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Title: Management diversity begets biodiversity in production forest landscapes

Year: 2022

Version: Published version

Please cite the original version:

Duflot, R., Fahrig, L., & Mönkkönen, M. (2022). Management diversity begets biodiversity in
production forest landscapes. Biological Conservation, 268, Article 109514.
https://doi.org/10.1016/j.biocon.2022.109514

Perspective

Management diversity begets biodiversity in production forest landscapes

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ABSTRACT

How to manage forest for biodiversity conservation is an ongoing debate. We argue that maximizing biodiversity in managed forest landscapes requires a diversity of forest management regimes in space and time. This will generate high levels of habitat heterogeneity at a landscape scale, which in turn will support various groups of forest species. Based on concepts from landscape ecology, we formulate five hypotheses on how management diversity, *i.e.* combining various management approaches can benefit overall biodiversity across a production forest landscape. First, management diversity will increase habitat diversity and, therefore, beta diversity (the *habitat diversity hypothesis*). Second, asynchrony in management timing will enhance long-term availability of different habitat types (the *spatio-temporal heterogeneity hypothesis*). Third, management to create spatial adjacency or proximity of stands with different management or successional stages will increase biodiversity by providing simultaneous access to multiple resources (the *interspersion hypothesis*). Fourth, heterogeneous unmanaged set-aside forests, interspersed with managed forests, are needed for complete biodiversity conservation (the *natural forest hypothesis*). Fifth, management diversity will create functional landscape connectivity between protected forests for multiple species through time (the *temporary corridor hypothesis*). Although strongly grounded in landscape and forest ecology, these five hypotheses remain largely under-investigated, and we suggest methods for how they can be tested. In the meantime, we suggest that increasing forest management diversity represents a risk-spreading approach for adaptation to global change, and therefore is likely a reasonable objective for sustainable forestry moving forward.

1. Introduction

By reducing vegetation complexity and supressing disturbance-succession dynamics at both local and landscape scales, intensive forestry has greatly restricted habitat availability and quality, and led to threatened forest-associated species (Kuuluvainen, 2002; Lindenmayer, 2016). Protected unharvested forests are often scarce in regions where forests are managed for timber production. Production forest landscapes, where the primary management objective is the production of timber, fiber, bioenergy and/or non-wood forest products, occupied in 2020 about 31% of the forest area globally (FAO, 2020). In contrast, only 11% of forest was primarily designated for biodiversity conservation, with large regional variability. Therefore, maintaining forest biodiversity at a global scale largely depends on how production forests are managed and how they contribute to biodiversity conservation (Gustafsson et al., 2010; Kuuluvainen, 2009).

Maintaining biodiversity and non-timber ecosystem services in production landscapes is challenging because of increasing demand for forest fuels and biomass for the bio-economy (Eyvindson et al., 2018). To reconcile timber production with biodiversity conservation, researchers and practitioners have proposed that sustainable forest management should "mimic" natural disturbance regimes and succession dynamics, and emphasise typical forest structures and habitat variability (Angelstam, 1998; Kuuluvainen, 2002; Long, 2009). The rational is that information on the natural variation of ecological conditions in forest landscapes should provide general guidelines on how biodiversity-rich forest landscapes should look (*e.g.* Kuuluvainen et al., 2021).

We suggest that the concept of landscape spatio-temporal heterogeneity is useful for understanding biodiversity patterns in managed forest landscapes and for designing improved management approaches. Landscape heterogeneity is a key concept of landscape ecology. It can be defined as the variation of ecological conditions in space and time. Spatial heterogeneity has two components (i) landscape composition, which refers to the types, their relative amounts and the diversity of land

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covers in the landscape and (ii) landscape configuration, which refers to the pattern or spatial organization of these covers relative to each other (Duelli, 1997; Fahrig et al., 2011; Fahrig and Nuttle, 2005). Compositional heterogeneity determines the number of local communities that can be present in a landscape (beta-diversity). Configurational heterogeneity affects landscape-scale processes that link habitats and communities across the landscape through movement of organisms, including landscape connectivity (Fahrig and Merriam, 1985), meta-population dynamics (Hanski, 1998), landscape complementation and supplementation (Dunning et al., 1992), and source-sink dynamics (Pulliam, 1988).

Both components of landscape spatial heterogeneity are subject to temporal dynamics, *i.e.* variation over time in availability and spatial distribution of land covers. Such dynamism in landscape pattern can have an overwhelming influence on population abundance (Fahrig, 1992). The temporal dynamics of forest landscapes is a long-recognized phenomenon (Bengtsson et al., 2000; Kuuluvainen, 2009; Schütz et al., 2016). Natural (*e.g.* windthrow and fire) and human-induced (*e.g.* clear-cut) disturbances create new open habitats, followed by successional stages. Even non-stand-replacing processes such as natural tree death, or thinning or selective logging, repeatedly modify the stands, thus creating different cover types on the landscape through time that are suitable to different species. Where the rate of such processes remains constant over a very long time and over very large areas, they can in theory lead to a shifting mosaic steady-state landscape, where local vegetation changes through time, while at a landscape scale the proportion of different seral stages and associated habitats remains more or less stable (Turner et al., 2001).

There is abundant research on how to increase heterogeneity at the scale of individual forest stands by using alternative management regimes that aim to reconcile timber production with environmental protection (Mönkkönen et al., 2018). The objective is to create forest elements that support biodiversity, such as deadwood or large old trees that host micro-habitats, and are absent or rare in intensively managed forests, whether naturally regenerated or planted (Bouget et al., 2014; Kuuluvainen and Gauthier, 2018; Larrieu et al., 2017). Indeed, management determines stand structure and tree species composition, which are strong drivers of forest biodiversity (*e.g.* Tinya et al., 2021). Such alternative management regimes include, for example, green (alive) tree retention (Gustafsson et al., 2012) and continuous cover forestry (Pukkala and Gadow, 2012). The debate continues regarding which management strategies can best reach conservation goals in various forest types (*e.g.* Nolet et al., 2018; Savilaakso et al., 2021; Schall et al., 2018).

In contrast to within-stand heterogeneity, the role of spatio-temporal variation in forest management at a landscape scale for maintaining biodiversity and ecosystem processes is not well studied empirically (Lindenmayer, 2016). For instance, in boreal forests, landscape studies often focus on a particular age class (*e.g.* old forest; Olsson et al., 2012) or vegetation type (*e.g.* broadleaved tree forest; Paltto et al., 2006), or on total amount of deadwood (Rubene et al., 2017). These studies describe the landscape based on habitat availability but ignore habitat heterogeneity and spatial configuration. Earlier research has suggested that diversifying forest management to promote heterogeneity is a key strategy to maintain biodiversity at a landscape scale (Mönkkönen et al., 2014a; Triviño et al., 2017). However, a mechanistic understanding has remained thin.

We combine spatial concepts of landscape ecology and temporal concepts of forest disturbance ecology (Lindenmayer, 2016) to formulate five hypotheses on how forest management diversity can be used to increase biodiversity in production forest landscapes. A forest landscape is a heterogeneous mosaic of patches at various forest successional stages having various environmental conditions that offer potential habitats for a wide range of forest species. These forest species include generalists as well as specialists on each forest stage, from early-stage open habitat specialists to old-growth specialists. A forest landscape can include both naturally-regenerating and planted stands. We define

management diversity as the combination of a variety of management practices across a production forest landscape. This means that forest stands, *i.e.* management units, within a landscape are harvested using different forestry practices. Our hypotheses describe why and how a diversity of management regimes is required to generate high levels of habitat heterogeneity over large spatial extents, and why this in turn should generate a high level of biodiversity across the landscape. After describing the hypotheses, we discuss some existing relevant research and sketch out how future research could test them.

2. Five hypotheses on how forest management diversity can benefit biodiversity in production forest landscapes

2.1. The habitat diversity hypothesis: forest management diversity increases landscape-scale beta species diversity (Fig. 1)

If we consider that different forest management regimes generate habitats that are suitable for forest species with various requirements, increased diversity of management regimes across a landscape should increase overall biodiversity (Fig. 1). For instance, a diversity of saproxylic species groups could co-exist in a landscape across different locations varying in numbers of large trees, canopy density, amount of deadwood, and tree species present (Bouget et al., 2014; Tikkanen et al., 2006). Landscape-scale variation in management would produce such variation in forest structure over space. Overall diversity in such a forest landscape will be high because of increased beta-diversity – variation in species composition across space (Gossner et al., 2013a; Tscharntke et al., 2012). The benefit to biodiversity is expected to be larger when all management regimes are equally represented in the landscape compared to a landscape where one or a few management regimes dominate (Fig. 1a–c). Increasing evenness of representation of the different habitat types should allow persistence of most species because most species associated with each cover types will have sufficient habitat. In contrast, the use of a single, even low-intensity, management regime over a large spatial extent is unlikely to maintain all components of biodiversity as it will lead to homogenization of forest stands, thus reducing beta-diversity (Redon et al., 2014; Schall et al., 2018).

2.2. The spatio-temporal heterogeneity hypothesis: asynchrony in management timing enhances long-term availability of different habitat types (Fig. 2)

A diversity of management timing across stands (asynchrony) can ensure continuity of habitat availability in the landscape through time (Fig. 2a, Turner et al., 2001), such that all habitat types are provided somewhere in the landscape at all times. The suitability of stands for different species groups varies in time due to forest succession (*e.g.* Hilmers et al., 2018). However, biodiversity associated with all habitat types will be maintained when different stands within the landscape occur at different successional stages, ensuring continuity over time for each habitat type (Nordén et al., 2014). In contrast, synchronous management operations, creating a similar stand age across the landscape at any one time, generates large fluctuations in habitat availability over time for individual species. This can lead to potential habitat bottlenecks, *i.e.* periods of time when some habitat types are absent or scarce (Fig. 2b), thereby increasing extinction risk of species associated with them (Ranius et al., 2016; Roberge et al., 2015, 2018). Using various rotation times among stands, including some with extended rotation times, increases asynchrony in a landscape (Fig. 2c).

2.3. The interspersion hypothesis: spatial adjacency or proximity between stands with different management or successional stages increases biodiversity (Fig. 3)

Interspersion of stands with different management or successional stages creates spatial adjacency or proximity of habitats with different
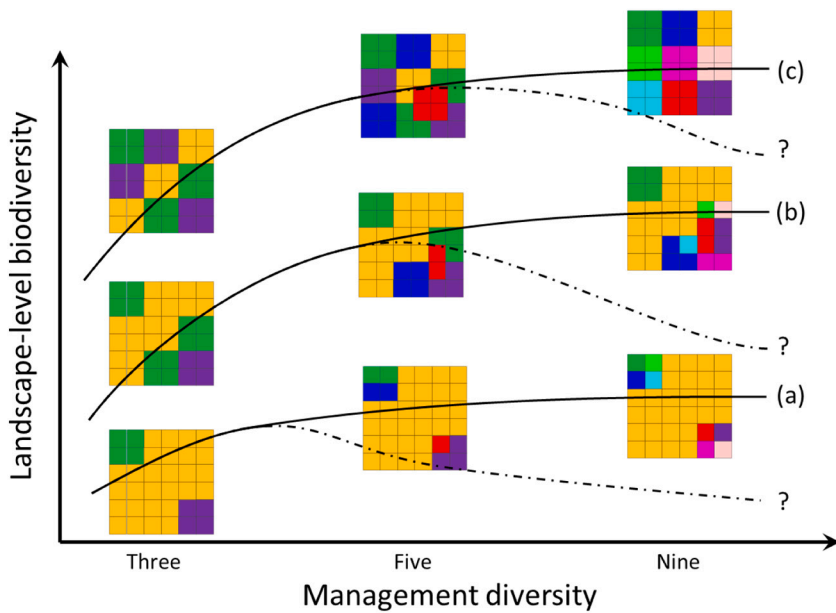
Fig. 1. Landscape-scale (gamma) biodiversity as a function of management diversity at (a) low, (b) intermediate, and (c) high evenness (in proportion of area) among management regimes. Hypothetical landscapes show examples with three, five or nine management regimes. At a constant level of management diversity, an increase in evenness among management regimes increases species diversity. As different forest management regimes are suitable for different species, increased diversity of management regimes at a landscape scale should increase overall biodiversity. However, beyond a certain threshold the area-heterogeneity trade-off could lower the benefits of management diversity (dashed line), especially when management is highly uneven (a) – see Discussion Section 3.1.
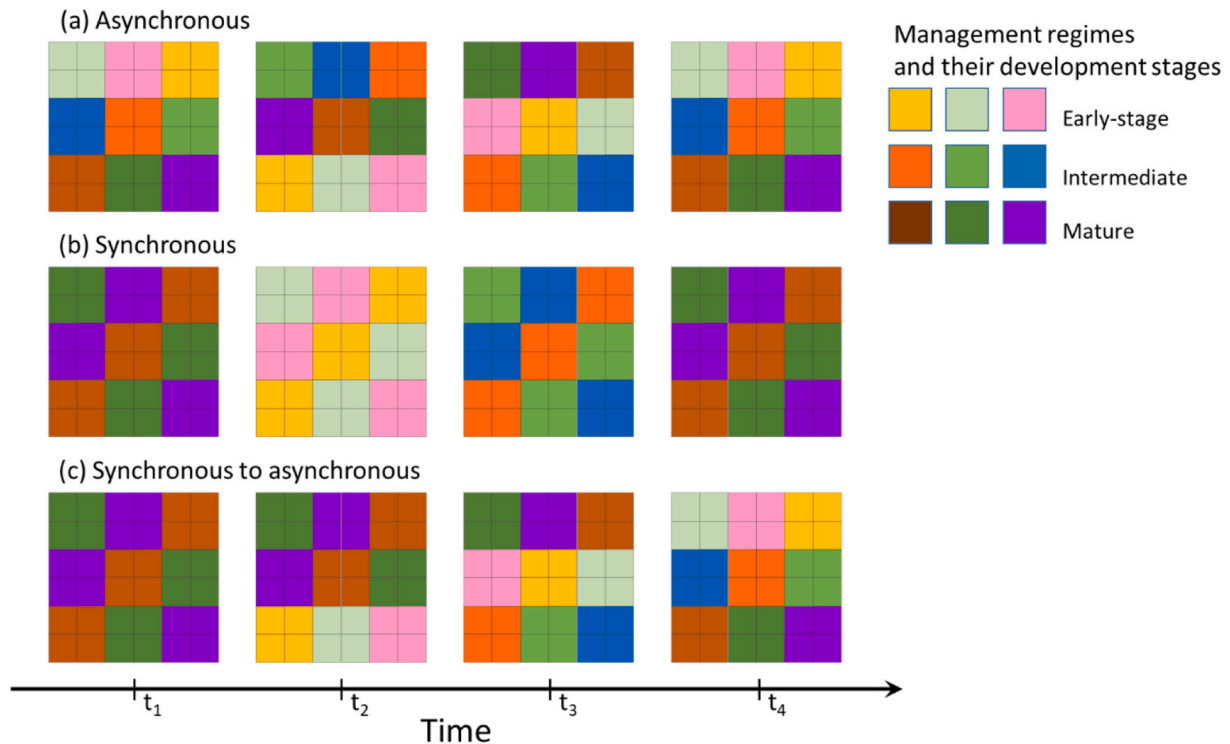

Fig. 2. Example of hypothetical landscape trajectories at four consecutive time steps (t1-t4). The three management regimes are equally represented, but the initial state (t$_1$) differs: (a) each development stage is equally represented at initial and consecutive stages, *i.e.* steady-state shifting mosaic; (b) all stands are synchronized, *i.e.* at the same development stage; (c) all stands are synchronized at the initial stage, but various lengths of delayed harvest re-establish asynchrony, *i.e.* each development stage is equally represented at the final the time step. (a) and (b): the fourth time step is equal to the first time step (full rotation).

attributes (Fig. 3a–b). Such interspersion can promote landscape complementation, where species obtain different resources such as shelter and food in different habitats (Dunning et al., 1992). Edges between adjacent stands (Fig. 3a) can also benefit particular species that differ from those found in interior habitats (*e.g.* van Halder et al., 2011). For species with good dispersal capacity (*e.g.* mammals, birds, or flying beetles), direct adjacency between habitats may not be necessary and spatial proximity may be sufficient for such species to benefit from

complementary resources found in different stands (3b). In contrast to an aggregated distribution (Fig. 3c), interspersing different management regimes will also result in a dispersed distribution of habitats over the landscape. This will further benefit beta diversity due to variation in micro-habitats across space (Deane et al., 2020; Lasky et al., 2013). As different patches of each habitat type will intersect larger extents of environmental gradients, they will also intersect more species distributions.
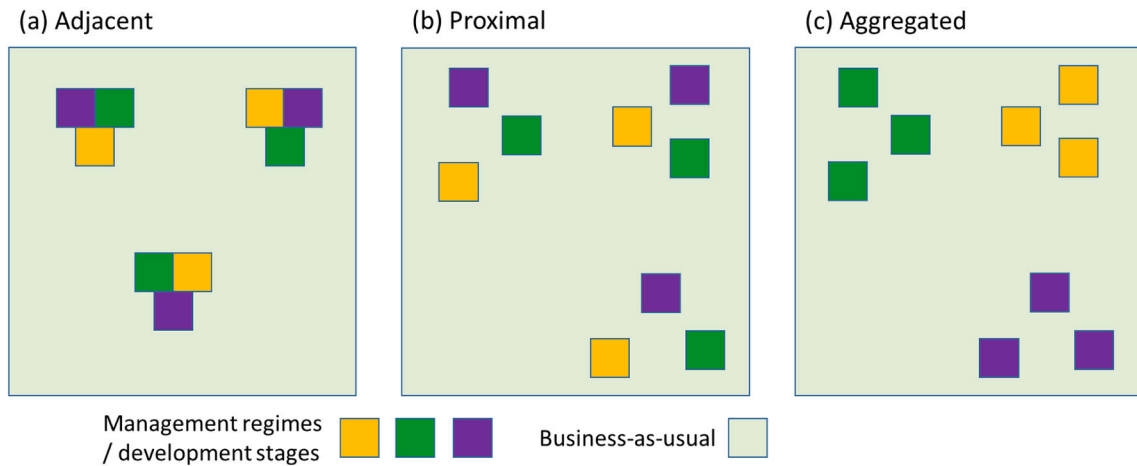
Fig. 3. Example of three hypothetical landscapes showing (a) adjacent, (b) proximal, and (c) aggregated distributions of forest covers created by alternative management regimes. Adjacency and proximity, *i.e.* interspersion, of forest areas under different management regimes would facilitate access to different habitats, providing species with multiple resources within their movement ranges (landscape complementation), as compared to the aggregated distribution. All landscapes are dominated by intensively managed production forests (business-as-usual: pale green), which are unsuitable habitat for many forest species. All landscapes also contain three alternative management regimes or three different forest development stages covering about 10% of the landscape area and providing habitats with higher quality than business-as-usual areas for many species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.4. The natural forest hypothesis: heterogeneous unmanaged set-aside forests are needed for complete biodiversity conservation

Managed forest – even alternatively managed – can never fully replicate the habitat quality of natural unmanaged forest because tree harvest removes and alters habitats (Schütz et al., 2016; Stockdale et al., 2016). Between 10% and 40% of species are restricted to natural old-growth forest, depending on the taxonomic group (Niemelä, 1999), and many red-listed species are associated with old-growth natural forests (Tikkanen et al., 2006). Therefore, a component of landscape-scale forest management should be to set aside a certain amount of forest where no human interventions are allowed. A related consideration is the degree to which protected areas actually represent the diversity of natural gradients in a region. Current protected areas are often in areas of lower primary productivity and so as a whole they intersect only a portion of the natural environmental gradients present in a region (Kuuluvainen, 2009). Overall biodiversity will be maintained when protected areas represent the whole gradient of environmental conditions (Gossner et al., 2013a).

2.5. The temporary corridor hypothesis: management diversity creates non-permanent connections between protected forests for multiple species (Fig. 4)

Management diversity can create temporary corridors between protected forests that are more cost-effective than protecting permanent habitat corridors (Fig. 4). Landscape connectivity is usually evaluated at a given time, without accounting for the temporal dynamics of changing landscapes (Martensen et al., 2017). However, metapopulation functioning does not necessarily require permanent connectivity between habitat fragments. Temporary though frequent connections may be enough for the movement of sufficient numbers of individuals for population persistence. For instance, extended rotation can prolong the existence of old forest habitats that can function as temporary corridors for old-growth-dependent species. Delaying harvest can be achieved by the use of temporary conservation contracts between forest owners and environmental agencies (Ahtikoski et al., 2018; Juutinen et al., 2012). The economic cost of such actions is modest as the income from timber production is only postponed, not eliminated. In addition, the use of multiple management regimes that promote high spatio-temporal variability in production forest landscapes can provide different pathways for different species groups between protected forests that vary through
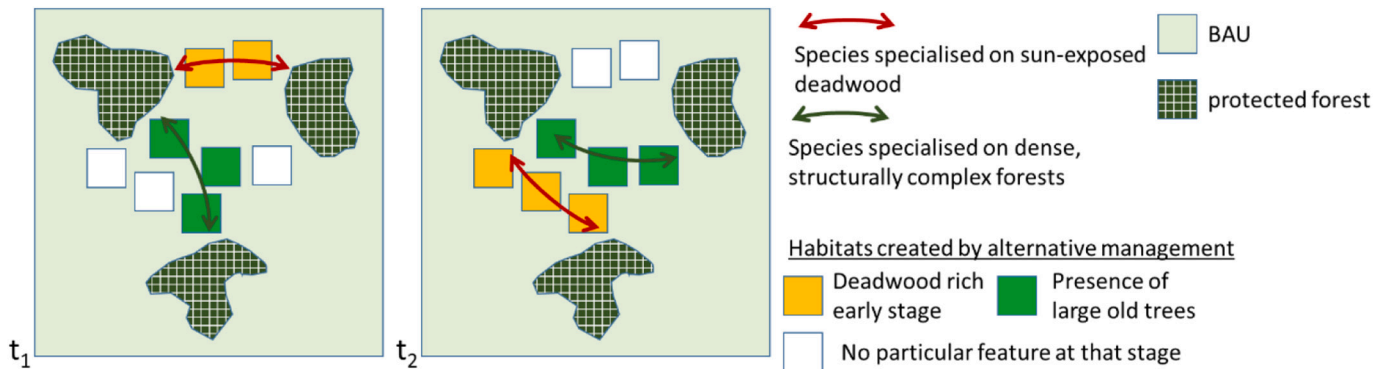

Fig. 4. Example of a landscape at two different time steps (t_1 and t_2) where protected forests are connected by alternatively managed stands. Different types of forest management can create high-quality habitat patches and serve as temporary corridors or stepping-stones between protected areas for different species groups. BAU = business-as-usual.

time (Fig. 4).

3. Discussion

3.1. The habitat diversity hypothesis

Although not directly tested by comparing landscapes with various management diversity levels, empirical observations support the assumption that different management regimes create various forest structures that support different species communities. First, forest management diversity that leads to spatial variation in canopy density can enhance habitat heterogeneity. Indeed, canopy closure determines light and microclimatic conditions, which are strong drivers of species composition for many taxa in forest ecosystems (Horak et al., 2014; Tikkanen et al., 2006; Tomao et al., 2020). This can be achieved using various harvest intensities across a production forest landscape. For example, variation in tree retention levels, from a few scattered trees to continuous cover forestry, results in different species compositions of local spider assemblages, where forest specialist species are replaced by open-habitat generalist species over a gradient of harvest intensity (Pinzon et al., 2016). Therefore, at the landscape scale, use of variable tree retention levels can enhance the conservation of more species through increased beta diversity.

Second, the variety of forest elements produced by different alternative management regimes can enhance beta-diversity as well. For instance, continuous cover forestry can enhance local biodiversity by creating vertical vegetation complexity, maintaining large trees and favouring tree species mixtures, but does not necessarily offer high amounts of deadwood (Gossner et al., 2013b; Hjältén et al., 2017; Mönkkönen et al., 2018; Peura et al., 2018). Higher amounts of deadwood can be achieved by other management regimes, such as extended rotation, *i.e.* a longer return time of harvests than is usually practiced, or absence of thinning (Felton et al., 2017; Tikkanen et al., 2012). These practices also produce denser forests, contributing to the diversity of canopy density (Roberge et al., 2016, 2018). Finally, specific habitats, such as burned wood substrate necessary for specialist pyrophilous saproxylic species, require specific interventions, in this case prescribed burning (Heikkala et al., 2016; Suominen et al., 2015). Importantly, many practices are not exclusive to each other and can be used in different combinations to further increase beta-diversity. For instance, different combinations of prescribed burning (or absence of burning) with varying amounts of deadwood enrichment, artificial tree uprooting, and various tree species among stands create a diversity of habitats hosting different species communities (Hekkala et al., 2014; Laarmann et al., 2013; Toivanen and Kotiaho, 2007). Similarly, combining different harvesting methods and intensities with active deadwood enrichment of diverse tree species can benefit saproxylic beta diversity, *e.g.* in polypores (Elo et al., 2019; Gossner et al., 2016).

However, there can be very many potential combinations of management regimes, and the specific combinations employed should take into consideration their complementarity. Indeed, depending on local context, some management regimes may have limited values for biodiversity, or only host a subset of the species found in other management regimes thus not adding to overall biodiversity. For instance, there is a weak complementarity between shelterwood and uneven-aged forestry in central European beech forests (Schall et al., 2018, 2020). Therefore, it may be more valuable for biodiversity conservation to focus on a carefully selected set of management regimes rather than using the full range of potential management variations (Duflot et al., 2022). In particular, management regimes should be determined based on their ability to generate forest habitats that are similar to those naturally found in the region (*e.g.* Kuuluvainen et al., 2021). Another potential limitation of the habitat diversity hypothesis is that, following the intermediate heterogeneity hypothesis (Fahrig et al., 2011), also called the area-heterogeneity trade-off hypothesis (Allouche et al., 2012), a very high level of management diversity will reduce the total area of each

habitat, reducing the persistence of some associated species (Fig. 1, dashed lines). Beyond a certain threshold, this could lower the benefits of management diversity. However, this pattern is by no means general (Ben-Hur and Kadmon, 2020; Heidrich et al., 2020).

3.2. The spatio-temporal heterogeneity hypothesis

The temporal dynamic of forest habitats due to succession is a widely recognized phenomenon (Turner et al., 2001). However, the landscape-scale consequences of this dynamic on biodiversity have received little attention so far (Lindenmayer, 2016). The primary effect of using a diversity of management timing across stands is to generate a diversity of forest stages over the landscape, thereby increasing the coexistence of various species groups (Hilmers et al., 2018; Roberge et al., 2018). This creates variation across the landscape in canopy openness. For instance, a diversity of management stages benefits total biodiversity of saproxylic beetles in deadwood-rich forest stands, as open and closed canopies host different assemblages (Kraut et al., 2016; McGeoch et al., 2007). In addition, the presence of early-stage habitats is beneficial to various groups of pollinators (Rodríguez and Kouki, 2017), while mature, or old-growth forests with various deadwood types benefit fungal and bryophyte diversity (Tikkanen et al., 2006). For complete biodiversity conservation, all forest stages should be distributed across environmental gradients and vegetation types, thus multiplying the diversity of habitats. For example, young and mature stands of dry boreal forests host saproxylic communities that are very different from each other and from those in other forest types in the same landscape (Kraut et al., 2016).

The response of biodiversity to habitat dynamics depends on the time needed for a given habitat to form, and the longevity of that habitat once formed. There is often a long delay before a management regime results in the creation of suitable habitat because of slow structural development of key elements (Nordén et al., 2014; Ranius et al., 2016). For instance, in boreal forest it took several decades and more than half a century for tree retention management to increase deadwood volume and the density of large deciduous trees respectively (Roberge et al., 2015). Long habitat life-time is important for species with long generation times, low reproduction, and limited colonization abilities (Nordén et al., 2014). For example, saproxylic beetles that specialize on long-lived habitats are affected by landscape pattern at smaller spatial scales, suggesting lower dispersal abilities (Percel et al., 2019). In contrast, habitat continuity at small scales may be less important for species inhabiting ephemeral habitat patches, such as early post-disturbance stages, and with good dispersal abilities, as they are able to colonize habitats over larger distances (Nordén et al., 2014; Percel et al., 2019). Thus, the temporal and spatial scales of habitat dynamics determine which species will be present in a forest landscape.

Management strategies should take these dynamics into account as overall biodiversity will be maintained when availability of each habitat type is high and stable through time, and when organisms can move between temporarily available areas of suitable habitat (spatio-temporal connectivity; Martensen et al., 2017). This is particularly challenging for species with limited dispersal abilities, which rely on habitat accessibility over small spatial scales (Roberge et al., 2015). When applied at fine scales, *e.g.* by delaying harvest in adjacent stands, the use of variable rotation time can make an even distribution of stand ages more uneven, increasing age-class variability, thereby increasing habitat heterogeneity and availability over time (Yoshimoto, 2001). Similarly, variation in prescribed burning over space and time can be used to create mosaics of post-fire age-classes, including retention of long-unburned forest (Cohn et al., 2015; Nimmo et al., 2012).

3.3. The interspersion hypothesis

The effects of habitat interspersion on biodiversity have primarily been studied through the role of edges; high interspersion generates higher edge density. In this perspective, interspersion can promote

biodiversity, as edges are specific habitats hosting typical species assemblages, *e.g.* of plants (Harper et al., 2015) or saproxylic organisms (Horak et al., 2014). However, how an interspersed distribution of forest management regimes can facilitate landscape complementation and contribute to create suitable habitats over the full range of environmental gradients has been overlooked. In the latter case, spreading the different management regimes and development stages in space can help to cover higher variability in topography and soils, and maintain different species communities (Kraut et al., 2016; see also discussion below).

Landscape complementation has been observed among stands at different successional stages; however, extrapolation of such processes to different management regimes has not yet been studied much. For example, deciduous woodland species of birds, carabids, and spiders (Barbaro et al., 2005, 2007), or butterfly species in temperate pine plantation forests (van Halder et al., 2011) have positive responses to adjacency and proximity between different development stages in the landscape, suggesting that many species use complementary habitats. Theoretically, it is possible that different alternative management regimes generate complementary forest resources as well, such as nesting sites (*e.g.* cavity bearing trees), shelter (*e.g.* dense understory vegetation) and food resources (*e.g.* deadwood). In practice, cutblocks in wood production landscapes often tend to be spatially and temporally clustered to reduce operational costs (*e.g.* transportation; Rönnqvist et al., 2015), potentially reducing proximity between various successional stages (Lindenmayer, 2016). Scheduling asynchronous harvests in adjacent stands would be an efficient way to create interspersion of age-classes but might pose difficulties for planning (Yoshimoto, 2001). Proximity of complementary management regimes might be easier to implement than direct adjacency, as it increases the number of options to find forest owners willing to apply alternative management regimes.

As discussed above, connectivity or spatial proximity between similar habitats can be important for the conservation of species groups with limited dispersal ability. Therefore, in contrast with the interspersion hypothesis, aggregating similar management regimes and consequently the habitats they generate may be beneficial for such species (Fig. 3c). For instance, aggregating deadwood rich patches increases saproxylic beetles diversity in harvested sites with retention trees and prescribed burning (Rubene et al., 2017). Similarly, Roberge et al. (2018) suggested the benefit of extending rotations could be enhanced by aggregating long-rotation stands together or by locating them nearby existing old-growth set-asides to facilitate their colonization. Some form of aggregation would be needed where stands are small relative to species habitat requirements and for species that specialize on interior habitat and avoid edges, where predation risk is higher or microclimate is less favourable, as found in some butterflies (van Halder et al., 2011) and polyporse (Ylisirniö et al., 2016). Therefore, an interspersion strategy combining small and large blocks of stands with the same management regimes or harvest timing can be a good approach to maintain landscapes with different patch sizes and edge densities (Schütz et al., 2016).

3.4. The natural forest hypothesis

The need to retain unmanaged forests to maintain all species is well established, as well as the idea that forest protection suffers from geographical biases. Even previously-managed protected forests host greater species richness and different species communities for most taxa, compared to low-intensity managed forest (Sitzia et al., 2017). However, how much protected forest is necessary, and which drivers of beta-diversity need to be accounted for in evaluating their representativeness, remain open questions. As a general guideline, Hanski (2011) suggested the "third-of-a-third" rule where a third of a region is managed as multifunctional forest (*i.e.* non-intensive), within which a third of the land area is unmanaged. However, the effectiveness of this rule remains to be tested. In a simulation study, Côté et al. (2010) predict that a

TRIAD approach, where forest is divided into protect areas, multifunctional forest (*i.e.* alternative management) and intensive production forest can be beneficial to biodiversity. In their Canadian landscape, a TRIAD approach with 12% protection and 60–74% multi-purpose management was the scenario that most resembled the absence of management (*i.e.* landscape with natural disturbances). However, the proportion of the landscape that should remain unmanaged remains subject to debate and is likely to vary among regions.

Current forest reserves are often concentrated in low-productivity land at northern latitudes or high elevations, or on shallow unfertile soils (*e.g.* in Finland, stat.luke.fi/en/forest-protection). The scarcity of reserves in high-productivity areas is highly problematic for biodiversity conservation because biodiversity generally increases with productivity (Hawkins et al., 2003). For example, low-productivity boreal forests host only a subset of the saproxylic beetle species present in high productivity sites (Hämäläinen et al., 2018). Note that this does not negate the role that low productivity sites play in biodiversity conservation, as some taxa, such as lichens, have high species richness in low-productivity sites (Hämäläinen et al., 2020). This highlights the importance of preserving heterogeneous sets of protected areas across environmental gradients, to preserve overall biodiversity. Other examples of important gradients driving beta-diversity include micro- and macro-scale gradients in altitude, potential solar radiation, soil humidity, and fire frequency (Angelstam, 1998; Chia et al., 2015; Johansson et al., 2017).

The spatial bias in protected areas can be mitigated by establishing younger or smaller protected areas proactively in regions and in conditions where protected areas are currently lacking. Importantly, protected areas do not necessarily need to be old-growth when initially established; as long as they are permanently protected they will eventually become mature forest, and will have high conservation value in the future (Kotiaho and Mönkkönen, 2017). The immediate conservation value of younger protected forests could be enhanced through, for example, deadwood enrichment (Sandström et al., 2019). Furthermore, old forests dominate in protected areas (Gustafsson and Perhans, 2010) and it has been proposed that young forests are also included to protect high-quality early successional habitats and associated endangered species (Rodríguez and Kouki, 2017; Tikkanen et al., 2006). Furthermore, young forests are usually cheaper per hectare to buy from private owners than old forests, so larger areas can be protected with equivalent financial resources (Ranius et al., 2016). In addition to establishing younger protected areas, establishing smaller protected areas in under-represented environmental conditions could contribute to a better coverage of environmental gradients. Such small reserves are regarded as effective to maintain biodiversity even if potentially isolated (Häkkilä et al., 2021; Mason and Zapponi, 2016; McGeoch et al., 2007). For instance, Laita et al. (2010) found that they contributed equally or more than larger protected areas to the conservation of rare forest habitat types in a region dominated by intensive forestry, thereby increasing the representativeness of protected forests.

3.5. The temporary corridor hypothesis

Functional connectivity between protected unmanaged forests is important for long-term biodiversity conservation. However, protected sites are often scarce and small, and may suffer from isolation, reducing their ability to maintain biodiversity. For example, bird richness declines with distance from larger protected areas in small old-growth protected forests embedded in managed forests (Mönkkönen et al., 2014b); and the species richness of red-listed wood-inhabiting fungi is much higher in well-connected habitats than in isolated ones (Nordén et al., 2013). It is often claimed that alternative management regimes can contribute to better connectivity, often with a vague definition of what is to be connected by them and for which species. It has been argued that green tree retention (Gustafsson et al., 2010; Kruys et al., 2013) and continuous cover forestry (Mönkkönen et al., 2018; Pinzon et al., 2016; Pukkala and Gadow, 2012) increase connectivity. However,

as yet these claims have not been formally tested, *e.g.* using radio-tracking data or species composition similarity analysis between sites connected by forests managed with such methods.

Permanent micro-reserves of high-quality habitats within a managed forest matrix can increase habitat availability and complement more conventional large natural reserves, and can also enhance the connectivity through the matrix of managed forests (Laita et al., 2010). Because micro-reserves are scattered across the landscape, they only benefit species that can disperse far enough to reach them; therefore, a higher density of micro-reserves will be more effective for increasing connectivity. Temporary habitats through specific forest management methods could play the same role. For this approach to succeed, it will be important to determine how long a temporary reserve should be maintained for species to colonize it, develop a population in it, and disperse from it (Nordén et al., 2014; Tomao et al., 2020).

3.6. Evaluating the management diversity hypotheses

The fives hypotheses can be evaluated using the regular tools of forest ecology, *i.e.* empirical biodiversity observation in selected or manipulated sites and forest simulations. However, instead of replicate sites as forest stands, here they would be replicate forest landscapes. In other words, a given study would compare the biodiversity in landscapes containing different combinations of forest management regimes.

The influence of different aspects of heterogeneity generated by management diversity can be assessed by measuring gamma diversity across different landscapes that vary, for example, in diversity of management regimes (habitat diversity), diversity of age-classes (spatio-temporal hypotheses), amount of set-aside (natural forest), or edge density between various management and/or age classes (interspersion). Adequate evaluation of the relative effects of these variables will require a pseudo-experimental approach. In such a design, study landscapes are carefully selected so that: (i) they represent the widest possible range of each of the heterogeneity variables of interest, (ii) the heterogeneity variables are not spatially autocorrelated, and (3) the heterogeneity variables are independent of each other (*i.e.* not correlated; Pasher et al., 2013). In each landscape, estimation of beta and gamma diversity will require a whole-landscape sampling design, where multiple plots are sampled within each landscape (Bennett et al., 2006).

Because of the standardization of forestry operations, it may prove difficult to find landscapes with many different management regimes (but see Elliot State Research Forest recent experimental proposal: OSU College of Forestry, 2020). One possibility to overcome this limitation is to simulate virtual landscapes and populate them using empirical biodiversity data collected in stands experiencing various management regimes and at different development stages (*e.g.* see Schall et al., 2020). In this approach, biodiversity data can be used to evaluate virtual landscapes with increasing number or varying proportions of alternative management regimes and/or of age classes (habitat diversity and the spatio-temporal hypotheses). Biodiversity samples would then be randomly selected according to these management diversity scenarios and aggregated at landscape scale as gamma and beta-biodiversity measures.

However, this approach cannot be used to evaluate hypotheses that include aspects of spatial configuration and temporal change, such as the spatio-temporal heterogeneity hypothesis, the interspersion hypothesis and the temporary corridor hypothesis. The challenge here is that information would be needed about how species move across and between stands as they change through time. Simulation modelling (*e.g.* forest growth simulator and connectivity analyses) can be used to make predictions about which combinations of management regimes in space and time are likely to increase biodiversity using a variety of assumptions about habitat dynamics and species movements (Roberge et al., 2015; Tittler et al., 2015). Such simulations can be used to predict the long-term impact of various forms of management diversity. The most promising management combinations could then be applied in real landscapes. Because simulation tools offer only a simplified representation of real-world systems, application of simulation-derived scenarios should carefully consider the special conditions of the given case. These landscapes could be monitored over time by successive forest ecologists to determine whether the predictions do indeed hold up.

4. Conclusion

We suggest that management diversity (including the absence of management in some stands) can increase biodiversity in production forest landscapes. The importance of local-scale structural heterogeneity for biodiversity in forest ecosystems is well recognized. However, the role of management diversity at a landscape scale across space and time is less well studied. By providing hypotheses to be tested, we hope to stimulate further research in this area. Different species differ in their dispersal abilities and behaviours in relation to habitat heterogeneity. Thus, although we present the hypotheses at a landscape scale, they could also be applied within stands (*e.g.* in regions with large stand areas), where spatial units would be individual trees or groups of trees. We also hope to encourage forest managers to begin applying these ideas in real landscapes, along with biodiversity monitoring through time. This will provide invaluable information to future forest ecologists about the role of forest management diversity in maintaining biodiversity. At the same time, if the hypotheses are valid, application of them now will provide concrete benefits to forest biodiversity in the coming decades.

We acknowledge that our perspective is largely inspired by experimental, observational, and theoretical research conducted in the temperate and boreal forests in Europe and North America, while Mediterranean and tropical forests are less well integrated in our framework. However, it is very possible that similar principles apply to forest landscapes of these biomes as well, as they are also heterogeneous mosaics of habitats resulting from natural disturbance-succession dynamics and subject to homogenization from forestry activities (*e.g.* Chambers et al., 2013). In addition, we are well aware that sustainable forest management is a vast domain that does not only target biodiversity conservation but also encompasses risk mitigation (*e.g.* flood, fire, landslide), livelihoods of local communities, and climate change adaptation. In this respect, management diversity might also contributes to balance multiple societal objectives (Eyvindson et al., 2021), and may offer a larger range of adaptive options in a changing and uncertain future (Kuuluvainen et al., 2021).

CRediT authorship contribution statement

Rémi Duflot, Lenore Fahrig & Mikko Mönkkönen: Conceptualization, Rémi Duflot: Writing - original draft; Lenore Fahrig & Mikko Mönkkönen: Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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