Review

A gaping hole in boreal conservation research: Effects of size and aggregation of conservation areas on species diversity at the landscape scale

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ARTICLE INFO

ABSTRACT

Area-based conservation measures are the main approach to preserve forest biodiversity. However, there is no common view on the best strategy in relation to spatial aggregation of conservation areas, for a given total area preserved. We conducted a systematic literature review to evaluate the effect of mean patch size and aggregation of conservation areas on landscape-scale biodiversity in boreal forest. Our main objectives were to find empirical evidence regarding whether few large or several small conservation areas protect more biodiversity and investigate how the spatial aggregation of conservation areas affects biodiversity. We searched specifically for studies comparing biodiversity across many small vs. few large and dispersed vs. aggregated conservation areas, controlling for total area protected. Although our initial search resulted in a large number of articles, not a single study assessed landscape-scale biodiversity in many small vs. few large, or dispersed vs. aggregated conservation areas, of a spatial scale relevant to average-sized or even small nature reserves (i.e. $\geq$ 10 ha). We did find 5 studies comparing many small vs. few large conservation patches within clear-cuts, and one study of forest patches within a national park (ca 7 ha). The conservation areas on clear-cuts were patches of retained trees, with the smallest patches being single trees. The effect of patch size on biodiversity varied among studies, mostly indicating neutral effects of patch size. While the results of these studies are relevant to clear-cuts, their relatively small spatial extent (the largest retained patch being 1.2 ha) precludes extrapolation to scales relevant to reserves in boreal forest. Our review exposes an extensive knowledge gap regarding consequences of the sizes of conservation areas on landscape-scale boreal forest biodiversity. Until such information is available, we recommend a combined approach involving both small and large conservation areas in boreal forest.

1. Introduction

Setting aside protected areas is one of the most common conservation measures to protect biodiversity (Gaston et al., 2008). Knowing how species respond to different protected area designs is crucial for decision-making in nature conservation. Since the 1970 s, there has been an ongoing debate (the SLOSS debate; SLOSS=single large or several small) about the best design principles to apply to protected areas for preserving biodiversity (May 1975; Boecklen, 1997; Wiersma & Nudds, 2009). This debate has been about the relative importance of protected area size and replication: are a few *large* protected areas better for biodiversity conservation than many *small* areas (Boecklen, 1997; Diamond, 1975; Ovaskainen, 2002; Rösch et al., 2015)?

Large protected areas are often considered the primary conservation measure, despite uncertainties about their performance in comparison to several small protected areas of the same total size (Ovaskainen,

2002; Hokkanen et al., 2009; Tjørve, 2010; Fahrig et al., 2022). Based on island biogeography theory (MacArthur & Wilson, 1967) and other species-area relationships (Connor & McCoy, 1979), it has been suggested that for a fixed total area, one large protected area is more effective in conserving biodiversity than several small ones (May 1975; Diamond, 1975; Terborgh, 1974; Wilson & Willis, 1974). This prediction mostly derives from the assumption that variation in extinction rate dominates the outcome of the extinction–colonization dynamic, and that small patches have smaller populations and thus higher extinction rates (Fahrig et al., 2022).

However, it has been suggested that when the colonization rate dominates the outcome, several small patches may have more species due to higher migration rates (Fahrig et al., 2022). Furthermore, more species are expected to be present in several small patches than in a few large ones if the beta diversity in the landscape is large. This is because, given that the occurrence of species or habitats is spatially autocorrelated within a landscape, a large number of small patches will intersect more habitats and species compared to a small number of large patches (Fahrig et al., 2022). Modelling studies using different approaches to resolving the SLOSS dispute, however, point out that several factors may affect the optimal size and number of protected areas. These factors include the level of decreased species density caused by isolation, the level of overlap in the habitat provision (Tjørve, 2010), which measure of population persistence is used (Etienne & Heesterbeek, 2002), and the management history of the landscape (Ranius & Kindvall 2006).

Apart from the size of protected areas, the spatial aggregation of conservation measures is another potentially important factor in biodiversity conservation. In particular, it may make a difference whether protected areas are more evenly *dispersed* or *aggregated* within the landscape. This is because landscapes with the same amount of habitat and with the same number of areas of the same size, but with the areas situated in different locations, exhibit different functional connectivity and habitat reachability (Villard & Metzger, 2014 and references therein). Therefore, the spatial arrangement of protected areas might affect a species' ability to persist. When Diamond (1975) originally argued for single large protected areas rather than several small ones, he also argued that it is an advantage if protected areas are well-connected, to facilitate dispersal between them. This is in line with conclusions drawn from metapopulation ecology suggesting that the persistence of a metapopulation is higher if habitat patches are aggregated (clumped into aggregations) within a landscape, because of the increased connectivity (Hanski, 2011). Spatial aggregation of protected areas has likewise been found to have a strong effect, both positive and negative, on some species (Aben et al., 2012; Kajtoch et al., 2012; Lehtilä et al., 2020). On the other hand, landscapes with a more even distribution of protected areas might cover a larger variety of habitats, and thus support more species (Fahrig et al., 2022). Similar to SLOSS evaluations, assessing the full consequences of alternative spatial arrangements requires empirical landscape-scale studies that measure gamma diversity in locations with the same amount of aggregated or dispersed habitat, and with landscape histories such that species richness is at equilibrium (Bennett et al., 2006).

In many regions of the world, boreal forest has been extensively altered by the introduction of intensive forest management practices (Östlund et al., 1997). For example, in Fennoscandia the transformation of large forest areas into monospecific even-aged stands has resulted in dramatic changes to the overall dynamic and structure of ecosystems (Berglund & Kuuluvainen, 2021). This has strong negative effects on many species, especially those associated with old trees or dead wood (reviewed in Duflot et al., 2022). For these species, unmanaged forest often provides habitat of the highest quality, followed by old managed forests, while young forest and clear-cuts provide habitats of lower quality (e.g. Ekbom et al., 2006). Thus, for the most sensitive species, a managed forest landscape can be highly fragmented, with only very small isolated patches of habitat available. In contrast, more generalist species, which are thought to have evolved to thrive in heterogeneous environments (Futuyma & Moreno, 1988), often persist in at least some types of managed forest. Therefore, the same landscape may harbor large areas of suitable forest habitat for generalist species, while more specialized species are disfavored by habitat loss.

The establishment of protected areas is a primary instrument in achieving biodiversity protection goals in forest ecosystems. Large reserves are argued to be important for maintaining forest biodiversity in the long term (Powers et al., 2013). However, with increasing habitat loss and degradation due to wood production-oriented forest management (Gustafsson et al., 2015), smaller reserves (e.g., 20 ha) are becoming more common (Angelstam et al., 2020; Baldwin & Fouch, 2018; Bengtsson et al., 2003). Moreover, retention forestry has become a common practice to preserve forest habitats within managed forest landscapes (Felton et al., 2020). This approach involves retention of living and dead trees, as individuals or small patches left intact within clear-cuts at the time of harvest (Lindenmayer et al., 2012). Since this has been applied only during the last few decades, the long-term benefits of aggregated vs. dispersed retention are largely unknown (Baker et al., 2015, but see also Lee et al., 2017; Roberts et al., 2016).

Here, we review the existing literature to find empirical studies testing the effects of size and spatial aggregation of conservation areas on biodiversity at a landscape scale (gamma diversity), controlling for the total area protected. We focus on boreal and hemi-boreal forests, and aim to address the following two key questions: (Q1) How does the size of conservation areas affect the provision of biodiversity? (Q2) How does the aggregation of conservation areas affect the provision of biodiversity? To answer these questions, we systematically searched for relevant empirical evidence within studies that compared the effects on landscape-scale biodiversity of the size of the conservation areas over whole sets of patches with the same total area but with different numbers and sizes of patches, or with different levels of aggregation within landscapes (Fig. 1).

2. Methods

2.1. Literature search

We explored studies in boreal forests that evaluated the effect of sizes and spatial aggregation of conservation areas, for a given total area of the conservation areas, on landscape-scale biodiversity. The initial research question also included the effect of sizes and spatial aggregation of conservation areas on ecosystem services, but this part of the search was not used in this study. Thus, the search was done for a broader scope of articles than we include here. We searched in Scopus: (https://www.scopus.com/home.uri) and in Web of Science Core collection (https://clarivate.com/). The Web of Science topic search covered all years within Science Citation Index Expanded (1945-present), Social Sciences Citation Index (1956-present), Arts & Humanities Citation Index (1975-present), Conference Proceedings Citation Index-Science (1990-present), Conference Proceedings Citation Index- Social Science & Humanities (1990-present), Emerging Sources Citation Index (2015-present). General search statistics are reported in accordance to PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analysis, https://www.prismastatement.org) guidelines in Fig. 2 (PRISMA checklist included as S1 Checklist).

We used the following search strings (Web of Science format):

TS=(*Forest** OR *"Plantation*"* OR *Woodland** OR *"Silvicultur*"*).

• AND

TS=(*biodivers** OR *"divers*"* OR *species** OR *"red listed"* OR *"red-listed"*) OR (*recreat** OR *touris** OR *social** OR *cultur** OR *herita** OR *preference** OR *people** OR *public**) OR (*mushroom** OR *berry** OR *berrie** OR *meat** OR *game** OR *hunt** OR *reindeer** OR *non-timber*) OR (*pest** OR *pathogen** OR *outbreak**) OR (*fire** OR *wildfire**).
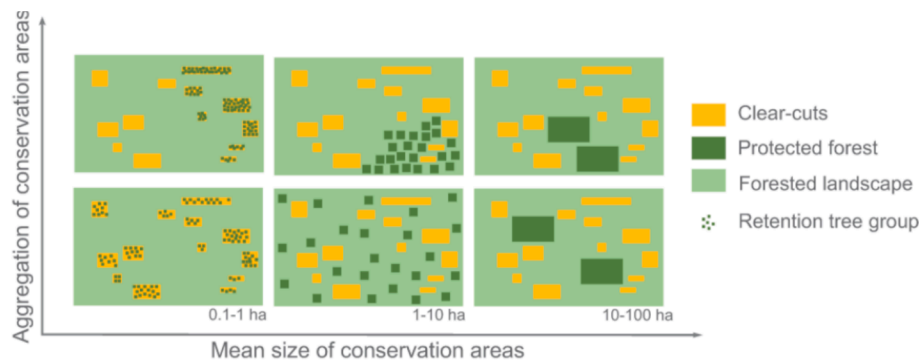
Fig. 1. Schematic representation of hypothetical variation in size and spatial aggregation of conservation areas. Each large rectangle is a landscape. For a given total conservation area in a forest landscape (the sum of the dark green areas in a landscape), the sizes of conservation areas may vary from individual retention trees or small tree clusters (two left side panels), to small protected areas (two middle panels), to large reserves (two right panels), as visualized along the x-axis (with indicated approximate sizes of conservation areas). Similarly, forest landscapes could have the same number of conservation areas of the same size, but the conservation areas could be dispersed evenly throughout the landscape, or aggregated in some parts of the landscape, as visualized along the y-axis.

- AND

TS=(*"Conservat*"* OR *"Biological legac*"* OR *"Buffer strip*"* OR *"Buffer zone*"* OR *"Buffer area*"* OR *deadwood*ies OR *"dead wood*"* OR *"snag*"* OR *"green tree*"* OR *"protected area*"* OR *"Remnant tree*"* OR *"Reserve"* OR *reservation* OR *"Residual tree*"* OR *"Restorat*"* OR *"Retention*"* OR *"set aside*"* OR *"set-aside*"* OR ((*"aggregat*"* OR *"dispers*"* OR *"distrib*"* OR *"connectiv*"* OR *"fragment*"* OR *"patch*"* OR *"SLOSS"* OR *"size"* OR *"scale"*) AND (*"manage*"* OR *"forestry"* OR *"landscape"* OR *"reserve"* OR *"conservat*"*))).

- AND

(CU=(*RUSSIA* OR *LATVIA* OR *SWEDEN* OR *CANADA* OR *LITHUANIA* OR *NORWAY* OR *ESTONIA* OR *FINLAND)* OR AD=(*MICHIGAN* OR *WISCONSIN* OR *MINNESOTA* OR *"NORTH DAKOTA"* OR *"ALASKA"*) OR TS=(*Boreal** OR *Hemiboreal** OR *Nordic** OR *Fennoscand** OR *Scandinavi** OR *Canad** OR *Russia** OR *Finland* OR *Finnish* OR *Swed** OR *Norw** OR *"Michigan"* OR *"Wisconsin"* OR *"Minnesota"* OR *"North Dakota"* OR *"Alaska"*)).

The main search was performed on 15–20 March 2018 and the additional search for later articles was done on 11 January 2022. Both searches were done through Swedish University of Agricultural Sciences institutional access to the above-mentioned academic databases. After excluding duplicates, the combined search resulted in 52,417 articles (for studies on both biodiversity and ecosystem services). The initial screening for relevance on the title-level resulted in 13,208 records (for studies on both biodiversity and ecosystem services). After reviewing publication abstracts, 1,308 articles (only on biodiversity) were kept for further full-text scrutinizing (Fig. 2). Most duplicate removal, title and abstract screening was performed in EPPI-Reviewer 4.0 (Thomas et al., 2010) and the screening of articles from the 2022 search was done in EndNote X8 and 20 (The EndNote Team, Philadelphia, PA, USA). The screening of abstracts and full text was performed following the predefined inclusion criteria described below.

2.2. Inclusion criteria

Our goal was to examine relationships between the sizes and spatial aggregation of conservation areas and landscape-scale biodiversity (Fig. 1). We only included studies that were conducted in forests within the boreal and the hemi-boreal zone (Ahti et al., 1968; Brandt, 2009). To be included, articles needed to present direct measures of biodiversity, such as species composition, diversity, abundance, richness or data on reproduction or persistence of a species of conservation value (i.e. all species except pests and invasive species). We searched for conservation

areas at a range of possible spatial scales, from retention of individual trees within clear-cuts to large reserves (Fig. 1). Specifically, we searched for studies comparing many small conservation areas to one or a few large conservation areas controlling for total area protected. We included field-based empirical studies, as well as review papers and simulation studies that used primary data.

Articles were screened in two stages by four researchers, first by title and abstract (LW, SF, KJ and JK) and then full text (SF and JK). All reviewers followed the same protocol (produced after discussion among LW, TR, AF and KJ) to ensure consistency during the abstract screening stage (S1 Review protocol). If a reviewer was unsure whether to include or exclude an article at the title or abstract stage, the article was included. At the full text stage, the articles that a reviewer was unsure about were discussed with other research group members.

2.3. Data extraction

For each retained article, we recorded general information on the scale and duration of the study, conservation area type (reserve or retention patch) and conservation area details (total area, mean patch size and retention level). One of the most important criteria in our review was related to the area measured; we thoroughly read the descriptions of the study designs to ensure that only studies where the total area of the smaller protected patches equaled the total area of the larger protected patch(es) were included. Finally, we documented statistical analyses, significance and the direction of responses, and summarized the relevant findings for each article.

From the selected studies, for each species biodiversity responses (e. g. species richness, abundance etc.) the results of statistical comparisons between several small and few large areas were recorded as "positive", "negative" or "neutral". The effects were summarized for each organism group. Since the relevant tests were few and heterogenous, it was impossible to conduct a *meta*-analysis.

3. Results

We found no studies investigating the effect of spatial aggregation of conservation areas on landscape-scale biodiversity, i.e. comparing landscapes differing in whether the conservation areas are dispersed or aggregated but similar in other aspects (scenarios along the y-axis in Fig. 1). Further, we found no studies comparing landscape-scale biodiversity in several small vs. a few large conservation areas at the scale of a forest landscape (scenarios along the x-axis in Fig. 1). However, we found 5 articles comparing many small vs. few large conservation patches within clear-cuts (i.e. at a smaller scale) and one study comparing forest patches of different sizes within a larger protected
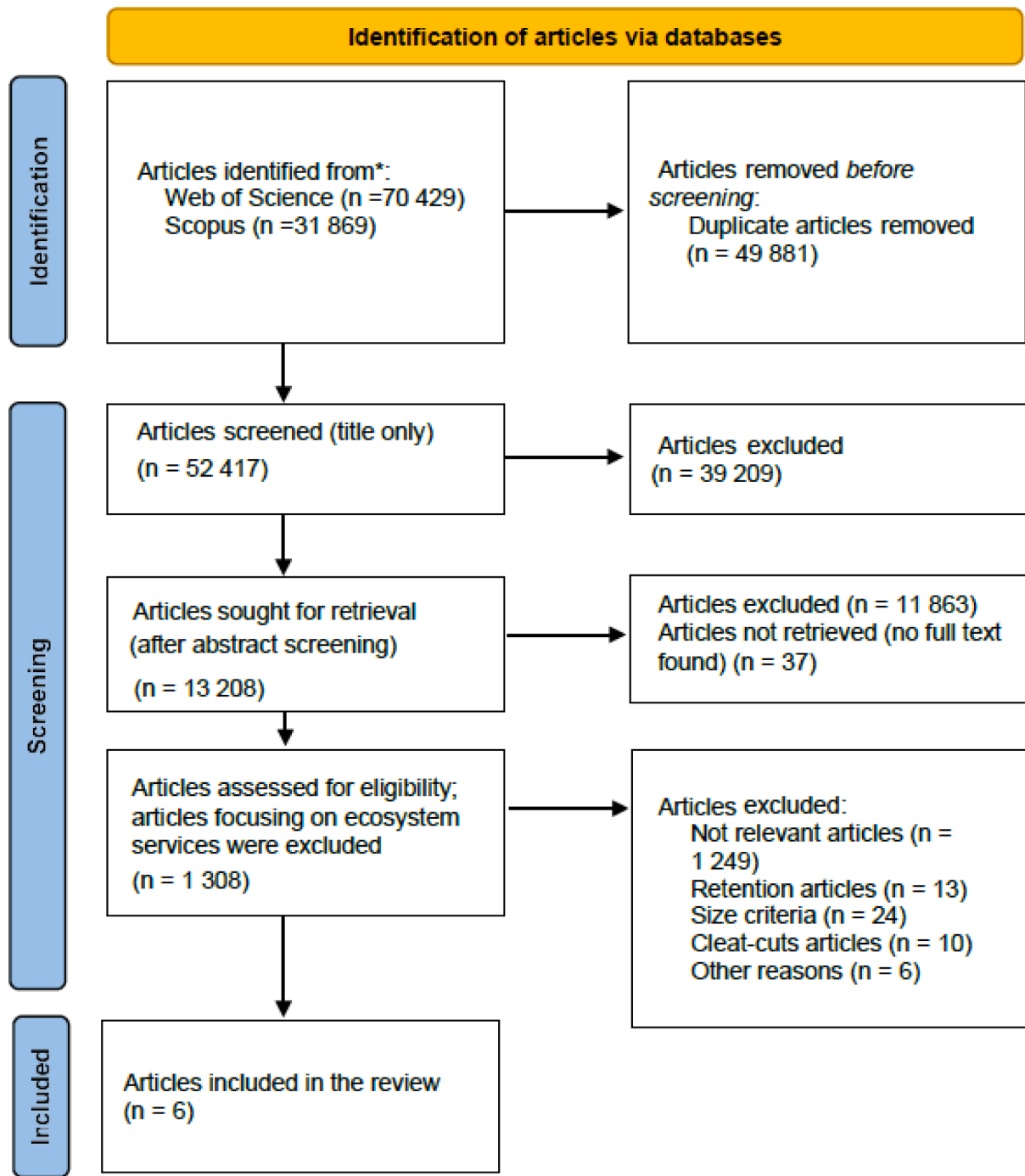
Fig. 2. Study selection. PRISMA flow diagram of selected articles for inclusion. Although the initial search resulted in a large number of articles, only a few articles fulfilled our predefined criteria and were included in the review. *Note that the search was done for a broader scope of articles than we include here: the numbers of articles screened and sought for retrieval represent articles on effects of either size or spatial aggregation of conservation areas on biodiversity and ecosystem services, while here we only included articles on biodiversity (see *Literature search* section for more details).

patch (S1 Fig). In all clear-cut studies, the total area covered by retention trees was the same per clear-cut, and the comparison was done between different levels of tree clustering: either single retention trees vs. groups of retention trees, or smaller vs. larger groups of retention trees within a clear-cut. The sizes of the larger patches of retention trees on clear-cuts varied between 0.1 and 1.2 ha and the sizes of the smaller patches varied between individual retained trees and 0.8 ha. One study was done on forest patches within a national park for which the studied forest patches varied in size between 0.05 and 6.93 ha (S1 Table).

In the 6 studies, a total of 17 statistical comparisons were made

between many small and few large conservation patches. Among those comparisons, 59 % of species biodiversity responses (species richness, abundance, diversity and dispersal) showed neutral effects of increasing the mean size of patches, 23 % were positive and 18 % were negative (Fig. 3). In the 5 studies conducted on clear-cuts, a total of 15 statistical comparisons were made of single retention trees vs. groups of retention trees or of smaller vs. larger groups of retention trees. Among those comparisons, 67 % of species biodiversity responses showed neutral effects of increasing the mean size of patches, 27 % were positive and 6 % were negative. The studies were conducted in Canada, USA, and
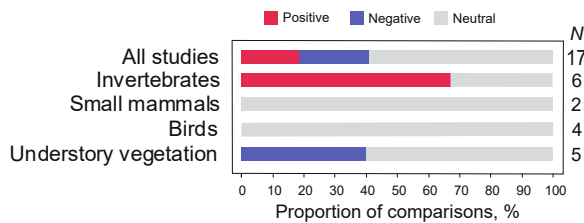
Fig. 3. The effects of increasing mean size of conservation patches on biodiversity responses, for a given total area conserved, based on 17 statistical comparisons in six studies in boreal forest. All tests compared species biodiversity responses (species richness, abundance, diversity, and dispersal) in few large areas to several small ones ("Positive" – the species metric increased with increasing mean size of the conservation patches; "Neutral" – the species metric did not correlate with increasing mean size of the conservation patches; "Negative" – the species metric decreased with increasing mean size of the conservation patches). Five of the six studies evaluated patches of retained trees within clear-cuts. The sixth study evaluated patches of different types of forest within a national park. *N* denotes the total number of tests for each category.

Finland.

Despite the small number of studies and comparisons, the measured biodiversity responses were spread across four major taxonomic groups (Fig. 3).

4. Discussion

The most important result of this review is the complete lack of empirical studies comparing landscape-scale biodiversity responses to many small vs. few large, or to dispersed vs. aggregated protected areas, in managed boreal forest landscapes. Five of the six studies that we did find compared many small vs. few large clusters of retained trees within clear-cuts, and the sixth compared many small vs. few large patches of particular forest types within a national park. Our research was extensive: we reviewed the titles of 52,417 potential studies (including studies on ecosystem services), a subset of 13,000 abstracts, and the full text of the 1,300 remaining articles that were eligible. Thus, we are confident in our conclusion that SLOSS studies at a landscape scale within boreal forest are scarce.

In this review we intentionally focused on studies that assessed biodiversity metrics at a landscape scale. There are studies investigating the effects of patch size on alpha diversity in boreal forest (Tjørve, 2010; Sahlin & Schroeder, 2010; Liu et al., 2022), as well as studies exploring variation in species composition within forest landscapes (beta diversity) (Gossner & Müller, 2011; Rubene et al., 2015). However, as species diversity patterns are shaped by ecological processes operating on different scales (Willis & Wittaker, 2002), there is a need for information on gamma diversity, i.e. landscape-scale biodiversity across sets of many small patches vs. across one or a few large patches (Franklin, 1993). Hence, the main result of our study is to reveal a large hole in the scientific literature on boreal forest biodiversity, namely a lack of knowledge about the effects of mean patch size or aggregation of conservation areas at a beta and gamma scale.

To some extent our results may not be surprising, especially in the context of boreal forest ecosystems. Even with access to the resources needed for designing a replicated landscape-scale experiment, it is challenging to conduct such a study in an appropriate way. One reason for this is that there is a natural heterogeneity in habitat quality among and between forest landscapes, due to variation in, for instance, forest productivity and historical land use. Furthermore, it may take many decades before biodiversity is in equilibrium after an experiment is initiated (Takashina, 2021). For this reason, species richness can be higher in old-growth forest remnants in recently harvested production forest landscapes, in comparison to forest patches of the same size that have been isolated for longer periods of time (Berglund & Jonsson, 2005). Thus, it is critical to determine whether a stronger extinction debt

occurs across several small than few large patches, or vice versa (Hämäläinen & Fahrig 2024). This can be done by monitoring changes in species richness over time using the controlled resampling of empirical data (e.g. Öckinger & Nilsson, 2010). An alternative approach is to compare sites varying in mean size, but with similar time since disturbances, for instance since the last intervention in forests previously managed for production. Altogether, these difficulties can explain why the focus in landscape ecology since the 90′s has largely shifted from the SLOSS question towards more narrowly defined sub-questions, such as the importance of habitat connectivity and edge effects (Harper et al., 2015; Martensen et al., 2017).

We did find five studies of conservation patches in clear-cuts, and one study on forest patches within a national park (S1 Table). Most of the comparisons in these studies found no difference between many small and few large conservation patches. However, there were also some comparisons that showed either a higher diversity in few large than many small conservation patches, or a higher diversity in many small conservation patches. Two previous reviews summarized the effects of conservation areas in production forests (Fedrowitz et al., 2014; Häkkilä et al., 2021), but neither of these tested SLOSS, as they compared scenarios with different amounts of total conservation area. This is in contrast to our review that only included studies with the same total area protected. The first of these reviews, a *meta*-analysis on the effect of green tree retention found that richness is higher in retention cuts than in clear-cuts, and that positive effects of retention cuts on forest species richness increases with the proportion of retained trees and time since harvest (Fedrowitz et al., 2014). A second systematic review found that retained patches within production forests act as a complement to the larger protected areas within a landscape, by providing habitat for species with restricted dispersal abilities; but these patches do not replace larger reserves, as they harbor distinct communities (Häkkilä et al., 2021). In our review, the absence of species responses to the mean size of conservation patches in most of the 15 comparisons in the five clear-cut studies could be due to the small sizes of the patches tested (single trees and small clusters of trees). In such circumstances individual retention trees in clear-cuts may function as habitat, either because they are sufficiently close to each other such that the total amount of habitat exceeds minimum habitat demands, or because the surrounding matrix serves as habitat or provides complementary resources (Andersson & Bodin, 2009). For instance, we found no evidence that birds and small mammals respond to an increasing mean size of retention patches, probably because the territories of such species are large enough to exceed that provided by one single tree or one group of trees. Thus, the processes behind the observed patterns may well be driven by the surrounding availability of resources, rather than dispersal limitation. This is distinct from what has been considered in, for example, island biogeography theory that predicts colonization and extinction at much larger spatial scales.

Given the fine scale of the studies conducted within clear-cuts, caution is warranted when extrapolating these results to the design of protected areas in boreal forest. The largest retained area was less than 1.2 ha, which is very small compared to the size of protected areas in Europe's boreal forest, which typically range between 10 and 100 ha (Elbakidze et al., 2013), but can encompass areas of hundreds of thousands of ha. Therefore, while these five studies provide useful information on the effects of the size of retention tree groups, other studies are needed at spatial scales that are relevant to reserve design.

5. Conclusions

Our review shows that for boreal forest landscapes there is a lack of empirical studies investigating the effect on landscape-scale biodiversity of the average size of conservation areas or the spatial aggregation of conservation areas, while holding total area constant, and at scales corresponding to the typical scale of reserves (even small ones). One likely reason is that conducting studies that cover large areas is time and

resource demanding. Even with large amounts of resources available, it is difficult to design studies where patch sizes vary but the total area is constant among otherwise similar landscapes. Nevertheless, this is a key question in nature conservation, and thus there is a pressing need for empirical studies evaluating large scale gamma diversity across sets of patches of different sizes. As long as this question remains unanswered, a mixed approach that combines both many small and at least some large conservation areas, as advocated by Arroyo-Rodríguez et al. (2020) and Filyushkina et al. (2022), is likely the best option available for protected areas design in boreal forest landscapes.

CRediT authorship contribution statement

Julia Kyaschenko: Writing – review & editing, Writing – original draft, Visualization, Investigation. **Lina Widenfalk:** Writing – review & editing, Visualization, Methodology, Investigation, Conceptualization. **Sarah L. Facey:** Methodology, Investigation, Conceptualization. **Adam Felton:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Lenore Fahrig:** Writing – review & editing. **Thomas Ranius:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Adam Felton reports financial support was provided by Swedish Research Council Formas. Julia Kyaschenko reports financial support was provided by Stora Enso AB. Other 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.

Data availability

Data will be made available on request.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2024.126704.

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