# Short- and long-term benefits for forest biodiversity of retaining unlogged patches in harvested areas

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## ABSTRACT

Aggregated retention, in which patches of trees (aggregates) remain unlogged within larger harvested units, was first applied commercially in 1986. A primary goal was to maintain greater diversity of forest-dependent species through harvest, relative to conventional clearcutting. Despite its global application, the long-term benefits for biodiversity and the comparative responses of disparate taxonomic groups to aggregated retention are largely unknown. A critical knowledge gap relates to the role of 'forest influence' – whether and to what extent aggregates affect biodiversity in neighboring harvested areas. We sampled plants, beetles, and spiders/harvestmen in the world's three oldest aggregated-retention sites (21–26 years old), matched with three recently harvested sites (5–8 years old). For each taxonomic group, we compared species composition between undisturbed aggregates and regenerating forests to assess the 'lifeboating' function of aggregates. For each group, we also modeled changes in species composition, and in the numbers of aggregate- and regeneration-affiliated species, with distance from the aggregate edge into the regenerating forest along transects at north-facing edges. For all three taxa, species composition differed between aggregates and regenerating forests in both older and recent sites, confirming the long-term effectiveness of aggregates for lifeboating. The compositional difference between habitats was significantly greater at recent than at older sites for plants, but not for invertebrates. Plants and spiders/harvestmen responded to forest influence, with a marginal response for beetles. Responses for plants and spiders generally manifested as increased numbers of aggregate-affiliated species and decreased numbers of regeneration-affiliated species in regenerating areas closer to edges. Our results indicate that aggregated retention has short- and long-term benefits for biodiversity reflecting both the lifeboating and forest-influence functions of aggregates. However, variation in the responses of plants, beetles and spiders suggests that these benefits cannot be generalized among taxa. We advocate broader application of aggregated retention in forests managed for timber production and encourage managers to incorporate the benefits of forest influence in harvest designs by arranging aggregates to reduce average distances from harvested areas to unlogged habitats.

## 1. Introduction

Aggregated retention, the practice of leaving unlogged patches within logged areas is a form of retention forestry that has gained increasing use globally as an alternative to clearcut logging (Gustafsson et al., 2012; Lindenmayer et al., 2012; Mori and

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Kitagawa, 2014). In contrast to clearcutting, retention forestry maintains habitat for species affiliated with closed forest—thus mitigating the negative effects of timber harvest—while also providing habitat for early-seral species (Fedrowitz et al., 2014). Developed in the late 1980s, retention forestry incorporates the benefits of retained forest elements for ecosystem recovery and habitat connectivity after disturbance. Nevertheless, widespread adoption of retention forestry is relatively recent, and much broader application is desirable since clearcutting is still prevalent in many regions (Lindenmayer et al., 2012).

Retention of undisturbed patches within harvest units is intended to sustain some forest-dependent species through disturbance—the 'lifeboating' function of aggregates (Franklin et al., 1997). In addition, aggregates may facilitate species' re-establishment within adjacent harvest areas through effects of 'forest influence'—a type of edge effect (Baker et al., 2013). Two edge-related mechanisms may contribute to re-establishment: microclimatic amelioration (shading) near the edge and greater proximity to source populations (Keenan and Kimmins, 1993; Heithecker and Halpern, 2007; Baker et al., 2013). Few studies have assessed the timing and or extent to which forest edges influence re-establishment in the harvest area (but see Helle and Muona, 1985; Tabor et al., 2007; Larrivée et al., 2008), particularly in the context of retention forestry. Small aggregates may be susceptible to edge and area effects, thus compromising both their lifeboating and forest-influence functions (Aubry et al., 2009; Baker et al., 2013).

Biotic responses to retention forestry have rarely been investigated in the long-term (e.g., Lõhmus and Lõhmus, 2010; Halpern et al., 2012). However, it is likely that habitat changes and ecological succession alter the importance of retained structure over time (Halpern et al., 2012). For example, the structural contrast between harvested and retained forest, and the strength of edge influence on microclimate in the harvested area, change with regrowth of the regenerating forest (Baker et al., 2014)—particularly the pace at which the canopy closes. As a consequence, the relative importance of aggregates as refuges for forest-dependent species or as structures that influence ecological processes in the harvested area may change with time since disturbance.

Studies of biological responses to forest management rarely consider multiple taxonomic groups. In the absence of empirical data, natural resource or conservation managers may thus assume that responses of forest-dependent or early-seral species in one taxonomic group apply to other taxa. For example, if responses of invertebrates are keyed to changes in vegetation (de Andrade et al., 2014), then surveying plants may be sufficient. Whether plants serve as surrogates for other taxa remains unresolved: some studies show partial surrogacy (Panzer and Schwartz, 1998; Catterall et al., 2004; Kati et al., 2004; de Andrade et al., 2014) and others, no clear relationship (e.g., Oliver et al., 1998; Wolters et al., 2006). Few studies of invertebrates consider more than one major group, regardless of evidence suggesting varying responses to management (Buddle et al., 2006; Lovell et al., 2007; de Andrade et al., 2014). Even when multiple taxa are considered, rarely is a common methodology used to facilitate direct comparison. Where comparable methodology has been used, taxa have shown varying responses to retention harvests. For example, Halaj et al. (2008) found that spiders and carabid beetles showed contrasting responses to edge within forest aggregates. Coincidental sampling of taxa in time and space makes it possible to evaluate more fully the ecological consequences of forest management.

Our research was designed to address these gaps in knowledge. We sampled plants, and ground-active beetles and spiders/harvestmen in the oldest known sites subjected to aggregated retention, and in more recently harvested sites contemporaneous with the use of aggregated retention in most regions of the world. Our objectives were to elucidate the importance of lifeboating and forest-influence within these contexts:

(1) Lifeboating: To characterize (a) the differences in species composition between mature (aggregate) and adjacent regenerating forests, and whether these differences vary (b) with time since harvest and (c) among taxonomic groups.
(2) Forest influence: To assess (a) the strength of forest influence on species composition in the harvested area and whether it varies (b) with time since harvest or (c) among taxonomic groups. (d) To assess whether compositional gradients are driven by species associated with mature and/or regenerating forest, which we expected to decline or increase in number, respectively, with distance from edge.

Our results provide some of the first empirical evidence of the longevity and relative effectiveness of these dual ecological functions for a taxonomically diverse set of forest organisms. They provide strong support for aggregated retention as a strategy for balancing conservation of biological diversity with timber production in managed forest landscapes.

## 2. Materials and methods

### 2.1. Study sites

We studied aggregated-retention sites in Douglas-fir (*Pseudotsuga menziesii* (Mirb.)) dominated forests on federal, state and private forestlands in Washington State, USA. We utilized the only three available early operational sites (i.e., "older" sites, harvested 21–26 years previously) and three more recently harvested sites (i.e., "younger" sites, harvested 5–8 years previously) (Fig. 1). The harvested areas of the older sites were in the stem-exclusion (closed-canopy) phase of forest development; those in the younger sites were in the stand-initiation (pre-closure) phase (Franklin et al., 2002). Details of the management history, dominant plant species, and general ecological settings of the sites are provided in Tables A1 and A2 in Appendix A, Supplementary material.

### 2.2. Sampling design

Within each site, we established a transect originating from the center of each of two unlogged aggregates, extending along an approximately northern bearing across the aggregate-harvest area boundary (20–40 m away) to a distance of 50 m into the harvested area ("regenerating forest"; Fig. 2). We chose a northerly bearing to maximize shading; effects of forest influence are likely to be weaker along south-facing (warmer, brighter) edges.

Aggregates varied in size from 0.4 to 1.3 ha and all but one were 0.4 to 0.8 ha. Because the largest aggregate was long and thin and the sampling transect was located at its far end, edge effects were probably similar to those of smaller aggregates. We established vegetation plots every 5 m along each transect in both directions from the aggregate edge. We established pitfall traps for ground-active invertebrates (beetles and spiders/harvestmen) every 10 m in the regenerating forest, but usually every 5 m in the aggregates to ensure at least four traps per transect in this more restricted habitat.

### 2.3. Data collection

Data were collected in summer 2012. We sampled vascular plants in two 1 × 1 m subplots per plot. Within each subplot, we visually estimated the percentage cover of each vascular plant

**Fig. 1.** Map of study site locations in Washington USA. The three older sites are indicated with stars and the three younger sites with circles.

species to the nearest 1% (or 0.1% for cover <1%); subplot values were then averaged for each plot. We collected the invertebrates using standardised pitfall traps. We included harvestmen (Opiliones) with spiders because they are also arachnids, are functionally similar to ground-roaming spiders, and low vagility and sensitivity to drought make them potentially responsive to forest management. Their small sample size (see Section 3) precluded separate analysis. Traps used 100% propylene glycol as a preservative and were emptied once, at the end of a six-week trapping period. Of a total of 112 traps, 8 were disturbed and had missing data (see Section 2.4). All individuals were identified to species or morphospecies (hereafter, species). For spiders/harvestmen, whose juveniles often cannot be identified to species, only individuals identified to a unique taxonomic unit (family, genus, or species) were used in analyses. Full sampling details are presented in Appendix A.

### 2.4. Statistical analyses

Prior to analyses, we log transformed species' cover (plants) or trapped numbers (invertebrates) to down-weight the influence of dominant species. To graphically illustrate the variation in species composition among mature (aggregate) and regenerating forests at contrasting times since harvest (Objectives 1a and 1b) we conducted non-metric multidimensional scaling (MDS) on plot-scale data. Separate ordinations were run for complete datasets of each taxonomic group using Bray-Curtis similarity; results were rotated to aid interpretation of axes. Analyses were run using PRIMER v6 (Clarke and Gorley, 2006).

We performed exploratory quantitative analysis of each taxon with a mixed PERMANOVA using PRIMER v6 PERMANOVA+ software (Anderson, 2001; Anderson et al., 2008). This model was used to identify the variables and/or interactions to be considered in a more targeted approach. The full model included *habitat* (mature vs. regenerating forest; fixed effect), *distance* from edge (fixed effect), *age* (younger vs. older sites; fixed effect), *site* (random effect nested within *age*, reflecting the hierarchical nature of the design), and *transect* (random effect nested within *site*), as well as two- and three-way interactions among these variables.

We used PERMANOVA and the '*Distances among centroids*' procedures in PRIMER v6 PERMANOVA+ software to assess whether species composition differed between aggregates and adjacent harvested areas (Objective 1). Full PERMANOVA models yielded significant effects of age and habitat, as well as significant interactions of habitat with site and transect. Thus, we conducted a reduced set of models to assess differences between habitats within each age class (younger and older sites) and transect. For these reduced models, four plots were selected systematically from both the regenerating and mature (aggregate) forest portions of each transect. Given the small number of unique permutations (typically 35) for the transect-based tests, we set the significance threshold at $\alpha = 0.1$, following Moran's (2003) argument not to adjust for multiple comparisons. Given lack of true replication of habitats within transects, inferences were based on the consistency of response among transects.

To determine whether differences in species composition between mature (aggregate) and regenerating forest habitats vary with time since harvest and among taxa (Objectives 1b and 1c), we used the '*Distances among centroids*' procedure. Bray-Curtis dissimilarities (distances) between mature and regenerating forests were computed using principal coordinates analysis (PCO), based on two centroids per transect (each representing four plots per habitat). PCO is a metric multi-dimensional scaling approach and distances between centroids are proportional to their dissimilarities (Faith et al., 1987). Using these dissimilarities, we then performed a linear mixed-effects analysis (using the "lme4" package in *R*; (Bates et al., 2013) to assess whether the dissimilarity between habitats varied with time since harvest (age) or taxonomic group. Age and taxon were modeled as fixed effects (both with and without the interaction term), and transect, as a random effect. We obtained *P*-values by likelihood-ratio tests comparing the full model to a model without the effect in question (Neyman and Pearson, 1928). We then conducted Tukey's tests using the "multcomp" package in *R* (Hothorn et al., 2008) to identify the groups (ages or taxonomic groups) for which habitat dissimilarities differed significantly.

We used mixed-effects models (*R* library "lme4") to assess strength of forest influence within harvested areas and its dependence on time since harvest and taxonomic group (Objectives 2a–c). Preliminary analyses indicated substantial variation in species composition both among and within sites, thus forest influence was quantified at the scale of individual transects (i.e., as slopes representing responses to distance from edge). We first computed the Bray-Curtis similarity in species composition between each plot in the regenerating forest (i.e., each distance from edge) and each of four plots in the corresponding aggregate. The four values were then averaged to obtain a mean similarity for each distance. A preliminary model yielded a significant taxon × distance × age interaction. Thus distance and age effects were analysed separately for each taxonomic group.

We then assessed whether compositional gradients reflected the distributions of species associated with mature or regenerating forests (Objective 2d). For each plot (distance) in the regenerating forest, we tallied the number of species present among the four plots of the corresponding aggregate (i.e., aggregate-affiliated species) or absent from those plots (regeneration-affiliated species).
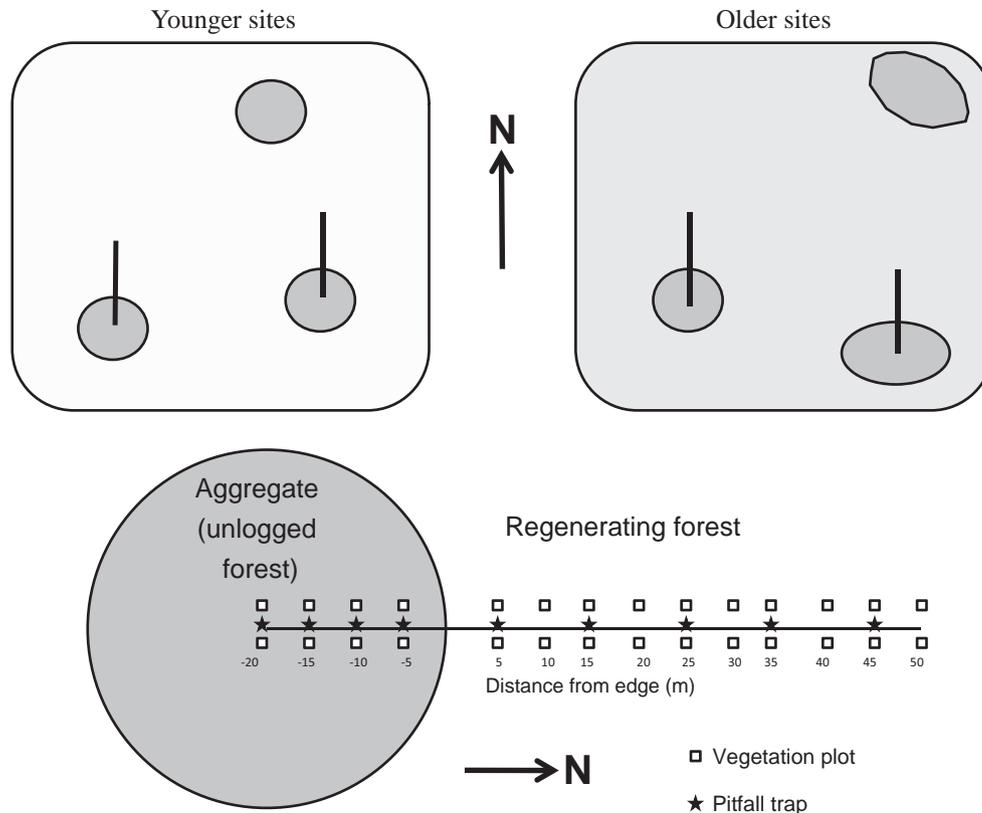
**Fig. 2.** Schematic of the sampling design: two transects per site replicated at each of three younger and older sites.

After examining diagnostics plots, we applied linear regression to the compositional similarity (Bray-Curtis) data and generalized linear regression with Poisson family and a log link function to counts of aggregate- and regeneration-affiliated species. Site was excluded from these models because it did not contribute to variation beyond that of the random transect effect (based on likelihood-ratio tests). We included a random intercept and slope when significant. Preliminary analyses indicated a better fit for linear than for logarithmic relationships with distance.

## 3. Results

In total, we observed 121 vascular plant taxa, 119 beetle species (1666 individuals), and 60 and 9 species of spiders and harvestmen (1451 and 372 individuals, respectively). We list all species and their general habitat affiliations in Appendix A (Supplementary Results).

### 3.1. Lifeboating (Objective 1)

MDS produced comparable results with two and three dimensions; for simplicity, we present the former. MDS ordinations produced some degree of separation in the composition of aggregates and regenerating forests, especially at younger sites (Fig. 3). There was clear separation of plots representing younger and older sites (times since harvest; Fig. 3), regardless of habitat, for all three taxonomic groups. PERMANOVAs conducted on the composition of both younger and older sites indicated significant interactions between habitat (aggregate vs. regenerating forest) and site or transect for all taxonomic groups. Subsequent PERMANOVAs for individual transects yielded a significant effect of habitat ($P \leqslant 0.1$) in more than half of the tests for each combination of

taxon and age—the majority for plants and spiders/harvestmen (Table 1).

All taxa showed a trend for reduced compositional dissimilarity between habitats in older than in younger sites (Table 2). However, the age × taxon interaction was marginally significant ($P = 0.056$), with the age-related difference in dissimilarity significant only for plants ($P < 0.001$; Tukey's multiple comparison tests). Conversely, there were no differences among taxa within each age class ($P > 0.1$) (Table 2).

### 3.2. Forest influence (Objective 2)

The strength of forest influence varied among taxonomic groups (significant taxon × age × distance interaction; likelihood-ratio test: $\chi^2_{obs} = 72.562$, $df = 8$, $P < 0.0001$). Taxon- and age-specific models were used to tease apart this interaction. Compositional similarity to aggregates declined significantly with distance from edge for plants and spiders/harvestmen, but only marginally so for beetles (Table 3a). In addition, similarity to aggregates was significantly greater in older than in younger sites for plants, but not for beetles or spiders/harvestmen (Fig. 4a).

For plants, the number of aggregate-affiliated species tended to decline with distance from edge in younger, but not older sites (marginally significant age × distance interaction; Table 3b; Fig. 4b). The AIC value for the model containing the interaction term was lower, suggesting a better fit. For beetles, the number of aggregate-affiliated species did not vary consistently with distance (Table 3b). For spiders/harvestmen, the distance-related decline in aggregate-affiliated species (Fig. 4b) was non-significant ($P = 0.148$), although inclusion of distance in the model reduced AIC, providing some support for the effect of forest influence.
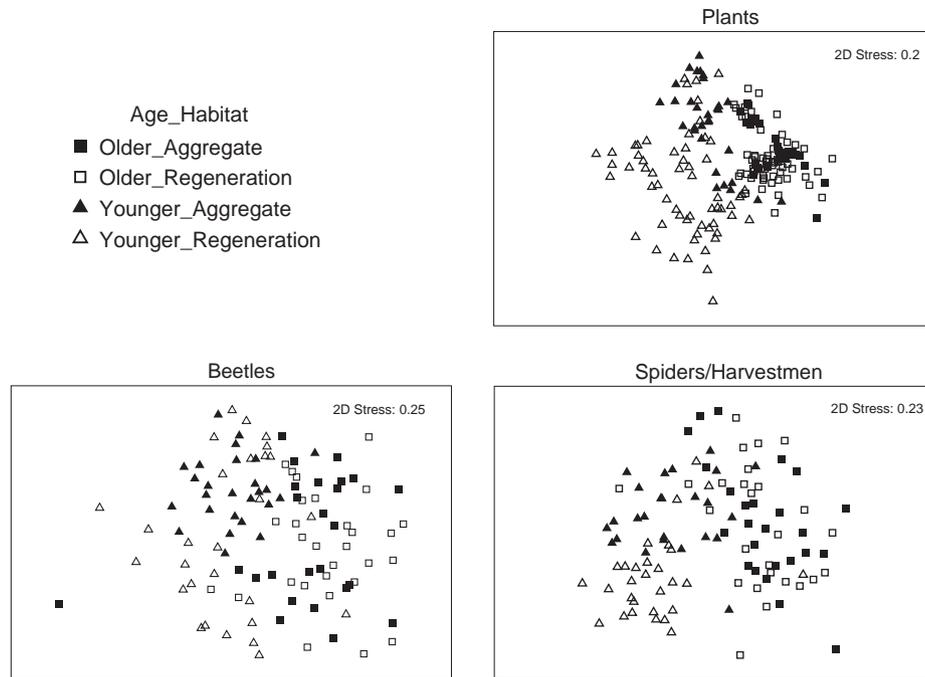
**Fig. 3.** MDS ordination illustrating variation in species composition of plants, beetles, and spiders/harvestmen in plots representing contrasting habitats (aggregate vs. regenerating forest) and times since harvest (younger vs. older sites).

**Table 1**
Significance (*P*) values[†] from one-way PERMANOVA models testing for a habitat difference (aggregate vs. regenerating forest) for each transect.

| Transect | Plants | Beetles | Spiders/harvestmen |
|---|---|---|---|
| *Younger sites* | | | |
| Quartz Vein T1 | 0.027* | 0.030* | 0.029* |
| Quartz Vein T2 | 0.030* | 0.029* | 0.026* |
| Out Post T1 | 0.32 n.s. | 0.057# | 0.17 n.s. |
| Out Post T2 | 0.030* | 0.028* | 0.027* |
| Upwind T1 | 0.028* | 0.49 n.s. | 0.027* |
| Upwind T2 | 0.031* | 0.059# | 0.025* |
| | | | |
| *Older sites* | | | |
| Cougar Ramp T1 | 0.029* | 0.059* | 0.029* |
| Cougar Ramp T2 | 0.11 n.s. | –[‡] | 0.14 n.s. |
| Big Dog T1 | 0.86 n.s. | 0.080# | 0.032* |
| Big Dog T2 | 0.023* | 0.082# | 0.028* |
| PacifiCorp T1 | 0.028* | 0.37 n.s. | 0.029* |
| PacifiCorp T2 | 0.030* | 0.11 n.s. | 0.10# |

[†] Significance codes: *, 0.01 < *P* ⩽ 0.05; #, 0.05 < *P* ⩽ 0.1; n.s., *P* > 0.1.

[‡] –: data unavailable.

**Table 2**
Mean (SD) Bray-Curtis dissimilarity between habitats (aggregate and regenerating forests) in older vs. younger sites. Significance (*P*) values are from Tukey's tests, assessing whether the degree of dissimilarity between habitats varied between age classes. The corresponding comparisons among taxa within each age class were non-significant (*P* > 0.1).

| Taxa | Older sites | Younger sites | *P*-value[†] |
|---|---|---|---|
| Plants | 32.6 (12.5) | 58.6 (22.4) | 0.0016** |
| Beetles | 42.1 (6.2) | 47.4 (9.8) | 0.97 n.s. |
| Spiders/harvestmen | 47.7 (9.0) | 52.7 (9.0) | 0.98 n.s. |

[†] Significance codes: **, *P* ⩽ 0.01; n.s., *P* > 0.1.

The number of regeneration-affiliated species increased significantly with distance from edge for plants and marginally so for spiders/harvestmen (*P* = 0.090; AIC values supported including distance), especially at younger sites, however there was no trend for beetles (Table 3c, Fig. 4c).

In addition to effects of forest influence, numbers of aggregate- and regeneration-affiliated plants and spiders/harvestmen tended to be greater in younger than in older sites (significantly larger intercepts; Fig. 4b and c; Table 3). These trends reflected the higher overall richness of species in younger sites (S.C.B., unpublished data).

## 4. Discussion

### 4.1. Lifeboating

Our results are consistent with past studies of retention forestry that demonstrate the 'lifeboating' function of aggregates (reviewed in Rosenvald and Lõhmus, 2008; Fedrowitz et al., 2014). Undisturbed patches supported distinctly different assemblages of plants, beetles, and spiders/harvestmen from those of adjacent harvested areas. Our study is one of very few that demonstrates the capacity of relatively small (<1 ha) aggregates to support forest-dependent species for multiple decades after timber harvest (Halpern et al., 2012; Fedrowitz et al., 2014).

For plants, the differences between aggregates and regenerating forests were substantially greater at younger sites where forest generalist and late-seral species dominated the aggregates and early-seral species, the harvested areas (Table S3 in Appendix A). At older sites, structural (Table S1 in Appendix A), and presumably therefore microclimatic (Baker et al., 2014) differences between aggregates and regenerating forest were much reduced compared to younger sites, which may relate to the variation in plant response with forest age. However, this contrast was less apparent for ground-active beetles and spiders/harvestmen. This variation among taxa suggests that ground-active invertebrates respond, at least in part, to factors other than plant species composition, even though the leaf-litter habitat is largely plant-derived. Nevertheless, absence of an interaction with age was surprising, given the strong contrast in microclimate between mature forest and recently harvested areas (Chen et al., 1999), and that microclimate and stand density are known to influence the composition of both

**Table 3**

Results of mixed-effects models for each of three taxonomic groups testing for effects of distance from edge, age, and their interaction on similarity in (a) species composition to aggregates, (b) number of aggregate-affiliated species, and (c) number of regeneration-affiliated species. Gaussian distributions were used for Bray-Curtis similarity and Poisson distributions for number of species. Note that the error distribution influences the scale of model estimates.

| | | Plants | Beetles | Spiders/harvestmen |
|---|---|---|---|---|
| *(a) Bray-Curtis similarity to aggregates* | | | | |
| Distance | *P*-value[†] | 0.0029** | 0.0840# | 0.0087** |
| | Slope | −0.204 | −0.133 | −0.227 |
| | (95% CI) | (−0.334, −0.073) | (−0.282, 0.015) | (−0.389, −0.064) |
| Age | *P*-value | 0.0018** | 0.376 n.s. | 0.987 n.s. |
| | Intercept difference[‡] | −25.71 | −5.664 | −0.082 |
| | (95% CI) | (−38.76, −12.67) | (−18.014, 6.687) | (−9.591, 9.427) |
| Distance × age | *P*-value | 0.16 n.s. | 0.251 n.s. | 0.756 n.s. |
| *(b) Number of aggregate−affiliated species* | | | | |
| Distance | *P*-value | – | 0.577 n.s. | 0.148 n.s. |
| | Slope | Older: 0.002 | −0.003 | −0.007 |
| | (95% CI) | (−0.005, 0.009) | (−0.013, 0.007) | (−0.016, 0.002) |
| | | Younger: −0.006 | | |
| | | (−0.118, −0.0006) | | |
| Age | *P*-value | – | 0.138 n.s. | 0.0016** |
| | Intercept difference | 0.398 | 0.210 | 0.530 |
| | (95% CI) | (−0.372, 1.169) | (−0.068, 0.488) | (0.260, 0.799) |
| Distance × age | *P*-value | 0.091# | 0.749 n.s. | 0.894 n.s. |
| *(c) Number of regeneration-affiliated species* | | | | |
| Distance | *P*-value | <0.0001*** | 0.999 n.s. | 0.090# |
| | Slope | 0.013 | −0.000 | 0.010 |
| | (95% CI) | (0.007, 0.019) | (−0.011, 0.011) | (−0.002, 0.022) |
| Age | *P*-value | 0.014* | 0.759 n.s. | 0.084# |
| | Intercept difference | 0.0792 | −0.088 | 0.524 |
| | (95% CI) | (0.223, 1.360) | (−0.099, −0.077) | (−0.054, 1.102) |
| Distance × age | *P*-value | 0.288 n.s. | 0.750 n.s. | 0.274 n.s. |

[†] Significance codes: ***, $P \leqslant 0.001$; **, $0.001 < P \leqslant 0.01$; *, $0.01 < P \leqslant 0.05$; #, $0.05 < P \leqslant 0.1$; n.s., $P > 0.1$.

[‡] Intercept difference describes the difference in predicted values (younger minus older sites) at the aggregate-regenerating forest boundary.

beetle and spider assemblages (Halaj et al., 2008; Prieto-Benítez and Méndez, 2011; Gillingham et al., 2012). Other potentially important influences on ground-active invertebrates include the structural complexity of the forest and the abundance of leaf litter, moss, and coarse woody debris (Peltonen et al., 1997; Halaj et al., 2008; Larrivée et al., 2008; Pinzon et al., 2012), factors that we did not assess in this study.

Relatively small aggregates are susceptible to edge effects, potentially compromising the intended lifeboating function (Nelson and Halpern, 2005; Halaj et al., 2008). That said, in retention forestry, aggregates are not intended as forest-interior habitats, but are more analogous to unburned patches that escape wildfire, the dominant natural disturbance in Douglas-fir forests (Franklin et al. 1997). Riparian buffers are often the primary component of unlogged forest within production forestry landscapes, but by their nature are of confined landscape position and support different species composition than do upslope areas reserved in aggregates (Baker et al., 2006). Our results demonstrate that small upland patches are effective at lifeboating forest-dependent plants and invertebrates for multiple decades after timber harvest, enabling species' persistence within the managed forest landscape.

## 4.2. Forest influence

We detected gradients in forest influence, although they varied in strength among taxonomic groups. For example, we observed clear edge-related gradients for plants and spiders/harvestmen, but only marginally significant trends for beetles. In previous studies, all three groups (and other taxa) have shown responses to forest influence (reviewed in Baker et al., 2013). For plants and spiders/harvestmen, similarity in species composition to aggregates decreased, and number of regeneration-affiliated species increased, with distance from edge, irrespective of age. For spiders/harvestmen, number of aggregate-affiliated species declined with distance, regardless of age; for plants, the decrease occurred only at younger sites. Thus, for at least some groups at one or more points in time, edge-related gradients in composition reflect the responses of both forest-dependent and open-habitat species, as observed in other single taxon studies (e.g., Pearce et al., 2005; Larrivée et al., 2008). Our results suggest that it is possible to distribute aggregates within harvest units in ways that benefit species from contrasting, but equally important, functional groups (i.e., shade-tolerant, late-seral species vs. open-site, early-seral species) (Swanson et al., 2011; Fedrowitz et al., 2014). Aggregates serve to reduce distances to unlogged forest, although additional research is needed to elucidate the contributions of patch size and inter-patch distance to biological responses in the harvest matrix. We sampled along north-facing edges where forest influence gradients were expected to be maximised, thus assessment of forest influence gradients along other edge bearings would also be useful.

The absence of any detectable effect of forest influence on aggregate-affiliated plants at older sites was surprising. Although rapid closure of the regenerating forest may create conditions suitable for re-establishment of mature-forest species (Swanson et al., 2011), we expected establishment to be somewhat dispersal-limited (particularly for late-seral species), hence, to decline with distance from edge (Matlack, 1994; Baker et al., 2013). In the absence of pre-harvest data—particularly for species that are patchily distributed—it can be difficult to identify the processes that contribute to post-harvest distributions (Nelson and Halpern, 2005). The marginal edge response in beetles, with no gradients observed for regeneration-affiliated or aggregate-affiliated species, was also unexpected because others have detected a significant effect of forest influence in ground-active beetles within clearcuts (T. Work pers. comm., Pearsall, 2003; Fountain-Jones et al., 2015). Clearly, the differing responses of the groups sampled in this study, underscore the potential danger in generalizing about biodiversity responses to forest influence and to retention forestry in general.

The existence of strong edge-related gradients in plant and invertebrate response has important implications, not only for retention forestry, but for forest edges and disturbed areas more broadly. Our understanding of forest influence derives, in large part, from studies of clearcuts adjacent to much longer and deeper edges (e.g. Tabor et al., 2007). An important finding from this study is that relatively small aggregates (∼0.5–1.0 ha) can have positive effects on biodiversity of the surrounding harvest matrix. This has been documented for mycorrhizal fungi (Outerbridge and Trofymow, 2004; Jones et al., 2008) and frogs (Chan-McLeod and Moy, 2007), but to our knowledge, not previously for plants or invertebrates.

Our assessment of forest influence provides empirical support for current approaches to variable retention in some regions of world. For example, strict forest-influence guidelines are applied to harvests that qualify as retention forestry in coastal British Columbia (Mitchell and Beese, 2002) and SE Australia (Baker and Read, 2011). Specifically, 50% of the harvested area must lie within one canopy-tree-height from long-term retention in forest aggregates
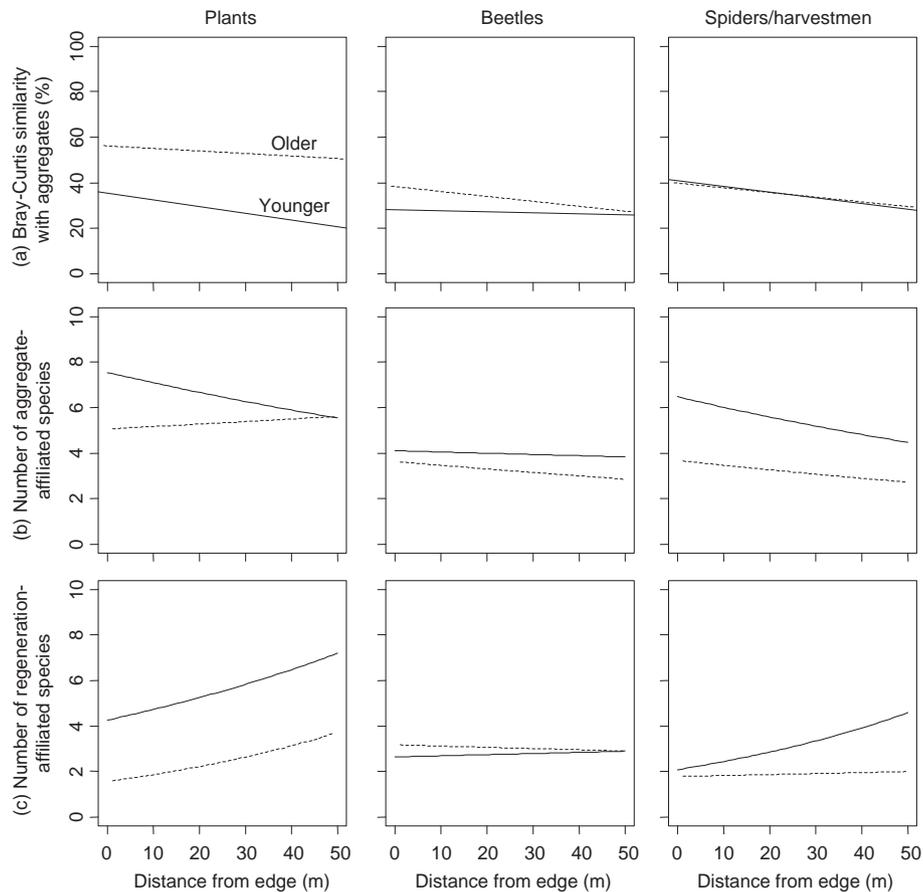
**Fig. 4.** Fitted relationships with distance from edge for plants, beetles, and spiders/harvestmen from mixed-effect models: (a) Bray-Curtis similarity with aggregate plots from the same transect; (b) number of aggregate-affiliated species; and (c) number of regeneration-affiliated species. For (b) and (c) where Poisson models with log-link functions were used, data were back-transformed for plotting. Independent slopes and intercepts were plotted for the two age classes in all cases (see Table 3 for their significance).

or edges. In other regions, some degree of forest influence is attained by prescribing a maximum distance between retained forest elements (Baker, 2011). On State lands in western Washington (USA) distances among individual leave trees and/or aggregates cannot exceed 120 m (reflecting the spacing of song-bird breeding territories). Our findings suggest that this spacing (which applied to our Younger study sites) also provides enough forest influence to encourage re-establishment of aggregate-affiliated plants and spiders/harvestmen while also providing habitat conditions for early-seral species. However, in most regions where retention forestry is practiced, forest influence is not the primary motivation for retention of aggregates; rather, it is the lifeboating function (Franklin et al., 1997; Gustafsson et al., 2012), borne out by numerous empirical studies (Rosenvald and Lõhmus, 2008; Gustafsson et al., 2012; Halpern et al., 2012). By demonstrating the long-term benefits of forest influence for biodiversity, we hope to raise greater awareness of this benefit in the application of retention forestry across the world. We therefore recommend explicit adoption of forest-influence guidelines for aggregated retention.

### 4.3. Conclusions

The benefits to biodiversity of retaining mature forest aggregates were evident two decades after harvest, greatly extending the longevity of lifeboating effects reported in previous studies. Also, relatively small forest aggregates exert significant influence on the composition and diversity of species in adjacent harvest areas, affecting the distributions of both forest-dependent and open-site species. Given an emphasis, to date, on the internal stability of aggregates, and the paucity of information on the benefits to adjacent harvest areas, it is not surprising that managers have rarely incorporated the notion of forest influence in the design of harvest units. We advocate that forest managers consider the multiple functions of aggregates in designing retention harvests to meet the dual objectives of timber production and maintenance of biological diversity. We urge land managers currently implementing aggregated retention to continue to do so, and urge those who still use clearcutting to adopt this biologically more sustainable approach (Lindenmayer et al., 2012).

Further research effort is required in the topic of landscape context. Site-level retention of aggregates with retention forestry is usually in addition to any landscape-level retention (Gustafsson et al., 2012). However, if there were to be trade-offs between site-level and landscape-level retention, then consideration of the SLOSS (single large or several small areas for conservation) debate is warranted (e.g. Lindenmayer et al., 2015). Furthermore, biological responses may vary depending on the history of frequency and intensity of landscape-level disturbance; for example, if poorly dispersing taxa are more common in older than younger landscapes (Ranius, 2006; Hopper, 2009) then this could impact re-establishment into harvested areas.

Finally, although assemblages of plants, beetles, and spiders/harvestmen respond somewhat similarly to changes in forest structure and age, their sensitivity to forest influence differs. We therefore urge caution in generalizing about the responses of forest-dependent taxa to retention harvests.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.05.021.

## References

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46.

Aubry, K.B., Halpern, C.B., Peterson, C.E., 2009. Variable-retention harvests in the Pacific Northwest: a review of short-term findings from the DEMO study. For. Ecol. Manage. 258, 398–408.

Baker, S.C., 2011. Seeking a balance between forestry and biodiversity – the role of variable retention silviculture. Insights from western USA and Canada. FWPA Project Report PGD167-0910. FWPA, Melbourne, Australia, p. 60.

Baker, S.C., Read, S.M., 2011. Variable retention silviculture in Tasmania's wet forests – ecological rationale, adaptive management and synthesis of biodiversity benefits. Aust. For. 74, 218–232.

Baker, S.C., Richardson, A.M.M., Barmuta, L.A., Thomson, R., 2006. Why conservation reserves should not always be concentrated in riparian areas: a study of ground-dwelling beetles in wet eucalypt forest. Biol. Conserv. 133, 156–168.

Baker, S.C., Spies, T.A., Wardlaw, T.J., Balmer, J., Franklin, J.F., Jordan, G.J., 2013. The harvested side of edges: effect of retained forests on the re-establishment of biodiversity in adjacent harvested areas. For. Ecol. Manage. 302, 107–121.

Baker, T.P., Jordan, G.J., Steel, E.A., Fountain-Jones, N.M., Wardlaw, T.J., Baker, S.C., 2014. Microclimate through space and time: microclimatic variation at the edge of regeneration forests over daily, yearly and decadal time scales. For. Ecol. Manage. 334, 174–184.

Bates, D., Maechler, M., Bolker, B., 2013. lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2.

Buddle, C.M., Langor, D.W., Pohl, G.R., Spence, J.R., 2006. Arthropod responses to harvesting and wildfire: Implications for emulation of natural disturbance in forest management. Biol. Conserv. 128, 346–357.

Catterall, C.P., Kanowski, J., Wardell-Johnson, G., Proctor, H., Reis, T., 2004. Quantifying the biodiversity values of reforestation: design issues and outcomes in Australian forest landscapes. In: Lunney, D. (Ed.), Conservation of Australia's Forest Fauna. Royal Zoological Society of New South Wales, Mosman, Australia, pp. 359–393.

Chan-McLeod, A.C.A., Moy, A., 2007. Evaluating residual tree patches as stepping stones and short-term refugia for red-legged frogs. J. Wild. Manag. 71, 1836–1844.

Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L., Franklin, J.F., 1999. Microclimate in forest ecosystem and landscape ecology. Bioscience 49, 288.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth, UK.

de Andrade, R.B., Barlow, J., Louzada, J., Mestre, L., Silveira, J., Vaz-de-Mello, F.Z., Cochrane, M.A., 2014. Biotic congruence in humid tropical forests: a multi-taxa examination of spatial distribution and responses to forest disturbance. Ecol. Indic. 36, 572–581.

Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegatio 69, 57–68.

Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A., Gustafsson, L., 2014. Can retention forestry help conserve biodiversity? A meta-analysis. J. Appl. Ecol. 51, 1669–1679.

Fountain-Jones, N.M., Jordan, G.J., Baker, T.P., Balmer, J.M., Wardlaw, T., Baker, S.C., 2015. Living near the edge: being close to mature forest increases the rate of succession in beetle communities. Ecol. Appl. 25, 800–811.

Franklin, J.F., Berg, D.R., Thornburgh, D.A., Tappeiner, J.C., 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. In: Kohm, K.A., Franklin, J.F. (Eds.), Creating a Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington DC, USA, pp. 111–139.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J.Q., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155, 399–423.

Gillingham, P.K., Palmer, S.C.F., Huntley, B., Kunin, W.E., Chipperfield, J.D., Thomas, C.D., 2012. The relative importance of climate and habitat in determining the distributions of species at different spatial scales: a case study with ground beetles in Great Britain. Ecography 35, 831–838.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W., Brodie, A., Kouki, J., Lindenmayer, D.B., Lõhmus, A., Martínez Pastur, G., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A., Franklin, J.F., 2012. Retention forestry to maintain multifunctional forests: a world perspective. Bioscience 62, 633–645.

Halaj, J., Halpern, C.B., Yi, H., 2008. Responses of litter-dwelling spiders and carabid beetles to varying levels and patterns of green-tree retention. For. Ecol. Manage. 255, 887–900.

Halpern, C.B., Halaj, J., Evans, S.A., Dovciak, M., 2012. Level and pattern of overstory retention interact to shape long-term responses of understories to timber harvest. Ecol. Appl. 22, 2049–2064.

Heithecker, T.D., Halpern, C.B., 2007. Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. For. Ecol. Manage. 248, 163–173.

Helle, P., Muona, J., 1985. Invertebrate numbers in edges between clear-fellings and mature forests in northern Finland. Silva Fenn. 19, 281–294.

Hopper, S.D., 2009. OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. Plant Soil 322, 49–86.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biomet. J. 50, 346–363.

Jones, M.D., Twieg, B.D., Durall, D.M., Berch, S.M., 2008. Location relative to a retention patch affects the ECM fungal community more than patch size in the first season after timber harvesting on Vancouver Island, British Columbia. For. Ecol. Manage. 255, 1342–1352.

Kati, V., Devillers, P., Dufrene, M., Legakis, A., Vokou, D., Lebrun, P., 2004. Testing the value of six taxonomic groups as biodiversity indicators at a local scale. Conserv. Biol. 18, 667–675.

Keenan, R.J., Kimmins, J.P., 1993. The ecological effects of clear-cutting. Environ. Rev. 1, 121–144.

Larrivée, M., Drapeau, P., Fahrig, L., 2008. Edge effects created by wildfire and clear-cutting on boreal forest ground-dwelling spiders. For. Ecol. Manage. 255, 1434–1445.

Lindenmayer, D.B., Franklin, J.F., Lohmus, A., Baker, S.C., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Martinez Pastur, G., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A., Gustafsson, L., 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. Conserv. Lett. 5, 421–431.

Lindenmayer, D.B., Wood, J., McBurney, L., Blair, D., Banks, S.C., 2015. Single large versus several small: the SLOSS debate in the context of bird responses to a variable retention logging experiment. For. Ecol. Manage. 339, 1–10.

Lõhmus, A., Lõhmus, P., 2010. Epiphyte communities on the trunks of retention trees stabilise in 5 years after timber harvesting, but remain threatened due to tree loss. Biol. Conserv. 143, 891–898.

Lovell, S., Hamer, M., Slotow, R., Herbert, D., 2007. Assessment of congruency across invertebrate taxa and taxonomic levels to identify potential surrogates. Biol. Conserv. 139, 113–125.

Matlack, G.R., 1994. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology 75, 1491–1502.

Mitchell, S.J., Beese, W.J., 2002. The retention system: reconciling variable retention with the principles of silvicultural systems. Forest Chron. 78, 397–403.

Mori, A.S., Kitagawa, R., 2014. Retention forestry as a major paradigm for safeguarding forest biodiversity in productive landscapes: A global meta-analysis. Biol. Conserv. 175, 65–73.

Nelson, C.R., Halpern, C.B., 2005. Edge-related responses of understory plants to aggregated retention harvest in the Pacific northwest. Ecol. Appl. 15, 196–209.

Neyman, J., Pearson, E.S., 1928. On the use and interpretation of certain test criteria for purposes of statistical inference Part I. Biometrika 20A, 175–240.

Oliver, I., Beattie, A.J., York, A., 1998. Spatial fidelity of plant, vertebrate, and invertebrate assemblages in multiple-use forest in eastern Australia. Conserv. Biol. 12, 822–835.

Outerbridge, R.A., Trofymow, J.A., 2004. Diversity of ectomycorrhizae on experimentally planted Douglas-fir seedlings in variable retention forestry sites on southern Vancouver Island. Can. J. Bot. 82, 1671–1681.

Panzer, R., Schwartz, M.W., 1998. Effectiveness of a vegetation-based approach to insect conservation. Conserv. Biol. 12, 693–702.

Pearce, J.L., Venier, L.A., Eccles, G., Pedlar, J., McKenney, D., 2005. Habitat islands, forest edge and spring-active invertebrate assemblages. Biodivers. Conserv. 14, 2949–2969.

Pearsall, I.A., 2003. Study to assess the efficacy of ground beetles (Coleoptera: Carabidae) as ecological indicators in north and south island operational sites. Year 3 final report. Pearsall Ecological Consulting Nanaimo, BC, Canada.

Peltonen, M., Heliövaara, K., Väisänen, R., 1997. Forest insects and environmental variation in stand edges. Silva Fenn. 31, 129–141.

Pinzon, J., Spence, J.R., Langor, D.W., 2012. Responses of ground-dwelling spiders (Araneae) to variable retention harvesting practices in the boreal forest. For. Ecol. Manage. 266, 42–53.

Prieto-Benítez, S., Méndez, M., 2011. Effects of land management on the abundance and richness of spiders (Araneae): a meta-analysis. Biol. Conserv. 144, 683–691.

Ranius, T., 2006. Measuring the dispersal of saproxylic insects: a key characteristic for their conservation. Popul. Ecol. 48, 177–188.

Rosenvald, R., Lõhmus, A., 2008. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. For. Ecol. Manage. 255, 1–15.

Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B., Swanson, F.J., 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Front. Ecol. Environ. 9, 117–125.

Tabor, J., McElhinny, C., Hickey, J., Wood, J., 2007. Colonisation of clearfelled coupes by rainforest tree species from mature mixed forest edges, Tasmania, Australia. For. Ecol. Manage. 240, 13–23.

Wolters, V., Bengtsson, J., Zaitsev, A.S., 2006. Relationship among the species richness of different taxa. Ecology 87, 1886–1895.