



## Forest Management

# Potential Recolonization Benefits of Retention Forestry Practices

Craig Loehle<sup>o</sup>, Kevin A. Solarik<sup>o</sup>, Daniel U. Greene, Laura Six,<sup>o</sup> and Darren J.H. Sleep

Tree retention after forest harvest is often used to enhance biodiversity in forests that are otherwise managed using even-aged systems. It remains unclear to what extent scattered trees and residual patches (i.e., retained structures) actually facilitate recolonization of species in logged areas. For assessing recolonization benefits, it is necessary to consider both survival in retained structures postharvest and recolonization in cleared areas. We conducted a literature review to assess recolonization responses of birds, mammals, reptiles, amphibians, vascular plants, invertebrates, lichens/bryophytes, and mycorrhizal fungi. The clearest benefits of retention were for poorly dispersing plants. Seed dispersal type may be a key life-history trait relative to effectiveness of recolonization, with animal-dispersed seeds having the greatest dispersal range. We found that lichens/bryophytes are likely not dispersal limited (with possible exceptions) but are slow growing and require the development of moist microsite conditions. Significant literature gaps exist for amphibians, nonvolant invertebrates, and mycorrhizal fungi. Overall, recolonization success postharvest is taxon specific, where the benefits of implementing retention systems will depend on the region and species within that region. Species that require a long growth period (some lichens) or are poor dispersers (some herbaceous species) may benefit more from the creation of forest reserves than from retention practices.

**Keywords:** biodiversity, clearcut logging, dispersal, forest management, lifeboat, recolonization, retention patches, variable retention, retained structures

Tree retention to help conserve biodiversity is a widespread practice in forestry (Lindenmayer et al. 2012). These practices were initially suggested as a means to emulate natural disturbances (e.g., Seymour et al. 2002). Because these practices, especially clearcuts with scattered trees and small tree patches, do not emulate natural disturbances very precisely in either type or scale, it is not obvious that they achieve desired conservation goals. For example, a timber harvest is not strictly comparable to fire, windthrow, or insect disturbances. Retained patches may not match the size or environmental conditions (e.g., sheltered and/or wet) of patches left after a natural disturbance. Thus, we cannot assume a priori that these practices will benefit all taxa of concern. For a species to benefit from the postharvest environment, it must be able to persist in retained patches and recolonize the surrounding or adjacent clearcut by either propagules or dispersers. We are not concerned here with high levels of retention because in those cases, recolonization may not be an issue.

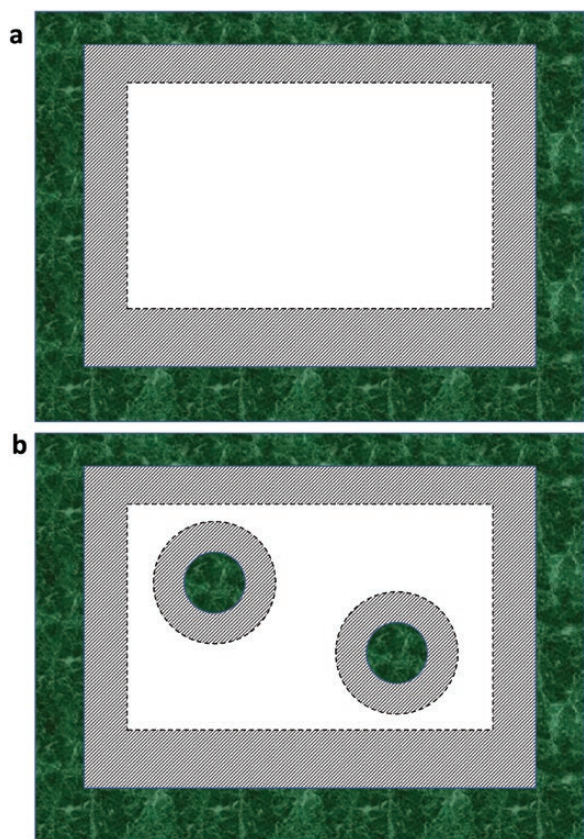
The benefits of retention practices have been evaluated by numerous researchers in terms of similarity to natural disturbances,

retention of snags and down wood, persistence of species in the retained patch, and biodiversity of a harvested unit (with retention) (e.g., Swanson and Franklin 1992, Hunter and Bond 2001, Spence 2001, Franklin et al. 2002, 2018, Mitchell and Beese 2002, Gustafsson et al. 2012, Lindenmayer et al. 2012, Fedrowitz et al. 2014, Baker et al. 2015). Many studies have attempted to evaluate biodiversity responses to structural retention (e.g., McDonald 1995, Roy et al. 1995, Carey 2003, Rempel 2007, Rosenvald and Lóhmus 2008, Parrish et al. 2017). However, the issue of recolonization is also critical and has received little attention. The time between timber harvests (20–60 years) may be much shorter than a particular forest's natural disturbance regime interval. This may cause poorly dispersing species to be gradually lost from a system if they do not tolerate an open canopy condition (e.g., Matlack and Monde 2004, Matlack 2005). This may, in turn, alter ecosystem structure and function. Although it seems logical that retained tree patches or isolated trees could provide a source for recolonization (a lifeboat function) of the cut stand with shorter dispersal distances (Figure 1), retained structures are subject to enhanced

Manuscript received March 9, 2020; accepted November 30, 2020; published online January 20, 2021

**Affiliations:** Craig Loehle ([cloehle@ncasi.org](mailto:cloehle@ncasi.org)), National Council for Air and Stream Improvement, Inc., 1258 Windemere Avenue, Naperville, IL 60564, USA. Kevin A. Solarik ([ksolarik@ncasi.org](mailto:ksolarik@ncasi.org)), National Council for Air and Stream Improvement, Inc., 2000 McGill College Avenue, Montréal, QC H3A 3H3, Canada. Daniel U. Greene ([Daniel.Greene@weyerhaeuser.com](mailto:Daniel.Greene@weyerhaeuser.com)), Weyerhaeuser Company, Environmental Research South, 29 Tom Rose Road, Columbus, MS 39701, USA. Laura Six ([Laura.Six@weyerhaeuser.com](mailto:Laura.Six@weyerhaeuser.com)), Weyerhaeuser Company, Timberlands Environmental Research, 505 N Pearl Street, Centralia, WA 98531, USA. Darren J.H. Sleep ([Darren.Sleep@sfiprogram.org](mailto:Darren.Sleep@sfiprogram.org)), The Sustainable Forestry Initiative (SFI), 1306 Wellington Street West, Suite 400, Ottawa, ON K1Y 3B2, Canada.

**Acknowledgments:** Thanks to D. Miller, J. Verschuyf, and K. Vice for helpful suggestions.



**Figure 1.** (a) For species that are lost from clearcuts, traditional methods implicitly assume that species will recolonize from surrounding stands. (b) Lifeboat theory focuses on retained patches as sources. With patches, more area can be reached by dispersers. Green areas are forest, blank areas are clearcut, and gray areas are reachable by dispersal. Gray areas (dispersal distances) are implicitly taxa and species specific.

tree mortality and edge effects (e.g., Solarik et al. 2012, Bezzola and Coxson 2020). They may also be too small for persistence of some species. Ultimately, this is an empirical question that is the goal of our study: Do retention structures enhance recolonization of harvested stands by acting as lifeboats? Our focus is on temperate and boreal forests where retention practices have been well studied.

Individual trees or patches retained at the time of harvest might serve a critical role as lifeboats, particularly for dispersal-limited species that would otherwise be unable to recolonize postharvest (Baker et al. 2015). If a species is highly mobile and can recolonize a disturbed area as soon as conditions are favorable, a lifeboat may not be needed. As we discuss lifeboating, we are not referring to only short-term benefits (i.e., whether the species persists in the retained structures), but rather whether there is a lifeboating function that helps a species recolonize adjacent areas where forest harvest has occurred. For example, Fedrowitz et al. (2014) conducted a meta-analysis of retention studies, where they considered benefits to biodiversity mostly in the short term (less than or equal to five years). Using this approach, a species that remained in unharvested patches and did not recolonize a harvested area was still considered a biodiversity benefit. In this review, however, we are interested in documenting the value of retention structures for recolonization over longer time periods. Retained structures in a recent clearcut

within which species persist and from which they can recolonize a site could theoretically provide a benefit by reducing dispersal distances (Figure 1; also Solarik et al. 2010, Baker et al. 2015). Persistence in retained structures is necessary to facilitate recolonization. Lifeboats may be particularly beneficial if harvested areas are large relative to organism dispersal and/or much of the landscape will be disturbed after prolonged management.

Responses to different patterns and levels of retention vary by species and region (Rosenvald and Löhmus 2008, Fedrowitz et al. 2014). Because of their mobility, many species of birds, mammals, and reptiles can likely easily recolonize harvested stands. Mobile species such as birds or bats that use snags or large trees may benefit from retention but our specific interest here is recolonization of the cleared portion, not the benefit of large trees or snags, which are well documented (see above references). Among amphibians, salamanders have low dispersal capabilities because of their small home ranges and intolerance of desiccation. Many arthropods can disperse long distances (Edwards 1986, Greenstone et al. 1987, Den Boer 1990, Work et al. 2004) and exhibit a rapid response to natural and anthropogenic disturbance (Pinzon et al. 2012, 2016, Lee et al. 2017). Such species would not be likely to depend on lifeboats. Other less-mobile invertebrates (e.g., worms, snails) may not colonize as well and warrant further examination. Vascular plants with poor dispersal capacity and lacking a suitable seedbank may benefit from retention patches, whereas plants requiring a disturbed microsite (e.g., exposed mineral soil) would benefit from soil disturbance from harvesting (e.g., Solarik et al. 2010). Finally, some concern has been expressed about recolonization of bryophytes, lichens, and mycorrhizal fungi, the latter being a critical symbiont for many tree species. Together, these less-mobile species make up a large portion of the biodiversity in forest ecosystems, including many rare species, and affect nutrient cycling. Our goal then is to evaluate the benefits of retention practices specifically for recolonization of harvested forest areas for less-mobile taxa that are negatively affected by logging.

## Methods

Our literature review focused on recolonization of forest openings created by timber harvest. We define recolonization as the dispersal into logged areas of individuals or propagules of species lost following clearcut logging such that a population is reestablished before the next harvest. We are therefore not considering large retention patches, which may not be economically feasible and verge on a reserve system. We also do not consider high levels of dispersed retention (e.g., >15% of original basal area), which may not be suitable for regeneration of many tree species being managed. Our focus was on lichens and bryophytes, mature forest vascular plants (generally shade tolerant), mycorrhizal fungi (essential to tree growth), amphibians, and nonvolant invertebrates, including wingless arthropods. We excluded mammals, birds, and reptiles from evaluation because of their mobility. Further, we also excluded most arthropods because of their winged life stages. As an initial entry to the literature, we manually searched (i.e., table of contents read) the complete contents of *Forest Science* (2014–2018), *Canadian Journal of Forest Research* (2012–2018), and *Forest Ecology and Management* (2012–2018) and read more closely when titles and abstracts seemed related. We also searched academic databases (Google Scholar and Web of Science) in early 2019 using relevant keywords (e.g.,

retention forestry, retained structure, lifeboat, green-tree retention, variable retention, and others) and associated Boolean operators to locate publications that examined responses of taxa of interest to retained structures for recolonization of logged areas. We also searched the literature cited within the papers selected, especially reviews and summaries such as Fedrowitz et al. (2014), Baker et al. (2015), and Franklin et al. (2018). Overall, we evaluated more than 6,000 papers (title, abstract, or full read). Our search uncovered hundreds of papers on the general topic, of which all those touching on recolonization are cited here.

We described what is known about taxa with limited dispersal abilities in the context of lifeboats. We limited our review primarily to Canada and the temperate forests in the United States, where retention practices are more common, with some literature from Europe when data on a particular taxon (e.g., lichens and bryophytes) were lacking in North America.

## Review of Existing Studies

We reviewed what is known about recolonization following clearcut logging. We organized the literature by selected taxa, as taxa often share similar mobility and site requirement characteristics. We were able to locate references ( $n = 99$ ) for lichens/bryophytes ( $n = 23$ ), mature forest vascular plants ( $n = 31$ ), mycorrhizal fungi ( $n = 14$ ), amphibians ( $n = 24$ ), and less-mobile invertebrates ( $n = 7$ ). We reviewed studies across the range of operational clearcut block sizes, which range from a few tens to several hundreds of hectares. Retained structures ranged from scattered individual trees to patches a few hectares in size in the reviewed studies.

### Mature Forest Vascular Plants

Effects of retention harvesting on understory vegetation has been studied in many forest types worldwide (e.g., Battles et al. 2001, Deal 2001, Macdonald and Fenniak 2007, Fedrowitz et al. 2014). Diversity and abundance of understory plants are directly influenced by pre- and postharvest forest cover and composition (Macdonald and Fenniak 2007), where site characteristics like soil pH, soil nutrients, light, litter quality, and moisture ultimately contribute to understory community composition. Microclimate conditions in a clearcut can vary sharply from those in a closed canopy forest (Huggard and Vyse 2002), leading to a decline of late-successional understory plants and communities in harvested areas (Aubry et al. 2009, Halpern et al. 2012). These late-successional species can become quickly outcompeted by an influx of early successional species that are better adapted to open-light conditions postharvest. Some understory plants typical of a mature forest do not seem to have good dispersal capabilities, especially if they mostly depend on vegetative reproduction and do not have a viable seed bank (Duffy and Meier 1992, Halpern et al. 1999). Nelson and Halpern (2005) found that even in retained patches, proximity to edges caused larger declines in herbaceous species abundance compared with woody species. Scattered remnant trees may not be beneficial because they do not provide sufficient shade (e.g., Traut and Muir 2000, Johnson et al. 2014) except at high retention levels (e.g., Aubry et al. 2009, Halpern et al. 2012).

Some species or groups, such as late-successional herbaceous plants, may take a prolonged period to recover. For harvested stands in Appalachian cove forests in the United States, Wyatt and Silman

(2010) found that 100 to 150 years was insufficient for understory herbaceous community recovery following harvesting and natural regeneration. It has been shown that herbaceous vegetation in stands in the Appalachians does not appear to fully recover following clearcut harvest within the time until the next harvest would occur, such as 60 to 90 years (Duffy and Meier 1992). Vellend (2004) found that on reforested agricultural land in New York, United States, a species of trillium (*Trillium* spp.) had not fully recovered after 70 to 100 years. Similarly, former agricultural land can still be distinguished from never-tilled (but harvested) land even after many decades, with distinct species composition and lower species richness and diversity (Hedman et al. 2000, Ramovs and Roberts 2003). Whether this is due to altered microclimate and soil conditions (e.g., Burke et al. 2016) or failure to recolonize remains unclear. Recovery rates and pathways on reforested agricultural land, however, may be longer and divergent from those on always-forested land (Dyer 2010). In contrast, 20 years was shown to be sufficient in a West Virginia forest for understory cover and species richness to match mature second growth (Gilliam 2002), though species-level comparisons were not performed.

For shade-requiring understory plants, not all retained structures have equal value. Isolated retained trees are unlikely to ameliorate site conditions sufficiently to maintain such species (Jalonen and Vanha-Majamaa 2001, Lachance et al. 2013, Johnson et al. 2014). Patches large enough to have an interior unaltered by edge effects may be necessary. However, if these species are unable to recolonize the cut area quickly enough (i.e., before the next harvest), then such species are not really benefiting from retention compared with the same area simply being set aside in a reserve. Field studies that can take advantage of historically harvested landscapes would help clarify this issue.

Dispersal ability seems to limit recolonization for many plants. A study by Takahashi and Kamitani (2004) took advantage of a Japanese black pine (*Pinus thunbergii*) forest planted on sand dunes (i.e., no prior forest), where they compared species types versus distance to an existing forest and found that the greatest dispersal was exhibited by plants with ingested or adhering seeds. Those with wind or hoarding (i.e., animal cache) dispersal were found only close to natural forest. Ant-dispersed seed species were not found. Dzwonko (1993) found, for a 70-year-old forest on abandoned agricultural land near Kraków, Poland, that species with limited dispersal capabilities (herbaceous and woody) were still more prevalent closer to old forest edges, whereas good dispersers were more common farther away. Direct measurement of dispersal rates (recolonization with distance from mature forest) found in a temperate study site in Poland (Dzwonko 2001) that on drier sites, rates ranged from 0.0 to 0.38 m year<sup>-1</sup>, whereas, on more mesic sites, rates exceeded 1.5 m year<sup>-1</sup>. Additional studies of this nature may be needed to evaluate recovery possibilities for species of concern. For species that persist after timber harvesting in low numbers, demography may be important, with some forest herbs having very slow population growth rates.

In some forested systems, understory plant diversity increases with frequent disturbances. In fire-prone systems such as southern US pine forests, plant diversity mirrors that of a recent clearcut, where an open pine canopy promotes grasses and other shade-intolerant species (i.e., early seral species, Waldrop et al. 1992, Brockway and Lewis 1997). Similarly, in forests where grazing



occurs concurrently, the understory may have a higher proportion of forbs and a lower proportion of woody species (Six et al. 2014). In these systems, the low number of species requiring closed canopy conditions suggests that lifeboating may not be necessary to maintain or restore preharvest conditions (e.g., Iglay et al. 2014, 2018).

In general, lower-intensity harvests have been shown to be more successful at conserving species that are shade tolerant (i.e., late seral species), whereas higher-intensity harvests favor more shade-intolerant species. In the case of clearcuts, the potential for dispersal limitation does suggest a role for retention patches for plants, but most retention studies we found were focused on other taxa. Dispersal ability appears to be a key trait determining recolonization, but slow population growth and requirements for moist microsite conditions may also limit recovery rates.

## Lichens and Bryophytes

Lichens and bryophytes (e.g., mosses and liverworts) make up a substantial and important component of the biodiversity of northern forests, with lichens being a primary food for caribou (*Rangifer* spp.). In some cases, they are specifically protected by endangered species legislation such as vole ears (*Erioderma mollissimum*) and boreal felt lichen (*E. pedicellatum*) in Canada.

Lichens and bryophytes generally exhibit declines in abundance/presence in harvested clearings and retained structures following harvest, probably because of desiccation (Nelson and Halpern 2005, Rosenvald and Löhmus 2008), especially for bryophytes (Caners et al. 2013). Halpern et al. (2012) and Aubry et al. (2009) documented short-term forest-floor bryophyte abundance declines under all patterns and levels of retention tested in Oregon and Washington, United States. Löhmus et al. (2006) found that after two years, bryophyte diversity, cover, and vitality on scattered residual trees were significantly reduced compared with preharvest conditions, as also found by Perhans et al. (2009) in Sweden and Gustafsson et al. (2010) in Scandinavia. These early declines were also observed by Oldén et al. (2014), who concluded that recovery to what they considered a viable population level took approximately 20–30 years for some bryophyte species. Löhmus and Löhmus (2010) also found a short-term decline of lichens and bryophytes on retained trees in Estonia, with the largest source of mortality being tree windthrow. In contrast, Jairus et al. (2009) found epiphytic lichens in Estonia to be tolerant of canopy removal. Harper et al. (2015) reviewed the magnitude and distance of edge influence on bryophytes, lichens, and other vegetation postharvest in boreal forest and concluded that the effect is generally seen only in close proximity (<30 m) to a forest edge. In contrast, Bezzola and Coxon (2020) found that some lichens of coastal northwestern British Columbia are very sensitive to edge effects at distances of 80 m or more. Thus, small residual patches could exhibit detrimental edge effects.

Responses have been found to be species specific. Sillett et al. (2000) studied two lichens associated with old-growth forest in the Pacific Northwest using inoculation and transplant experiments in clearcut and young forests. They found that *Lobaria oregana* grew as well in the young forest as in an old forest, whereas *L. pulmonaria* did at least as well in clearcuts as in the young and old forests. Similar results were found in transplant experiments with *L. oregana* and *Pseudocyphellaria rainierensis* (Sillett and McCune 1998). They concluded that low dispersal ability (inferred, not demonstrated)

and slow growth limit colonization of these species more than does microclimate, which means they would theoretically benefit from colonization sources within harvested areas. In this case, more dispersed residual trees could be better than large, aggregated patches. Related work (Sillett 1994) showed that epiphytic lichen species differed in their response to patch edges, a consideration when projecting benefits of retained patches.

Some long-term natural experiments have been used to study the benefits of residual trees on lichen recovery. In a retrospective study, Peck and McCune (1997) located mature second-growth stands (55–120 years old) with and without remnant old-growth trees in them at both low- and midelevation sites in western Oregon, United States. This study mimicked a dispersed retention design. They found mixed results: biomass of alectorioid and cyanolichen litter were greater in low-elevation sites with remnant trees. However, green-algal foliose lichen litter was 80% greater in midelevation sites without remnant trees. Total lichen litter was not significantly different with versus without remnant trees at either elevation. Sillett and Goslin (1999) located a stand disturbed by past fires in western Oregon. Remnant trees were mostly 600-year-old Douglas-fir (*Pseudotsuga menziesii*) at a very wide spacing but with some clusters, with a matrix of mostly 100-year-old second growth, also Douglas-fir. With this spatial arrangement, they had a near facsimile of individual tree/patch retention designs, but 100 years old (i.e., not recently harvested). Two abundant lichens were found mostly within 15 m of the remnant trees, with most other species showing weak or no relationship to the old trees. In the similar coastal forests of British Columbia with some residual trees, Price et al. (2017) found that it took more than 200 years for the epiphyte community structure to be equivalent to old growth.

Tests of colonization from mature or old-growth forest edges have yielded contradictory results. In the midboreal zone of Sweden, Hylander (2009) found no colonization effect of proximity overall for bryophytes, though close proximity did benefit a few species, perhaps because of microclimate effects. Dettki et al. (2000) found that in the northern boreal region of Sweden, epiphytic lichens on Scots pine (*Pinus sylvestris*) colonized more with proximity to old-growth stands than farther away. In contrast, Lättman et al. (2009), in a study of a rare lichen found on oaks (*Quercus* spp.) in Sweden, found that genetic uniformity across scattered oak stands suggested good gene flow, and thus dispersal, across distances of at least several kilometers between scattered oak stands. Boudreault et al. (2012) also found that distance did not affect epiphytic lichen recolonization of black spruce (*Picea mariana*) forest in western Quebec except for *Bryoria* spp., which disperses mainly via thallus fragments.

The net result of these cited studies is that a general benefit of proximity to either mature edges or residual trees cannot be assumed for lichens or bryophytes. Distance does not appear to be a limiting factor, in general, for recolonization, but slow growth and microsite requirements may be limiting factors. For example, Coxson and Marsh (2001) documented extended, predictable successional-type changes in lichen and bryophyte communities in a lodgepole pine (*Pinus contorta*) forest in northern interior British Columbia. There may be a benefit from retention for certain species or on certain sites. Caners et al. (2013), for example, speculated that bryophyte species with rare sporophyte production, larger spores, dioicous sexuality, or higher moisture requirements may have more restricted dispersal and thus benefit more from retention.







widely separated retained trees or discrete patches would likely not. A better understanding of the recovery dynamics of this species group would be necessary to provide more detail, especially for longer time frames than the studies we reviewed. The only study on community recovery that we located (Philpott et al. 2018) found good recovery in clearcut areas in wet west coast forests of the United States by 13 years postharvest, which is encouraging. It is not possible to say whether these results generalize to drier forest types.

For amphibians, it seems likely that dry soil conditions in open areas following harvesting generally have negative consequences, especially for salamanders. We did not find evidence that isolated trees can ameliorate this moisture limitation sufficiently to provide a benefit for recolonization or population recovery. Although retained patches might provide such a benefit, we did not find information on the size of patch or slope position of retention necessary to be useful to salamanders, nor whether amphibians in a retained patch provide a source for recolonization. Stand regrowth may be the limiting factor because of amphibian requirements for moist conditions. For amphibian species that live in decayed logs, loss of large logs over time in second-growth forest may be the limiting factor rather than dispersal distance, but this is probably species specific. Logs provided by live-tree retention over time might help these species persist, but we could find no literature on this per se. In areas where harvesting raises the water table (e.g., boggy areas of Canada or the US Coastal Plain), moisture conditions for amphibians might actually improve, as noted for a case in British Columbia (Beese et al. 2019).

For LMIs, data gaps exist for effects of timber harvest (i.e., mortality or loss from a site), persistence in retained structures, and dispersal and recolonization. These are likely to vary a great deal across these very different taxa.

In the studies we reviewed, the metric sometimes used for comparison was species richness. However, many early seral species will be found in recent clearcut units (Swanson et al. 2014), increasing richness, so that this is not a valid comparison to mature forest. It is helpful to keep in mind that these early seral species may include those on various special status (i.e., endangered) lists (Ribic et al. 2009, Swanson et al. 2014). Some studies do track these separately (e.g., Fedrowitz et al. 2014).

Although it might superficially seem that very long-term studies are necessary to evaluate lifeboating benefits of retained structures, this is not entirely true. Persistence of snags (e.g., Kroll et al. 2012) and residual trees (e.g., Solarik et al. 2012) can be evaluated on a decadal timescale, as can persistence of populations of amphibians or arthropods (Pinzon et al. 2016, Lee et al. 2017). Several studies cited here made use of long-term natural experiments (e.g., disturbance-created remnant trees or older forest edges) to help answer questions about recolonization of plants, lichens, and bryophytes. We suggest that additional studies of this type could help provide answers to the remaining questions about lifeboat benefits of retained structures.

In this review, we evaluated the potential of retention patches to serve as lifeboats for recolonization of harvested areas for dispersal-limited taxa only. There may be landscape-scale or long-term benefits that accrue from increased structural complexity,

but we did not address these benefits here. To design an optimal retention arrangement, specifying goals is critical because benefits of retention do not generalize across taxa (Baker et al. 2015).

Conflicts may exist among the needs of different taxa. For example, the very short dispersal distance of mycorrhizal fungi suggests that dispersed retention might be most beneficial (though perhaps still not adequate for some purposes), whereas dispersed retention may not provide enough shade to benefit shade-requiring plants. It has been suggested by Franklin et al. (2018) that leaving dispersed residuals surrounded by aggregated patches could provide a better means of protecting and preserving lifeboat function than patches alone, but this conclusion seems speculative. It is perhaps useful to modify retention designs to take into account actual recolonization responses of desired taxa.

Both spatial and time scales need to be considered when planning and evaluating retention practices. Although such practices do increase structural complexity, it is useful to ask which species specifically benefit and over what span of years. Colonization lags may make it difficult to detect responses with studies in the years immediately postharvest. The fact that some species may not persist in retained structures or may not be able to colonize a cut area before the next harvest suggests that for certain species, typically obligate old-growth types, the land set aside as retention patches might be more effective as larger permanent reserves. In some landscapes (e.g., the US Pacific Northwest), such reserves already exist for some forest types. In most regions, buffers around water bodies required by regulations (e.g., Parrish et al. 2018), and inoperable areas (e.g., cliff faces), also provide permanent protected areas for some species. In regions where fire regimes create open forest conditions (e.g., western US pine forests), the fire regime and lack of closed canopy lead to questions about whether true old-growth conditions (i.e., dark, moist, stable) ever exist and thus whether classic old-growth species are likely to be found there. In the boreal forests of central Canada, fires are typically very large and would seem to require that species are either tolerant of fire or have good dispersal abilities to persist.

These factors indicate that the need for and benefits of retention cannot be assumed but must instead be closely related to the ecology of a biome and the natural disturbance regime. A more explicit statement of conservation goals would be beneficial in each case. That is, the assumption that a more “natural” harvest that emulates a typical disturbance will automatically be beneficial may not be valid at the timescales (before the next harvest) involved or for the particular species of concern. For example, very large western and Canadian fires may take more than a century to fully recover, which is not a useful end point to emulate. In addition to efficacy, the increased operating costs (Phillips 2004) and reduced revenues (Mitchell and Beese 2002, Zobrist and Lippke 2007, Beese et al. 2019) that are associated with increased retention mean that more targeted retention design(s) would be economically useful. This is particularly so where windthrow or other mortality affects retained tree persistence over the long term (Busby et al. 2006, Lavoie et al. 2012, Solarik et al. 2012, Beese et al. 2019). We believe that the issue of recolonization needs to be more thoroughly examined, particularly for species of conservation concern.





- HAYES, M.P., T. QUINN, K.O. RICHTER, J. SCHUETT-HAMES, AND J.T.S. SHEAN. 2008. Maintaining lentic-breeding amphibians in urbanizing landscapes: The case study of the northern red-legged frog (*Rana aurora*). In: Mitchell JC, Jung RE, Bartholomew B (eds) . Urban Herpetology. Society for the Study of Amphibians and Reptiles, Herpetological Conservation 3, Salt Lake City, pp 445–461.
- HEDMAN, C.W., S.L. GRACE, AND S.E. KING. 2000. Vegetation composition and structure of southern coastal plain pine forests: An ecological comparison. *For. Ecol. Manage.* 134:233–247.
- HOMYACK, J.A., AND C.A. HAAS. 2009. Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders. *Biol. Conserv.* 142:110–121.
- HOMYACK, J.A., AND C.A. HAAS. 2013. Effects of repeated-stand entries on terrestrial salamanders and their habitat. *Southeast. Nat.* 12(2):353–366.
- HOMYACK, J.A., C.A. HAAS, AND W.A. HOPKINS. 2011. Energetics of surface-active terrestrial salamanders in experimentally harvested forest. *J. Wildl. Manage.* 75(6):1267–1278.
- HOMYACK, J.A., AND A.J. KROLL. 2014. Slow lives in the fast landscape: Conservation and management of plethodontid salamanders in production forests of the United States. *Forests* 5(5):2750–2772.
- HUGGARD, D.J., AND A. VYSE. 2002. *Edge effects in high-elevation forests at Sicamous Creek. Extension Note 62.* British Columbia Ministry of Forests, Forest Science Program, Victoria, B.C., Canada.
- HUNTER, J.E., AND M.L. BOND. 2001. Residual trees: Wildlife associations and recommendations. *Wildl. Soc. Bull.* 29(3):995–999.
- HYLANDER, K. 2009. No increase in colonization rate of boreal bryophytes close to propagule sources. *Ecology* 90(1):160–169.
- IBÁÑEZ, I., AND S. MCCARTHY-NEUMANN. 2016. Effects of mycorrhizal fungi on tree seedling growth: Quantifying the parasitism-mutualism transition along a light gradient. *Can. J. For. Res.* 46(1):48–57.
- IGLAY, R.B., R.E. GREENE, B.D. LEOPOLD, AND D.A. MILLER. 2018. Bird conservation potential of fire and herbicide treatments in thinned pine stands. *For. Ecol. Manage.* 409:267–275.
- IGLAY, R.B., B.D. LEOPOLD, AND D.A. MILLER. 2014. Vegetation responses to fire and herbicide in intensively managed, mid-rotation pine. *For. Ecol. Manage.* 328:69–78.
- JAIRUS, K., A. LÖHMUS, AND P. LÖHMUS. 2009. Lichen acclimatization on retention trees: A conservation physiology lesson. *J. Appl. Ecol.* 46:930–936.
- JALONEN, J., AND I. VANHA-MAJAMAA. 2001. Immediate effects of four different felling methods on mature boreal spruce understorey vegetation in Finland. *For. Ecol. Manage.* 146:25–34.
- JOHNSON, S., J. STRENGBOM, AND J. KOUKI. 2014. Low levels of tree retention do not mitigate the effects of clearcutting on ground vegetation dynamics. *For. Ecol. Manage.* 330:67–74.
- KRANABETTER, J.M., L. DE MONTIGNY, AND G. ROSS. 2013. Effectiveness of green-tree retention in the conservation of ectomycorrhizal fungi. *Fungal Ecol.* 6:430–438.
- KROLL, A.J., M.J. LACKI, AND E.B. ARNETT. 2012. Research needs to support management and conservation of cavity-dependent birds and bats on forested landscapes in the Pacific Northwest. *West. J. Appl. For.* 27(3):128–136.
- LACHANCE, É., D. POTHIER, AND M. BOUCHARD. 2013. Forest structure and understorey plant communities inside and outside tree retention groups in boreal forests. *Écoscience* 20(3):252–263.
- LÄTTMAN, H., L. LINDBLOM, J.-E. MATSSON, P. MILBERG, M. SKAGE, AND S. EKMAN. 2009. Estimating the dispersal capacity of the rare lichen *Cliostomum corrugatum*. *Biol. Conserv.* 142:1870–1878.
- LAVOIE, S., J.-C. RUEL, Y. BERGERON, AND B.D. HARVEY. 2012. Windthrow after group and dispersed tree retention in eastern Canada. *For. Ecol. Manage.* 269:158–167.
- LEE, S.-I., J.R. SPENCE, AND D.W. LANGOR. 2017. Combinations of aggregated and dispersed retention improve conservation of saproxylic beetles in boreal white spruce stands. *For. Ecol. Manage.* 385:116–126.
- LINDENMAYER, D.B., J.F. FRANKLIN, A. LÖHMUS, S.C. BAKER, J. BAUHUS, W. BEESE, A. BRODIE, ET AL. 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conserv. Lett.* 5:421–431.
- LINDO, Z., AND S. VISSER. 2004. Forest floor microarthropod abundance and oribatid mite (Acari: Oribatida) composition following partial and clear-cut harvesting in the mixedwood boreal forest. *Can. J. For. Res.* 34:998–1006.
- LÖHMUS, A., AND P. LÖHMUS. 2010. Epiphyte communities on the trunks of retention trees stabilize in 5 years after timber harvesting, but remain threatened due to tree loss. *Biol. Conserv.* 143:891–898.
- LÖHMUS, P., R. ROSENVALD, AND A. LÖHMUS. 2006. Effectiveness of solitary retention trees for conserving epiphytes: Differential short-term responses of bryophytes and lichens. *Can. J. For. Res.* 36(5):1319–1330.
- LUOMA, D.L., C.A. STOCKDALE, R. MOLINA, AND J.L. EBERHART. 2006. The spatial influence of *Pseudotsuga menziesii* retention trees on ectomycorrhiza diversity. *Can. J. For. Res.* 36:2561–2573.
- MACDONALD, S.E., AND T.E. FENNIAC. 2007. Understorey plant communities of boreal mixed wood forests in western Canada: Natural patterns and response to variable retention harvesting. *For. Ecol. Manage.* 242:34–48.
- MARSH, D.M., K.A. THAKUR, K.C. BULKA, AND L.B. CLARKE. 2004. Dispersal and colonization through open fields by a terrestrial, woodland salamander. *Ecology* 85(12):3396–3405.
- MATLACK, G.R. 2005. Slow plants in a fast forest: Local dispersal as a predictor of species frequencies in a dynamic landscape. *J. Ecol.* 93(1):50–59.
- MATLACK, G.R., AND J. MONDE. 2004. Consequences of low mobility in spatially and temporally heterogeneous ecosystems. *J. Ecol.* 92(6):1025–1035.
- MCDONALD, L. 1995. Relationships between northern flying squirrels and stand age and structure in aspen mixedwood forests in Alberta. P. 227–240 in *Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta*, STELFOX, J.B. (ed.). Alberta Environment Centre (AECV95-R1), Vegreville, AB, Canada; and Canadian Forest Service (Project No 00014), Edmonton, AB, Canada.
- MITCHELL, S.J., AND W.J. BEESE. 2002. The retention system: Reconciling variable retention with the principles of silvicultural systems. *For. Chron.* 78(3):397–403.
- NELSON, C.R., AND C.B. HALPERN. 2005. Short-term effects of timber harvest and forest edges on ground-layer mosses and liverworts. *Can. J. Bot.* 83(6):610–620.
- OLDÉN, A., O. OVASKAINEN, J.S. KOTIAHO, S. LAAKA-LINDBERG, AND P. HALME. 2014. Bryophyte species richness on retention aspens recovers in time but community structure does not. *PLoS One* 9(4):e93786.
- OUTERBRIDGE, R.A., AND J.A. TROFYMOW. 2009. Forest management and maintenance of ectomycorrhizae: A case study of green tree retention in south-coastal British Columbia. *J. Ecosyst. Manage.* 10(2):59–80.
- OVASKA, K., L. SOPUCK, AND D. ROBICHAUD. 2016. Short-term effects of variable-retention logging practices on terrestrial gastropods in coastal forests of British Columbia. *Northwest Sci.* 90(3):260–277.
- PARRISH, M.C., S. DEMARIS, T.B. WIGLEY, P.D. JONES, A.W. EZELL, AND S.K. RIFFELL. 2017. Breeding bird communities associated with land cover in intensively managed pine forests of the southeastern U.S. *For. Ecol. Manage.* 406:112–124.
- PARRISH, M.C., S. DEMARIS, T.B. WIGLEY, S.K. RIFFELL, A.W. EZELL, AND P.D. JONES. 2018. Operational green tree retention and land cover patterns in intensively managed pine forest landscapes of the southeastern United States. *For. Sci.* 64(5):564–576.
- PECK, J.E., AND B. McCUNE. 1997. Remnant trees and canopy lichen communities in western Oregon: A retrospective approach. *Ecol. Appl.* 7(4):1181–1187.
- PERHANS, K., L. APPELGREN, F. JONSSON, U. NORDIN, B. SÖDERSTRÖM, AND L. GUSTAFSSON. 2009. Retention patches as potential refugia for bryophytes and lichens in managed forest landscapes. *Biol. Conserv.* 142:1125–1133.



- A comparative study of two terrestrial salamanders in the U.S. Pacific Northwest. *Biol. Conserv.* 141:1149–1160.
- WOLF, A.J., R.B. RENKEN, D.K. FANTZ, X. GAO, AND J.J. MILLSPAUGH. 2016. Effects of 3 forest management systems on herpetofaunal diversity over 23 years in the Missouri Ozarks. *For. Ecol. Manage.* 379:252–264.
- WORK, T.T., D.P. SHORTHOUSE, J.R. SPENCE, W.J.A. VOLNEY, AND D. LANGOR. 2004. Stand composition and structure of the boreal mixedwood and epigeaic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. *Can. J. For. Res.* 34(2):417–430.
- WYATT, J.L., AND M.R. SILMAN. 2010. Centuries-old logging legacy on spatial and temporal patterns in understory herb communities. *For. Ecol. Manage.* 260:116–124.
- ZOBRIST, K.W., AND B.R. LIPPKE. 2007. Economic costs of different riparian management regulations in the Pacific Northwest. *West. J. Appl. For.* 22(1):36–41.