

Living near the edge: Being close to mature forest increases the rate of succession in beetle communities

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Abstract. In increasingly fragmented landscapes, it is important to understand how mature forest affects adjacent secondary forest (forest influence). Forest influence on ecological succession of beetle communities is largely unknown. We investigated succession and forest influence using 235 m long transects across boundaries between mature and secondary forest at 15 sites, sampling a chronosequence of three forest age classes (5–10, 23–29, and 42–46 years since clear-cutting) in tall eucalypt forest in Tasmania, Australia. Our results showed that ground-dwelling beetle communities showed strong successional changes, and in the oldest secondary forests, species considered indicators of mature forest had recolonized to abundance levels similar to those observed within adjacent mature forest stands. However, species composition also showed forest influence gradients in all age classes. Forest influence was estimated to extend 13 m and 20 m in the youngest and intermediate-aged secondary forests, respectively. However, the estimated effect extended to at least 176 m in the oldest secondary forest. Our environmental modeling suggests that leaf litter, microclimate, and soil variables were all important in explaining the spatial variation in beetle assemblages, and the relative importance of factors varied between secondary forest age classes.

Mature-forest beetle communities can recolonize successfully from the edge, and our results provide a basis for land managers to build mature habitat connectivity into forest mosaics typical of production forests. Our results also indicate the importance of forest influence in determining potential conservation value of older secondary forest for beetles.

Key words: *Coleoptera*; *ecotone*; *Eucalyptus*; *forest influence*; *gradient forests modeling*; *litter input*; *secondary forest*.

INTRODUCTION

Natural and human-induced disturbance have led to forest landscapes that are increasingly fragmented, especially in production forest. Species with a strong dependence on mature forest can be particularly vulnerable in such landscapes, and biodiversity conservation strategies usually focus on protecting these species in large reserves. However, these reserves are often disconnected and distant from production forest areas, and are unlikely to be large enough on their own to maintain viable populations of all these species. Complementary management of production forest landscapes may improve the long-term survival prospects of many such species (Spence et al. 1996). However, this management depends on understanding how mature-forest species recolonize secondary forest, and particularly the biotic effects of the forest edges found throughout fragmented landscapes (Hopp et al. 2010, Baker et al. 2013a).

The extensive literature describing edge effects largely focuses on the biotic impacts of disturbed forest on the

interior of mature forest remnants (Harper et al. 2005). However, relatively few studies have assessed the opposite effect: how mature forest affects adjacent disturbed habitat (Baker et al. 2013a). This forest influence (Keenan and Kimmins 1993, Beese et al. 2003) involves a complex set of biotic and abiotic factors affecting the survival and establishment of many elements of the biota. In particular, proximity to mature forest may endow disturbed forest with mature forest environmental attributes that can facilitate survival and/or reestablishment by species adapted to mature forest conditions (Tabor et al. 2007). Shading from the edge, for example, results in cooler and moister conditions that favor rainforest species (Tabor et al. 2007). Forest influence effects have been shown for vascular plants (e.g., Matlack 1994, Tabor et al. 2007), non-vascular plants (Baker et al. 2013b), amphibians (Demaynadier and Hunter 2008), and invertebrates (e.g., Koivula et al. 2002, Siira-Pietikäinen and Haimi 2009). For invertebrates, several studies show declines in species affiliated with mature forests with distance from old-growth forest (Spence et al. 1996, Buddle et al. 2006, Jonsson and Nordlander 2006). Forest influence can facilitate recolonization for a variety of groups and in a variety of

Manuscript received 16 February 2014; revised 30 July 2014; accepted 12 August 2014. Corresponding Editor: A. K. Brody.

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systems, though the underlying mechanisms are poorly understood.

Forest influence on regeneration operates through mature forest both providing a source of species for recolonization and moderating the environment of the regenerating forest. Major disturbance will typically eliminate mature forest microhabitat and the subset of species with strict dependence on such microhabitats (Spence et al. 1996), and such species are typically presumed to recolonize from adjacent mature forests (Lemieux and Lindgren 2004, Chazdon et al. 2009, Hopp et al. 2010). Gradients of forest influence within regenerating forest may therefore involve dispersal limitation; species which are dispersal limited are more likely to recolonize areas closer to the source mature forest (Niemela et al. 1993, Michaels and McQuillan 1995, Koivula et al. 2002). The successional processes of colonization and stand development naturally lead to changes in the forest environment, particularly in the forest understory, which in turn can facilitate the recolonization of mature-forest species from other taxa. For example, plant detritus, forest canopy cover, and microclimate all change with vegetation succession in ways that can be relevant to recolonization by invertebrates (Magura et al. 2002, Hopp et al. 2010, Roume et al. 2011). Leaf litter and coarse woody debris provide food resources, predator protection, and increased insulation against microclimate extremes (Koivula et al. 1999, Jonsson and Nordlander 2006, Entling et al. 2007, Nakamura et al. 2009, Grove and Forster 2011). Other factors related to succession, e.g., soil chemistry, can affect invertebrates (Schwerk and Szyszko 2007, Antvogel and Bonn 2008, Cornellise and Hafernik 2009, Walker et al. 2010). Shading provided by the mature forest causes microclimatic gradients that are important in determining beetle community composition (Spence et al. 1996, Nakamura et al. 2009), by affecting the beetles directly and indirectly through impacts on vegetation and soil characteristics (Matlack 1994). In particular, canopy closure is typically associated with large changes in microclimate that are pertinent to arthropod community succession (Niemelä et al. 1996, Nakamura et al. 2009).

Litter-dwelling beetles (Coleoptera) are a particularly suitable group for investigating forest influence, as they are both ecologically important and amenable to study. They are abundant, relatively easy to sample and identify, and many taxa are sensitive to forest disturbance, including disturbance created by forest harvesting (e.g., Rosenvald and Lohmus 2008, Baker et al. 2009a, Hyvarinen et al. 2009). Determining the main factors driving forest influence on beetle communities is important for developing forest management practices that improve outcomes for biodiversity conservation through the maintenance or restoration of landscape connectivity. How far the forest influence effect extends into secondary forest and how this pattern changes across successional time is largely unknown.

This study therefore aims to assess how ground-dwelling beetle communities respond to forest influence and community turnover from mature into secondary forest by using a chronosequence approach. In particular, we focus on the spatial scale of forest influence (as measured using depth of forest influence, DFI). We hypothesize that dispersal is a critical factor that drives forest influence on successional change post harvest. Furthermore, we investigate and report on which environmental factors are driving edge gradients and beetle recolonization in three forest age classes (5–10, 23–29, and 42–46 years since clear-cutting) in tall eucalypt forest in Tasmania, Australia.

METHODS

Study sites

Fifteen sites were selected in Tasmania's Southern Forests region (see Fig. 1), within and adjacent to the Warra Long-Term Ecological Research (LTER) area (see Brown et al. 2001). Each site was established to contain a boundary between mature unlogged forest and a harvested area in its first rotation after clear-fell, burn, and sow silviculture (see Hickey [1994] for details). Mature forest was defined as forest possessing reproductively active eucalypt and rainforest species at the time of logging and that had not been significantly disturbed by wildfire for at least 40 yr before the site was harvested. The unlogged mature forest had at least one age cohort of eucalypts older than 110 yr (Turner et al. 2009) that formed the upper canopy up to 50 m tall, had not been significantly disturbed by wildfires for at least 70 yr, and had an understory stratum comprising a heterogeneous mix of sclerophyllous and rainforest tree species. Sclerophyllous species dominate the understory during the initial period after a fire, with a progressive enrichment by rainforest elements as the interval since that last fire increases.

The experiments employed a balanced design with five replicate sites for each of three age classes of silviculturally regenerated forest. The three age classes comprised sites averaging ~45 yr (harvested between 1966 and 1970), ~27 yr (harvested between 1983 and 1989), and ~7 yr (harvested between 2002 and 2007) post disturbance (see Appendix A: Table A1). Forests ~7 yr old were dominated by emerging eucalypts and sclerophyllous species both up to 7 m in height, with the sedge *Gahnia grandis* forming a ground cover. After a further 20 yr, the eucalypts and sclerophyllous species had formed a dense canopy on average 22 m in height and the sedge was in decline. In ~45-yr-old forest, the canopy reached approximately 27 m.

At each site, three transects were established perpendicular to the boundary between mature and silvicultural forest, starting 35 m within mature forest and ending 200 m inside the harvested site. We used designs with unequal distances between plots to focus sampling where edge effects are more likely (Harper et al. 2005, Baker et al. 2007, Ewers and Didham 2008). Plots were

established in the mature forest at -35 and -15 m from the edge (35 and 15 m into the mature forest, respectively) and into the harvested areas at 15, 35, 70, 120, and 200 m. Thus there were 315 plots (15 sites \times 3 transects \times 7 distances). The height of mature forest at our study sites was approximately 40–65 m, hence plot distances were located both within and beyond one mature-forest tree height into harvested areas. Spatial autocorrelation and depletion effects are not significant for pitfall-trap sampling in this forest type (Baker and Barmuta 2006).

Each site was controlled for slope (no greater than 10°), altitude (100–350 m above sea level), and distance from the next site of the same age class (>5 km). We excluded sites close to rivers and major creeks, but tolerated small creeks and streams, as they are ubiquitous in the landscape. Sites bisected by roads were excluded and all plots were at least 40 m from any road or track.

Beetle sampling

Pitfall trapping is a common method of collecting beetle community data in wet forests (Niemela et al. 1993, Baker et al. 2007, 2009). We deployed a single pitfall trap in each of the 315 plots. To replace traps lost through flooding or disturbance, we placed an additional trap ~ 20 m from the main pitfall in the middle transect of each site. Only 33 of these additional pitfalls were required. Each trap was constructed from 150 mm lengths of 8.5 cm diameter PVC pipe buried in the soil, with plastic cups (8.6 cm diameter, 12.2 cm height) inside the pipe, flush with the soil surface. Approximately 200 mL of 100% propylene glycol (Fronine, Riverstone, Australia) was added to each trap as a preservative. A protective plastic plate (180 mm diameter) was positioned 2 cm above the trap to prevent flooding and disturbance. Traps were operational for exactly 30 d for each of three sampling periods (spring, summer, and autumn 2011, 2012). Traps were then collected and the contents transferred immediately to 96% ethanol (Merck, Kilsyth, Australia).

All beetles were then identified to morphospecies (sensu Oliver and Beattie 1996). Of these morphospecies, 27% were assigned to species, another 58% to genus, and the remainder (15%) to subfamily or family using keys (Lawrence et al. 1999), specimen matching to the Tasmanian Forest Insect Collection (TFIC; Forestry Tasmania, Hobart, Australia), or by expert assistance. Seasonal effects were not central to our hypotheses, so data were pooled across seasons to maximize community signals.

Vegetation and environmental data

We measured 17 environmental and biotic variables from all plots and two microclimatic variables from the middle transect plots (Table 1). Vegetation cover, plant species diversity, average tree diameter, and percent cover of litter, moss, and coarse woody debris (CWD)

were measured in 10×10 m quadrats adjacent to the pitfall trap. Maximum diameter of woody material was also measured at each quadrat (minimum diameter 5 mm). At each quadrat, four 0–10 cm depth soil cores were taken and combined together. Within 48 h of collection, each sample was stored in a paper bag in a cool, dry area until ready for analysis. Soil was sieved using a 2-mm sieve to remove leaf litter, roots, and rocks, and then ground in a mortar and pestle. The soil pH and conductivity were measured using a Palintest pH meter (Gateshead, UK) and an Elmetron CPC-411 conductivity meter (Zabrze, Poland), calibrated on each day of testing. We followed the Palintest procedure of shaking a 1:4 solution of soil to distilled water for 1 min prior to taking the pH meter reading. For conductivity, we used a 1:5 solution of soil to distilled water shaken for 2 min, and allowed this to settle before reading as per the manufacturer's instructions. Nitrogen and carbon were analyzed using a Perkins Elmer Series II 2400 CHNS/O Elemental Analyzer (Waltham, Massachusetts, USA), following the manufacturer's protocol.

Litter depth was also recorded, with four measurements taken to the nearest millimeter with vernier calipers (Mitutoyo, Kawasaki, Japan) within 1 m of pitfall traps and then averaged. Leaf area index (LAI) was measured directly over the trap using hemispherical photography and analyzed using Scion Image (Bréda 2003). Hobo temperature and humidity loggers (Onset, Bourne, Massachusetts, USA) were placed within a 2 m radius of each trap 20 cm above the ground on the middle transect at each site, and measured temperature and relative humidity every 15 min for the duration of the study.

Statistical analysis

To test for distance and age effects on species abundance and richness, a two-way factorial ANOVA was conducted with forest age and distance as factors. Indicator species analysis was performed for each age class on common species (>5 individuals). This analysis (presented in Appendix D: Table D1) was designed to provide information about likely habitat preferences of individual species. To enable this, plots were divided into mature (-15 , -35 m), near edge (15, 35 m), and far from edge (120, 200 m) categories for each forest age, and 70-m plots were excluded to keep a balanced design. This analysis was performed using the package *indicspecies* in R (De Cáceres et al. 2012). However, to ensure objectivity, unless otherwise stated, species categorized as mature-forest indicators for further testing of the response of such species to distance or succession were based on a previous study (Baker 2006), rather than the analysis of species from the present study.

For multivariate analyses, we used Bray-Curtis similarity matrices of square-root-transformed abundance data. We predicted DFI using nonlinear canonical analysis of principle coordinates (NCAP) to estimate the logistic gradient in the beetle community data (Millar et

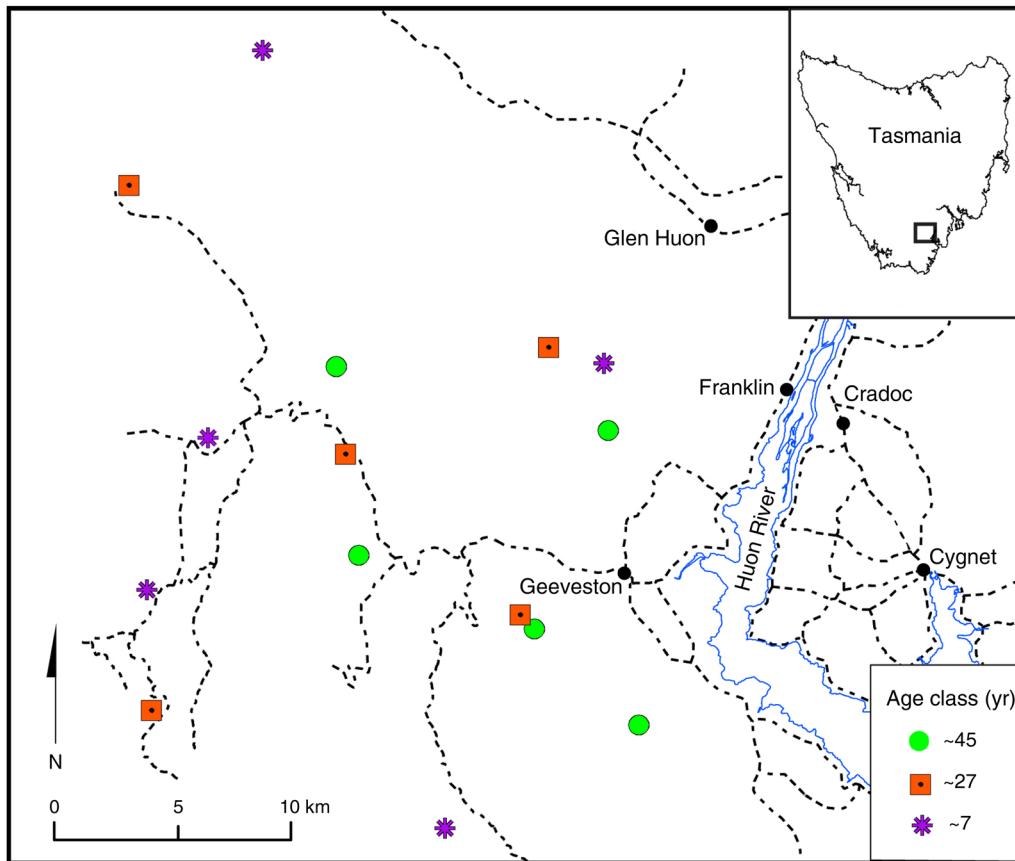


FIG. 1. Map of the study region in southern Tasmania, Australia. Forest chronosequences are shown by age class, dashed lines show major roads.

al. 2005). NCAP is an extension of canonical analysis of principle coordinates (CAP; Anderson and Willis 2003), with a link function to fit nonlinear models. Logistic curves were appropriate for our data, as we assumed that the community gradient would be steepest at the edge (Millar et al. 2005), particularly for the ~7-yr-old

sites. To test if distance was linked to community change, permutation tests were performed on community data, and confidence limits of the logistic model were generated by bootstrapping (see Millar et al. [2005] for details). DFI was defined as the point at which the community composition was estimated to be 95%

TABLE 1. Environmental variables used in the gradient forests model for each age class.

Variable	Unit	Sampling details
Carbon	concentration (%)	four soil subsamples within 5 m of the trap
Nitrogen	concentration (%)	four soil subsamples within 5 m of the trap
C:N ratio	C:N	four soil subsamples within 5 m of the trap
Soil pH	pH	four soil subsamples within 5 m of the trap
Conductivity	µS/cm	four soil subsamples within 5 m of the trap
Rock cover	percent cover	10 × 10 m quadrat at the plot
Bare ground cover	percent cover	10 × 10 m quadrat at the plot
Vegetation cover	percent cover	10 × 10 m quadrat at the plot
Litter cover	percent cover	10 × 10 m quadrat at the plot
Moss cover	percent cover	10 × 10 m quadrat at the plot
CWD cover	percent cover	10 × 10 m quadrat at the plot
Litter depth	mm	average of six measurements around the pitfall trap
Tree diameter	mm	average diameter at breast height of stems (cm) within 10 × 10 m quadrat at the plot
Plant diversity	N_1	exponential Hill's number (N_1 ; Chao et al. 2013) of plant species within the 10 × 10 m quadrat
Leaf area index	unitless	measured directly above the pitfall trap
CWD diameter	mm	largest CWD diameter within a 5 m radius of the trap
Distance	m	plot distance from mature forest edge; negative distances are in the mature forest

Note: Throughout the table, CWD describes coarse woody debris.

similar to interior disturbed forest along our 200-m transects in harvested secondary forest. Rare species were omitted from analyses if they occurred in <5 plots. NCAP was conducted in R version 3.02 (R Development Core Team 2013) using 9999 randomizations (see Supplement). The forest influence effect on the abundance of Tasmanian mature wet-forest indicator species (see Baker 2006) was analyzed using quasi-Poisson regression, as the variance was much greater than the mean.

The effects of site and distance from edge on beetle community composition were tested for each age using a mixed permutational MANOVA (PERMANOVA) model (Anderson 2001), treating site as a random effect and distance as a fixed effect. The permutation tests of significance were based on 9999 unrestricted permutations of the raw data where the three transects were considered replicates. PERMANOVAs were also used to test for successional age differences. In this case, only data sampled from mature forest (−15 and −35 m) and from 120 and 200 m into secondary forest were analyzed to avoid the edge transition zone. As mature plots were not independent of adjacent secondary forest plots, one-way fixed PERMANOVA was used to test for differences between mature forest and adjacent secondary forest for each age. Differences between secondary-forest communities were separately tested using a two-way PERMANOVA with age fixed and site as a random factor. CAP analysis was also used to test and visualize the differences between mature forest and each of the age classes. The CAP ordination was constrained by distance. These tests were conducted using PRIMER 6 PERMANOVA+ (Anderson et al. 2008). Two-way factorial ANOVA was also used to test the differences in abundance of species associated with mature forests (Baker 2006) between each secondary forest stage and corresponding mature forest, with age and disturbance (i.e., mature or secondary forest) as factors.

Distance-based linear models (DISTLM; Anderson and Legendre 1999, McArdle and Anderson 2001) were used to model community response to the environmental predictors (Table 1). The complete environmental data set was screened for multi-collinearity and, as DISTLM fits a linear model, leaf litter, rock, and bare ground cover were log-transformed to normalize variance. The procedure was performed using the BEST selection procedure in PRIMER 6 PERMANOVA+ (Anderson et al. 2008). Gradient forest modeling was not appropriate for use on the successional data set as, unlike DISTLM, this modeling procedure is not suitable when only a low number of plots are considered (<100; R. Thomson, *personal communication*).

To understand how vegetation and environmental covariates affected community turnover within age classes, we used gradient forest modeling (GFM; Ellis et al. 2012) on the beetle abundance data set. GFM is an extension of the random forests machine learning tree ensemble model that analyzes community-wide

responses to environmental gradients (Ellis et al. 2012). Random forest methods are useful for understanding community responses to gradients because they do not assume linearity of predictor or response variables and are not sensitive to highly correlated environmental variables (Strobl et al. 2008). GFM modeling assembles a large number of decision trees, and collates the distribution of splits in the tree (Thomson et al. 2014). Cumulative distribution of splits or cumulative importance curves are generated for each species and provide a measure of community change in n -dimensional environmental space (Thomson et al. 2014). Each tree is generated using a random partitioning procedure based on a subset of plots and cross-validated using the remaining plots. Each split is selected from ~27% of the predictor variables, in our case five out of 19 environmental variables. Covariate importance is calculated by randomly permuting each variable and estimating the degradation of explanatory performance (see Ellis et al. [2012] for more details). We modeled changes in community composition in each age class using 17 of the environmental variables measured (Table 1; two of the 19 variables measured were collinear, and thus excluded from analysis). Microclimatic variables were excluded because they were only available for one transect per site. All plots were included, beetle abundance data was square-root-transformed, and species were omitted from analysis if they occurred in <5 plots in each age. In total, 1000 trees were generated for each species. GFM analysis was conducted in R using the package *gradientForest* (package *available online*).⁵ R script is provided in the Supplement.

Nonlinear regressions were conducted in R to further assess the relationships between distance and temperature, humidity, and other important variables identified in the GFM for each age.

RESULTS

Beetle forest influence gradient

In total, 11 830 beetles from 271 species were collected. There was no overall significant relationship between distance from edge and total beetle abundance and species richness in any age class, although average beetle abundance was highest in the 15-m plots in all ages. The NCAP results, however, showed that beetle assemblage composition was strongly correlated with distance from edge (Fig. 2). The DFI and community composition varied between secondary forest age classes. The NCAP model showed a sharp community composition gradient from mature forest at the edge of both the ~7- and ~27-yr-old classes of secondary forest with only a narrow predicted DFI (~13.2 and 20.4 m respectively; Fig. 2). In contrast, the gradient was gradual across the edge of the ~45-yr-old age class of

⁵ <https://r-forge.r-project.org/projects/gradientforest>

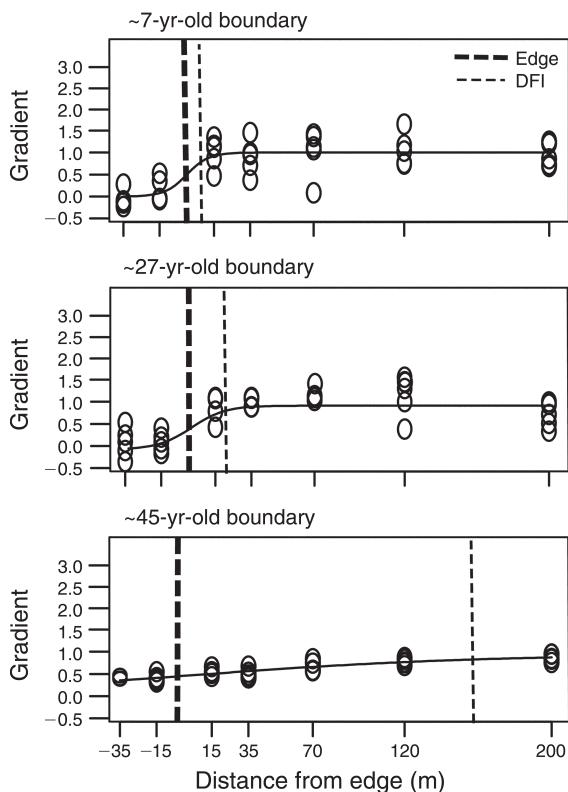


FIG. 2. Nonlinear canonical analysis of principle coordinates (NCAP) ordination of three forest ages (shown as a transect encompassing the boundary between a secondary forest and a mature forest) fitted (solid line) to beetle community data (open circles) using the logistic model. Gradient refers to the gradient of community change across the edge on the Bray-Curtis scale (i.e., 0–1). Estimated depth of forest influence (DFI) for each age class is 13.23 m (total $R^2 = 0.6317$, 95% confidence interval [CI] = 2.2–161.3 m, $P < 0.001$) for ~7-yr-old secondary forest; 20.4 m (total $R^2 = 0.6264$, 95% CI = 2.2–103.6 m, $P < 0.001$) for ~27-yr-old regrowth; and 175.8 m ($R^2 = 0.8148$, 95% CI 127.7–254.6 m, $P < 0.001$) for ~45-yr-old regrowth. DFI was defined as the point at which the community composition was estimated to be 95% similar to interior disturbed forest along our 200 m long transects in secondary forests.

secondary forest, which had an estimated DFI of 176 m (Fig. 2). The curve did not plateau at 200 m from the forest boundary and confidence intervals extended beyond 200 m, which suggests that the transects were not long enough to incorporate the entire edge gradient for this age class. The magnitude of community change was also much less for this age (~0.2, i.e., 20%) over the transect, compared to ~1 (i.e., 100%) for the younger stages. The confidence intervals were large for each forest age class (Fig. 2).

The PERMANOVA results confirmed that distance from mature forest was an important factor for beetle communities in each age class (PERMANOVA pairwise tests: for ~7-yr-old, pseudo $F_{6,6} = 1.366$, $P = 0.008$; for ~27-yr-old, pseudo $F_{4,6} = 1.47$, $P = 0.018$; for ~45-yr-old, pseudo $F_{4,6} = 1.31$, $P = 0.013$).

The relationship of pooled abundance of known mature-forest indicator species with distance from edge also varied among successional stages (Fig. 3). There were significant distance gradients in mature-forest indicator abundance across ~7- and ~27-yr-old edges (for ~7-yr-old: $P < 0.001$, deviance = 166.71; for ~27-yr-old, $P = 0.017$, deviance = 265.62; Fig. 3a, b) but not for ~45-yr-old edges ($P = 0.108$, deviance 197.68; Fig. 3c). All beetle species that were common in mature forest were also found in ~45-yr-old forest, and all but

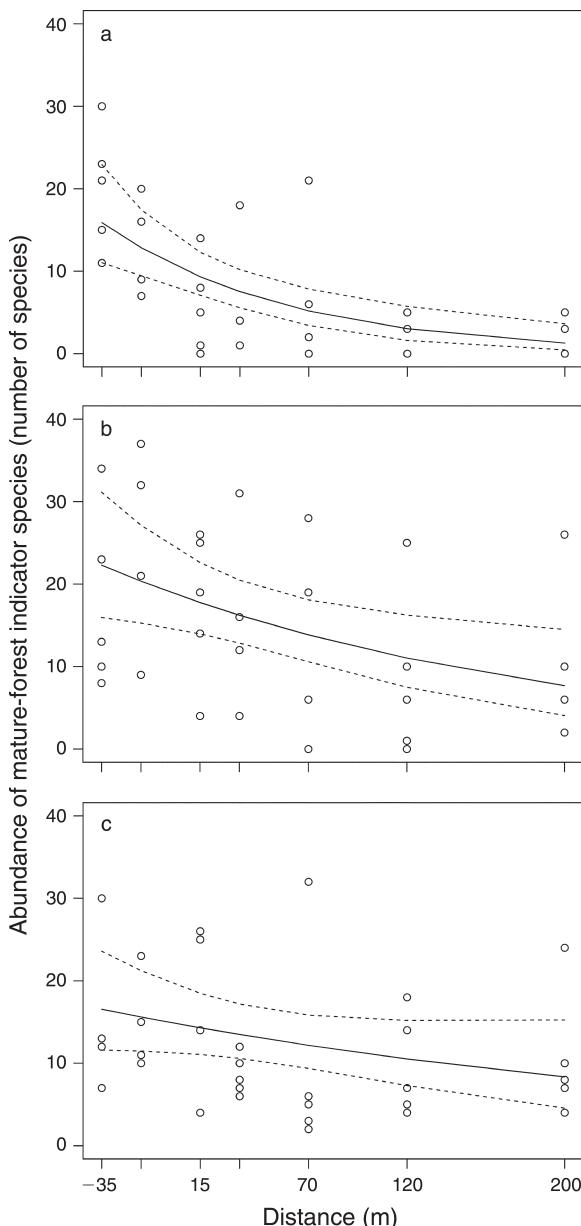


FIG. 3. Quasi-Poisson regressions (solid lines) of pooled mature-forest indicator species abundance vs. distance from mature into secondary forest of three ages: (a) ~7-yr-old forest ($P < 0.001$), (b) ~27-yr-old forest ($P = 0.017$), and (c) ~45-yr-old forest ($P = 0.112$). Dashed lines indicate 95% CI.

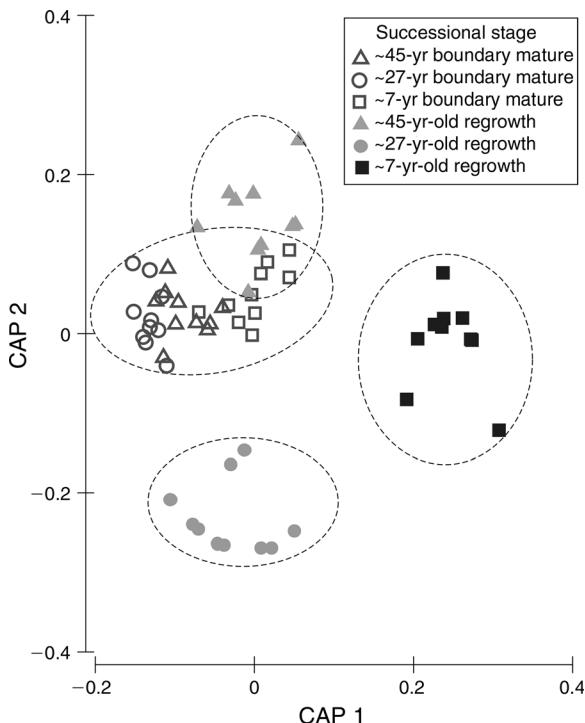


FIG. 4. Canonical analysis of principle coordinates (CAP) constrained ordination of beetle succession data comparing the mature forest communities (boundary mature) to the secondary (regrowth) forest ($R^2 = 0.9285$, $P < 0.001$). Dashed ovals indicate groups distinguished by PERMANOVA pairwise tests.

one of these (*Austronemadus* TFIC sp. 03 (Leiodidae)) was relatively common (see Appendix E).

Beetle succession

The CAP ordination examining differences in beetle community between forest age classes showed a clear separation ($R^2 = 0.9285$, $P < 0.001$) of both ~7- and ~27-yr-old secondary forest on the CAP 2 axis from the mature forest plots (Fig. 4). However, the beetle community in ~45-yr-old regrowth was only weakly differentiated from mature forest. The one-way PERMANOVA confirmed that each age of regenerating forest was distinct from mature forest (for ~7-yr-old, pseudo $F_{1,18} = 2.89$, $P < 0.001$; for ~27-yr-old, pseudo $F_{1,18} = 2.29$, $P = 0.009$; for ~45-yr-old, pseudo $F_{1,18} = 2.04$, $P = 0.002$).

The pooled abundance of species associated with mature forests showed a similar pattern (Fig. 5). Factorial ANOVA was significant for age ($F_{2,54} = 4.78$, $P = 0.012$) and disturbance (mature forest or secondary forest; $F_{1,54} = 36.120$, $P < 0.001$) effects, but not significant for the age \times disturbance interaction ($F_{2,54} = 2.377$, $P = 0.103$). Holm-Sidak post hoc comparisons showed no significant difference in abundance of species affiliated with mature forest in the mature forests associated with the different secondary forest age classes. The abundance of beetles affiliated with mature

forest in ~45-yr-old secondary forest was statistically indistinguishable that in from mature forests, but in both ~7- and ~27-yr-old forest, the pooled abundance of those beetles was significantly lower than in mature forest communities.

The DISTLM procedure showed that litter cover was the factor most strongly associated with differences in beetle assemblages among age class (16.72% of the model variance, $P < 0.001$). Other major factors were soil C:N (15.67% of model variance, $P < 0.001$) and LAI (7.9% of model variance, $P < 0.001$). Nitrogen and rock cover were excluded from the model, as they were strongly collinear with other variables in the model. There was a significant age effect on litter cover (ANOVA $F_{2,54} = 13.502$, $P < 0.001$) and LAI ($F_{2,54} = 10.791$, $P < 0.001$), with average litter cover and LAI greater in the ~45- and ~27-yr-old sites than the ~7-yr-old sites. There was also a significant age effect on C:N ratio ($F_{2,54} = 10.704$, $P < 0.001$), but conversely, the C:N ratio was higher in the young forest than in the older secondary forest. None of these factors showed a significant difference in the mature forest plots between age classes of the associated secondary forest (see Appendix B: Fig. B1).

Gradient forest modeling

The environmental variables selected by the GFM model and their relative importance in explaining the beetle community composition varied among age classes (Fig. 6). The most important factors in ~7-yr-old sites were leaf litter depth and soil C:N ratio. The C:N ratio

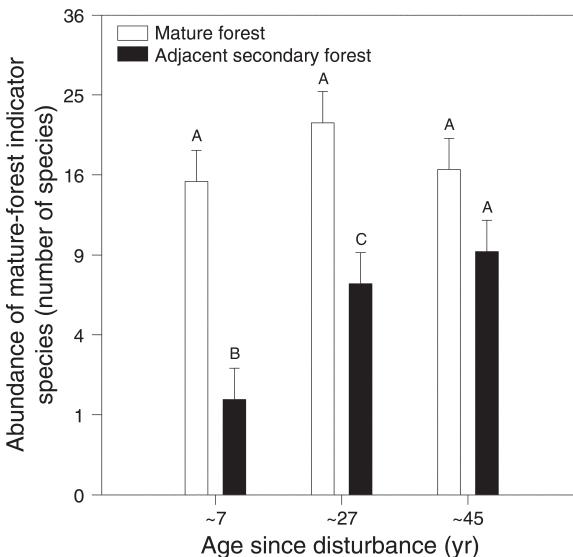


FIG. 5. Abundance of mature-forest indicator species (mean + standard error) by age class. There were significant age (ANOVA, $F_{2,54} = 4.78$, $P = 0.012$) and disturbance (mature vs. secondary forest; ANOVA, $F_{1,54} = 36.120$, $P < 0.001$) effects. Classes marked with a common letter were not significantly different from each other at the 0.05 level of confidence in the Holm-Sidak post hoc comparisons.

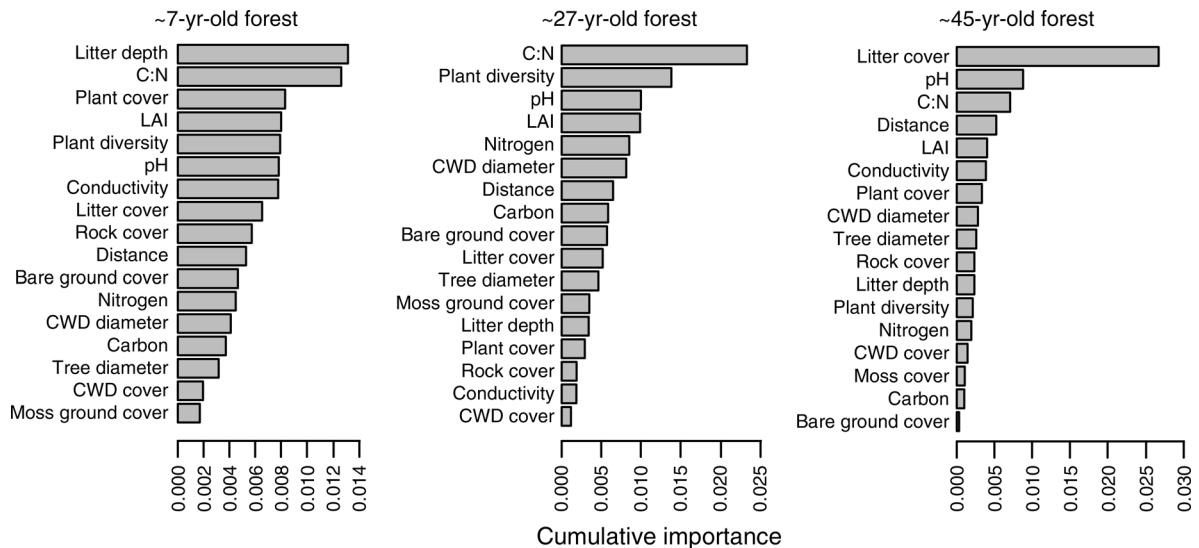


FIG. 6. Gradient forests model ranking each environmental variable by relative importance (cumulative importance) in predicting species assemblage within forest age class. Here, CWD is coarse woody debris, and LAI is leaf area index.

and plant diversity were also important in ~27-yr-old sites, but less so in ~45-yr-old sites. Litter cover was only of high importance in ~45-yr-old sites, where it had by far the greatest cumulative importance, whereas litter depth was the factor explaining the most variation in young forest. LAI, pH, and distance were relatively important in all three age classes. Running the GFM excluding mature forest plots provided congruent results, but we have presented the complete models because GFM is more reliable with a greater number of plots (preferably >100; R. Thomson, *personal communication*).

The three age classes showed different cumulative importance curves for environmental factors (see Appendix C). With increasing LAI, for example, the community turnover was quite steep in ~7- and ~27-yr-old forest, but much more gradual in older secondary forest. Similarly, as the C:N ratio increased, species turnover changed rapidly in the early and intermediate stages, but in the ~45-yr-old forest beetle community, the turnover was more gradual. The most rapid turnover in ~45-yr-old sites related to litter cover. Consistent with the NCAP analysis results, the distance curves for the ~7- and ~27-yr-old communities showed most of the species turnover occurred within 50 m of the forest boundary, but in the old forest there was only a shallow gradual change.

Only two of the environmental parameters ranking among the top five in the GFM models were significantly associated with distance from mature forest using linear and nonlinear regression (only significant regressions [$P \leq 0.05$] are presented in Appendix D: Figs. D1–D3). Litter depth was negatively correlated with distance, but only in the ~7-yr-old age class. In this age class, litter depth was also correlated with total beetle abundance. LAI was correlated with distance in

each age class, with mature forest LAI rapidly declining at the edge into secondary forest. There was no relationship between C:N, pH, nitrogen, plant diversity/cover, or litter cover with distance from edge in any age class.

The average midday temperature data showed positive relationships with distance from mature forest in ~7- and ~27-yr-old secondary forest, but not in ~45-yr-old secondary forest. There was no correlation between total beetle abundance and temperature.

DISCUSSION

Edge gradients and succession

Our results showed not only that the beetle communities showed strong succession, with composition approaching that of mature forest by ~45 years (Figs. 4 and 5), but forest influence also persisted until at least that stage, albeit with decreasing magnitude. Associated with this declining magnitude was an increase in the estimated DFI, from ~13 m in the youngest forest class to ~175–200 m in the oldest forest (Fig. 2). Even though the estimated DFI in the young forest was less than the distance to the first plot in the clear-fell, CAP ordination confirmed that the 15-m plots were associated with the gradient of species composition within the harvested area (N. M. Fountain-Jones, *unpublished data*). As indicated by the wide confidence intervals associated with the NCAP, there is uncertainty associated with the distance estimate of DFI, which may be greater than 13 m. It is also possible that the DFI actually extends beyond our 200-m transect length, although testing this is difficult because the maximum length of transects is limited by the size of clearcuts in these forests. These distances are all greater than that reported for beetles by Roume et al. (2011), possibly because the eucalypt

forests on either side of our boundaries showed greater biotic and abiotic similarities than the woodland and agricultural fields in the French study. For example, even ~7 years after logging, emerging eucalypts provide some shade and litter resources that may lessen the severity of the gradient. Furthermore, unlike in agricultural fields, the substantial coarse woody debris remaining after logging may aid species recovery, since many of the species we collected are known to be saproxylic. Our results also indicate that mature-forest species continue to occur in secondary forest, although their abundance declines with distance from mature forest. This illustrates that forest edges are permeable boundaries for beetles (Ries et al. 2004), even when there are large differences in habitat conditions, as, for instance, occurs soon after harvesting.

The longer but much weaker forest influence gradients in older (~45-year-old) secondary forest (Fig. 2) indicate that either mature forest is still acting as a source population for beetle recolonization, or beetles affiliated with mature forests are gradually moving further into harvested areas with time. Although the latter process could be due to constraints on mobility of mature-forest beetles, it could also reflect other aspects of forest influence, such as a greater density of regenerating rainforest tree species nearer the edge (Tabor et al. 2007). By ~45 years after harvesting, these trees will approach maturity and provide litter and shade.

Our observations that ~45-year-old forest beetle communities were relatively similar to those of mature forests (Figs. 4 and 5) are broadly consistent with the 35–50 years suggested for near-complete beetle assemblage recovery in Atlantic forest in Brazil (Hopp et al. 2010) and 50–70 years for carabids in boreal forests (Koivula et al. 2002, Buddle et al. 2006). However, the persistence of edge gradients shows that this rate of ecological reassembly of mature forest source communities is constrained by how close the secondary forest is to mature forest. This relatively long edge gradient is comparable to estimated dispersal distances from mature into long-established secondary forest for Scandinavian beetle fungivores (Jonsson and Nordlander 2006). Thus, it would be worthwhile to investigate whether differences between secondary forest and mature forest beetle communities may be persistent, as was found in hemlock forests (Latty et al. 2006).

Species responses to succession

This study clearly demonstrates distinct beetle successional assemblages in each forest age. In Tasmania, most species considered indicators of young (~3-year-old) forest by Baker (2006) were also indicators in our ~7-year-old plots (see Appendix E). These species may be pyrophilic, or responding to the changed habitat conditions such as increased light or altered food resources. For example, the early seral indicator *Mecyclothorax ambiguus* (Carabidae: Psydrinae) has also been collected in native grassland (Michaels

1999), which may suggest a preference for open conditions. As observed in other studies in Tasmanian wet forests, young seral species were uncommon in ~27-year-old forest, and not collected at all at the ~45-year-old sites (Michaels and McQuillan 1995, Baker 2006). The overall change in community gradient in the ~27-year-old regenerating forest appears to be mainly driven by mid-successional specialist species, including *Microsilpha* ANIC Thayer sp. 15 (Staphylinidae: Microsilphinae) and *Decilaus* TFIC sp. 03 (Curculionidae: Cryptorynchinae) (see Appendix E for species abundance data). However, mature-forest specialists are generally more abundant in the ~27-year-old regenerating forest than in ~7-year-old forests, and the slope of their decline in abundance with distance from edge is shallower (Fig. 3).

Environmental modeling

The observation that leaf litter attributes were the most important explanatory variables in ~7- and ~45-year-old sites (Fig. 6) makes sense, because leaf litter is the primary habitat for forest ground-dwelling beetle species and affects the microspatial distribution of some species that prefer open ground (Magura et al. 2005). The decline in litter depth with distance in the ~7-year-old sites suggests that mature forest is providing additional inputs of leaf litter near edges, and this habitat provision might be significant for facilitating beetle recolonization. These results are consistent with previous studies indicating that litter is an important predictor of beetle recolonization and succession (Michaels and McQuillan 1995, Magura et al. 2005, Nakamura et al. 2009).

The importance of plant diversity as an explanatory variable for forest influence in young and intermediate edges may reflect its relationship with diversity of leaf litter chemistry (Bardgett and Shine 1999). Since monotypic litter contains lower abundance and diversity of micro-arthropods than litter from several plant species, plant diversity is likely to have cascading effects on arthropods (Hansen 2000). The increased structural diversity supplied by rainforest plants typically present near mature edges (Tabor et al. 2007; J. Balmer, *unpublished data*) may also facilitate recolonization of beetle species affiliated with mature forests.

The importance of soil C:N ratio in the community gradient model for each forest age class as well as the beetle succession model (Fig. 6) may reflect impacts on predatory beetles resulting from the sensitivity of common prey (e.g., mites and springtails) to this ratio (Noti et al. 2003, Jensen et al. 2006). The lack of a relationship between distance and C:N ratio may be due to high spatial variability in levels of both C and N (Shaw et al. 2008). C:N was affected by forest age, with ~7-year-old stands having a higher C:N than the older secondary forest, presumably due to the migration of nitrogen from the soil into the canopy as the forest ages (Finzi et al. 1998). Few studies have measured beetle

community responses to soil C:N ratio, yet other soil variables are known to be important (Schwerk and Szyszko 2007, Antvogel and Bonn 2008). Soil pH affects carabid communities (McCracken 1994, Schwerk and Szyszko 2007, Antvogel and Bonn 2008) and was an explanatory factor in the GFM. However, as with all variables, the association of beetle communities with pH may not be causal, it may simply reflect a strong link between pH, soil moisture, and LAI (Antvogel and Bonn 2008).

The strong predictive power of LAI (Fig. 6) suggests that forest cover has a significant impact on beetle communities, presumably mediated by effects on microclimate. High LAI results in significantly lower temperatures and evaporative demand in these forests (Baker et al. 2014). There were strong temperature and LAI gradients across the ~7-year-old edges, but the gradients in later successional stages were less pronounced. Even ~7 years after harvest, the 15-m and 35-m plots had a greater LAI and were cooler compared to plots further away from the boundary, showing a strong forest influence effect. In the GFM, increasing LAI explains species turnover predominantly in the early and intermediate age sites and little in ~45-year-old sites. LAI was also important in explaining the beetle community successional changes. Canopy closure occurs in this forest type at ~20 years after harvest and clearly had an impact on community composition in both our older regrowth age classes. Canopy closure facilitates increased moisture content of the surface soil and a decrease in temperature and humidity fluctuations (Entling et al. 2007). For some mature-forest species, canopy closure may therefore be the most important factor enabling successful recolonization beyond shaded edge conditions (Koivula et al. 2002, Grimbacher et al. 2006, Nakamura et al. 2009). However, collinearity of variables in the model results in some ambiguity about which factors drive the patterns observed here. Experimental work on the effects of environmental variables on beetle recolonization would help resolve this ambiguity.

Conservation and management outcomes

This study clearly illustrates the importance of maintaining mature forest in production forest landscapes through its impacts on the successional trajectory of beetle communities in adjacent secondary forest. Not only do these mature forests have ecologically important effects on leaf litter inputs, microclimate, and shading on nearby regenerating forest, but they also provide sources of mature-forest species. The nearly complete reassembly of mature forest communities within ~175–200 m by ~45 years after harvest shows how retained mature forest can assist species reestablishment and persistence in secondary forest landscapes (Chazdon et al. 2009, Hopp et al. 2010).

Our results are relevant to forest managers looking to build connectivity into fragmented landscapes, as sec-

ondary forests with mature forest boundaries may harbor a comparable beetle community over time. Maintaining sufficient mature forest embedded within harvested landscapes should be a high priority, since our study demonstrates that as well as providing habitat for species requiring this successional stage, they appear to influence successional dynamics of the entire landscape. Furthermore, this study shows the conservation potential of retention forestry approaches like aggregated retention, where unlogged patches are retained within harvested areas (Baker et al. 2009). Current practices for designing aggregated retention harvests sometimes require that the harvested area is no more than one mature tree height from retained mature forest (forest influence target; Baker and Read 2011). The almost complete recovery of beetle assemblages associated with mature forests up to 200 m from mature forest by ~45 years indicate that this one-tree height target is relatively conservative for beetles, at least for this age class, although the estimated DFI was substantially less than one mature forest tree height for ~7- and ~27-year-old age classes. However, since our study surveyed clear-cut edges rather than gradients from small isolated aggregates, the poorly understood effects of mature forest patch size or total quantity of mature forest in the surrounding landscape may also be important limitations to the reestablishment of beetles, which require further study.

This study was one of the first to analyze the long-term impacts of forest influence on forest biodiversity. The relatively rapid recovery of mature-forest successional communities was driven by edge recolonization coupled with litter input and microclimate factors. Mature forest stands are not necessarily islands in a secondary forest mosaic, but instead are critical components facilitating connectivity and succession in fragmented landscapes.

ACKNOWLEDGMENTS

This project was funded by the Australian Research Council Linkage Grant LP100100050. We thank Tom Spies and Jerry Franklin for their advice. We also thank Kaely Kreger and Bianca Deans for field/lab assistance and soil data, Kevin Bonham and Lynne Forster for assistance with beetle identification and sorting, and Peter Harrison and Russell Thomson for statistical advice. We also thank Forestry Tasmania for financial and logistical support and access to the Tasmanian Forest Insect Collection (TFIC). We are grateful for reviewer comments that improved the manuscript.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–E and the Supplement are available online: <http://dx.doi.org/10.1890/14-0334.1.sm>

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.10c30>