

2.3 Connectivity and fragmentation: island biogeography and metapopulation applied to old-growth elements

Kris Vandekerkhove, Arno Thomaes and Bengt-Gunnar Jonsson

Large quantities of deadwood and a high density of old and hollow trees (further called “habitat trees”, see chapter 2.1) are characteristic elements of natural forests, especially of the old-growth phases (Harmon et al. 1986). These phases can cover up to 50 % of the area in natural forests (e.g. Meyer and Schmidt 2008) but are often absent or rare in managed forests, even in forests under close-to-nature management. Indeed, in commercial forests, only rejuvenation and mature stand phases are common, and other developmental phases are “shortcut” by the final harvest of the stand (Christensen and Emborg 1996; Bobiec 2002). Also, in selective harvests and thinnings, “defective” trees referring to these old-growth phases (hollow, dead, and languishing trees) are often removed. Yet, an important share of forest biodiversity is strictly or primarily dependent on these elements for its survival, especially saproxylic species, that is species that depend on deadwood (Stokland et al. 2012). Siitonen (2001) calculated that a decline of the total amount of coarse woody debris by over 90 % may lead to the disappearance of at least 1/4, and more probably over 1/2, of all saproxylic species. If this habitat loss is combined with habitat fragmentation, this proportion is expected to be even larger. As a result, most species dependent on old-growth elements and phases have become threatened.

Conservation of biodiversity in commercial forest stands is mainly a question of retention of specific elements to overcome the “harvest shortcut”

Old-growth elements such as hollow trees and deadwood emerge on their own if the manager allows them to develop. For instance, the net build-up of deadwood in recently set-aside stands in mid-European forests (which have a low initial deadwood amount) can reach on average 1–1.5 m³/ha/year without any heavy disturbance taking place (e.g. Vandekerkhove et al. 2009). At this pace, they may reach “natural” levels of deadwood after 50 to 100 years. Some old-growth elements may take even longer to redevelop once they are gone, such as old standing decorticated trees and highly decayed large logs. Reservation and retention of these elements is essential, as “restoration” may literally take ages (see Box 17). Still, even in sites where restoration is the only option, it is important to make the effort and slowly but gradually work towards the redevelopment of old-growth elements.

Box 17. Management strategies for conservation of old-growth elements: “the triple R”

- **Reserve:** safeguard existing relics of old-growth (or other patches with high value or potential) from harvest, by conserving them in delineated areas such as forest reserves and national parks, but also in smaller delineated patches, often called “set-aside patches”, “key habitats”, or “îlots de scénescence”.
- **Retain:** intentionally keep a number of dead, old, or other habitat trees in the stand during thinning and final harvests. Such retention trees are key elements in the managed forest “matrix”.
- **Restore:** even when none such old-growth elements are present at the moment, a policy can be applied to allow them to develop in a premeditated pattern and network.

This concept has been originally developed and applied as the “Variable Retention Harvest System” for the old-growth forests of the Pacific Northwest (Franklin et al. 1997, Lindenmayer and Franklin 2002). However, it can also be applied to temperate forests where no old-growth elements remain, but where a “management for old-growthness” is integrated in the silvicultural practice (Bauhus et al. 2009). It is mainly a question of intentionally “letting things happen”. Indeed, hollow trees and deadwood emerge by themselves if the manager allows them to develop and build up.

In order to be effective for the conservation of saproxylic biodiversity, these old-growth elements should be arranged in a functional network

The successful survival of a population of a species is only possible if its reproduction and immigration are able to compensate for losses through dispersal, mortality, and predation. Saproxylic species are peculiar in that their habitat is ephemeral: indeed, hollow and dead trees are only temporarily available and may only be suitable as a habitat for certain species for an even shorter period of time (Jonsson 2012). Thus, the survival of a population of a species will depend on the ability and opportunity to colonise newly available habitat before the original habitat is lost.

Saproxylic organisms can be considered as populations that live on melting icebergs and that need to be able to reach the next suitable iceberg before the original one is gone

Box 18. The theory of island biogeography and metapopulations

The **principles of island biogeography** were developed by MacArthur and Wilson (1967), who examined species diversity on larger and smaller islands, closer and farther away from the mainland.

Their basic conclusion was that species richness is higher on larger islands than on smaller ones, and higher on islands closer to the mainland than on remote ones. It is basically explained by the fact that the influx of species from the mainland (the source population) to an island decreases with the distance to be crossed. On larger islands, more habitat diversity may be present, making the island suitable for more species, and larger, less extinction-prone populations can build up.

Set-aside areas and habitat trees are for old-growth-dependent species like a network of “old-growth islands” and stepping stones in a “sea” of young and mature forest. Like in the typical island biogeography, larger habitat patches may support larger (sub-) populations for longer periods (lower extinction risk), and patches closer to large source populations also have a greater chance of being colonised.

The theory of **metapopulations** was mainly developed and described by Hanski (1999). It states that a population of a species can be composed of a number of separate subpopulations, each living in discrete patches of suitable habitat, but able to swiftly migrate from one site to another. All these subpopulations together form one so-called “metapopulation”.

Individual sites and sub-populations may go extinct, but as long as the sum of interchanging subpopulations is viable, the population may survive. In some cases (for example, an archipelago with breeding cormorants), the discrete sites are stable over time. In some cases, such as for dead trees, suitable sites will disappear over time and reappear elsewhere. Some individuals (or seeds) may disperse from one site to reach these new sites by chance (e.g. fungi, see further), while others may actively search for new sites (e.g. beetles). In this case, we speak of a “habitat tracking dynamics”

As long as enough habitat patches are available and within reach for colonisation, a viable metapopulation of a species can be built-up or sustained and guarantee the survival of a species. By contrast, when establishment rates are too low, the metapopulation will decline and eventually go extinct. This process can be slow and lag behind the loss of habitat. Species may still be present although their habitat requirements are no longer met. This is called an “extinction debt” (e.g. Hanski 1999). Similarly, recolonisation of newly established suitable habitats may also be delayed because species are not able to reach them or have not yet established new populations, the so-called “immigration credit” (e.g. Jackson and Sax 2009).

The colonisation of suitable habitat by a species is the joint result of successful dispersal and successful recruitment (e.g. Jonsson et al. 2005). Dispersal is the ability to actively spread. This can be done through seeds, spores, or flying adult individuals and can be random or target-directed. Recruitment is the ability to establish and reproduce on the newly reached

habitat patch. This strongly depends on the suitability of the habitat itself. Some species may be very selective, while others more indiscriminate. Success is strongly determined by species-dependent dispersal and recruitment potential.

A functional network of old-growth elements enables target species to develop and sustain viable metapopulations. Continuity and connectivity in time and space are essential elements

Such a network involves smaller and larger non-intervention patches that are interconnected by “corridors” and “stepping stones” of habitat trees in the managed forest matrix. The functionality of the design is dependent on the habitat requirements and dispersal ability of species.

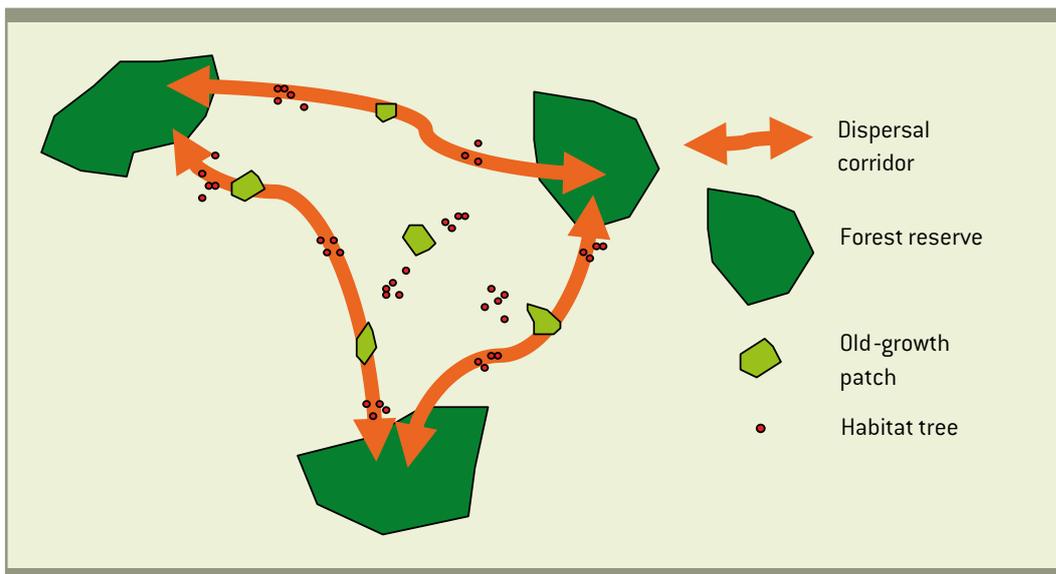


Figure 30. Schematic representation of a functional network of old-growth elements: larger set-asides (reserves >10 ha) are interconnected through set-aside patches (1–5 ha) and individual habitat trees. Areas with higher densities of habitat trees can form “corridors”, but a qualitative “matrix” can also be crossed by most target species. Source: Lachat and Bütler 2007.

Like other organisms (e.g. vascular plants), saproxylic species can be subdivided into different life-strategies, from fast-colonising ruderals to stress-tolerant sedentary survivors

Some species have a typical “ruderal” strategy: they invest in high reproduction and high dispersal capacities. They manage to quickly colonise newly available habitat over a long distance and produce a large number of offspring. Bark beetles are typical examples of such species. They need this strategy because time is short; they live on very short-lived habitat (such as freshly dead cambium) or must be first in order to successfully compete with other species.

On the other side of the spectrum are species that are very slow colonisers, producing little offspring, often only reproducing after several years. They have a strategy of “persistence”, with long individual life spans. Typical species here are beetles living in wood mould in cavities of very old living and dead trees. The mould is very hard to digest, with little nutritious value, so development is slow, but the cavities may persist for many decades, even centuries. Many other species have an in-between strategy, with high or low dispersal abilities. They may have specific habitat requirements or may be able to survive in harsh environments where hardly any other species can survive.

The required configuration of a functional network of habitat is strongly dependent on these life strategies: fast colonisers require a continuous supply of (often very short-lived) habitat over larger areas; slow colonisers are often dependent on the conservation and enlargement of relict habitat islands

As the saproxylic community is so diverse in its life strategies, the design of the network of old-growth elements should account for all these differences in order to be functional. It should guarantee continuity in time and space of suitable and renewing habitat.

We illustrate this theory with some species groups:

Forest birds are a well-studied group of good dispersers. Woodpeckers are often used as indicators for forest biodiversity. The habitat requirements of woodpecker species are indeed quite diverse. The Great Spotted Woodpecker (*Dendrocopos major*) and the Black Woodpecker (*Dryocopus martius*) are less restrictive than others; they can feed on living middle-sized trees and only need a few suitable nesting trees in their territory in order to survive. Others, such as the Middle Spotted Woodpecker (*Dendrocopos medius*), are more selective as they need large broadleaved trees with moss-rich branches to feed on (e.g. Pasinelli 2007). Finally, Three-toed (*Picoides tridactylus*) and White-backed Woodpeckers (*Dendrocopos leucotos*) are very selective in their habitat and need high densities of standing dead trees for feeding and breeding (at least 30 m³/ha, and over 50 m³/ha, respectively) (Angelstam et al. 2003; Bütler et al. 2004; Müller and Bütler 2010). It is clear that a few retention trees per ha may be a sufficient functional network for the first species, but the Middle Spotted Woodpecker will also need a sufficient amount of old-growth patches and a high density of old retention trees in the matrix (Pasinelli 2007; Müller et al. 2009). This was clearly illustrated in areas like Belgium and Holland, where Great Spotted and Black Woodpeckers quickly responded to improved habitat

conditions, while the Middle Spotted Woodpecker took much longer but now also successfully recolonises newly suitable habitat (Vandekerkhove et al. 2011). For White-backed and Three-toed Woodpeckers, several larger old-growth patches of at least 20–100 ha are needed to form a successful breeding territory, so they are often restricted to conservation areas. Still, retention trees and key habitats in managed forest may constitute the necessary stepping stones in between the reserves in order to create a wide-scale regional functional network for a viable metapopulation of these species.

Saproxylic fungi are in principle very good dispersers; they produce millions of spores that can be spread over hundreds of kilometres (e.g. Stenlid and Gustafsson 2001). However, only a very small fraction of the spores actually spread over longer distances. The vast majority of spores fall within a few meters of the fruiting body. Given the enormous number of spores, there is still a fair chance for some spores to travel over long distances. This small fraction is crucial to establish new populations in distant localities (Stenlid and Gustafsson 2001). In contrast to birds and insects, the spores cannot actively search for suitable substrate to germinate and thus depend entirely on chance, although some may be dispersed by insects (Jonsson 2012). Moreover, even when a viable spore reaches a distant new substrate and is able to germinate, another compatible spore must reach the same substrate in order to mate and produce a dikaryotic mycelium that in its turn is able to produce fruit bodies and new spores (Stenlid and Gustafsson 2001). This process makes the development of a reproductive new mycelium at longer distances much less likely than would be expected from its reproductive and dispersal capacity. A study on the colonisation capacity of *Fomitopsis rosea* in Sweden (Edman et al. 2004) showed that even with deposition rates of 10 spores per m² per hour and the availability of suitable substrate, no colonisation was registered after 5 years. The mere occurrence of spores and presence of suitable substrate does not necessarily guarantee colonisation (Jonsson et al. 2005). Examples have shown that for many species of fungi that are not too specific in their substrate requirements, the actual density of suitable habitat appears sufficient to allow the steady development of new viable populations (Vandekerkhove et al. 2011). However, a number of highly selective species, such as the Bearded Tooth (*Hericium erinaceus*), are still rare or absent. They are often related to very specific, rare and transient substrates (such as wounds or rot holes of overmature trees). If their habitat is temporarily missing or the density of suitable habitat is too low, these species may easily fail to arrive in time, especially if source populations are distant (Christensen et al. 2005). Sites with a high occurrence of suitable substrate such as forest reserves, retention islands, and old tree rows not only locally increase the incidence of spores reaching suitable habitat and thus the chances of successful establishment, but also allow further development of larger local populations with a lower risk of local extinction. These new satellites may in the future develop to become new sources for further expansion (Siitonen 2001; Jonsson et al. 2005). Some species, however, appear to be restricted to large areas with amounts of deadwood over 100 m³/ha, such as *Antrodia citrinella* (Bässler and Müller 2010). Such species are “out of reach” for integrative management and require larger non-intervention areas.

For **saproxylic beetles**, habitat requirements and availability influence the possibility for recolonisation in much the same way as they do for saproxylic fungi, but the process is complicated by the extremely diverse dispersal potential of the different species (Jonsell et al. 1999). Some species, which are often linked with highly ephemeral habitats (such as bark beetles) have a high dispersal capacity, and are short-lived themselves. Species inhabiting stable deadwood microhabitats (such as species in wood mould) have low dispersal rates and also live longer (first described by Southwood 1977). Brunet and Isacsson (2009) found that non-

Box 19. Setting up a functional network: some ‘rules of thumb’

For fauna, **minimum viable metapopulations** (to ensure population survival and maintenance of genetic variation) require an estimated minimum population size of 4,000 to 5,000 individuals (Frankham 1995). For species with multi-year lifecycles, viable metapopulations may be smaller (for species with a generation time of 5 years, an “effective breeding” population of at least about 200 individuals, corresponding with a total population of 2,000 individuals, is needed to avoid inbreeding – Hamilton, 2009).

For some beetle species such numbers may occur on a single tree, while others need at least ten to several dozens of suitable trees within the dispersal range (e.g. *Osmoderma*). For most species, distances of 1–2 km are within this range, while others (again, such as *Osmoderma* and *Lucanus*) rarely cross distances of over a few hundred meters.

Depending on the target species, the design of the network will be more diffuse (appropriate for most species) or concentrated around relict populations (appropriate for slow colonisers, often rare target species).

For many species, a typical network of old-growth elements (as described above) will work if they are not “spread too thin”. A consistent network should therefore combine the following elements:

- one or several larger non-intervention areas (>10 ha, up to several hundred hectares)
- a network of “key habitats” (minimum size for set-aside patch >1 ha – Müller et al. 2012)
- a distance of 1–2 km between these set-aside areas is fine for most species but may be problematic for some (Brunet and Isacsson 2009).
- a suitable, qualitative matrix that allows good dispersal to the set-asides, but also provides habitat in itself for many species. Preserve at least 5–10 habitat trees per ha (large dead trees, old trees, hollow trees, etc.), both clusters and individual trees, and both sun-exposed and shaded trees (*for more details: see also chapter 2.1 on habitat trees*).
- for the specific group of dispersal-limited species requiring habitat continuity, look for “hotspots” and relict areas where a dense and local functional network of set-asides can be created in order to allow long-term viable (meta)populations to develop. Also take into account the relict hotspots for these species that are located outside the strict boundaries of the forest.
- and finally, be realistic. Typical “Urwald” indicator species will not settle for less; larger conservation areas will remain indispensable for their conservation. Integrative management can contribute by providing a better transit-matrix, but will not be able to harbour viable populations of these species.

Beyond the forest complex: the need for functional networks on a larger landscape scale

On a larger landscape scale, metapopulation authority Ilkka Hanski recently suggested his “third of a third” rule of thumb (Hanski 2011). He states that in a landscape where

at least one-third of the area consists of suitable habitat for a “habitat specialist”, loss of metapopulations due to fragmentation is not expected. Within this one-third, again one-third of the habitat should be managed (or set aside) to create ideal conditions for conservation (of the species). In this approach, he is stressing the need for some kind of aggregation of conservation efforts and set-asides to reach a sufficient amount of suitable habitat in functional “interweaving” networks at a larger landscape scale. At the same time, it is also stressed that these networks should not only cover less productive and more remote areas, but should encompass all habitat types.

selective species were not affected by isolation from old-growth forest, but for more selective or dispersal-limited species (that are therefore often rare and red-listed), there was already a significant effect after just a few hundred meters. Some species appeared unable to cross a 2 km section of unfavourable habitat. Jonsell et al. (1999) concluded that the fungi-inhabiting species they studied could colonise suitable substrate within 1 km of their point of origin, but already observed reduced colonisation over a distance of 150 m. For some species, such as *Osmoderma eremita*, dispersal over distances of over 200 m is even unlikely (Hedin et al. 2008). Thomaes (2009) calculated that stag beetle (*Lucanus cervus*) colonisation over a period of about 30 years does not exceed a radius of about 1 km. Moreover, some of these non-mobile species are very selective in their habitat. They are dependent on sites with high spatio-temporal continuity of habitat related to natural forests (“Urwaldreliktarten”) and are therefore often used as indicator species for habitat continuity (Müller et al. 2005). For most saproxylic beetles, an integrative retention network approach with clusters of habitat trees and retention islands at reachable distances (of a few hundred meters) will provide a functional network to build viable populations. For the non-mobile species of wood mould, a conservation strategy should be focused on the localisation of relict populations and the conservation and extension of their habitat in the immediate surroundings (Hedin et al. 2008; Thomaes 2009). At present many of these species are mainly found in pollard trees and orchards in the open countryside (Alexander 2008), sometimes bordering the forest. Connectivity networks for these species should therefore also focus outside the strict boundaries of the forest.

► *A functional network of old-growth elements should be tailored to these different life strategies and therefore requires the combination of larger and smaller set-asides, intertwined with a dense enough network of habitat trees, both dead and alive*

We can conclude that functional networks of retention trees and islands in managed forests are indispensable for the conservation of old-growth-related biodiversity. Integrative and segregative conservation approaches in forests are indeed complementary and essential in order to reach overall forest biodiversity conservation goals (Frank et al. 2007). A recent paper by Gossner et al. (2013) indeed concluded that the complete species richness of saproxylic species can only be guaranteed through a combination of managed forests with an ambitious

retention strategy (resulting in an average deadwood amount of at least 20 m³/ha), combined with a network of strict conservation areas that function as source-populations for the managed areas and simultaneously harbour the most critical species that are restricted to “Urwald” conditions.

Box 20. From theory to practice: the network of retention trees and set-aside areas of the Sonian Forest (Flanders-Belgium).

The Sonian forest, located at the southern edge of Brussels, has a specific management history that has resulted in a very high density of old trees and forest stands, mainly beech. In the part of the forest managed by the Flemish Forest Administration alone (2,500 ha), almost 400 ha of forest stands are over 180 years old, some even more than 230 years. These stands contain high densities of very large trees, sometimes up to 20–30 trees per ha. Over the whole inventoried area, more than 7,000 trees of > 3 m girth were registered. About half of these trees occur in the old stands, and the rest are widely spread over the area as individual trees and old avenues. Amounts of deadwood in the managed stands are currently still low (< 10 m³/ha). The whole area is registered as a Special Area of Conservation (Habitat directive) and Protected Landscape. The site is a hotspot for many species groups that are related to old beech forests, such as bats, mycorrhizal and saproxylic fungi, epiphytic mosses and lichens, saproxylic hoverflies, and beetles (e.g. *Stictoleptura scutellata*, *Gnorimus nobilis*).

A functional network of retention trees and set-asides was developed in the framework of the new management plan (Brichau et al. 2013). This network contains one large strict forest reserve (over 200 ha) and 75 ha of smaller strict set-aside areas (5–10 ha each). They are interconnected by 250 ha of “senescence islands” and a dense network of retention trees comprising individuals and groups. For these trees, a dynamic approach is used: individual trees may still be cut (dangerous or exceptionally high value trees) but should be compensated by ingrowth from smaller size classes. The overall number should remain at least at the current level of 7,000, and the senescence islands should retain their “old-growth character”, so no final cuts will be done there, only very selective fellings. When they eventually break down completely and lose their old-growth function, they can be reintegrated in the managed stand, but should be replaced by a new site.

Selection of the islands and retention trees is primarily based on their current occurrence, starting the selection in the remaining old stands. However, interconnection between retention areas and individual old retention trees was also taken into account.

The retention elements will be integrated in a matrix where a management of selective harvest and group fellings with retention trees will be applied that will guarantee the required ingrowth of old trees, and should also lead to higher amounts of deadwood. Dead and dying trees remain in the retention islands, and also in the other stands, at least up to the threshold of approximately 10 m³/ha.

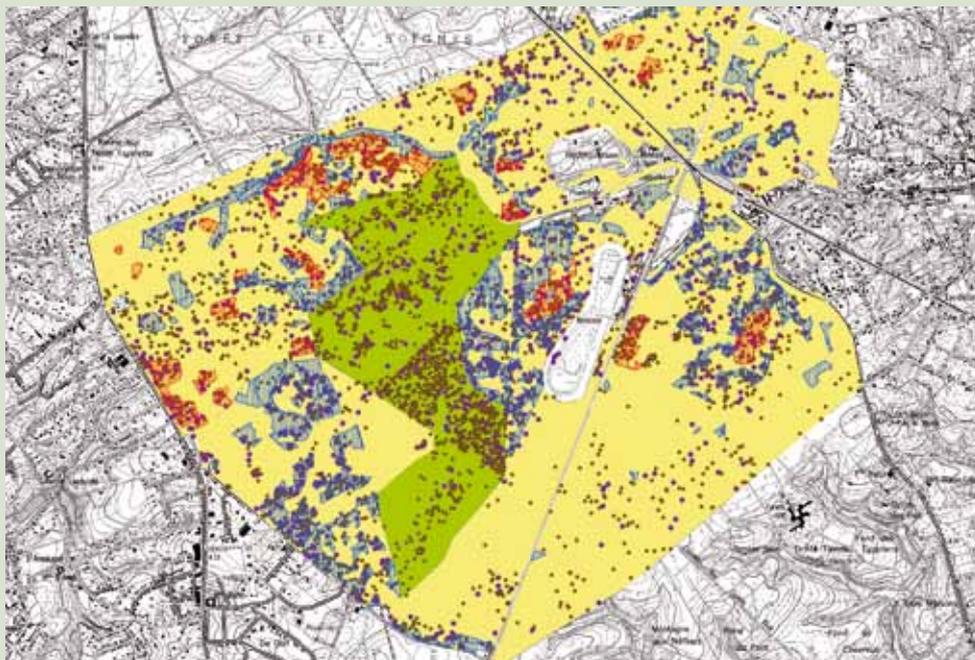


Figure 31. Part of the Sonian forest, showing the strict forest reserve (green), set aside areas (red), senescence islands (blue), and position of very large trees >3 m (brown) and > 3.50 m girth (purple).

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