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A cross-continental comparison of plant and beetle responses to retention of forest patches during timber harvest

Susan C. Baker,[1,2,3,13] Charles B. Halpern,[3] Timothy J. Wardlaw,[1,2] Christel Kern,[4] Graham J. Edgar,[5] Russell J. Thomson,[5] Richard E. Bigley,[6] Jerry F. Franklin,[3] Kamal J. K. Gandhi,[7] Lena Gustafsson,[8] Samuel Johnson,[8] Brian J. Palik,[9] Thomas A. Spies,[10] E. Ashley Steel,[11] Jan Weslien,[12] and Joachim Strengbom[4]

[1]*School of Biological Sciences, University of Tasmania, Private Bag 55, Hobart, Tasmania 7001 Australia*
[2]*ARC Centre for Forest Value, University of Tasmania, Private Bag 55, Hobart, Tasmania 7001 Australia*
[3]*School of Environmental and Forest Sciences, University of Washington, Box 352100, Seattle, Washington 98195 USA*
[4]*USDA Forest Service, Northern Research Station, 5985 Highway K, Rhinelander, Wisconsin 54501 USA*
[5]*Institute for Marine and Antarctic Studies, University of Tasmania, GPO Box 252-49, Hobart, Tasmania 7001 Australia*
[6]*Washington State Department of Natural Resources, Forest Resources, Olympia, Washington 98504 USA*
[7]*Daniel B. Warnell School of Forestry and Natural Resources, University of Georgia, 180 E Green St, Athens, Georgia 30602 USA*
[8]*Department of Ecology, Swedish University of Agricultural Sciences (SLU), P.O. Box 7044, SE-750 07, Uppsala, Sweden*
[9]*USDA Forest Service, Northern Research Station, 1831 Hwy 169 E, Grand Rapids, Minnesota 55744 USA*
[10]*USDA Forest Service, PNW Research Station, 3200 SW Jefferson Way, Corvallis, Oregon 97331 USA*
[11]*USDA Forest Service, PNW Research Station, 400 N 34th Street, Suite 201, Seattle, Washington 98103 USA*
[12]*The Forestry Research Institute of Sweden (Skogforsk), SE751 43, Uppsala, Sweden*

Abstract. Timber harvest can adversely affect forest biota. Recent research and application suggest that retention of mature forest elements (retention forestry), including unharvested patches (or aggregates) within larger harvested units, can benefit biodiversity compared to clearcutting. However, it is unclear whether these benefits can be generalized among the diverse taxa and biomes in which retention forestry is practiced. Lack of comparability in methods for sampling and analyzing responses to timber harvest and edge creation presents a challenge to synthesis. We used a consistent methodology (similarly spaced plots or traps along transects) to investigate responses of vascular plants and ground-active beetles to aggregated retention at replicate sites in each of four temperate and boreal forest types on three continents: Douglas-fir forests in Washington, USA; aspen forests in Minnesota, USA; spruce forests in Sweden; and wet eucalypt forests in Tasmania, Australia. We assessed (1) differences in local (plot-scale) species richness and composition between mature (intact) and regenerating (previously harvested) forest; (2) the lifeboating function of aggregates (capacity to retain species of unharvested forest); and whether intact forests and aggregates (3) are susceptible to edge effects and (4) influence the adjacent regenerating forest. Intact and harvested forests differed in composition but not richness of plants and beetles. The magnitude of this difference was generally similar among regions, but there was considerable heterogeneity of composition within and among replicate sites. Aggregates within harvest units were effective at lifeboating for both plant and beetle communities. Edge effects were uncommon even within the aggregates. In contrast, effects of forest influence on adjacent harvested areas were common and as strong for aggregates as for larger blocks of intact forest. Our results provide strong support for the widespread application of aggregated retention in boreal and temperate forests. The consistency of pattern in four very different regions of the world suggests that, for forest plants and beetles, responses to aggregated retention are likely to apply more widely. Our results suggest that through strategic placement of aggregates, it is possible to maintain the natural heterogeneity and biodiversity of mature forests managed for multiple objectives.

Key words: *aggregated retention; forest influence; ground-active beetles; lifeboating; retention forestry.*

Introduction

Forest harvest generally alters the composition of plant and animal communities, and industrial-scale harvesting can have substantial effects on biological diversity. In recent decades, considerable research and management have been devoted, worldwide, to forestry practices that improve outcomes for biodiversity. These practices are frequently informed by understanding of natural successional processes (Pulsford et al. 2014), of biological responses to natural disturbances such as wildfire or wind storms (Bergeron et al. 1999), and of fragmentation and edge effects (Didham et al. 1998, Baker et al. 2009). It is tempting to assume that similar forestry practices will have similar effects on biodiversity, irrespective of forest type or location. However, this assumption has never been tested empirically using consistent methodology.

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[13]E-mail: sue.baker@forestrytas.com.au

Biogeographic variation related to differences in disturbance regime, climate, soils, and species' phylogeny and biology, as well as differences in management practices, could lead to varying effects on biodiversity. Conversely, if effects are comparable, forest managers worldwide should have a degree of confidence that similar approaches to forest harvest will produce similar outcomes.

Retention forestry is an emerging approach to managing forests for multiple objectives, including timber production and maintenance of biodiversity. In contrast to the traditional practice of clearcutting, it involves partial cutting, leaving some (including merchantable) trees as structural or biological legacies within harvest units to enhance the heterogeneity of habitat conditions. Compared to clearcutting, retention forestry creates post-harvest stands that are more similar in structure to those left by natural disturbance (e.g., unburned patches in a wildfire; Franklin et al. 1997). Retention forestry is applied globally and has been advocated as the harvesting system of choice for 85% of the world's forests (Lindenmayer et al. 2012). Within this broader context, aggregated retention, wherein small (e.g., ~0.1–2 ha) patches of unharvested forest are retained within harvest units, shows particular promise (Fedrowitz et al. 2014).

Post-harvest (regenerating) forests support communities of species that differ, to varying degrees, from those of unmanaged forests, a consequence of disturbance, changes in the physical environment, and succession (Halpern and Spies 1995). Aggregates can support many of the species and structures associated with unmanaged forests, thus providing a lifeboating role (Franklin et al. 1997). However, small isolated aggregates, with a high perimeter-to-area ratio, may be more susceptible to edge effects than larger blocks of unmanaged forest. Edge effects can reflect changes in microclimate (Heithecker and Halpern 2007), instability and physical disturbance at the forest edge (Esseen 1994, Jönsson et al. 2007), or incursion of disturbance-associated species (Murcia 1995). Over time, these effects may compromise the ability of aggregates to support species that are sensitive to disturbance or to changes in the physical or biotic environment.

In theory, aggregates can also facilitate reestablishment of disturbance-sensitive and dispersal-limited forest species within adjacent harvested areas (Franklin et al. 1997, Turner et al. 1998), although this has rarely been quantified. Aggregates can exert forest influence (Franklin et al. 1997, Gustafsson et al. 2012, Baker et al. 2013*b*) by altering physical and biotic environments and serving as local propagule sources within the harvest area (Baker et al. 2013*b*). However, small, isolated aggregates may be less effective at providing these benefits than the longer and deeper edges formed by larger blocks of intact forest.

We examine the responses of two very different taxonomic groups, vascular plants and ground-active beetles, to aggregated retention in four biogeographic regions of the world: Douglas-fir forests in Washington, USA; aspen forests in Minnesota, USA; spruce forests in central Sweden; and wet eucalypt forests in Tasmania, Australia. We chose these taxonomic groups because they are diverse and distinctive, are readily sampled using consistent methodology, and past work suggests that both can be sensitive to forest management and, potentially, to edge effects (Nelson and Halpern 2005, Baker et al. 2007, Halaj et al. 2008, Fountain-Jones et al. 2015). We explore harvest and edge effects on community-level responses (composition and richness) at a local scale (the sampling unit), but not at the larger scales needed to capture the diversity of rarer or specialized taxa (taxa requiring a very different sampling approach). In the absence of pre-treatment data, we assess harvest effects and edge-related patterns with data from contrasting habitats (large blocks of intact forest, adjacent post-harvest regenerating forests, and unharvested aggregates within these) and from varying distances to edge within each habitat. For each geographic region, we compare community responses between (1) intact vs. regenerating forests (effects of harvesting) and (2) aggregates vs. intact forests (lifeboating function). For plants, we then explore the extent to which aggregates and intact forests (3) experience edge effects and (4) exert influences on adjacent regenerating forests. We use the consistency of responses among regions and taxa as a basis for generalizing about the benefits of aggregated retention for the maintenance and recovery of biological diversity in managed forest landscapes.

Methods

Study sites

This study was conducted in operational aggregated-retention harvest units on three continents (North America, Europe, and Australia; Table 1). These included temperate *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) forests in Washington State, USA; subboreal *Populus tremuloides* Michx. (aspen) forests in Minnesota, USA; boreal *Picea abies* (L.) H. Karst (Norway spruce) forests in Sweden; and temperate wet *Eucalyptus* L'Hér. forests (usually dominated by *E. obliqua* and sometimes by *E. regnans*) in Tasmania, Australia. The principal form of natural disturbance in these forests is fire, whose effects can vary from stand replacing to mixed severity.

Study design

Three to six study sites were selected in each region (six in Washington and Tasmania, five in Sweden, and three in Minnesota). Except for Minnesota, two transects were established in each site: one aggregate and one intact forest transect (Fig. 1). To be suitable, aggregates had to be ≥20 m in radius and >100 m from any other unharvested habitat in the direction of the transect. Intact forest needed to be >200 m wide and deep. The aggregate transect originated in the center of an unharvested aggregate and extended 50 m into the adjacent harvest area (regenerating forest; Fig. 1). The distance from

TABLE 1. Characteristics of the study sites in the four study regions.

	Washington	Minnesota	Sweden	Tasmania
Biome	temperate coniferous	sub-boreal mixedwood	boreal coniferous	temperate hardwood
Average temperature range (°C)†	0–26	−18 to 26	−12 to 20	2–22
Annual precipitation (mm)	1,900	715	515	1,200
Elevation (m)	200–950	400–500	200–500	100–600
Time since harvest (yr)	5–9	11–12	4–9	6–9
Tree regeneration method	planted (mostly Douglas-fir) 1–3 yr after harvest; some herbicide application to control weeds	natural aspen regeneration from root suckers; no weed control	scarification and planting (mostly Norway spruce) ~2–3 yr after harvest; no weed control	broadcast burning of slash then aerial sowing with eucalypt seed within 1 yr of harvest
Aggregate area (ha)	0.25–0.5	0.12–0.2	0.3–0.8	0.6–2.6
Transect length into aggregates (m)	20–40	20	20–30	25–55
Height of intact forest (m)	41–49	11–19	19–23	37–46
Height of regenerating forest (m)	2–4	6–10	1–2	3–11

†Includes average minimum temperature for the coldest month and average maximum temperature for the hottest month.

center to edge (20–55 m) of an aggregate varied with aggregate size and shape but always represented the shortest distance to edge. The intact forest transect originated in a larger block of unmanaged forest, 50 m from the edge and extended 50 m into the adjacent regenerating forest; two additional interior plots were established in the intact forest at 95 and 100 m from edge (Fig. 1). We directed each transect northward (southward in Tasmania) from the aggregate/intact forest to standardize and maximize the shading effect (and presumably the degree of forest influence). However, the need to avoid other unharvested habitats led to some variation in transect bearings. Distances among transects within a site ranged from ~75 to 500 m; distances among sites within a region ranged from ~2 to 180 km.

Constraints on site availability in Minnesota and Sweden required that we adjust the general design. In Minnesota, the six transects were distributed among three sites, yielding two transects per edge type. In Sweden, there were five sites and, in one, the aggregate and intact forest transects were in separate but nearby (1.3 km) harvest units matched for vegetation characteristics.

Data collection

Data for plants and beetles were collected during summer 2012. Along each transect, we sampled vascular plants in plots spaced at 5-m intervals from the edge (the edge itself was not sampled). Each plot (distance) consisted of a pair of quadrats (1 × 1 m) placed 2 m from each side of the transect line (occasionally as far as 3 m, if a quadrat coincided with an unsuitable habitat, e.g., stump, log, or wet area comprising >33% of the quadrat). Within each quadrat, we visually estimated the cover (%) of each vascular plant species to the nearest 1% (or 0.1% for values <1%). Visual reference guides showing a range of cover values were used to assist in estimation. Within regions, observers calibrated their estimates to ensure consistency. An expert botanist was present to confirm identifications and to assist other observers as needed. When necessary, unknown plants were collected for identification in the lab. Cover was averaged for the two quadrats at each distance (plot) and richness was expressed as the total number of species per plot (2 m^2).

We sampled ground-active beetles (adults of all families) along the same transects using pitfall traps. Traps were spaced at 10-m intervals in the intact and regenerating forests, but in the aggregates spacing varied with aggregate size: 10 m in larger aggregates and 5 m in smaller aggregates (to ensure at least four traps in this habitat). Traps were established directly on the transect line between the pairs of vegetation quadrats. We used a standardized pitfall trap consisting of two 450-mL plastic drinking cups, one inside the other. These were inserted into the soil, ensuring that the top of the cup was level with the soil/litter surface and did not form a barrier to invertebrate movement. To exclude rainwater, we used lids made from picnic plates (~18 cm diameter) supported by thin sticks. Traps were not placed where water could accumulate (drainage hollows or channels) or in areas of high ungulate activity. After 4–6 weeks, we removed the traps and emptied the contents into plastic jars for identification in the laboratory. Some traps (15%) were disturbed, resulting in missing data. Beetles were pinned or pointed and identified under a dissecting microscope. Expert coleopterists identified reference specimens to the finest taxonomic resolution practical. Given the diversity of forest beetles (including numerous undescribed taxa) and the availability of regional expertise, beetles were identified to a range of taxonomic resolutions. All specimens were identified to family and, where possible, to genus and species. When the latter was not possible, we classed specimens by "morphospecies" (unnamed but distinguishable by morphology). This is a robust approach that provides data of high consistency

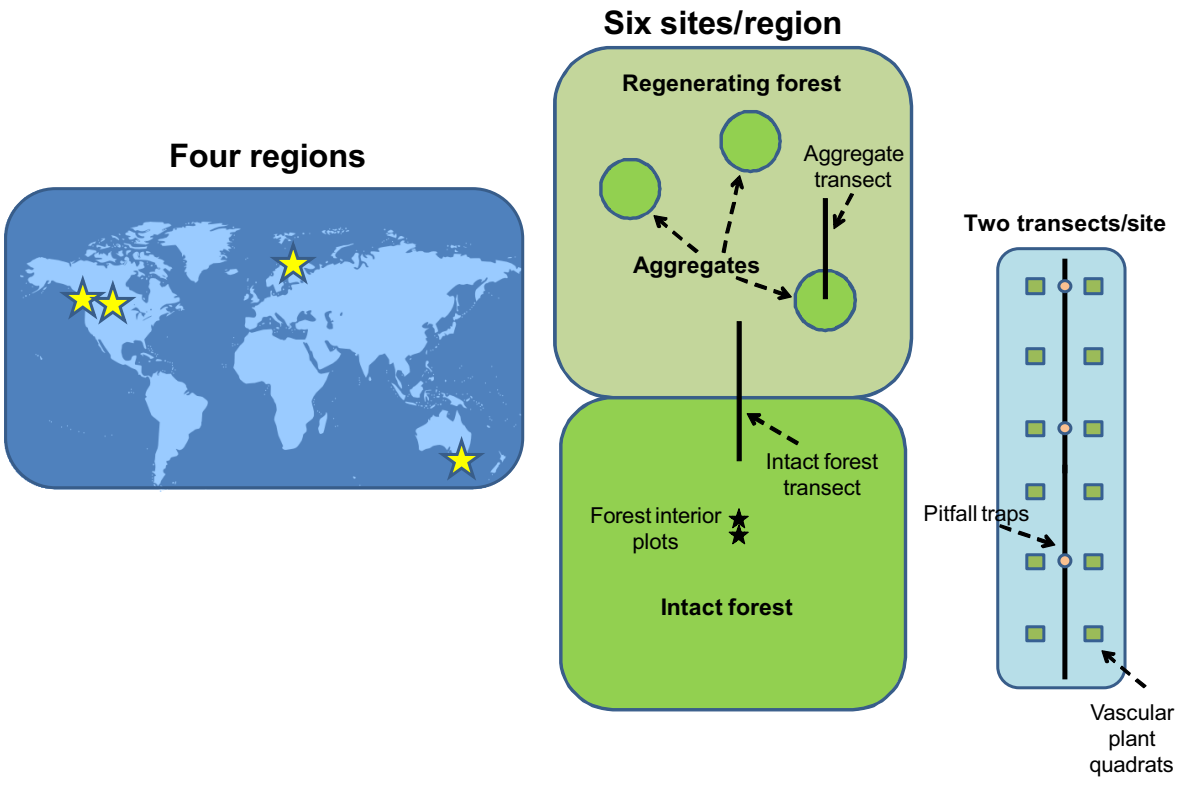

FIG. 1. Common sampling design at each site among the four regions. Each site contains one aggregate transect and one intact forest transect. Each transect extends into mature (aggregate or intact) forest and regenerating forest. Pairs of 1 × 1 m vegetation quadrats are spaced every 5 m and pitfall traps are spaced every 5 or 10 m from the edge.

(identifications were made by professional entomologists) and allows for many more surveys because it removes the need for taxonomic specialists (Oliver and Beattie 1996).

Beetle specimens were archived at the following institutions: the James Entomological Museum and the Oregon State Arthropod Collection, Corvallis, Oregon, USA; the Daniel B. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia, USA; Skogforsk, Uppsala, Sweden; and the University of Tasmania and the Tasmanian Forest Insect Collection, Tasmania, Australia.

Sampling was not designed to ensure a complete inventory of plant or beetle species among habitats or regions. Rather, we used a consistent methodology, sampling during a period of expected high beetle activity to ensure that the local (plot-scale) density and composition of species could be compared between habitats within a region. Our inferences do not extend to rare species or to species active at other times of year.

Statistical analyses

Analyses were conducted separately for each of the eight datasets (two taxa × four regions). Although the sampling design differed in Minnesota, the two transects per edge type in each site were treated as independent replicates to facilitate comparisons with other regions (see statistical analyses sections relating to *effects of harvesting* and *Edge effects and forest influence*). Where multiple statistical tests are presented, we follow the recommendation of Moran (2003) and assess the consistency of response rather than risk inflating Type II error rates with a Bonferroni correction.

Variation in species composition among and within habitats.—To characterize the variation in species composition among and within habitats (intact forest, aggregates, and regenerating forest), we first conducted nonmetric multidimensional scaling (MDS) of species abundance data. Bray–Curtis was used as the similarity measure. Cover and count data were log-transformed to down-weight the influence of dominant species. Analyses were conducted in PRIMER version 6 (Clarke and Gorley 2006). We conducted a separate ordination for each region × taxon using the matrix of plots (distances from edge) × species. For comparability among regions, we present two-dimensional solutions for each ordination. For ease of interpretation, we display centroids (means) of plots representing each site × habitat.

Species composition and richness in intact vs. regenerating forests (effects of harvesting).—We used permutational

ANOVA (PERMANOVA) to compare species composition and richness between intact (unharvested) and regenerating forests. Separate models were run for each taxonomic group and region. For composition, cover/abundance data were log transformed (to down-weight the influence of dominant species), Bray–Curtis was used as the similarity measure, and significance was based on 9,999 permutations. Analyses were conducted with PRIMER version 6 PERMANOVA+ software (Anderson 2001, Anderson et al. 2008). Using data from intact forest transects (both sides of the harvest boundary including forest interior plots), the model tested for differences between habitats (intact vs. regenerating forests; fixed effect), variation among sites (random effect), and their interaction. Variation associated with distance from edge was accounted for in the residual term. We used the variance components produced by PERMANOVA to compute the percentage of variation explained by each model term. PERMANOVA uses expected mean squares to obtain unbiased estimates of the components of variation in the model in an approach analogous to estimating variance components in univariate ANOVA (Anderson et al. 2008).

We used the same model structure to compare the average richness of species (number of taxa per plot or trap) between intact and regeneration forest habitats. We did not estimate richness at larger spatial scales; this would have required greater intensity of sampling. Models utilized untransformed data and a Euclidean distance matrix. For Minnesota, models also included a transect term (nested within site) and associated interaction terms. However, the variance explained by site was generally similar to that of the simpler models, thus the latter were presented for comparability among regions. In addition to the PERMANOVAs, we compared the magnitude of the habitat effect using a log response ratio (LRR), which expressed the proportional change in richness due to harvest,

$$\mathrm{LRR} = \ln(X_R / X_I),$$

where X_R and X_I are mean richness in the regenerating and intact forests, respectively (see Poore et al. 2012). LRR was computed for each site and a mean and standard error were computed for each region. Values <0 indicate greater richness in the intact forest; values >0 indicate greater richness in the regenerating forest.

Species composition and richness in aggregates vs. intact forests (lifeboating function).—We used the same PERMANOVA approach to assess the lifeboating function of aggregates. Models compared composition and richness between aggregate and intact forest habitats. We then computed a log response ratio, ln (X_A/X_I), expressing the proportional change in richness in aggregate (X_A) relative to intact (X_I) forest habitats.

Edge effects and forest influence.—We used mixed-effects models to explore the nature and strength of edge effects and forest influence. These analyses were restricted to plant species composition because beetle traps were spaced too widely (10 m) to model edge-related gradients. To quantify the effects of edge, we computed the Bray–Curtis similarity between each plot (distance from edge) in the unharvested forest (aggregate or intact forest) and each of four comparison plots in the regenerating forest (i.e., at 15, 25, 35, and 45 m from the edge on the same transect). For each distance, the four similarity values were averaged to obtain a mean similarity to regenerating forest. Mean similarity was then used as the measure of response in a mixed-effects model with two predictors: distance from edge (fixed effect) and site (random effect). An edge effect was inferred from a significant decline in similarity with distance from edge (one-tailed test). Preliminary analyses indicated a better fit for linear than for logarithmic relationships, hence linear models were used.

We used the same approach to quantify forest influence, the effects of aggregates or intact forests on adjacent regenerating forests. Here, each plot (distance) in the regenerating forest was compared to four comparison plots in the aggregate or intact forest (i.e., at 5, 10, 15, and 20 m from the edge on the same transect). For Minnesota, where each site had two transects per edge type, site did not contribute to variation beyond that of transect (based on likelihood ratio tests). Site was thus dropped from the models and transect was used as the random term. Models were developed in the *lme4* package in R (Bates et al. 2013).

Results

Total richness and abundance of species varied among regions. For plants, 142 species were observed in Washington, 135 in Minnesota, 46 in Sweden, and 87 in Tasmania. For beetles, 115 species (2,169 beetles) were collected in Washington, 159 species (7,196 beetles) in Minnesota, 89 species (2,711 beetles) in Sweden, and 221 species (1,427 beetles) in Tasmania.

Variation in composition among habitats

MDS ordinations of plant and beetle data illustrated considerable variation in species composition among sites and habitats within each region. Unharvested and harvested habitats occupied fairly distinct portions of the ordination space (red/orange vs. green/blue/black symbols, respectively; Fig. 2). Yet, for both types of habitats, there was considerable variation in composition, even in the same site (Fig. 2). Within each region, harvesting had a fairly consistent effect on the direction of compositional change, but the magnitude of change varied from site to site (compare directions and lengths of red arrows; Fig. 2). In contrast, plots representing aggregate and intact forests (including forest interiors) were closer in the ordination space with no consistency in their relative positions (see directions of black arrows; Fig. 2).

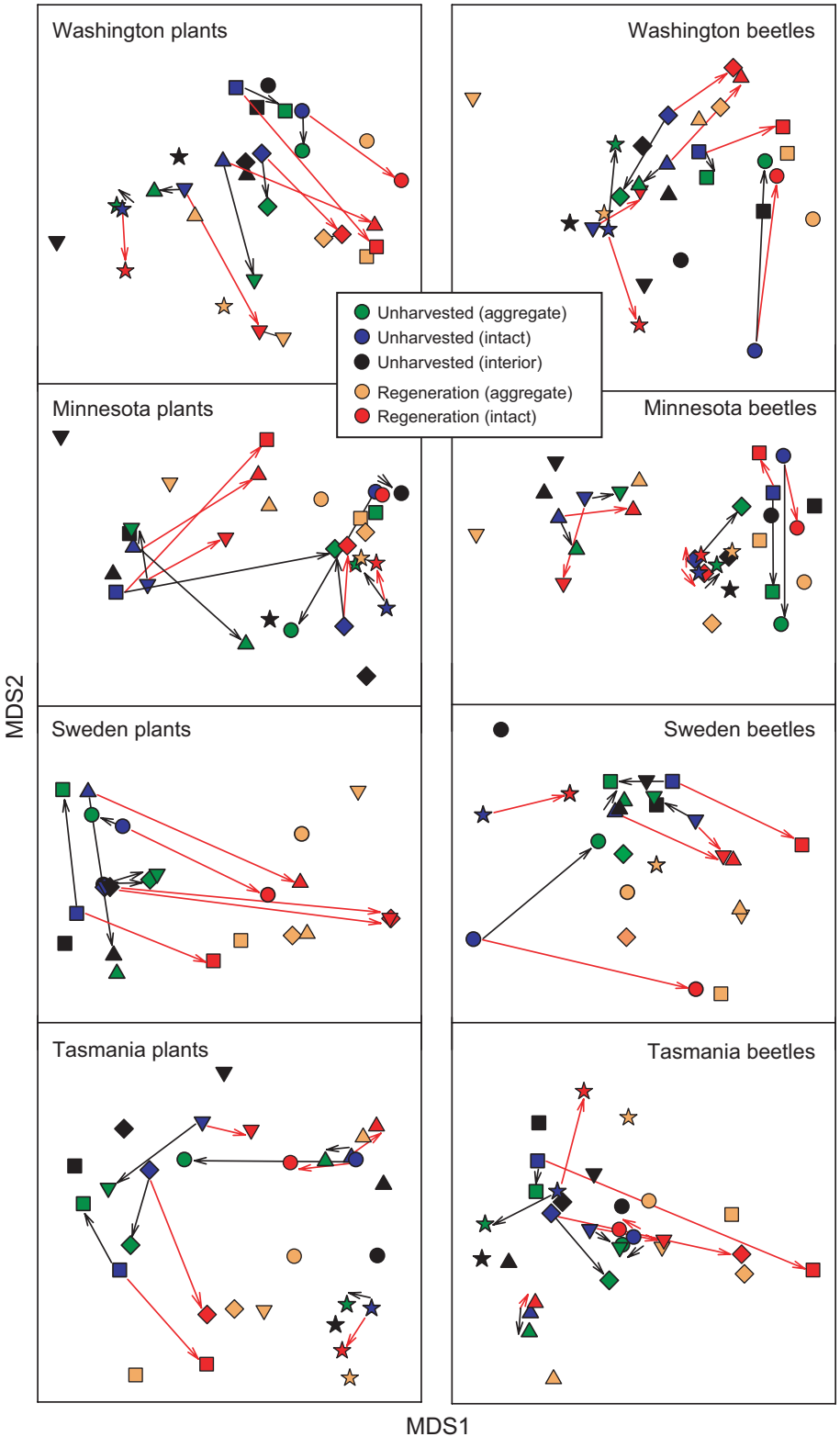

FIG. 2. MDS ordinations of plant and beetle composition among and within habitats in each region. Ordinations are based on compositional data from plots (two 1 × 1 m quadrats) or traps. However, for simplicity, we show plot or trap averages (centroids) for each site × habitat. Colors indicate habitats and symbols indicate study sites. Black arrows connect intact (non-interior) and aggregate forests at each site; red arrows connect intact (non-interior) and regenerating forests at each site.

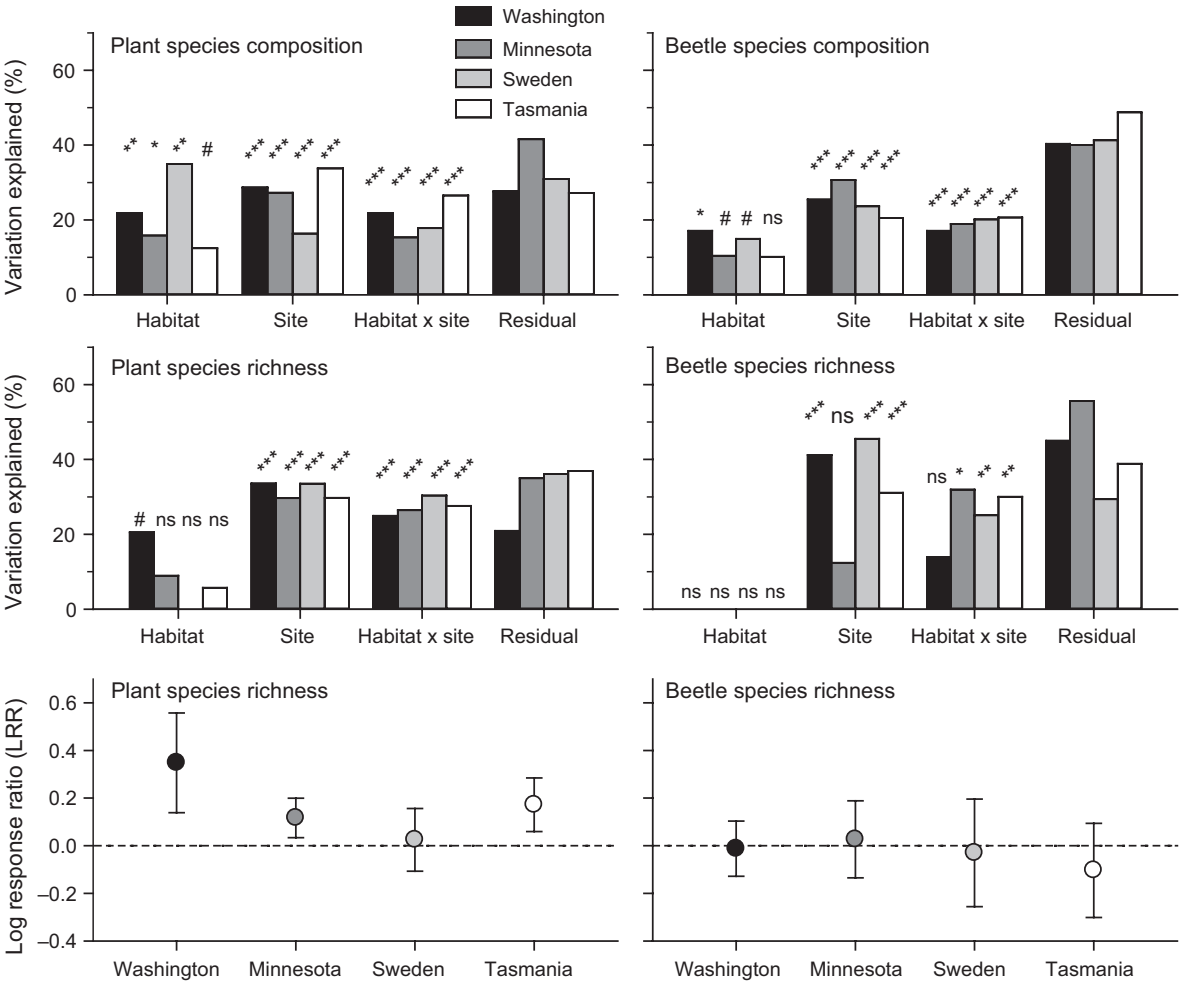

FIG. 3. Metrics of species composition and richness comparing intact and regenerating forest habitats. Components of variation (% variation explained) and their significance are assessed by PERMANOVA. Log response ratios (LRR; mean ± 1 SE) represent the proportional change in species richness between regenerating and intact forest habitats. Positive values indicate greater richness in the regenerating forest. *** $P \leq 0.001$, ** $0.001 < P \leq 0.01$, * $0.01 < P \leq 0.05$, # $0.05 < P \leq 0.1$, ns $P > 0.1$.

Regenerating vs. intact forests (effects of harvesting)

For nearly all comparisons of composition and richness, there was a significant interaction between habitat (intact vs. regenerating forest) and site (Fig. 3). Most variation was accounted for by site, habitat × site, and residual (among-plot) terms, suggesting substantial spatial heterogeneity among and within sites. Habitat explained a small proportion of the variation in composition (typically <20%) and little or no variation in plot-level richness for plants or beetles. Despite limited significance of the habitat term in the PERMANOVAs, log response ratios suggest greater richness of plants in the regenerating forest (except in Sweden), but no difference in richness of beetles.

Aggregates vs. intact forests (lifeboating function)

For nearly all comparisons of composition and richness, there was a significant interaction between habitat (aggregate vs. intact forest) and site (Fig. 4). The habitat term was generally nonsignificant, explaining very little (<10%) of the variation. There was one exception, however: in Sweden, plant species richness was consistently higher in aggregates than intact forest. Most variation in composition and richness was attributable to site, habitat × site, and residual terms, suggesting substantial spatial heterogeneity among and within unharvested habitats.

Edge effects and forest influence

Edge effects within intact forests and aggregates.—Edge effects (tested only for plant composition) were contingent on edge type (intact forest vs. aggregates) and region (Fig. 5a). Similarity in composition to regenerating forest declined significantly with distance from edge in intact forests in two of four regions (Washington,

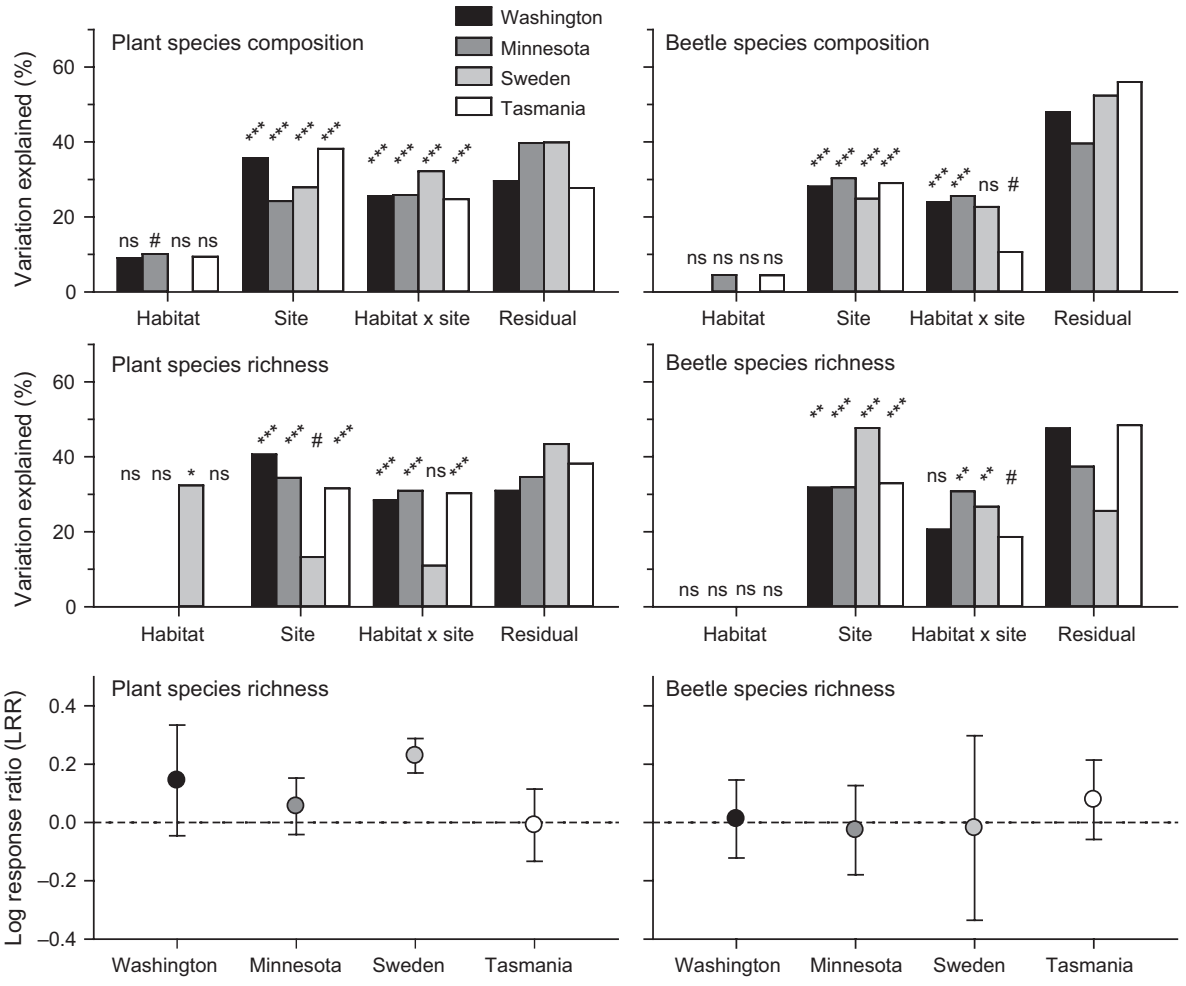

FIG. 4. Metrics of species composition and richness comparing aggregate and intact forest habitats. Components of variation (% variation explained) and their significance are assessed by PERMANOVAs. Log response ratios (LRR; mean ± 1 SE) represent the proportional change in species richness between aggregates and intact forest habitats. Positive values indicate greater richness in the aggregates. *** $P \leq 0.001$, ** $0.001 < P \leq 0.01$, * $0.01 < P \leq 0.05$, # $0.05 < P \leq 0.1$, ns $P > 0.1$.

$P < 0.001$; Minnesota, $P < 0.01$), but in aggregates, only in Tasmania ($P < 0.01$). For aggregates in Sweden, the direction of the edge effect ran counter to expectation, due to strongly negative slopes at two sites. In both aggregates, plots near the center had high cover of the bunchgrass *Deschampsia flexuosa,* which was typically more common in regenerating forests.

Forest influence adjacent to intact forests and aggregates.—Forest influence into regenerating forests was more common than edge effects (Fig. 5b). Similarity in composition declined with distance from intact forest in three of four regions (significant effects in Washington, $P < 0.01$, and Sweden, $P = 0.028$; marginally significant effect in Minnesota, $P = 0.088$). Compositional trends were even stronger adjacent to aggregates (significant in Washington, $P < 0.001$; Sweden, $P < 0.0001$; and Minnesota, $P < 0.001$). Effects of forest influence were not observed in Tasmania.

DISCUSSION

Harvesting of forest ecosystems can have severe and long-lasting effects on biological diversity (Lindenmayer and Franklin 2002). In the absence of local research or expertise, managers must rely on research from other regions to guide management, research that may or may not be applicable. Our comparative analyses of temperate and boreal forests on three continents demonstrate that vascular plants and ground-active beetles respond similarly to aggregated retention and that retained forest aggregates can fulfil their intended lifeboating function by supporting the diversity of species found in larger blocks of mature, relatively undisturbed forest. From an ecological perspective, it is interesting that responses to harvest-related disturbance and habitat fragmentation were similar for very different communities of plants and beetles. From a management perspective, this consistency provides strong support for

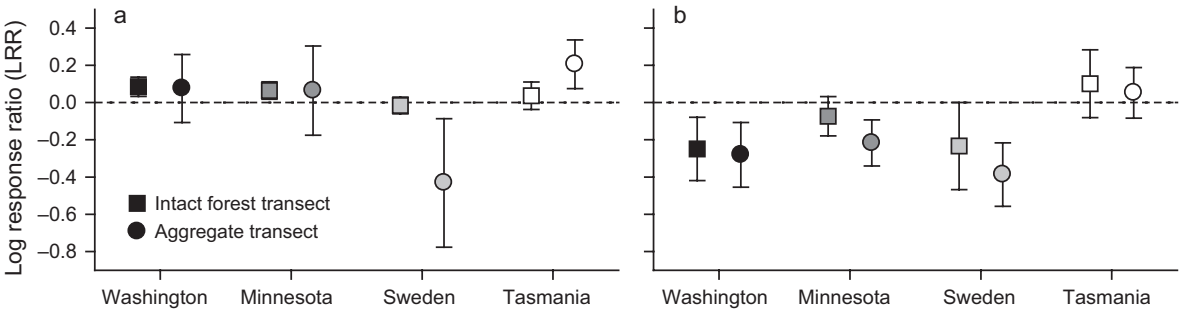

FIG. 5. Slopes of regression models for (a) edge effects and (b) forest influence gradients on plant species composition. Values are means with 95% confidence intervals for transects representing intact forests (squares) and aggregates (circles) within each region (with regions shaded as in Figs. 3, 4). Slopes in the expected direction are positive for edge effects and negative for forest influence.

broader adoption of this approach to regeneration harvesting.

Encouragingly, relatively small, isolated aggregates supported similar communities of plants and beetles as did larger blocks of intact forests. Moreover, aggregates generally were not compromised by edge effects and had a positive influence on plant composition in the regenerating forest (aggregates in Tasmania were an exception). Our analyses also underscore the inherent spatial heterogeneity of mature, unmanaged forests and the potential to distribute aggregates within managed stands in ways that sustain (via lifeboating) and enhance (via forest influence) the recovery of biodiversity.

Regenerating vs. intact forests (effects of harvesting)

Consistent with disturbance and succession theory and empirical work in many forest ecosystems (Franklin and MacMahon 2000, Pulsford et al. 2014), harvesting had a substantial effect on the composition of vascular plant and ground-active beetle communities. We detected harvest-related changes in plant and beetle communities despite the absence of pre-treatment data and substantial variation in composition among and within sites. Effects of harvesting appeared to be stronger for plants than for beetles, but this may relate, in part, to the lower sampling intensity and very high natural variability in species composition of beetles. In addition to removal of the forest canopy, post-harvest site preparation (e.g., use of herbicides in Washington, scarification in Sweden, and broadcast burning in Tasmania) is also likely to have affected the composition of plant and beetle communities. Ordinations showed significant separation of unharvested and harvested (regenerating) forests. However, variance components from PERMANOVA indicated that less variation was explained by habitat (harvesting effect) than by factors related to spatial location (site or site × habitat). The distributions of habitats in ordination space offer insight into the sources and spatial scales of this variation: although the directions of compositional change from the unharvested to the harvested portions of transects tended to be similar, the magnitude of change varied considerably among sites. The significance of the site × habitat interaction thus appears to be driven by variation in the degree of species turnover between habitats, not by an inconsistent response to harvesting among sites. This heterogeneity in species composition prior to harvest is expected to facilitate re-organization and recovery after disturbance (Folke 2006).

Although these effects of logging are not surprising (Halpern et al. 2012), they are notable in demonstrating consistency in the direction of compositional change among very different taxa and forest biomes of the world. At the same time, the effects on local (plot-level) richness of species was weak, reinforcing the notion that simple community attributes such as richness can mask important changes in species composition (e.g., Magurran et al. 2015). This study did not assess seral associations of species, but numerous studies have found that logging can lead to at least partial (or temporary) replacement of late-seral by early-seral species (e.g., Halpern and Spies 1995, Baker 2006). In Sweden, species' pools were generally similar in the regenerating and intact forests and plant species richness was comparable. Compositional differences between habitats reflect the replacement of several interior species by several disturbance-adapted species in the regenerating forest. In contrast to the other regions, however, there was not a large pool of early-seral species to enhance richness following harvest.

Lifeboating

The general absence of compositional differences between aggregates and intact forests suggests that aggregates can be effective in maintaining forest-dependent plants and ground-active beetles in managed landscapes. This is encouraging, because aggregates are intended as temporary refugia and dispersal sources, roles played by remnants of intact forest that escape natural disturbance (Lindenmayer and Franklin 2002). However, comparisons to natural forest remnants are needed to confirm that aggregates function similarly as there is evidence from some systems that they may not (Gandhi et al. 2004, Buddle et al. 2006). Whether aggregates can predictably serve as refugia for rarer or specialized taxa remains unclear given the inherently patchy distributions of these

species and the limitations of our sampling effort. Isolation in small fragments can leave these species susceptible to demographic or environmental stochasticity (Gilpin and Soulé 1986, Hanski 1998).

Several factors may have contributed to the overall effectiveness of aggregates in this study. First, with the exception of the old-growth sites in Tasmania, harvests were conducted in younger or mature forests, which tend to have fewer sensitive or specialist species. Second, aggregates had been isolated for relatively short periods of time (4–12 years), whereas the extinction debt of fragmentation (Tilman et al. 1994) may not be expressed for decades. Whether aggregates can serve as refugia in the longer term, until conditions in adjacent harvest areas become suitable for establishment, remains a critical unanswered question. With time, physical disturbance (e.g., edge-related windthrow; Esseen 1994, Jönsson et al. 2007, Steventon 2011) or the cumulative effects of short-rotation harvest (Lindenmayer and Franklin 2002) could compromise this function. Retention of small aggregates may be inappropriate in some regions or in topographic positions that are susceptible to extreme wind events (Mitchell 2013). Third, some aggregates in this study were larger than those retained in typical forest operations; greater size increases the area-to-edge ratio thus reducing any negative influences of edge (but see *Discussion: Edge effects and forest influence on plants*).

Although for most comparisons, the main effect of habitat (aggregate vs. intact forest) was nonsignificant, the interaction with site was highly significant. Absence of pre-harvest data limits our ability to interpret this interaction, although the results of MDS offer insight. Pairs of intact and aggregate forest habitats showed little consistency in their relative positions in ordination space, thus no consistency in species' turnover. The site × habitat interaction likely reflects natural heterogeneity in species composition attributable to topographic, edaphic, or other factors that vary at the spatial scales at which we sampled. Knowledge of this heterogeneity can be informative in the design of harvest units (Lindenmayer and Franklin 2002). For example, operational guidelines (e.g., for Tasmania, Baker and Read 2011) can include recommendations that encourage managers to distribute aggregates within forest stands to capture this natural diversity of habitats—diversity that is fundamental to the ecological complexity and post-harvest resilience of plant and animal communities (Gustafsson et al. 2012).

Edge effects and forest influence on plants

We detected significant effects of edge on the composition of plant communities in unharvested forest but only for a subset of edge types × regions. Contrary to expectation (e.g., Soga et al. 2013), effects were no more frequent in the smaller, more exposed aggregates than in the larger blocks of intact forest, which presumably were more buffered. The general absence of edge effects highlights the potential for forest aggregates to remain compositionally stable (e.g., Halpern et al. 2012) despite changes in microclimate (e.g., Heithecker and Halpern 2007) or susceptibility to wind disturbance (Jönsson et al. 2007).

Interestingly, we were unable to detect effects of forest influence in the regenerating forests of Tasmania, even adjacent to larger blocks of intact forest. It is possible that in these systems, reestablishment of forest species in the harvested area is limited by dispersal or microclimatic conditions that are inhospitable to germination or survival. Evidence of increasing forest influence on tree regeneration in clearfelled stands of increasing age in Tasmania suggests that these limitations may diminish with time (Tabor et al. 2007, Baker et al. 2013*a*). Baker et al. (2014) similarly showed that, although microclimatic stress is moderated by proximity to edge, the strength of this effect increased with time since harvest (peaking nearly three decades after harvest) reflecting changes in the canopy structure of the regenerating forest.

Given the contrasts in disturbance history, resource availability, and physical environment on opposite sides of the edge, it is not surprising that compositional gradients were stronger in the regenerating forests. Here, they reflect reassembly of post-harvest communities along sharp gradients in resource availability, stress, and shading along which early-seral and forest species are differentially favored (Franklin and MacMahon 2000, Baker et al. 2013*b*). In contrast, in the intact forest, established species can be highly resilient to edge-related gradients in microclimate (Harper et al. 2015) and to incursion by early-seral species (Pulsford et al. 2014).

Management implications

Retention of mature forest has been advocated in managed forest landscapes to maintain the species, structures, and habitats that contribute uniquely to biodiversity (Lindenmayer and Franklin 2002). This study provides strong and broad-based support for the hypothesized functions of aggregated retention, providing local refugia for mature-forest species and facilitating their recovery in the regenerating matrix (Baker et al. 2015). Previous studies have demonstrated the effectiveness of retention forestry for specific taxonomic groups (including fungi, nonvascular plants, and ground-dwelling vertebrates) in particular forest ecosystems (Rosenvald and Lõhmus 2008, Fedrowitz et al. 2014). We demonstrate the benefits of aggregated retention for two distinctly different taxonomic groups, vascular plants and ground-active beetles, in four regions of the world with very different biotas, forest histories, and management practices: in Sweden, with historically intensive forest management and virtually no remaining old-growth; in Tasmania, where old-growth had been harvested for the first time; and in Minnesota and Washington, with disturbance histories intermediate to these. Clearly, further research is needed to understand how the benefits of aggregated retention are likely to vary with other potentially

important factors, including aggregate size, forest age at harvest, and time since disturbance.

Although we found strong consistency in biological responses across continents, we also observed significant variation, both within and among sites, in the composition of mature forest communities. Spatial heterogeneity in community composition enhances the potential for ecological redundancy and ecosystem resilience to disturbance or stress (Walker 1992, Naeem 1998, Messier et al. 2013). The spatial scale of heterogeneity observed in this study underscores the need to retain unharvested patches of forest within the broader managed landscape. In most forested regions of the world, there is little potential to sustain this heterogeneity by adding large reserves; moreover, relying on large reserves may be inadequate for biodiversity conservation (McAlpine et al. 2007), as suggested by the debate over land sparing vs. land sharing (Phalan et al. 2011). Instead, a combination of approaches is probably most effective (Lindenmayer and Cunningham 2013). Retaining intact forest patches in locally managed forests is relatively easy, even in regions where harvesting is conducted on small private tenures such as Fennoscandia (Gustafsson et al. 2010). Small aggregates may contribute substantially to biodiversity conservation in areas targeted for this purpose.

Conclusions

Clearcut logging can have adverse effects on biodiversity, fragmenting forest habitats, reducing the size and connectivity of relatively undisturbed habitats and increasing forest exposure to edge. Retention forestry, inspired by models of natural disturbance processes, is likely to benefit species that are adapted to the patchy landscapes that result from periodic natural disturbance such as wildfire and windthrow (Gustafsson et al. 2012). We found that retention of small patches of intact forest within larger harvest units fosters persistence and enhances recovery of mature forest plant and animal communities. Our results provide support for adopting retention forestry in landscapes in which managers seek to enhance the ecological values of forests managed for timber production (Lindenmayer et al. 2012). However, additional research is needed to fully understand how aggregate size, shape, and edge effects influence the functioning of aggregates as refugia and dispersal sources, particularly for rarer species or those that are sensitive to disturbance or environmental changes. Future research should also address the longevity of aggregate functioning and the cumulative effects of multiple harvests. Strategies that incorporate the characteristic heterogeneity of mature forests in harvest designs are likely to be most effective in meeting the biodiversity objectives of retention forestry.

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Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.md045