non-pyrophilous beetle species. Other studies suggest that species requiring a more specific habitat may be dispersal limited, which is often the case for threatened species (Gibb et al. 2006; Schiegg 2000a, b; Seibold et al. 2015).

Hollows in living trees are considered an extremely stable habitat as they may persist for many decades (Ranius and Hedin 2001), potentially providing a suitable habitat for many generations of species inhabiting those hollows. Tree hollow specialists are therefore expected to have more limited dispersal abilities and a lower dispersal propensity than species inhabiting more transient deadwood habitats. Direct measurements of dispersal abilities of one specialist, the Hermit beetle *Osmoderma eremita* Scopoli, 1763, suggest more limited dispersal abilities in comparison to other saproxylic insects (Hedin et al. 2008; Ranius 2006). Likewise, Nilsson and Baranowski (1997) found the beetle fauna in hollow trees to be impoverished in previously disturbed stands and argue that this is due to dispersal limitation. On the other hand, the naturally patchy distribution of tree hollows should favor dispersal abilities. In addition, the potentially small population size of a particular species within a tree hollow may select for a high dispersal propensity of at least one sex to avoid inbreeding (Perrin and Mazalov 2000; Waldbauer and Sternburg 1979) and potentially competition among relatives (see below).

15.2.2 Influence of Feeding Strategies on Dispersal

Dispersal is defined as the movement from the natal or breeding site to another breeding site. This includes not only the departure from a patch and settlement in the (new) breeding site but also the movement between those patches (Clobert et al. 2009). The movement strategy and potential dispersal distance of saproxylic insects will be strongly influenced by nutritional and habitat requirements of the dispersing life stage—which are usually the adult insects.

While larvae of many saproxylic species are dependent on decomposing wood in some form, adult life stages may rely on very different food sources. At one extreme, adults may not feed at all, which will limit the maximum distance that can be covered during dispersal as only the stored biomass can be utilized for flight or movement and is traded off against reproduction. Nonfeeding species therefore tend to have a more sedentary lifestyle than those feeding as adults (Hanks 1999). A comparison of the life history and dispersal behavior of two cerambycid beetles, the Japanese pine sawyer *Monochamus alternatus* Hope, 1843 and the Sugi bark borer *Semanotus japonicas* Lacordaire, 1869, suggests that dispersal propensity is strongly influenced by adult feeding behavior. While *M. alternatus* Hope, 1843 adults must feed on the bark of twigs of healthy pine trees for maturation and then have to search for weakened or newly killed pine trees to oviposit, *S. japonicus* Lacordaire, 1869 is more sedentary as oviposition may take place on the same tree that larvae developed in and no maturation feeding of the adult is required (Shibata 1986a, b).

Other insects that have to undergo maturation feeding are many saproxylic species of syrphid flies that require protein-rich pollen in order to fully develop their reproductive organs and achieve egg maturation (Speight 2012). Saproxylic syrphid flies therefore require open stands with a rich herb layer within forests (Fayt et al. 2006) and are also frequently found in meadows (Branquart and Hemptinne 2000). In order to meet nutritional demands, they potentially need to cover quite a distance before entering deadwood structures again to reproduce or deposit eggs.

15.2.3 Inbreeding Avoidance

Mating between related individuals results in inbreeding. Inbreeding can occur in both large and small populations. In large populations, nonrandom mating of related individuals may occur simply due to geographic proximity of these individuals. In small populations however, the probability of inbreeding is much higher, even with random mating because most individuals within the population will be related.

Local population sizes of saproxylic insects may often be small, which may result in substantial levels of inbreeding if mobility of the species is low. A local population may comprise individuals within the same forest or forest fragment, but may be as small as the group of individuals living in the same habitat patch, which can be a deadwood structure like a tree hollow, a fallen log, or the sporocarp of a bracket fungus. Especially bark and ambrosia beetles show very high levels of inbreeding in some species when mating takes place among kin within the same galleries (Keller et al. 2011; Kirkendall 1983; Kirkendall et al. 2015). Other saproxylic insect species also show considerable levels of relatedness within the same breeding structure such as a particular tree hollow, e.g., the two cetoniine beetles *Osmoderma barnabita* Motschulsky, 1845 and *Protaetia marmorata* Herbst, 1786 (Oleksa et al. 2013) or the beetle *Anaspis ruficollis* Fabricius, 1792, the syrphid fly *Criorhina floccosa* Meigen, 1822, and the wood-soldier fly *Xylomya maculata* Meigen, 1804 (Schauer et al. 2018b).

As inbreeding has been shown to reduce fitness in many insects (Henter 2003), mechanisms to avoid inbreeding are expected to be selected in order to reduce negative fitness effects (Pusey and Wolf 1996). Inbreeding can be avoided either by dispersal (of at least one sex) from natal sites to reduce contact with relatives (Waldbauer and Sternburg 1979) or, when dispersal is not possible, inbreeding may be avoided by mechanisms that prevent breeding with close relatives (Blouin and Blouin 1988).

Sex-biased dispersal has been observed in several species of saproxylic beetles. In *Melandrya barbata* Fabricius, 1792 and *Melanotus villosus* Gmelin, 1789, a larger proportion of males was found to colonize recent forest fragments, suggesting male-biased dispersal (Bouget et al. 2015). In the stag beetle *Lucanus cervus* Linnaeus, 1758, both sexes disperse. However, females fly for shorter distances in comparison to males and then move around on the ground in search for an oviposition site (Rink and Sinsch 2007). Likewise, the sex ratio was more female biased at shorter dispersal distances and unbiased at larger distances in *Ips typographus* Linnaeus, 1758 (Dolezal et al. 2016), which can be explained by males being the pioneer sex. In contrast, tethered flight experiments on *Osmoderma eremita* Scopoli, 1763 suggest that females may have higher flight capacities (Dubois et al. 2010). Several authors point out the observed patterns with potential sex-biased dispersal may be due to differences in the likelihood of catching beetles of one of the sexes (often the males). Thus, recapture rate of male Rosalia longicorn beetles was higher than that of females, but no sex difference in cumulative dispersal distance was found (Drag et al. 2011).

15.2.4 Delayed Dispersal, Flightless Males, and Outbreeding Depression in Cooperatively Breeding and Social Saproxylic Insects

A special case of sex-biased dispersal can be found in ambrosia beetles (Scolytinae) where inbreeding polygyny has evolved repeatedly as mating system (Kirkendall 1983). Female ambrosia beetles mate with close kin (brothers) before they disperse (Kirkendall et al. 2015). Adult females often stay within natal galleries where fungus is grown and delay dispersal after mating in order to provide parental care to closely related offspring (Peer and Taborsky 2007). Dispersal of mated females is triggered by a low number of close kin dependent on alloparental care (Biedermann and Taborsky 2011). Males in such species are usually flightless, resulting in highly sex-biased dispersal patterns (Kirkendall et al. 2015). In addition, mating with related individuals may by now be favored in these species as outbreeding has been shown to reduce fitness (Peer and Taborsky 2005).

Likewise in the lower dry-wood feeding termite *Cryptotermes secundus* Walker, 1853, inclusive fitness gains that can be attained by individuals delaying dispersal. Individuals stay as helpers in the natal nest and delay dispersal to found a new colony themselves when the piece of wood they nest in is still large and food abundant. When food becomes scarce, workers develop into winged sexuals more readily and disperse (Korb and Schmidinger 2004).

15.2.5 Competition-Colonization Trade-Offs

Differences in dispersal ability among species may be selected by competitive interactions. Individuals of smaller species are often inferior competitors during scramble or interference competition, i.e., when they have to compete for resources directly and a superior individual can displace an inferior competitor or prevent access to the resource. However, if inferior competitors have better dispersal abilities, coexistence may be enabled. Such a competition-colonization trade-off seems to allow species coexistence of species of spore-feeding beetles on a wood-decaying bracket fungi *Ganoderma* spp. in New Zealand. Here the beetle *Zearagytodes maculifer* Broun, 1880 evades competition with the superior competitor *Holopsis sp.* by dispersing and colonizing distant habitat patches not yet colonized by the latter species (Kadowaki et al. 2011).

15.3 Measurement of Dispersal

While dispersal is an important life-history trait influencing the persistence of a species locally and regionally as well as its range, it is notoriously difficult to observe or measure, especially in rare species or those with a mainly cryptic lifestyle such as many saproxylic insect species. Dispersal can be measured either directly or indirectly. Direct measurement of dispersal implies that individuals (or a cohort) are observed during the whole dispersal process from the departure point to the point of settlement. This usually requires that individuals are marked in some way so that they can be identified. Direct measurements of dispersal have the advantage that exact dispersal distances and movement patterns of particular individuals can be measured. Based on the distribution of observed dispersal distances of many individuals, a dispersal kernel, i.e., a probability distribution of the distance traveled by any individual, can be calculated (Etxebeste et al. 2016). In addition to the distance traveled, information on movement behavior can be gained during direct measurements. In contrast, indirect measurement of dispersal is usually based on the interpretation of patterns generated by dispersing individuals. Indirect methods comprise population genetic analyses or patterns of occurrence of saproxylic insects (usually in relation to landscape structure and spatial distribution of potential habitat patches). Direct and indirect measures of dispersal are complementary and not redundant methods (Lowe and Allendorf 2010; Ranius 2006).

15.3.1 Direct Measurement of Dispersal: Radio Telemetry

Radio telemetry allows the measurement of exact dispersal distances and movement patterns of particular individuals of saproxylic insects (Chiari et al. 2013; Dubois and Vignon 2008; Hedinand Ranius 2002; Hedin et al. 2008; Moore et al. 2017; Svensson et al. 2011). By closely following movements of single individuals through the habitat, radio telemetry can uncover the use of hitherto unknown or cryptic breeding sites (Moore et al. 2017) or time spent in other habitats (Chiari et al. 2013), which may contribute to increased distances from the natal patch to a breeding site. The most important limiting factor in such studies is the trade-off between the weight of the transmitter that is attached to the insect and the power of the transmitter. Active transmitters used in radio telemetry are powered by batteries and are usually relatively heavy (200–1000 mg), but the signal is transmitted over larger distances of up to 500 m on the ground (Kissling et al. 2014). While a 500 m radius may be enough to monitor movements and short-distance dispersal by telemetry, those individuals that fly beyond the range of the receiver are lost (Moore et al. 2017), and therefore long-distance dispersal events are rarely (if ever) detected with this method. Another problem arises due to the relatively large weight of the transmitter, which precludes their use in studies with smaller saproxylic insects as their normal movement and dispersal behavior may be altered. Consequently, most studies using radio telemetry have been conducted on large beetles such as *Osmoderma eremita* Scopoli, 1763 (Chiari et al. 2013; Dubois and Vignon 2008; Hedin and Ranius 2002; Svensson et al. 2011), the stag beetle *Lucanus cervus* Linnaeus, 1758 (Rink and Sinsch 2007), or rhinoceros beetles (Moore et al. 2017). Passive transmitters (without a power source) such as RFID tags are much lighter than active transmitters (weighing only 0.9 to 100 mg) which would allow the study of small saproxylic insects. However, as the range of the signal is <1 m, landscape-scale studies using transmitters are currently impossible (Kissling et al. 2014).

15.3.2 Direct Measurement of Dispersal: Capture-Mark-Recapture

Another method measuring exact dispersal distances is capture-mark-recapture (or mark-release-recapture). This method allows the determination of dispersal distances of particular individuals and dispersal rates of released cohorts (Rossi de Gasperis et al. 2016; Torres-Vila et al. 2017). Recapture efficiency may be increased using odor traps with species-specific semiochemicals if available for the respective species (Meurisse and Pawson 2017; Torres-Vila et al. 2015; Zauli et al. 2014), or traps with fermenting baits (Torres-Vila et al. 2017; Torres-Vila et al. 2012), that are placed at different distances from the release site. Using fermented bait traps to recapture *Cerambyx welensii* Küster, 1846 and *C. cerdo* Linnaeus, 1758, recapture rate ranged from 36% to 66%, which permitted the study of the influence of parameters such as wind speed and direction, air temperature, temporal patterns, and impact of season on dispersal behavior (Torres-Vila et al. 2017). As the study was conducted in two species in parallel, this allowed a direct comparison of dispersal behavior. Nonetheless, capture-mark-recapture studies are often biased toward those individuals that are captured again—often relatively close to the habitat patch they emigrated from. Long-distance dispersal events are rarely observed (Vlasanek et al. 2013), but can be estimated by extrapolation from the dispersal function at shorter distances (Drag et al. 2011; Torres-Vila et al. 2017). Another caveat may be that—depending on the method of marking—the movement abilities and thus movement patterns of insects may be altered (Gall 1984) or make them potentially more conspicuous to predators. In addition, movement behavior may be influenced by the translocation, e.g., if individuals are released in unfamiliar or matrix habitat (Heidinger et al. 2009). Both problems may be overcome by using a passive marking method, where individuals become marked when leaving their breeding site and are then captured after dispersal. Bark beetles have been successfully marked by coating or dusting infested logs with fluorescent dye or powder. As emerging beetles walked on the surface of the logs before flight, they became marked passively as grains of fluorescent powder adhered to cuticular hairs. After recapture, beetles can be inspected for the presence of fluorescent marker using a UV light source (Cronin et al. 1999; Dolezal et al. 2016).

15.3.3 Direct Measurement of Dispersal: Assignment Methods Using Genotypic Data of Individuals

Genotypic data (such as multilocus genotypes based on microsatellites) can also be used for direct measurement of dispersal. Such studies may yield comparable results to mark-recapture studies. While the dispersing individual is not directly observed, a particular dispersal event of an individual may be detected and distances measured when offspring can be assigned to their source parents based upon multilocus genotypes unambiguously. This, however, requires some genetic divergence of potential source populations and that these source populations have been sampled (Lowe and Allendorf 2010). This method is best applicable for species where groups of related individuals represent source populations with only a few individuals leaving such a kin group to disperse. Such a scenario can be found in bark beetles with high levels of inbreeding or subsocial beetle colonies as well as in eusocial ants and termites. Genotypes of source populations (or mature colonies) can then be compared with genotypes of individuals that have just dispersed to start new kin groups or colonies (Türke et al. 2010). Winged sexuals of the Formosan subterranean termite *Coptotermes formosanus* Shiraki, 1909 could be assigned unambiguously to their parental colonies based on multilocus genotypes and have been shown to disperse over at least 500 m (Simms and Husseneder 2009).

15.3.4 Direct Measurement of Dispersal: Colonization Experiments

Colonization experiments, where empty habitat patches (or odor traps) are provided and distances to potential source populations of colonizing insects are known, can also be utilized to measure dispersal distances. This method has been used to estimate dispersal abilities of beetles associated with bracket fungi (Jonsell et al. 1999; Jonsson and Nordlander 2006) and also for bark beetles and bark weevils on a very large scale (Chase et al. 2017; Nilssen 1984). In the latter study by Nilssen (1984), trap logs of spruce were laid out and colonized by the large pine weevil *Hylobius abietis* Linnaeus, 1758 at a distance of 171 km to the nearest occurrence of spruce forest. Chase et al. (2017), in contrast, used black panel insect traps with α-pinene and ethanol to attract the two bark beetle species *Hylurgus ligniperda* Fabricius, 1787 and *Hylastes ater* Paykull, 1800. Both species were trapped up to approximately 25 km away from the nearest pine stands. Colonization of deadwood structures after a large-scale forest fire can be seen as a natural experiment as abundant resources are generated over a vast area with a clearly visible distinction of burned and unburned parts of the forest. The colonization of large recently burned forest sites by pyrophilous saproxylic beetles as well as non-pyrophilous secondary users suggested that these groups were not negatively affected by up to 8 km distance to the border of the burned area (Saint-Germain et al. 2013).

15.3.5 Indirect Measurement of Dispersal: Population Genetic Analyses

Population genetic analyses are frequently used to infer population connectivity, i.e., the degree of gene flow on larger spatial and temporal scales, which is not feasible with direct measurements of dispersal. Population genetic inference is based on the principle that genetic divergence among local populations due to genetic drift (which causes subpopulations to diverge) is counteracted by the cohesive effects of gene flow due to individuals migrating from one population to another (Lowe and Allendorf 2010). The degree of genetic divergence can be used as an indicator of dispersal capacity of a species as it reflects past gene flow and thus dispersal (or absence thereof). When populations are subdivided (e.g., by fragmentation of forest habitats), the number of migrants can be estimated using classical F-statistics approaches. In species distributed continuously over space, limited gene flow (i.e., limited dispersal distances) leads to an increasing genetic differentiation among individuals as geographic distance increases, an effect known as isolation by distance (Allendorf et al. 2013).

Population genetic analyses also allow hierarchical analyses of populations on very different spatial scales within the same analysis. The relatedness and level of inbreeding of a group of individuals collected from a single structure such as a tree hollow can be measured (Schauer et al. 2018b) as well as genetic variation on the local (e.g., same forest patch) to regional scale as described above (Oleksa 2014; Oleksa et al. 2013, 2015; Schauer et al. 2018b). Dispersal distances can be estimated from spatial patterns of relatedness within local populations, where spatial autocorrelation among genotypes at varying distances is estimated. When individuals disperse over short distances, this will result in positive spatial genetic autocorrelation, i.e., the genotypes of individuals that are spatially closer are genetically more similar than at random (Epperson 2005; Oleksa et al. 2015).

Recent studies using population genetic analyses have shown that several saproxylic insects may be able to disperse over much longer distances than expected as no isolation by distance or population substructure was found among populations sampled over a distance of several hundred kilometers. For example, the cerambycid beetle *Rosalia alpina* Linnaeus, 1758 showed only very little genetic substructuring on a range of 600 km and potentially a rapid expansion of one genetic lineage within this area (Drag et al. 2015). Likewise beetles associated with bracket fungi such as *Bolitophagus reticulatus* Linnaeus, 1767 or *Diaperis boleti* Linnaeus, 1758 showed no spatial genetic substructuring over sites up to 200 km apart (Jonsson et al. 2003; Oleksa 2014). When landscape features are included in population genetic analyses, potential barriers to gene flow can be identified (or the lack of dispersal barriers that had been assumed before), which allows some inferences of dispersal behavior (Schauer et al. 2018b). However, this is also a potential drawback of landscape or population genetic analyses as for population substructure to arise gene flow must be lacking or hampered for a number of generation among subpopulations (Epps and Keyghobadi 2015). Furthermore, genetic analyses do not provide information about dispersal rate and exact dispersal distances of single individuals or on dispersal periods and patterns. Another drawback of population or landscape genetic analyses is that they are only feasible when a significant number of individuals per species [>30 to 50 at least, but the more the better (Lowe et al. 2004)] can be analyzed. For very rare species where only a handful of individuals can be analyzed, statistical noise would be too high to produce meaningful results.

15.3.6 Indirect Measurement of Dispersal: Analysis of Morphological Traits Impacting Light Performance

Dispersal ability can also be inferred indirectly by measuring traits associated with flight performance such as wing load (body mass divided by wing area) or wing aspect ratio (measure for shape of wings as wing length is divided by wing width) of the insect (Berwaerts et al. 2002). A lower wing load (i.e., less body weight per mm^2 of wing) supposedly translates into better flying ability because flight becomes energetically more efficient with decreasing wing load (Angelo and Slansky 1984). Relatively longer wings (higher aspect ratio) are thought to improve efficiency of prolonged flights and increase acceleration capacity or flight speed (Berwaerts et al. 2002; Marden 2000; Wootton 1992). Large body size reduces the mass-specific cost of flight and is thus associated with better dispersal ability (Roff 1991). Dispersal-associated morphological traits have been compared among (Gibb et al. 2006) as well as within (Bouget et al. 2015) species to differentiate between species or sexes with lower or higher dispersal abilities.

15.3.7 Indirect Measurement of Dispersal: Tethered Flight Experiments in Flight Mills

Tethered flight experiments are a suitable method to measure the physical dispersal capacity of individuals. As experiments are conducted under laboratory conditions with the surrounding “landscape” being similar for all individuals tested, it is assumed that motivational differences or differences due to environmental factors are reduced. Flight mills are the most common device used for tethered flight experiments, where an insect is attached to a flight arm that rotates due to the forces produced by the insect in flight. Flight time and speed are then used to calculate a maximum flight distance (Forsse and Solbreck 1985; Jactel and Gaillard 1991). Tethered flight experiments are suitable for the estimation of differences in dispersal abilities among species (Jonsson 2003) or within species (Dubois et al. 2010; Forsse and Solbreck 1985; Jactel 1993; Jactel and Gaillard 1991; Taylor et al. 2010). When life-history traits associated with dispersal capacity are compared in parallel among the individuals used for the tethered flight experiments, the proximate mechanisms underlying differences in dispersal ability can be uncovered, e.g., by measuring sex-specific differences or the influence of body condition on flight capacity such as the presence and status of wings and wing muscles (wing load) or fat content

(Akbulut and Linit 1999; David et al. 2014; Dubois et al. 2010; Forsse and Solbreck 1985; Jactel 1993; Jactel and Gaillard 1991; Jonsson 2003; Taylor et al. 2010).

A drawback of such experiments may be that flight behavior may be influenced by the insect being tethered. First insects must be handled and fixed to the device. Then, insects must accelerate the flight arm and have to overcome the friction of conventional bearings or the torsional resistance of magnetic mounds. This supposedly results in an underestimation of flight speed of the insects, which makes tethered flight experiments an excellent approach of measuring relative differences in dispersal capabilities but not absolute differences (Taylor et al. 2010).

15.3.8 Indirect Measurement of Dispersal: Inferring Dispersal Capabilities from Occurrence Patterns

The analyses of occurrence patterns (presence/absence) can be used to infer colonization abilities of saproxylic insects. Occurrence patterns of species result from their colonization abilities and local extinctions in respective habitat patches. In a number of studies, such occurrence patterns have been used as a proxy for colonization rates of specific habitat types and dispersal ability (Schiegg 2000a, b). However, as present occurrence patterns in habitat patches are confounded not only by current size and quality of the habitat patch itself but also by historical processes (Flensted et al. 2016; Gossner et al. 2008; Hanski and Ovaskainen 2002; Herrault et al. 2016; Janssen et al. 2016; Nordén et al. 2014), the estimation of dispersal abilities from such patterns is often difficult. Presence of a species within a habitat patch with low current connectivity to other habitat patches could either be due to a recent colonization event by a good disperser or the species has persisted locally if the habitat was formerly larger and/or less isolated and is therefore still found in spite of being a poor disperser (Herrault et al. 2016). This problem can be overcome when the same sites are sampled repeatedly, and thus colonization rate (and extinction rate in the metapopulation) can be inferred (Ranius et al. 2014). On the community level, colonization credit, i.e., lower than expected species richness in a habitat patch of a given area and quality, allows an estimation of the proportion of species that may be dispersal limited. After an increase in patch size, the number of species found would then be lower than expected in a habitat of a given size due to a time lag. For example, for hoverflies—a group that is thought to be highly mobile—Herrault et al. (2016) showed that they suffered a colonization credit in isolated woodlands, suggesting dispersal limitation.

In order to determine occurrence patterns, saproxylic insects need to be observed in a particular site or trapped. While direct observation in a particular site (e.g., by searching for individuals on the surface of potential host trees (Ranius et al. 2014) or opening deadwood structures) ensures that the particular insect really uses a site and is not only "passing through," using passive trapping is often preferred as it less labor intensive and captures a larger part of the saproxylic community. Emergence traps or flight interception traps are most often used to this end (Herrault et al. 2016; Irmler et al. 2010; Schiegg 2000a). By comparing the abundance of a particular species in flight interception traps within forest patches to that in traps in matrix habitat (open grassland), dispersal propensity and the potential of a species to cross matrix habitat can be tested, which helps to explain occurrence patterns.

Such an approach was used by Irmler et al. (2010), who showed that most of the 80 beetle species found in traps in the forest, as well as in grassland, were not very mobile, covering only distances of less than 30 m into the open grassland. Abundance of beetle species in forest patches was positively correlated with their mobility (Irmler et al. 2010).

15.3.9 Are Results of Different Methods Congruent?

Results obtained with the different methods described above yield different pictures of dispersal abilities of saproxylic insects (see Table 15.1 and overview of known dispersal distances below). Direct measurements of dispersal distances using telemetry or mark-release-recapture often suggest more limited dispersal abilities as distances measured are usually shorter than distances obtained in flight mill experiments or colonization experiments when conducted with the same species (e.g., several studies on *Bolitophagus reticulatus* Linnaeus, 1767, *Monochamus galloprovincialis* Olivier, 1795, or *Ips typographus* Linnaeus, 1758; for references see Table 15.1). This discrepancy may arise in capture mark-recapture-experiments due to the bias of individuals being recaptured. Recapture rate of those individuals dispersing over shorter distances only is higher than for those dispersing over longer distances. The potential for long-distance dispersal is captured more easily in tethered flight experiments. Likewise, the few population genetic analyses available to date often suggest that dispersal abilities are often better than hitherto thought. Here gene flow enabled by rare long-distance events is captured in absent or low genetic substructure or isolation by distance on larger spatial scales. As population genetic analyses also integrate over longer temporal scales, estimation of dispersal abilities is often not straightforward as genetic connectivity depends on the absolute number of dispersers among populations—and a few are enough to counteract population subdivision. For the persistence of a metapopulation of saproxylic insects, demographic connectivity is important though. Demographic connectivity means the relative contribution to population growth rates of dispersing individuals vs. survival and reproduction of residents (Lowe and Allendorf 2010). The use of a combination of different methods (direct and indirect measurement of dispersal) would therefore be important to gain a deeper understanding of the role of dispersal abilities in shaping community-level occurrence patterns of saproxylic insects locally and regionally.

Table 15.1 Studies addressing the dispersal abilities of saproxylic insects

	Dispersal strategy	Method	Distance	Author
Coleoptera				
Agrilus planipennis (Fairmaire 1888)	Flight	Flight mill	1.13 km	Fahrner et al. (2015)
Agrilus planipennis, (Fairmaire 1888)	Flight	Flight mill	>50% more than 750 m, 1% > 6 km	Taylor et al. (2010)
		Free flight experiment	>20 km	
Anaspis ruficollis (Fabricius 1792)	Flight	Genetic studies	No genetic differentiation in a ~10 × 10 km study area	Schauer et al. (2018b)
Anoplophora glabripennis (Motschulsky 1853)	Flight	Mark-recapture	2.6 km (98% of individuals recaptured within 920 m)	Smith et al. (2004)
Bolitotherus cornutus, (Panzer 1794)	Flight	Mark-recapture	50 m	Starzomski and Bondrup-Nielsen (2002)
Bolitotherus cornutus, (Panzer 1794)	Flight	Colonization experiment	365 m	Whitlock (1992)
Bolitophagus reticulatus (Linnaeus, 1767)	Flight	Field experiment	55 m	Sverdrup-Thygeson (2010)
Bolitophagus reticulatus (Linnaeus 1767)	Flight	Flight mill	29 h 36 min total flight time corresponding to 125 km	Jonsson (2003)
Bolitophagus reticulatus (Linnaeus 1767)	Flight	Genetic studies	200 km	Jonsson et al. (2003)
Cerambyx cerdo (Linnaeus 1758)	Flight	Mark-recapture	880 m for male, 1700 m for female	Torres-Vila et al. (2017)
Cerambyx welensii (Küster 1846)	Flight	Mark-recapture	1100 m for male, 580 m for female	Torres-Vila et al. (2017)
Dendroctonus frontalis (Zimmermann 1868)	Flight	Mark-recapture	500 m	Cronin et al. (1999)
Dendroctonus pseudotsugae (Hopkins 1905)	Flight	Flight mill	23 h continuous flight	Borden and Bennett (1969)
Diaperis boleti, (Linnaeus 1758)	Flight	Genetic studies	150 km	Oleksa (2014)
Elater ferrugineus, (Linnaeus 1758)	Flight	Mark-recapture	1.6 km, median 214 m	Zauli et al. (2014)
Elater ferrugineus (Linnaeus 1758)	Flight	Genetic studies	100 to ~650 m	Oleksa et al. (2015)

(continued)

Table 15.1 (continued)

	Dispersal strategy	Method	Distance	Author
Hylobius abietis, (Linnaeus 1758)	Flight	Flight mill	10–80 km	Solbreck (1980)
Hylastes ater (Paykull 1800)	Flight	Colonization experiment	27.6 km	Chase et al. (2017)
Hylurgus ligniperda (Fabricius 1787)	Flight	Colonization experiment	26.3 km	Chase et al. (2017)
Hylurgus ligniperda (Fabricius 1787)	Flight	Mark-recapture	960 m, model based estimates 46% > 1 km, 1.6% > 5 km	Meurisse and Pawson (2017)
Ips typographus (Linnaeus 1758)	Flight	Mark-recapture	1.1 km	Dolezal et al. (2016)
Ips typographus (Linnaeus, 1758)	Flight	Field experiment	8 km	Botterweg (1982)
Ips typographus (Linnaeus 1758)	Flight	Mark-recapture	1.2–1.6 km	Forsse and Solbreck (1985)
Ips typographus (Linnaeus 1758)	Flight	Mark-recapture	120 m (furthest trapping point)	Zolubas and Byers (1995)
Lucanus cervus (Linnaeus 1758)	Flight	Telemetry	2 km	Rink and Sinsch (2007)
Lucanus cervus (Linnaeus 1758)	Flight	Telemetry	200 m	Sprecher-Uebersax and Durrer (2001)
Lucanus cervus, (Linnaeus 1758)	Flight	Telemetry	2 km	Rink and Sinsch (2007)
Lucanus cervus (Linnaeus 1758)	Flight	Telemetry	250 m for males, 144 m for females	Tini et al. (2017)
Monochamus alternatus (Hope 1843)	Flight	Mark-recapture	59 m	Shibata (1986b)
Monochamus carolinensis (Olivier 1792)	Flight	Flight mill	2200 m ± 1100 m	Akbulut and Linit (1999)
Monochamus galloprovincialis (Olivier, 1795)	Flight	Mark-recapture	>400 m	Torres-Vila et al. (2015)
Monochamus galloprovincialis (Olivier 1795)	Flight	Modeling of dispersal kernels in a mark-recapture study	> 4 km	Etxebeste et al. (2016)
Monochamus galloprovincialis (Olivier 1795)	Flight	Flight mill	63 km	David et al. (2014)
Monochamus sartor (Fabricius 1787)	Flight	Flight mill	3.14 km	Putz et al. (2016)

(continued)

Table 15.1 (continued)

	Dispersal strategy	Method	Distance	Author
Monochamus sutor (Linnaeus 1758)	Flight	Flight mill	5.56 km	Putz et al. (2016)
Morimus asper (Sulzer 1776)	Walking	Mark-recapture	451 m	Rossi de Gasperis et al. (2016)
Odontotaenius disjunctus (Illiger 1800)	Flight, walking	Colonization experiment	Ø11.6 m	Jackson et al. (2009)
Oplocephala haemorrhoidalis (Fabricius 1787)	Flight	Flight mill	7 h 30 min total flight time corresponding to 29 km	Jonsson (2003)
Oplocephala haemorrhoidalis (Fabricius 1787)	Flight	Genetic studies	>12 km	Jonsson (2003)
Osmoderma barnabita (Motschulsky 1845)	Flight	Genetic studies	200 m	Oleksa et al. (2013)
Osmoderma eremita (Scopoli 1763)	Flight	Mark-recapture	190 m	Ranius and Hedin (2001)
Osmoderma eremita (Scopoli 1763)	Flight	Radio telemetry	1500 m	Chiari et al. (2013)
Osmoderma eremita (Scopoli 1763)	Flight	Radio telemetry	700 m	Dubois and Vignon (2008)
Osmoderma eremita (Scopoli 1763)	Flight	Flight mill	~2300 m	Dubois et al. (2010)
Protaetia marmorata (Herbst 1786)	Flight	Genetic studies	500 m	Oleksa et al. (2013)
Rhizophagus grandis (Gyllenhaal 1827)	Flight	Field experiment	4 km	Fielding et al. (1991)
Rosalia alpina (Linnaeus 1758)	Flight	Mark-recapture	1.6 km	Drag et al. (2011)
Rosalia alpina (Linnaeus 1758)	Flight	Genetic studies	600 km	Drag et al. (2015)
Spasalus crenatus, (MacLeay 1819)	Flight, walking	Colonization experiment	2–6 m	Galindo-Cardona et al. (2007)
Thanasimus dubius (Fabricius 1777)	Flight	Mark-recapture	1.25 km, 5% > 5 km, maximum one individual 8 km	Cronin et al. (2000)
Tomicus piniperda (Linnaeus 1758)	Flight	Field experiment	95.3% 400 m, 4.7% 780–2000 m	Barak et al. (2000)
Diptera				
Criorhina floccosa (Meigen 1822)	Flight	Genetic studies	No genetic differentiation in a ~10 × 10 km study area	Schauer et al. (2018b)

(continued)

Table 15.1 (continued)

	Dispersal strategy	Method	Distance	Author
Hammerschmidtia ferruginea (Fallén 1817)	Flight	Mark-recapture	5 km	Rotheray et al. (2014)
Xylomya maculata (Meigen 1804)	Flight	Genetic studies	No genetic differentiation in a ~10 × 10 km study area	Schauer et al. (2018b)
Hymenoptera				
Tetrastichus planipennisi (Yang 2006) *(parasitoid of Agrilus planipennis)*	Flight	Flight mill	1.81 km	Fahrner et al. (2015)
Isoptera				
Coptotermes formosanus (Shiraki 1909)	Flight	Mark-recapture	890 m	Messenger and Mullins (2005)
Coptotermes formosanus (Shiraki 1909)	Flight	Mark-recapture	1.3 km	Mullins et al. (2015)
Coptotermes formosanus (Shiraki 1909)	Flight	Genetic studies	510 m	Simms and Husseneder (2009)
Pseudoscorpiones				
Allochernes wideri (C.L. Koch 1837)	Phoresy	Genetic studies	Small but significant genetic substructure at sites up to 900 km apart	Ranius and Douwes (2002)
Larca lata (Hansen 1884)	Phoresy	Genetic studies	Small but significant genetic substructure at sites up to 900 km apart	Ranius and Douwes (2002)

If no range or further information is presented in the column “distance” the maximum distance measured or estimated in the study is given

15.4 Dispersal Distances: What Is Known for Particular Taxa?

15.4.1 Beetles

The knowledge on dispersal seems to be best for saproxylic beetles compared to other taxa (see Table 15.1). Still there is only knowledge of few species in terms of their dispersal ability.

In the family of Scarabaeidae, *Osmoderma eremita* Scopoli, 1763 is the one species where most direct measurements of dispersal were conducted. Recorded maximum dispersal distances reported in different studies for *O. eremita* Scopoli, 1763 ranged from 190 m (Ranius and Hedin 2001) to 1500 m (Chiari et al. 2013). Physically *O. eremita* Scopoli, 1763 seems to be able to fly over larger distances, as in a tethered flight experiment a distance of ~2300 m was recorded (Dubois et al. 2010). This suggests that dispersal distances are influenced by local landscape and spatial distribution of suitable habitats. Shorter dispersal distances were recorded in the Swedish population with a high local density of suitable habitats surrounded by unsuitable matrix habitat, while in other study areas (Italy, France), larger dispersal distances were found where the beetles inhabit cork oaks in a large woodland area or chestnut trees that are patchily distributed in the landscape (Chiari et al. 2013; Dubois and Vignon 2008). Occurrence patterns on a larger geographic scale strongly suggest that *O. eremita* Scopoli, 1763 is dispersal limited as the presence of the beetle is positively correlated with spatial connectivity of habitat patches (Ranius et al. 2011). In the closely related species *Osmoderma barnabita* Motschulsky, 1845, Oleksa et al. (2013) estimated an average dispersal distance of 200 m and approximately 500 m in *Protaetia marmorata* Herbst, 1786 based on genetic data. Over a sampling range of 100 km, both species showed significant isolation by distance and thus limited gene flow due to the limited dispersal abilities (Oleksa et al. 2013).

In the family Tenebrionidae, the dispersal abilities of several beetle species with a very similar ecological niche have been studied. All species studied to date develop in and feed on the sporocarps of tinder or bracket fungi. Dispersal abilities of *Bolitophagus reticulatus* Linnaeus, 1767 have been measured with several different methods. An observed dispersal distances of 55 m in a field experiment (Sverdrup-Thygeson 2010) suggested that this beetle is likely to be dispersal limited. However, the dispersal abilities of *B. reticulatus* Linnaeus, 1767 should be much higher as the longest total flight time in flight mill-experiments for a single individual was 29 h 36 min which would correspond to an estimated dispersal distance of 125 km and median of ~7 km (Jonsson 2003). These results are corroborated by genetic analyses where no differentiation was found among populations as far apart as 200 km (Jonsson et al. 2003). Dispersal abilities of *B. reticulatus* Linnaeus, 1767 were compared to those of the rarer tenebrionid *Oplocephala haemorrhoidalis* Fabricius, 1787, which also feeds exclusively on tinder fungi. Both, flight mill experiments and genetic analyses suggested that the dispersal abilities were not as good as in *B. reticulatus* Linnaeus, 1767. While the median length of flight was estimated to be >12 km in *O. haemorrhoidalis* Fabricius, 1787, the maximum estimated flight time and distance was shorter (7 h 30 min and 29 km), and dispersal propensity was lower than in *B. reticulatus* (Jonsson 2003). Likewise genetic differentiation was moderate to strong in this species over the same geographic distance where no differentiation was found in *B. reticulatus* Linnaeus, 1767 (Jonsson et al. 2003). Studies on occurrence patterns on the one hand suggest that the beetle has excellent long-distance dispersal capabilities and is not dispersal limited as it occurs wherever the host fungus occurs (Jonsell et al. 2003). In contrast, another study shows habitat fragmentation may lead to a much higher differentiation in a fragmented landscape compared to a continuous area (Knutsen et al. 2000). A lack of spatial genetic substructure was similarly found for the fungus-associated *Diaperis boleti* Linnaeus, 1758 over a spatial scale of 150 km (Oleksa 2014). In the North American species *Bolitotherus cornutus* Panzer, 1794, mark-recapture data suggested a very limited movement radius of around 50 m (like in *B. reticulatus* Linnaeus, 1767, see above) (Starzomski and Bondrup-Nielsen 2002), while dispersal distances of 365 m were found in a colonization experiment (Whitlock 1992).

Dispersal in the family of Curculionidae has been studied for the subfamily Scolytinae, the bark beetles, as major forest pest species of economic interest. Measured dispersal distances in *Ips typographus* Linnaeus, 1758 ranged from 120 m (max. Distance at which traps with lure were placed in this mark-recapture study) (Zolubas and Byers 1995) to a range of 1.1 to 8 km in other studies and field experiments (Botterweg 1982; Dolezal et al. 2016; Weslien and Lindelöw 1990). The percentage of recaptured individuals was still around 2% of all marked individuals at the maximum distance sampled in these latter studies, suggesting that longer dispersal distances may occur under natural conditions. In addition, *I. typographus* Linnaeus, 1758 flies above the tree crowns which may allow the small beetles to be passively dispersed over larger distances by wind (Forsse and Solbreck 1985). Marked individuals of *Dendroctonus frontalis* Zimmermann, 1868 were found between 100 and 500 m from their releasing point (Cronin et al. 1999) and those of the common pine shoot beetle *Tomicus piniperda* Linnaeus, 1758 mostly within 400 m of the releasing point but a few up to 2 km away (Barak et al. 2000). For other Scolytinae, the estimated dispersal distances were much higher, with an estimated 10 to 80 km in a flight mill experiment for *Hylobius abietis* Linnaeus, 1758 (Solbreck 1980) or 23 h continuous flight in *Dendroctonus pseudotsugae* Hopkins, 1905, respectively (Borden and Bennett 1969). In mark-recapture experiment, many individuals were recaptured after a dispersal distance of 920 m, which was the furthest distance of traps from the site of release. Based on diffusion models, the authors estimate that nearly 50% of individuals of *Hylurgus ligniperda* Fabricius, 1787 disperse over at least 1 km and 1.6% further away than 5 km (Meurisse and Pawson 2017). The good dispersal abilities of this as well as another pine bark beetle species, *Hylastes ater* Paykull, 1800, were corroborated by colonization experiments using odor traps. Both species were caught in traps as far away as 26 km from the nearest pine resources (Chase et al. 2017). Based on mark-recapture studies, the dispersal distances of at least 50% of individuals of *Thanasimus dubius* Fabricius, 1777 (Cleridae), a predator of bark beetles in North America, were estimated to disperse at least 1.25 km, but around 5% should disperse over distances >5 km. The maximum dispersal distance of a marked individual was 8 km. Thus, the predator seems to have better or at least similar dispersal ability in comparison to its prey (Cronin et al. 2000).

Dispersal abilities of flightless Curculionidae were indirectly inferred by comparing occurrence patterns of woodlands in Northern Germany. The flightless weevils of the subfamily Cryptorhynchina *Acalles ptinoides* Marsham, 1802, *Trachodes hispidus* Linnaeus, 1758, and *Kyklioacalles navieresi* Boheman, 1837 (belonging to the subfamily Molytinae) were found only in ancient woodlands but not recent ones (Buse 2012), suggesting very strong dispersal limitation.

For Cerambycidae, longhorned beetles, dispersal distances vary considerably in the species that were studied to date, even in related species. The Japanese pine sawyer *Monochamus alternatus* Hope, 1843 seems to be a species with limited dispersal abilities as a dispersal distance of 59 m was observed (Shibata 1986b) using mark-recapture. Flight mill experiments on the congeneric *M. carolinensis* Olivier, 1792 suggest a better dispersal ability of this species, with mean flight distances being 2.2 km for both sexes (Akbulut and Linit 1999). In yet another congeneric, *M. galloprovincialis* Olivier, 1795, marked individuals were found at a distance of >400 m from the release site, while mean dispersal distance was app. 120 m (Torres-Vila et al. 2015). Based on modeling of dispersal kernels in a mark-recapture study, the estimated dispersal distance of *M. galloprovincialis* Olivier, 1795 is still larger though with >4 km (Etxebeste et al. 2016). Flight mill experiments again underscore the good dispersal abilities of *M. galloprovincialis* Olivier, 1795 with a mean estimated potential dispersal distance of 16 km and a maximum of up to 63 km (David et al. 2014). The good dispersal capacity of beetles of this genus was corroborated in a study on another two European species *M. sartor* Fabricius, 1787 and *M. sutor* Linnaeus, 1758 using a flight mill. The maximum distance flown in a single bout by *M. sartor* Fabricius, 1787 was 3.14 km, and the cumulative dispersal distance over the life span of a beetle was 7.5 km. The smaller *M. sutor* Linnaeus, 1758 flew even further, with a maximum flight distance of 5.56 km (Putz et al. 2016). The majority of marked and recaptured Asian longhorned beetles *Anoplophora glabripennis* Motschulsky, 1853 were found to disperse less than 1 km from the release site, while some individuals were caught at distances of 2.6 km from the release site (Smith et al. 2004). Earlier studies of *A. glabripennis* Motschulsky, 1853 showed slightly shorter dispersal distances (Smith et al. 2001).

Dispersal abilities of the threatened Rosalia longicorn *Rosalia alpina* Linnaeus, 1758 were studied using mark-recapture as well as genetic analyses. The maximum distance covered (which included flights over unsuitable matrix habitat) was 1600 m (Drag et al. 2011), suggesting good dispersal abilities. No genetic substructure was found among populations of *R. alpina* Linnaeus, 1758 as far apart as 600 km (Drag et al. 2015), suggesting that the observed dispersal distance translates into high levels of gene flow over large distances, in spite of habitat fragmentation. Dispersal abilities of *Cerambyx welensii* Küster, 1846 and *Cerambyx cerdo* Linnaeus, 1758 were estimated using mark-recapture methods in Spanish populations. Both species showed a pronounced dispersal polymorphism. While some individuals showed a high dispersal propensity and much larger dispersal distances than other individuals (*C. welensii* Küster, 1846, maximum recorded distance of 1100 m for a male and 580 m for a female; *C. cerdo* Linnaeus, 1758, 880 m for a male and 1700 m for a female), many individuals were sedentary and hardly moved away from the site of release (Torres-Vila et al. 2017). This subset of individuals should allow colonization of habitat patches that are further away. In contrast, in the flightless cerambycid *Morimus asper* Sulzer, 1776, only very few individuals left the point where they were released after marking, and the furthest dispersal distance measured was 451 m (Rossi de Gasperis et al. 2016).

Among elaterids, information on dispersal distance is available only for *Elater ferrugineus* Linnaeus, 1758, a facultative predator of *O. eremita* Scopoli, 1763. Here dispersal distances of more than 1.6 km were found using mark-recapture and a median dispersal distance of 214 m, suggesting again similar or better dispersal capacities of the predator in comparison to its prey (see above the clerid *T. dubius* Fabricius, 1777 and its bark beetle prey) (Zauli et al. 2014). Genetic analyses suggest a dispersal distance of 100 to ~650 m as isolation by distance was found at a scale of ~9 km, albeit in a fragmented agricultural landscape where this click beetle can mostly be found in old hollow trees along rural avenues (Oleksa et al. 2015).

In *Lucanus cervus* Linnaeus, 1758 (Lucanidae), telemetry studies revealed dispersal distances between 200 m in a Swiss population (Sprecher-Uebersax and Durrer 2001) and 2 km in a German population (Rink and Sinsch 2007). In another telemetry study conducted in a relict lowland forest in a nature reserve in Italy, the mean dispersal distance of *L. cervus* Linnaeus, 1758 males was 250 m compared to an average of 144 m for females (Tini et al. 2017).

The buprestid *Agrilus planipennis* Fairmaire, 1888 (emerald ash borer) has been shown to fly over distances of up to 1.13 km (Fahrner et al. 2015) to >6 km (Taylor et al. 2010) in flight mill experiments. As insects may show slower flight speed when tethered (see discussion of tethered flight experiments, Sect. 15.3.7), Taylor et al. (2010) measured the speed of flight in free-flying experiments in parallel. Flight distances obtained in the flight mill experiment were then calibrated with flying speed in free-flight and dispersal distances corrected. The median corrected flight distance of females was >3 km and 1% of females flew >20 km.

The passalid beetle *Spasalus crenatus* MacLeay, 1819 was shown to have very limited dispersal abilities. In a colonization experiment, beetles dispersed for 2 to 6 m only from a release point before initiating a colony. The beetles were functionally flightless as their wing muscles were not developed, strong enough to enable flight and thus most likely dispersed by walking (Galindo-Cardona et al. 2007). Similarly, the passalid *Odontotaenius disjunctus* Illiger, 1800 primarily disperses over short distances of on average 11.6 m by walking (Jackson et al. 2009) and has rarely be shown to fly over longer distances (Jackson et al. 2012).

The predator *Rhizophagus grandis* Gyllenhaal, 1827 (Rhizophagidae) was also shown to have good dispersal abilities as individuals were found at their prey 4 km from the release site (Fielding et al. 1991). In the scraptiid beetle *Anaspis ruficollis* Fabricius, 1792, inhabiting tree hollows but also lying deadwood, population genetic analyses did not uncover genetic differentiation in a ~10 × 10 km study area of large forest fragments. However, genetic differentiation was slightly stronger in this beetle species in comparison to the two dipteran species compared in the same study (Schauer et al. 2018b).

15.4.2 Other Saproxylic Taxa

For hoverflies and other dipteran species, not much is known about their dispersal abilities. In a mark-recapture study on the syrphid fly *Hammerschmidtia ferruginea*

Fallén, 1817, a dispersal distance of 5 km was shown (Rotheray et al. 2014). Schauer et al. (2018b) could show no genetic differentiation of the syrphid fly *Criorhina floccosa* Meigen, 1822 and the xylomid fly *Xylomya maculata* Meigen, 1804 in a ~10 x 10 km managed forest, suggesting good dispersal abilities of these two species.

The hymenopteran *Tetrastichus planipennisi* Yang, 2006, a parasitoid of the emerald ash borer *Agrilus planipennis* Fairmaire, 1888, has been shown to be able to disperse slightly further than its host. While *A. planipennis* Fairmaire, 1888 flew a maximum distance of 1.13 km, the parasitoid showed a maximum flight distance of 1.81 km under similar conditions in a flight mill experiment (Fahrner et al. 2015).

Winged sexuals of the Formosan subterranean termite *Coptotermes formosanus* Shiraki, 1909 have been shown to disperse over at least 500 m to 1300 m in an urban setting in New Orleans. Dispersing individuals could be assigned unambiguously to their parental colonies either based on multilocus genotypes (Simms and Husseneder 2009) or in mark-recapture experiments (Messenger and Mullins 2005; Mullins et al. 2015). Small flightless arthropods such as pseudoscorpions and mites often hitch-hike on larger saproxylic insects for dispersal. Using population genetic analyses, Ranius and Douwes (2002) found very small genetic substructure among populations of *Allochernes wideri* C.L. Koch, 1837 and *Larca lata* Hansen, 1884 as far apart as 900 km, suggesting good passive dispersal through phoresy (Ranius and Douwes 2002). Nonetheless, *L. lata* Hansen, 1884 may still be dispersal limited as its occurrence was positively correlated with spatial connectance on larger spatial scales (Ranius et al. 2011).

15.5 Outlook and Conclusion

Researchers and naturalists alike often estimate dispersal abilities of particular taxa—or species—based on their morphology and notion of life-history traits as data on dispersal is often still scarce. To date dispersal distances have been measured mostly either for pest species or threatened species (often “flagship species”). Knowledge of dispersal behavior and its implications for gene flow, population persistence, and colonization of new habitats is still scarce. A better knowledge of dispersal abilities and behavioral aspects of dispersal are needed, especially with respect to the development of management strategies for saproxylic insects in managed forests or fragmented habitats.

Currently, there is ongoing debate in the field whether saproxylic insects are rather dispersal limited or habitat limited. Due to deforestation and ecological degradation of forests, connectivity and habitat availability are both low. Absence of a species in a seemingly suitable habitat patch is often interpreted as dispersal limitation. Local extinction may result from the absence of habitat, poor habitat quality, or unsuitable area around a habitat patch that is not crossed during dispersal (Fahrig 2013; Hanski et al. 1994). The relatively few population genetic analyses available to date suggest that saproxylic insects are often not dispersal limited on a local and regional scale—or at least not as much as assumed. However, this will depend strongly on the species studied as different taxa vary strongly in dispersal distances and dispersal abilities (e.g., passalids dispersing a few meters only in comparison to some flying cerambycids or scolytids that can disperse over several to dozens of kilometers). Studies on occurrence patterns over larger geographic scales have detected dispersal limitation for a broad range of different species. When forest fragments or other habitat structures are more isolated, fewer saproxylic insect species occur (Bergman et al. 2012; Ranius et al. 2011). Likewise, artificial deadwood structures mimicking tree hollows were less often colonized by saproxylic tree hollow specialists when placed further away from sources. As habitat quality was comparable, species have most likely been dispersal limited (Jansson et al. 2009).

Factors influencing different aspects of dispersal behavior, such as the decision to leave a patch, the movement pattern (e.g., what kind of matrix habitats are crossed during dispersal?), and the decision to settle at a particular site are often still unknown. These factors include the sex of an individual, body condition, feeding strategy, breadth of ecological niche, or competition. Even less is known about the interplay of several of these factors. However, such data is needed to assess whether structural connectivity among habitat patches also results in functional connectivity.

The use of a combination of methods that integrate several temporal and spatial scales would be desirable to characterize dispersal abilities of species. By combining mark-recapture techniques and population genetic analyses, the dispersal ability of a large proportion of individuals can be tested directly using the former, and the influence of the often small percentage of individuals dispersing over much larger distances on the population structure would be captured with the latter. And how strongly do dispersal distances vary with landscape and are they consistent over time? If such data was available for more species, this would allow for comparative analysis to be conducted, allowing more general conclusions of the dispersal abilities of species with similar ecological niches. For example, the suite of species of tenebrionid beetles feeding on fungal sporocarps seems to have relatively similar dispersal abilities, in spite of belonging to different genera and living on different continents. Does this hold for more groups of species with a similar ecological niche? How strongly is dispersal behavior influenced by spatial and temporal heterogeneity? In the light of climate change and anthropogenic habitat destruction, it is important to assess the plasticity or evolutionary potential of dispersal strategies for different species.

A better knowledge of dispersal of saproxylic insects is required for an understanding of ecological processes but also to inform management decisions for the conservation of threatened species. However, as dispersal is a highly complex phenomenon, more integrative studies would be vital that on the one hand examine physiological and behavioral aspects of dispersal and on the other hand measure dispersal distances using different methods. An increase in availability of data on dispersal collected with different methods will allow drawing more general conclusions and potentially also relatively well-informed predictions of the dispersal abilities of species.

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References

Akbulut S, Linit MJ (1999) Flight performance of *Monochamus carolinensis* (Coleoptera: Cerambycidae) with respect to nematode phoresis and beetle characteristics. Environ Entomol 28:1014–1020

Allendorf FW, Luikart G, Aitken SN (2013) Conservation and the genetics of populations. Wiley-Blackwell, Chichester

Angelo MJ, Slansky F (1984) Body building by insects—trade-offs in resource-allocation with particular reference to migratory species. Fla Entomol 67:22–41

Barak AV, McGrevy D, Tokaya G (2000) Dispersal and recapture of marked, overwintering *Tomicus piniperda* (Coleoptera: Scolytidae). Great Lakes Entomol 33:69–80

Benton TG, Bowler DE (2012) Dispersal in invertebrates: influences on individual decisions. In: Clobert J, Baguette M, Benton TG, Bullock JM (eds) Dispersal ecology and evolution. Oxford University Press, Oxford, pp 41–49

Bergman KO, Jansson N, Claesson K, Palmer MW, Milberg P (2012) How much and at what scale? Multiscale analyses as decision support for conservation of saproxylic oak beetles. For Ecol Manag 265:133–141

Berwaerts K, Van Dyck H, Aerts P (2002) Does flight morphology relate to flight performance? An experimental test with the butterfly *Pararge aegeria*. Funct Ecol 16:484–491

Biedermann PHW, Taborsky M (2011) Larval helpers and age polyethism in ambrosia beetles. Proc Natl Acad Sci U S A 108:17064–17069

Blouin SF, Blouin M (1988) Inbreeding avoidance behaviors. Trends Ecol Evol 3:230–233

Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, Gibbs M, Lehouk V, Mathysen E, Mustin K, Saastamoinen M, Schtickzelle N, Stevens VM, Vandewoestijne S, Baguette M, Barton K, Benton TG, Chaput-Bardy A, Clobert J, Dytham C, Hovestadt T, Meier CM, Palmer SCF, Turlure C, Travis JMJ (2012) Costs of dispersal. Biol Rev 87:290–312

Borden JH, Bennett RB (1969) A continously recording flight mill for investigating effect of volatile substances on flight of tethered insects. J Econ Entomol 62:782–785

Botterweg PF (1982) Dispersal and flight behavior of the spruce bark beetle *Ips typographus* in relation to sex, size and fat-content. Z Angew Entomol 94:466–489

Bouget C, Brin A, Tellez D, Archaux F (2015) Intraspecific variations in dispersal ability of saproxylic beetles in fragmented forest patches. Oecologia 177:911–920

Boulanger Y, Sirois L, Hebert C (2010) Distribution of saproxylic beetles in a recently burnt landscape of the northern boreal forest of Quebec. For Ecol Manag 260:1114–1123

Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol Rev 80:205–225

Branquart E, Hemptinne JL (2000) Selectivity in the exploitation of floral resources by hoverflies (Diptera : Syrphinae). Ecography 23:732–742

Brin A, Valladares L, Ladet S, Bouget C (2016) Effects of forest continuity on flying saproxylic beetle assemblages in small woodlots embedded in agricultural landscapes. Biodivers Conserv 25:587–602

Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445–449

Brunet J, Isacsson G (2009) Restoration of beech forest for saproxylic beetles-effects of habitat fragmentation and substrate density on species diversity and distribution. Biodivers Conserv 18:2387–2404

Buse J (2012) “Ghosts of the past”: flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. J Insect Conserv 16:93–102

Chase KD, Kelly D, Liebhold AM, Bader MKF, Brockerhoff EG (2017) Long-distance dispersal of non-native pine bark beetles from host resources. Ecol Entomol 42:173–183

Chiari S, Carpaneto GM, Zauli A, Zirpoli GM, Audisio P, Ranius T (2013) Dispersal patterns of a saproxylic beetle, *Osmoderma eremita*, in Mediterranean woodlands. Insect Conserv Divers 6:309–318

Clobert J, Le Galliard JF, Cote J, Le Galliard JF, Massot M (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecol Lett 12:197–209

Compton SG (2002) Sailing with the wind: dispersal by small flying insects. In: Bullock JM, Kenward RE, Hails RS (eds) Dispersal ecology. Blackwell Science, Oxford, pp 113–133

Cronin JT, Turchin P, Hayes JL, Steiner CA (1999) Area-wide efficacy of a localized forest pest management practice. Environ Entomol 28:496–504

Cronin JT, Reeve JD, Wilkens R, Turchin P (2000) The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey. Oikos 90:127–138

David G, Giffard B, Piou D, Jactel H (2014) Dispersal capacity of *Monochamus galloprovincialis*, the European vector of the pine wood nematode, on flight mills. J Appl Entomol 138:566–576

Denno RF, Roderick GK, Peterson MA, Huberty AF, Döbel HG, Eubanks MD, Losey JE, Langellotto GA (1996) Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. Ecol Monogr 66:389–408

Dolezal P, Okrouhlik J, Davidkova M (2016) Fine fluorescent powder marking study of dispersal in the spruce bark beetle, *Ips typographus* (Coleoptera: Scolytidae). Eur J Entomol 113:1–8

Drag L, Hauck D, Pokluda P, Zimmermann K, Cizek L (2011) Demography and dispersal ability of a threatened saproxylic beetle: a mark-recapture study of the Rosalia longicorn (*Rosalia alpina*). PLoS One 6:e21345

Drag L, Hauck D, Berces S, Michalcewicz J, Seric Jelaska L, Aurenhammer S, Cizek L (2015) Genetic differentiation of populations of the threatened saproxylic beetle Rosalia longicorn, *Rosalia alpina* (Coleoptera: Cerambycidae) in central and south-east Europe. Biol J Linn Soc 116:911–925

Dubois G, Vignon V (2008) First results of radio-tracking of *Osmoderma eremita* (Coleoptera: Cetoniidae) in French chestnut orchards. Rev Ecol Terre Vie:131–138

Dubois GF, Le Gouar PJ, Delettre YR, Brustel H, Vernon P (2010) Sex-biased and body condition dependent dispersal capacity in the endangered saproxylic beetle *Osmoderma eremita* (Coleoptera: Cetoniidae). J Insect Conserv 14:679–687

Epperson BK (2005) Estimating dispersal from short distance spatial autocorrelation. Heredity 95:7–15

Epps CW, Keyghobadi N (2015) Landscape genetics in a changing world: disentangling historical and contemporary influences and inferring change. Mol Ecol 24:6021–6040

Etxebeste I, Sanchez-Husillos E, Alvarez G, Gisbert MI, Pajares J (2016) Dispersal of *Monochamus galloprovincialis* (Col.: Cerambycidae) as recorded by mark-release-recapture using pheromone traps. J Appl Entomol 140:485–499

Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. J Biogeogr 40:1649–1663

Fahrig L, Merriam G (1994) Conservation of fragmented populations. Conserv Biol 8:50–59

Fahrner SJ, Lelito JP, Aukema BH (2015) The influence of temperature on the flight capacity of emerald ash borer *Agrilus planipennis* and its parasitoid, *Tetrastichus planipennisi*: implications to biological control. BioControl 60:437–449

Fayt P, Dufrene M, Branquart E, Hastir P, Pontegenie C, Henin JM, Versteirt V (2006) Contrasting responses of saproxylic insects to focal habitat resources: the example of longhorn beetles and hoverflies in Belgian deciduous forests. J Insect Conserv 10:129–150

Fielding NJ, Okeefe T, King CJ (1991) Dispersal and host-finding capability of the predatory beetle *Rhizophagus grandis* Gyll (Col., Rhizophagidae). J Appl Entomol 112:89–98

Flensted KK, Bruun HH, Ejrnaes R, Eskildsen A, Thomsen PF, Heilmann-Clausen J (2016) Red-listed species and forest continuity—a multi-taxon approach to conservation in temperate forests. For Ecol Manag 378:144–159

Forsse E, Solbreck C (1985) Migration in the bark beetle *Ips typographus* L—duration, timing and height of flight. Z Angew Entomol 100:47–57

Galindo-Cardona A, Giray T, Sabat AM, Reyes-Castillo P (2007) Bess beetle (Coleoptera : Passalidae): substrate availability, dispersal, and distribution in a subtropical wet forest. Ann Entomol Soc Am 100:711–720

Gall LF (1984) The effects of capturing and marking on subsequent activity in *Boloria acrocnema* (Lepidoptera, Nymphalidae), with a comparison of different numerical models that estimate population size. Biol Conserv 28:139–154

Gibb H, Hjalten J, Ball JP, Atlegrim O, Petterson RB, Hilszezanski J, Johansson T, Danell K (2006) Wing loading and habitat selection in forest beetles: are red-listed species poorer dispersers or more habitat-specific than common congenerics? Biol Conserv 132:250–260

Gossner M, Engel K, Jessel B (2008) Plant and arthropod communities in young oak stands: are they determined by site history? Biodivers Conserv 17:3165–3180

Gotelli NJ (1991) Metapopulation models—the rescue effect, the propagule rain, and the core-satellite hypothesis. Am Nat 138:768–776

Grove SJ (2002a) The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. Biol Conserv 104:149–171

Grove SJ (2002b) Saproxylic insect ecology and the sustainable management of forests. Annu Rev Ecol Syst 33:1–23

Hanks LM (1999) Influence of the larval host plant on reproductive strategies of cerambycid beetles. Annu Rev Entomol 44:483–505

Hanski I (1998) Metapopulation dynamics. Nature 396:41–49

Hanski I, Ovaskainen O (2002) Extinction debt at extinction threshold. Conserv Biol 16:666–673

Hanski I, Kuussaari M, Nieminen M (1994) Metapopulation structure and migration in the butterfly *Melitaea cinxia*. Ecology 75:747–762

Hedin J, Ranius T (2002) Using radio telemetry to study dispersal of the beetle *Osmoderma eremita*, an inhabitant of tree hollows. Comput Electron Agric 35:171–180

Hedin J, Ranius T, Nilsson SG, Smith HG (2008) Restricted dispersal in a flying beetle assessed by telemetry. Biodivers Conserv 17:675–684

Heidinger IMM, Poethke HJ, Bonte D, Hein S (2009) The effect of translocation on movement behaviour—a test of the assumptions of behavioural studies. Behav Process 82:12–17

Heikkala O, Martikainen P, Kouki J (2017) Prescribed burning is an effective and quick method to conserve rare pyrophilous forest-dwelling flat bugs. Insect Conserv Divers 10:32–41

Henter HJ (2003) Inbreeding depression and haplodiploidy: experimental measures in a parasitoid and comparisons across diploid and haplodiploid insect taxa. Evolution 57:1793–1803

Herrault PA, Larrieu L, Cordier S, Gimmi U, Lachat T, Ouin A, Sarthou JP, Sheeren D (2016) Combined effects of area, connectivity, history and structural heterogeneity of woodlands on the species richness of hoverflies (Diptera: Syrphidae). Landsc Ecol 31:877–893

Horak J, Vodka S, Pavlicek J, Boza P (2013) Unexpected visitors: flightless beetles in window traps. J Insect Conserv 17:441–449

Irmler U, Arp H, Notzold R (2010) Species richness of saproxylic beetles in woodlands is affected by dispersion ability of species, age and stand size. J Insect Conserv 14:227–235

Jackson HB, Baum KA, Robert T, Cronin JT (2009) Habitat-specific movement and edge-mediated behavior of the saproxylic insect *Odontotaenius disjunctus* (Coleoptera: Passalidae). Environ Entomol 38:1411–1422

Jackson HB, Baum KA, Cronin JT (2012) From logs to landscapes: determining the scale of ecological processes affecting the incidence of a saproxylic beetle. Ecol Entomol 37:233–243

Jactel H (1993) Individual variability of the flight potential of *Ips sexdentatus* Boern (Coleoptera, Scolytidae) in relation to day of emergence, sex, size, and lipid-content. Can Entomol 125:919–930

Jactel H, Gaillard J (1991) A preliminary study of the dispersal potential of *Ips sexdentatus* (Boern) (Col., Scolytidae) with an automatically recording flight mill. J Appl Entomol Z Angew Entomol 112:138–145

Janssen P, Cateau E, Fuhr M, Nusillard B, Brustel H, Bouget C (2016) Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in unfragmented montane forests. Biodivers Conserv 25:1167–1185

Jansson N, Ranius T, Larsson A, Milberg P (2009) Boxes mimicking tree hollows can help conservation of saproxylic beetles. Biodivers Conserv 18:3891–3908

Jonsell M, Nordlander G, Jonsson M (1999) Colonization patterns of insects breeding in wood-decaying fungi. J Insect Conserv 3:145–161

Jonsell M, Schroeder M, Larsson T (2003) The saproxylic beetle *Bolitophagus reticulatus*: its frequency in managed forests, attraction to volatiles and flight period. Ecography 26:421–428

Jonsson M (2003) Colonisation ability of the threatened tenebrionid beetle *Oplocephala haemorrhoidalis* and its common relative *Bolitophagus reticulatus*. Ecol Entomol 28:159–167

Jonsson M, Nordlander G (2006) Insect colonisation of fruiting bodies of the wood-decaying fungus *Fomitopsis pinicola* at different distances from an old-growth forest. Biodivers Conserv 15:295–309

Jonsson M, Johannesen J, Seitz A (2003) Comparative genetic structure of the threatened tenebrionid beetle *Oplocephala haemorrhoidalis* and its common relative *Bolitophagus reticulatus*. J Insect Conserv 7:111–124

Kadowaki K, Leschen RAB, Beggs JR (2011) Competition-colonization dynamics of spore-feeding beetles on the long-lived bracket fungi *Ganoderma* in New Zealand native forest. Oikos 120:776–786

Karpinski L, Rutkowski T, Szczepanski WT (2017) First record of phoresy of *Dendrochernes cyrneus* (L. Koch, 1873) (Pseudoscorpiones, Chernetidae) on *Cerambyx cerdo* Linnaeus, 1758 (Coleoptera, Cerambycidae) and their potential value as bioindicators. Anim Biodivers Conserv 40:187–192

Katlav A, Hajiqanbar H, Talebi AA (2014) First record of the genus *Acanthomastix* Mahunka, 1972 (Acari: Dolichocybidae) from Asia, with the description of a new species. Int J Acarol 40:7–14

Keller L, Peer K, Bernasconi C, Taborsky M, Shuker DM (2011) Inbreeding and selection on sex ratio in the bark beetle *Xylosandrus germanus*. BMC Evol Biol 11

Kettunen J, Kobro S, Martikainen P (2005) Thrips (Thysanoptera) from dead aspen (*Populus tremula*) trees in eastern Finland. Entomol Fenn 16:246–250

Kirkendall LR (1983) The evolution of mating systems in bark and ambrosia beetles (Coleoptera, Scolytidae and Platypodidae). Zool J Linn Soc Lond 77:293–352

Kirkendall LR, Biedermann PHW, Jordal BH (2015) Evolution and diversity of bark and ambrosia beetles. In: Vega FE, Hofstetter RW (eds) Bark beetles—biology and ecology of native and invasive species. Academic, London, pp 85–156

Kissling WD, Pattemore DE, Hagen M (2014) Challenges and prospects in the telemetry of insects. Biol Rev 89:511–530

Knutsen H, Rukke BA, Jorde PE, Ims RA (2000) Genetic differentiation among populations of the beetle *Bolitophagus reticulatus* (Coleoptera: Tenebrionidae) in a fragmented and a continuous landscape. Heredity 84:667–676

Korb J, Schmidinger S (2004) Help or disperse? Cooperation in termites influenced by food conditions. Behav Ecol Sociobiol 56:89–95

Kouki J, Hyvarinen E, Lappalainen H, Martikainen P, Similä M (2012) Landscape context affects the success of habitat restoration: large-scale colonization patterns of saproxylic and fire-associated species in boreal forests. Divers Distrib 18:348–355

Kuussaari M, Nieminen M, Hanski I (1996) An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. J Anim Ecol 65:791–801

Lowe WH, Allendorf FW (2010) What can genetics tell us about population connectivity? Mol Ecol 19:3038–3051

Lowe A, Harris S, Ashton P (2004) Ecological genetics—design, analysis, and application. Blackwell, Oxford

Marden JH (2000) Variability in the size, composition, and function of insect flight muscles. Annu Rev Physiol 62:157–178

Matthysen E (2012) Multicausality of dispersal: a review. In: Clobert J, Baguette M, Benton TG, Bullock JM (eds) Dispersal ecology and evolution. Oxford University Press, Oxford, pp 3–18

Messenger MT, Mullins AJ (2005) New flight distance recorded for *Coptotermes formosanus* (Isoptera: Rhinotermitidae). Fla Entomol 88:99–100

Meurisse N, Pawson S (2017) Quantifying dispersal of a non-aggressive saprophytic bark beetle. PLoS One 12:e0174111

Moore A, Barahona DC, Lehman KA, Skabeikis D, Iriarte IR, Jang EB, Siderhurst MS (2017) Judas beetles: discovering cryptic breeding sites by radio-tracking coconut rhinoceros beetles, *Oryctes rhinoceros* (Coleoptera: Scarabaeidae). Environ Entomol 46:92–99

Mullins AJ, Messenger MT, Hochmair HH, Tonini F, Su NY, Riegel C (2015) Dispersal flights of the Formosan subterranean termite (Isoptera: Rhinotermitidae). J Econ Entomol 108:707–719

Nilssen AC (1984) Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera, Scolytidae and Curculionidae) in northern Finland. Ann Entomol Fenn 50:37–42

Nilsson SG, Baranowski R (1997) Habitat predictability and the occurrence of wood beetles in old-growth beech forests. Ecography 20:491–498

Nordén B, Götmark F, Tönnberg M, Ryberg M (2004) Dead wood in semi-natural temperate broadleaved woodland: contribution of coarse and fine dead wood, attached dead wood and stumps. For Ecol Manag 194:235–248

Nordén B, Dahlberg A, Brandrud TE, Fritz Ö, Ejrnaes R, Ovaskainen O (2014) Effects of ecological continuity on species richness and composition in forests and woodlands: a review. Ecoscience 21:34–45

Oleksa A (2014) Weak isolation by distance in *Diaperis boleti*, a fungivorous saproxylic beetle. J Insect Sci 14

Oleksa A, Chybicki IJ, Gawronski R, Svensson GP, Burczyk J (2013) Isolation by distance in saproxylic beetles may increase with niche specialization. J Insect Conserv 17:219–233

Oleksa A, Chybicki IJ, Larsson MC, Svensson GP, Gawronski R (2015) Rural avenues as dispersal corridors for the vulnerable saproxylic beetle *Elater ferrugineus* in a fragmented agricultural landscape. J Insect Conserv 19:567–580

Peer K, Taborsky M (2005) Outbreeding depression, but no inbreeding depression in haplodiploid ambrosia beetles with regular sibling mating. Evolution 59:317–323

Peer K, Taborsky M (2007) Delayed dispersal as a potential route to cooperative breeding in ambrosia beetles. Behav Ecol Sociobiol 61:729–739

Perrin N, Mazalov V (2000) Local competition, inbreeding, and the evolution of sex-biased dispersal. Am Nat 155:116–127

Pusey A, Wolf M (1996) Inbreeding avoidance in animals. Trends Ecol Evol 11:201–206

Putz J, Vorwagner EM, Hoch G (2016) Flight performance of *Monochamus sartor* and *Monochamus sutor*, potential vectors of the pine wood nematode. Lesnícky Casopis For J 62:195–201

Ranius T (2006) Measuring the dispersal of saproxylic insects: a key characteristic for their conservation. Popul Ecol 48:177–188

Ranius T, Douwes P (2002) Genetic structure of two pseudoscorpions species living in tree hollows in Sweden. Anim Biodivers Conserv 25:67–74

Ranius T, Hedin J (2001) The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. Oecologia 126:363–370

Ranius T, Johansson V, Fahrig L (2011) Predicting spatial occurrence of beetles and pseudoscorpions in hollow oaks in southeastern Sweden. Biodivers Conserv 20:2027–2040

Ranius T, Bohman P, Hedgren O, Wikars LO, Caruso A (2014) Metapopulation dynamics of a beetle species confined to burned forest sites in a managed forest region. Ecography 37:797–804

Rink M, Sinsch U (2007) Radio-telemetric monitoring of dispersing stag beetles: implications for conservation. J Zool 272:235–243

Roff DA (1991) Life-history consequences of bioenergetic and biomechanical constraints on migration. Am Zool 31:205–215

Roff DA (1994) Habitat persistence and the evolution of wing dimorphism in insects. Am Nat 144:772–798

Ronce O (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annu Rev Ecol Evol Syst 38:231–253

Rossi de Gasperis SR, Passacantilli C, De Zan LR, Carpaneto GM (2016) Overwintering ability and habitat preference of *Morimus asper*: a two-year mark-recapture study with implications for conservation and forest management. J Insect Conserv 20:821–835

Rotheray EL, Bussiere LF, Moore P, Bergstrom L, Goulson D (2014) Mark recapture estimates of dispersal ability and observations on the territorial behaviour of the rare hoverfly, *Hammerschmidtia ferruginea* (Diptera, Syrphidae). J Insect Conserv 18:179–188

Saint-Germain M, Drapeau P, Buddle CM (2008) Persistence of pyrophilous insects in fire-driven boreal forests: population dynamics in burned and unburned habitats. Divers Distrib 14:713–720

Saint-Germain M, Drapeau P, Hibbert A (2013) Saproxylic beetle tolerance to habitat fragmentation induced by salvage logging in a boreal mixed-cover burn. Insect Conserv Divers 6:381–392

Schauer B, Steinbauer MJ, Vailshery LS, Müller J, Feldhaar H, Obermaier E (2018a) Influence of tree hollow characteristics on saproxylic beetle diversity in a managed forest. Biodivers Conserv 27:853–869. https://doi.org/10.1007/s10531-017-1467-9

Schauer B, Bong J, Popp C, Obermaier E, Feldhaar H (2018b) Dispersal limitation of saproxylic insects in a managed forest? A population genetics approach. Basic Appl Ecol. https://doi.org/10.1016/j.baae.2018.01.005

Schiegg K (2000a) Are there saproxylic beetle species characteristic of high dead wood connectivity? Ecography 23:579–587

Schiegg K (2000b) Effects of dead wood volume and connectivity on saproxylic insect species diversity. Ecoscience 7:290–298

Seibold S, Brandl R, Buse J, Hothorn T, Schmidl J, Thorn S, Müller J (2015) Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. Conserv Biol 29:382–390

Shaffer ML (1981) Minimum population sizes for species conservation. Bioscience 31:131–134

Shibata E (1986a) Adult populations of the Sugi bark borer, *Semanotus japonicus* Lacordaire (Coleoptera, Cerambycidae), in Japanese cedar stands—population parameters, dispersal, and spatial distribution. Res Popul Ecol 28:253–266

Shibata E (1986b) Dispersal movement of the adult Japanese pine sawyer, *Monochamus alternatus* hope (Coleoptera, Cerambycidae) in a young pine forest. Appl Entomol Zool 21:184–186

Siitonen J (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol Bull 49:11–41

Simms D, Husseneder C (2009) Assigning individual alates of the Formosan subterranean termite (Isoptera: Rhinotermitidae) to their colonies of origin within the context of an area-wide management program. Sociobiology 53:631–650

Smith MT, Bancroft J, Li GH, Gao R, Teale S (2001) Dispersal of *Anoplophora glabripennis* (Cerambycidae). Environ Entomol 30:1036–1040

Smith MT, Tobin PC, Bancroft J, Li GH, Gao RT (2004) Dispersal and spatiotemporal dynamics of Asian longhorned beetle (Coleoptera: Cerambycidae) in China. Environ Entomol 33:435–442

Solbreck C (1980) Dispersal distances of migrating pine weevils, *Hylobius abietis*, Coleoptera-Curculionidae. Entomol Exp Appl 28:123–131

Southwood T (1962) Migration of terrestrial arthropods in relation to habitat. Biol Rev 37:171–211

Speight MCD (1989) Saproxylic invertebrates and their conservation. Nature and environment series, vol 42. Council of Europe, Strasbourg, p 79

Speight MCD (2012) Species accounts of European Syrphidae (Diptera), 2012. Syrph the Net Publications, Dublin

Sprecher-Uebersax E, Durrer H (2001) Verhaltensstudien über den Hirschkäfer *Lucanus cervus* L. mit Hilfe der Telemetrie und Videobeobachtung. Mitteilungen der Naturforschenden Gesellschaften beider Basel 5:161–182

Starzomski BM, Bondrup-Nielsen S (2002) Analysis of movement and the consequence for metapopulation structure of the forked fungus beetle, *Bolitotherus cornutus* panzer (Tenebrionidae). Ecoscience 9:20–27

Stokland JN (2012) The saproxylic food web. In: Stokland JN, Siitonen P, Jonsson BG (eds) Biodiversity in dead wood. Cambridge University Press, Cambridge, pp 29–57

Svensson GP, Sahlin U, Brage B, Larsson MC (2011) Should I stay or should I go? Modelling dispersal strategies in saproxylic insects based on pheromone capture and radio telemetry: a case study on the threatened hermit beetle *Osmoderma eremita*. Biodivers Conserv 20:2883–2902

Sverdrup-Thygeson A (2010) Colonization of experimentally arranged resource patches—a case study of fungivorous beetles. Entomol Fenn 21:139–150

Taylor RAJ, Bauer LS, Poland TM, Windell KN (2010) Flight performance of *Agrilus planipennis* (Coleoptera: Buprestidae) on a flight mill and in free flight. J Insect Behav 23:128–148

Tini M, Bardiani M, Chiari S, Campanaro A, Marizi E, Toni I, Mason F, Audisio PA, Carpetano GM (2018) Use of space and dispersal ability of a flagship saproxylic insect: a telemetric study of the stag beetle (*Lucanus cervus*) in a relict lowland forest. Insect Conserv Divers 11:116–129

Torres-Vila LM, Sanchez-Gonzalez A, Ponce-Escudero F, Martin-Vertedor D, Ferrero-Garcia JJ (2012) Assessing mass trapping efficiency and population density of *Cerambyx welensii* Küster by mark-recapture in dehesa open woodlands. Eur J For Res 131:1103–1116

Torres-Vila LM, Zugasti C, De-Juan JM, Oliva MJ, Montero C, Mendiola FJ, Conejo Y, Sanchez A, Fernandez F, Ponce F, Esparrago G (2015) Mark-recapture of *Monochamus galloprovincialis* with semiochemical-baited traps: population density, attraction distance, flight behaviour and mass trapping efficiency. Forestry 88:224–236

Torres-Vila LM, Mendiola-Diaz FJ, Sanchez-Gonzalez A (2017) Dispersal differences of a pest and a protected *Cerambyx* species (Coleoptera: Cerambycidae) in oak open woodlands: a mark-recapture comparative study. Ecol Entomol 42:18–32

Travis JMJ, Delgado M, Bocedi G, Baguette M, Barton K, Bonte D, Boulangeat I, Hodgson JA, Kubisch A, Penteriani V, Saastamoinen M, Stevens VM, Bullock JM (2013) Dispersal and species' responses to climate change. Oikos 122:1532–1540

Türke M, Fiala B, Linsenmair KE, Feldhaar H (2010) Estimation of dispersal distances of the obligately plant-associated ant *Crematogaster decamera*. Ecol Entomol 35:662–671

Ulyshen MD (2011) Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. For Ecol Manag 261:1479–1489

Ulyshen MD (2016) Wood decomposition as influenced by invertebrates. Biol Rev 91:70–85

Ulyshen MD, Hanula JL, Horn S, Kilgo JC, Moorman CE (2004) Spatial and temporal patterns of beetles associated with coarse woody debris in managed bottomland hardwood forests. For Ecol Manag 199:259–272

Vlasanek P, Sam L, Novotny V (2013) Dispersal of butterflies in a new Guinea rainforest: using mark-recapture methods in a large, homogeneous habitat. Ecol Entomol 38:560–569

Waldbauer GP, Sternburg JG (1979) Inbreeding depression and a behavioral mechanism for its avoidance in *Hyalophora cecropia*. Am Midl Nat 102:204–208

Weslien J, Lindelöw A (1990) Recapture of marked spruce bark beetles (*Ips typographus*) in pheromone traps using area-wide mass trapping. Can J For Res Revue Canadienne De Recherche Forestiere 20:1786–1790

Whiteley AR, Fitzpatrick SW, Funk WC, Tallmon DA (2015) Genetic rescue to the rescue. Trends Ecol Evol 30:42–49

Whitlock MC (1992) Nonequilibrium population-structure in forked fungus beetles—extinction, colonization, and the genetic variance among populations. Am Nat 139:952–970

Wootton RJ (1992) Functional morphology of insect wings. Annu Rev Entomol 37:113–140

Zauli A, Chiari S, Hedenstrom E, Svensson GP, Carpaneto GM (2014) Using odour traps for population monitoring and dispersal analysis of the threatened saproxylic beetles *Osmoderma eremita* and *Elater ferrugineus* in central Italy. J Insect Conserv 18:801–813

Zeh JA, Zeh DW (2013) On the threshold of dispersal: hitchhiking on a giant fly favours exaggerated male traits in a male-dimorphic pseudoscorpion. Biol J Linn Soc 108:509–520

Zolubas P, Byers JA (1995) Recapture of dispersing bark beetle *Ips typographus* L (col, Scolytidae) in pheromone-baited traps—regression-models. J Appl Entomol Z Angew Entomol 119:285–289