Assessing rainforest restoration: the value of buffer strips for the recovery of rainforest remnants in Australia's Wet Tropics

LAURA J. SONTER[1], DANIEL J. METCALFE[2] and MARGARET M. MAYFIELD[1, 3]

Throughout the tropics, forest remnants are under increasing pressure from habitat fragmentation and edge effects. To improve the conservation value of forest remnants, restoration plantings are used to accelerate and redirect ecological succession. Unfortunately, many restoration projects undergo little to no evaluation in achieving project goals. Here we evaluate the success of one common restoration technique, "buffer strip planting," at the Malanda Scrub in North Queensland, Australia. Buffer strips are used to reduce the impacts associated with edge effects and improve overall forest quality. To evaluate the success of the Malanda project, we compared the microclimate, understorey community structure and functional trait-state diversity (functional diversity) for a range of plant functional traits along the original forest edge, a reference forest edge, and the interior forest of the Malanda reserve. We found the buffer strip restored the original forest edge to interior forest conditions for the majority of measured features. Edge effects were not found more than 5 m from any measured edge, and edge effects penetrated to even shorter distances along the buffer strip edge. The buffer strip appeared to have a similar microclimate (here represented by soil temperature) and physical structure; however, it did not (after 14 years) closely resemble the interior forest floristically nor did it have the same functional diversity for measured traits. Results suggest that the buffer strip was successful in reducing edge effects but not in restoring the forest to original conditions within 14 years.

Key words: Rainforest restoration, Buffer plantings, Edge effects, Plant functional traits, Functional diversity, Biodiversity

INTRODUCTION

It is well known that land clearing is a significant threat to biodiversity (Bierregaard *et al.* 1992; Lindenmayer and Fischer 2006). In many tropical regions around the world, forests are selectively cleared in patches, fragmenting the landscape and leaving forest remnants interspersed within a matrix of human land uses. While these remnants do have conservation value for some native plants and animals (Mayfield and Daily 2005), many are small, isolated and show extensive signs of degradation (DeFries *et al.* 2005).

Artificial edges created as the result of habitat fragmentation are a major cause of forest degradation, being both more abrupt and actively maintained than natural edges (Saunders *et al.* 1991). Numerous studies have shown how edge effects negatively impact biodiversity (e.g., Fahrig 2003). Though the dramatic physical and biological changes associated with artificial edges (known as edge effects) are a concern in all systems as they are also well known to vary among ecosystems (Turner 1996).

Rainforest remnants are extremely important for conserving biodiversity in fragmented tropical landscapes and thus their protection and rehabilitation is critical (Lamb *et al.* 2005). Techniques to increase forest conservation value and reduce the impacts of edge effects are diverse, but one common approach involves planting strips of native vegetation along artificial forest edges (Parrotta *et al.* 1997; Tucker and Murphy 1997). This approach is generally referred to as "buffer strip planting." The specific goals for using buffer strips are to increase forest area and to protect the interior forest from edge effects (K. Freebody, Personal Communication). Evidence of success in achieving these aims, however, is rare and unfortunately, few restoration projects undergo assessment of progress towards stated goals and little is known about general or site specific best practices (Freeman 2004; Freebody 2007).

Ecological studies that aim to evaluate the success of forest restoration projects to increase site conservation value are becoming more common (e.g., Kanowski *et al.* 2006). Our study adds to this literature as one of the first evaluations of a buffer strip planting and its ability to reduce the impacts of edge effects and create an ecosystem similar to interior forest conditions over a relatively short time period. To do this we evaluate a 14-year-old buffer strip at the Malanda Scrub in Australia's wet tropical highlands. The specific questions we ask about this conservation planting are:

1. Has the original (pre-planting) edge of the buffered forest become more similar to a mature interior forest compared to a non-buffered (reference) edge?
2. Do edge effects penetrate less far into the buffered forest than into the non-buffered forest?

[1]The University of Queensland, School of Biological Sciences, St Lucia Campus, Brisbane, Qld 4072 Australia
[2]CSIRO Ecosystem Sciences, Atherton, Qld 4883 Australia
[3]Corresponding author: m.mayfield@uq.edu.au, Tel: +617 3365 1685, Fax: +617 3365 1655

PACIFIC CONSERVATION BIOLOGY Vol. **16:** 274–288. Surrey Beatty & Sons, Sydney 2011.

3. Is the microclimate, community structure and functional diversity of the buffer strip itself more similar to mature interior forest than the non-buffered forest edge?

We expected that, after 14 years, the buffer strip would have begun to represent interior forest conditions. This was expected considering that: 1) other studies show recovery of species diversity and structural features in naturally regenerating forests by 15–20 years-post clearing (Nicotra *et al.* 1999; Kanowski *et al.* 2003; Kariuki and Kooyman 2005); and 2) the Malanda project underwent assisted regeneration, where the planted species acted to catalyse ecological succession for forest recovery.

We also expected the impacts of edge effects to penetrate 10-30 m into the forest from the new edge given studies of tropical forest edges in other locations (Hester and Hobbs 1992). Additionally, we expected "edge sealing" (the natural successional process through which forest edges become grown over to seal the interior forest from further damage; Gascon *et al.* 2000) to reduce the penetration distance of edge effects along the non-buffered reference edge compared to the newly buffered edge.

Finally, we expected species richness in the buffer strip to be similar to that of the interior forest. This was because of the high diversity of planted species associated with the "mixed species planting model" used for the Malanda buffer strip (Freebody 2007). This model involves planting numerous native species (in this case 80 species) representative of the interior forest (see Appendix A for planted species list).

METHODS

Study site

Our study took place in April 2008 in a large remnant of complex mesophyll vine forest at the Malanda Scrub Reserve on the Atherton Tablelands in North Queensland's wet tropics (S 17° 21', E 145° 36', 747 m asl). The Malanda Scrub (43.2 ha) is split by a road into the Malanda Falls Scenic Reserve (MFSR, 13.6 ha) and the Malanda Falls Conservation Park (MFCP, 29.6 ha; Fig. 1). The remnant was left when the surrounding area was cut in the early 1900s and the site is now surrounded by pasture and maintained lawns.

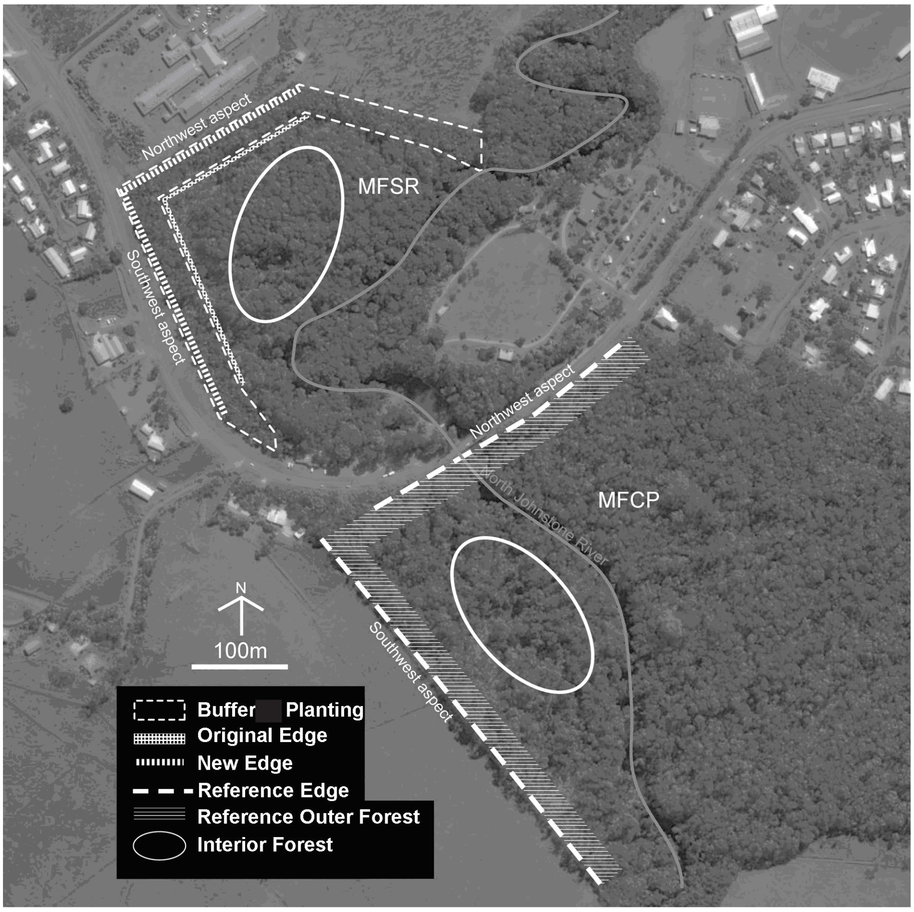

Fig. 1. Aerial photograph of the Malanda Scrub (source: GoogleEarth, March 2008). The northern forest patch is the Malanda Falls Scenic Reserve (MFSR) and the southern patch is the Malanda Falls Conservation Park (MFCP). Edge categories are shaded on the map to differentiate these from Forest categories. Shading is not to scale.

In 1992, a 30 m wide mixed species buffer strip was planted along the SW and NW facing edges of MFSR (henceforth "Buffered Forest"). No buffer was planted around MFCP (henceforth "Reference Forest"). Eighty local tree species representing elements of the presumed pre-disturbance community were planted in the buffer strip. Ninety percent of species were mid- and upper canopy tree species and 10% were early successional tree species (see Appendix A). Seedlings were planted uniformly 1.8 m apart.

Sampling design

We surveyed the microclimate (measured as soil temperature and canopy cover), community structure and understory plant diversity of the MFSR and the MFCP. Sampling was done in a semi-nested design for three Forest categories (Buffered Forest, Reference Forest, and Interior Forest; Fig. 2). For each Forest category, we sampled 10 replicate 40 m long transects with 1 × 1 m quadrats placed at 0, 2.5, 5, 10, 15, 20, 25, 30, 35 and 40 m from the edge. Buffered Forest and Reference Forest transects were positioned perpendicular to forest edge and Interior Forest transects were placed randomly throughout the forest but at least 50 m from any edge. All transects were spaced at least 50 m apart. Given the size of the reserve, this design limited pseudo-replication, which is somewhat inevitable in a single reserve study.

Microclimate and community structure

In each quadrat, we recorded microclimate and community structure features previously found to vary as a consequence of edge effects (Murcia 1995). All measured features are listed in Table 1 along with their measurement details. For all statistical analysis described below, all rainforest life forms (Table 1) were arcsine-transformed proportions to permit use of these bounded features in nested analyses of variance (ANOVA; Zar 1999).

In addition to the features listed in Table 1, we also calculated species richness (Hurlbert 1971), species evenness (Pielou 1966), Simpson's diversity index (Simpson 1949) and Shannon's diversity index (Pielou 1975). Each of these diversity metrics highlight a distinct component of species diversity, and have been shown to provide more detailed information about diversity than richness alone (Magurran 1988).

Functional trait data collection

The definition of functional diversity varies in the literature. Here, we defined it as the richness and composition of trait states of individual plant functional traits of known importance to ecological processes. We focused on individual traits as edge effects have been linked to biased losses of species from particular functional groups (Putz *et al.* 1990; Sieving and Karr 1997). Examination of individual functional traits allowed for a detailed assessment of which traits are most strongly influenced by edge effects. This approach is increasingly common in studies of human-impacted plant communities (McIntyre *et al.* 1999; Mayfield *et al.* 2005).

For all 106 angiosperm species sampled, we recorded data on six functional traits: growth form, fruit type, dispersal mode, seed size, specific leaf area (SLA) and pollination syn-

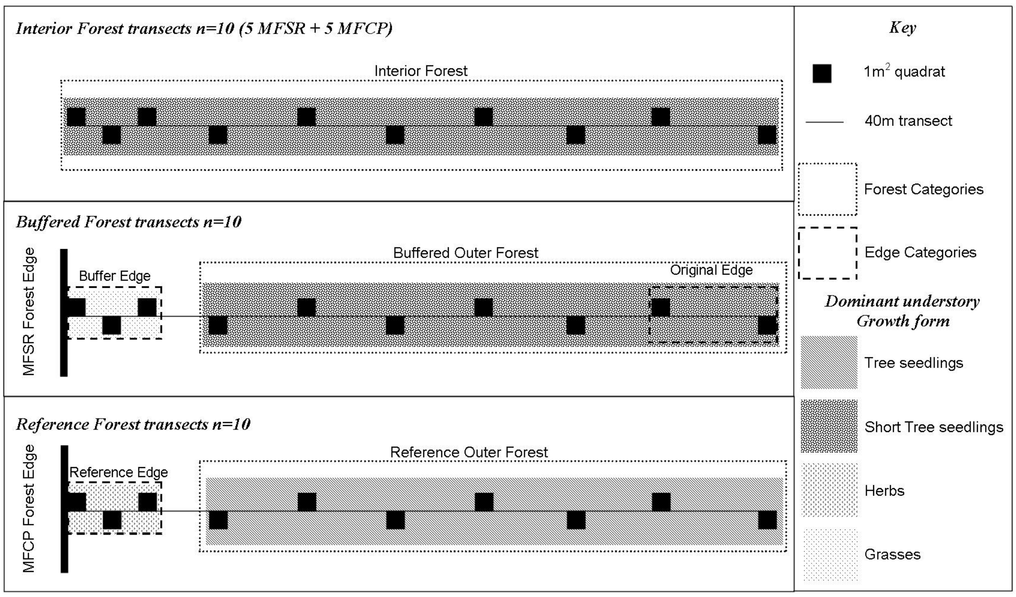

Fig. 2. Forest sampling design. For comparisons among Edge categories, quadrats within dashed boundaries were used. For analysis of edge effect penetration width, all quadrats were used. For comparisons among Forest categories, quadrats within dotted boundaries were used. The "Dominant understorey growth form" for each category is the growth form found most commonly in category quadrats, it does not necessarily reflect a significant dominance.

Table 1. Details of the microclimate and community structure features examined in this study. Features are reflective of edge effects and are of potential importance to ecosystem recovery following restoration.

Feature	Measurement details
Canopy cover	Measured four times (N, S, E, & W) for each quadrat using a spherical densiometer.
Soil temperature	Measured four times for each quadrat at a depth of 10 cm with a soil thermometer.
Leaf litter depth	Measured five times (each corner and centre) for each quadrat.
Vegetation cover (%)	Estimated for each quadrat (per m^2).
Grass cover (%)	Estimated for each quadrat (per m^2).
Understorey stem height	Measured height of all plants in quadrats with more than 10 leaves/leaflets and less than 1 m tall.
Understorey stem density	Recorded no. of stems in quadrats for plants with more than 10 leaves/leaflets and less than 1 m tall.
Understorey plant diversity	Recorded species identity in quadrats for plants with more than 10 leaves/leaflets and were less than 1 m tall.
Tree density	Recorded number of trees within 3 m either side of the 40 m transect.
Presence of rainforest life forms: • Vines • Lianas • Buttress roots • Vascular epiphytes	Recorded the number of trees (taller than 2 m, dbh greater than 5 cm, and within 3 m either side of the 40 m transect) that provided habitat to each rainforest life form.

drome (Table 2). These traits were selected for their known importance in forest restoration and functions in community development and ecological succession (Jordano 1995; Grubb and Metcalfe 1996; Petchey and Gaston 2006).

SLA was analysed as mean values measured from one leaf per species per quadrat using a standard methodology (Westoby 1998). Remaining trait state data were recorded from published floras (Grubb *et al.* 1998, Stanley 2002; Hyland *et al.* 2003; Cooper and Cooper 2004, US Forest Service 2008) and unpublished trait databases (J. Wells, Personal Communication). In this study seed size was used as a categorical trait due to our reliance on data from floras, which generally only report seed size ranges (e.g., 10–12 mm). SLA was converted to a categorical trait for MDS and ANOSIM analyses since these tests use categorical data for the calculation of similarity matrices. For all analyses, each species was permitted one trait state per categorical trait (Appendix B). When more than one trait state existed for a species we used the most commonly found trait state in published accounts (Stanley 2002; Hyland *et al.* 2003; Cooper and Cooper 2004). Species with missing trait state data were excluded from specific analyses. Missing trait state data were not clustered by Forest category or phylogenetic group. See Appendix B for sampled plants and their associated functional traits.

Functional diversity (trait states per trait) was calculated for all below analyses. This was done as trait state richness per m^2 for categorical

Table 2. Functional traits used for trait analyses. The number of recorded specimens with each trait state is given in parenthesis. The values given on the header row is the number of specimens used for the analysis of each trait.

Growth Form[a] (460)	Fruit Type (451)	Dispersal Mode[b] (449)	Seed Size[c,d] (449)	Specific Leaf Area[c,e] (421)	Pollination Syndrome (322)
Tall tree (164)	Berry (75)	Flying Endozoochory (339)	Average: (10.7)	Average: (179.6)	Bee (80)
	Capsule (51)				Beetle (194)
Short tree (158)	Cone (0)				Butterfly (8)
	Drupe (201)	Ground Endozoochory (25)	L (89)	H (79)	Fly (10)
Shrub (59)	Fig (3)		M (85)	I (266)	Insect (5)
Vine (45)	Follicle (2)		S (275)	L (76)	Moth (1)
Herb (34)	Nut (32)	Passive (12)			Wind (24)
Grass (0)	Pod (24)	Wind (73)			
	Samara (62)				
	Spike (1)				

Notes: **a** Growth form traits states: Tall trees were species with a maximum height greater than 30 m, short trees were single stemmed species with a maximum height between 10 and 30 m, shrubs were single or multi-stemmed woody species to 10 m, vines included scramblers. **b** Dispersal mode trait states: flying endozoochory species had fruits ingested by flying avian or mammal species; ground endozoochory species had fruits ingested by rodents, mammals or ground dwelling avian species; passively dispersed species included gravity dispersal or short-distance ballistic/explosive dispersal; wind dispersed species were those with adaptations for prolonged floating. **c** Traits were represented by both a continuous measurement and categorical trait states. **d** Seed size trait states: L (large) seeds were those greater in length than 30 mm, M (medium) seeds were between 10 and 30 mm, and S (small) seeds were less than 10 mm. All measurements included the length of the wing when present. **e** Specific leaf area (SLA) trait states: H (high) species had a SLA value greater than 200 g/mm^2, I (intermediate) species had a SLA between 100–200 g/mm^2, and L (low) species had a SLA value less than 100 g/mm^2.

traits and as the average trait value per m^2 for SLA and seed size.

Data Analysis

To assess the buffer strip's impact on the original edge we subdivided Forest categories into Edge categories (Fig. 2). Edge categories included "Original Edge" (the edge now protected by the buffer strip), "Buffer Edge" (the edge of the buffer strip) and "Reference Edge" (the edge of the Reference Forest). We compared all measured microclimate, community structure and functional diversity features among Edge categories using ANOVAs. To account for correlation within transects, the following nested design was used: Edge Category(Transect). Significant differences in features among Edge categories were assessed using Tukey honest statistical difference (hsd) post-hoc tests (JMP version 5.0.1; SAS 2003).

We used a fixed effect model with Tukey hsd pair-wise comparisons to assess edge penetration distances for all microclimate, community structure and functional diversity features from 0 m from edge to 40 m from edge. We calculated test effects from a coefficient of the expected mean square and a denominator synthesized from a linear combination of mean squares in the numerator that do not contain any fixed effects. The degree of freedom for the synthesized denominator is constructed using the Satterthwaite method (SAS. 2003). We defined "Edge penetration distance" as the distance from the edge into forest where plots no longer varied significantly from Interior Forest conditions. All Forest transects (n = 10) were used in this analysis.

For comparisons among Forest categories, we excluded the first 3 quadrats (0-5 m) of each transect (n = 10) from Buffered Forest (referred to as Buffered Outer Forest) and Reference Forest (Reference Outer Forest) so that distinct edge conditions in these quadrats did not impact comparisons (Fig. 2). To compare microclimate, community structure and functional diversity among Forest categories we used ANOVAs. We included edge "aspect" as a nested factor within Outer Forest categories because of its known influence on edge effects elsewhere in tropical Australia (Turton and Frieburgher 1997). We also included "patch" (MFSR or MFCP) as a nested factor within Interior Forest. This gave the following nested analysis design: Forest(patch or aspect(transect)). Significant differences in features among Forest categories were tested with Tukey hsd tests.

To compare floristic similarity among Forest categories we used multidimensional scaling (MDS) based on Bray-Curtis similarity coefficients (Bray and Curtis 1957) and a two-way nested analysis of similarity (ANOSIM; Carr 1997). For these analyses two transects were excluded from the presented analysis, the Interior Forest MFCP Transect 1 (identified as an extreme outlier) and the Buffered Outer Forest NW Transect 5 (only contained six quadrats and thus was not comparable to the others). To assess the functional trait similarity of Forest categories, we repeated ANOSIM tests for each categorical functional trait.

RESULTS

Edge recovery

Seed size ($F_{3, 24} = 10.1406$, $p = 0.003$), species richness ($F_{3, 24} = 11.7915$, $p < 0.0001$), stem density ($F_{3, 24} = 4.9889$, $p = 0.0055$), canopy cover ($F_{3, 24} = 6.8338$, $p = 0.0010$) and grass cover ($F_{3, 24} = 16.9547$, $p < 0.0001$) differed significantly among Edge categories, though the nature of these differences were factor specific (Fig. 3). For example, Interior Forest had significantly larger seeds on average than all other Edge categories, while species richness was significantly lower on average in Interior Forest than in Reference and Buffered Edge forests (Fig. 3). Stem density was significantly greater on average in the Reference Edge compared to other Edge categories, while canopy cover was significantly less dense in the Reference Edge than Original Edge and Interior Forest (Fig. 3).

Edge effect penetration distance

Differences at specific points along transects (metres from forest edge; Fig 4) were only detectable between Buffered Forest and Interior Forest for four measured features: canopy cover (Fig. 4), SLA (Fig. 4), grass cover (not shown) and vegetation cover (not shown). At 0 m from the Buffered Forest edge, mean canopy cover, mean SLA, grass cover, and vegetation cover were all significantly different from Interior Forest conditions (test at 0 m: $F_{2, 24} = 3.4340$, $p = 0.0469$; $F_{2, 24} = 24.9757$, $p < 0.0001$; $F_{2, 24} = 5.8921$, $p = 0.0075$; $F_{2, 24} = 15.8540$, $p < 0.0001$ respectively). Each of these features, however, was statistically indistinguishable by 2.5 m into the Buffered Forest. The only observed difference between the Reference Forest edge and Interior Forest was for canopy cover, which differed significantly up to 5 m from edge (test at 5 m $F_{2, 24} = 3.8271$, $p = 0.0459$).

Based on measured features, edge effects did not penetrate far into the Buffered or Reference Forests. We did, however, find significant differences in features at mid-point distances along transects in the Buffered Forest. For example, significant differences in canopy cover were found at 15 m from edge ($F_{2, 24} = 17.5119$, $p < 0.0001$) and 40 m from edge ($F_{2,}$

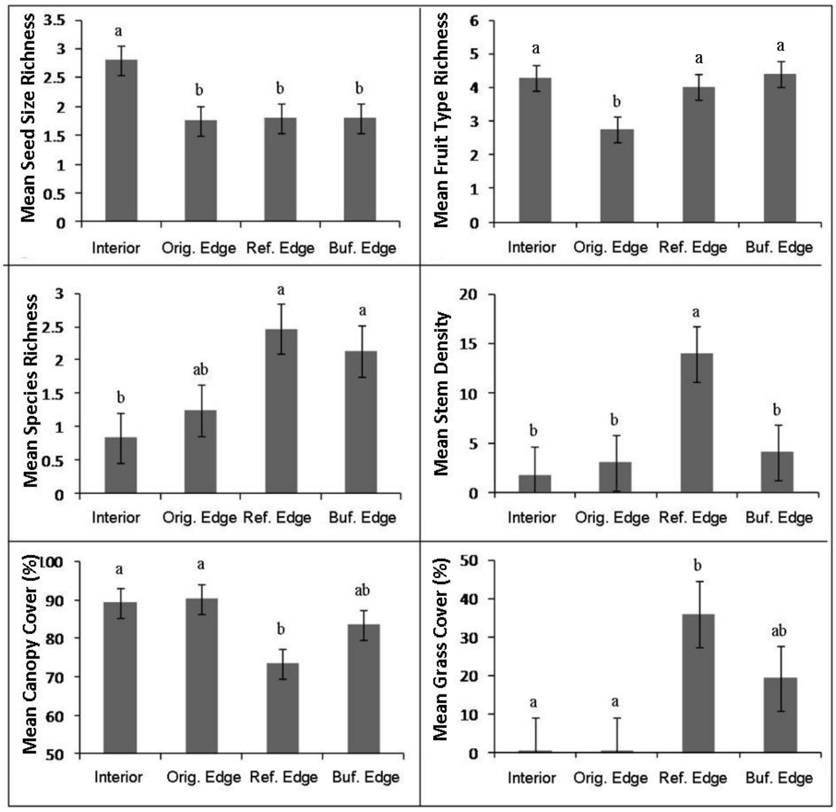

Fig. 3. Mean value of each feature (per m² +/- 1 SE) for Edge categories (χ –axis). For categorical traits (seed size, fruit type) values are the mean number of trait states per quadrat. Categories that do not share similar letters above error bars are significantly different (p<0.05).

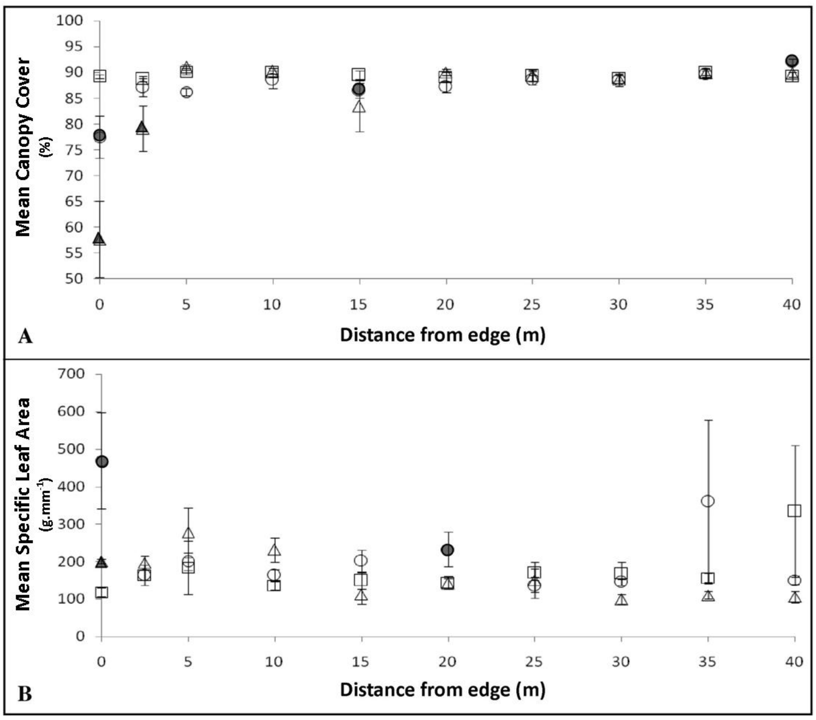

Fig. 4. Mean canopy cover (%) (A) and mean specific leaf area (g.mm^{-1}) (B). Symbols show the mean values +/- 1 SE (n=10) for all quadrats measured at the distance from forest edge indicated along the x-axis (metres from edge). Each mean value is based on 10 quadrats, sampled along 10 transects per Forest category. Squares show results for the Interior Forest, triangles for the Reference Forest and circles for the Buffered Forest. Reference and Buffered Forest values that differ significantly (p<0.05) from Interior Forest conditions are marked with filled symbols.

$_{24}$ = 3.9756, p = 0.0312; Fig. 4), in SLA at 20 m from edge ($F_{2, 24}$ = 3.3416, p = 0.0407; Fig. 4), in vegetation cover at 10 m from edge ($F_{2, 24}$ = 4.1735, p = 0.0263; not shown), and in grass cover from 5–25 m from edge (test at 5 m $F_{2, 24}$ = 3.5150, p = 0.0440; test at 25 m $F_{2, 24}$ = 7.3636, p = 0.0028; not shown). No significant mid-point differences were found at any other distance for measured features along Reference Forest transects.

Forest comparisons

We sampled 446 individual understorey plants from the three Forest categories, representing 38 families, 51 genera and 60 species. Eighty-four percent of surveyed plants and 82% of species were regionally native. The Interior Forest and Buffered Outer Forest understorey communities were dominated by seedlings (Fig. 2) of the short, disturbance-loving tree species *Neolitsea dealbata* (25.1 and 50.3% of individuals respectively). The Reference Outer Forest was dominated by tree seedlings (Fig. 2) of the species *Argyrodendron peralatum* (17.0% of individuals).

Many measured features differed among Forest categories (Appendix C; Fig. 5). Notably, grass cover was significantly higher for the Buffered Outer Forest than for both the Interior Forest and Reference Outer Forest ($F_{2, 24}$ = 36.77, p < 0.0001; Fig. 5).

Multidimensional scaling analyses of species and trait state composition among Forest categories (Fig. 6) showed that Buffered Outer Forest and Interior Forest differed significantly in species abundance (R = 0.282, p = 0.002), growth forms (R = 0.267, p = 0.005), and seed size (R = 0.155, p = 0.017). We also found significant compositional differences between the Buffered Outer Forest and Reference Outer Forest (Fig. 6) for fruit types (R = 0.418, p = 0.001), growth forms (R = 0.404, p = 0.001), species abundance (R = 0.4, p = 0.001), seed sizes (R = 0.257, p = 0.004), pollination syndromes (R = 0.249, p = 0.008) and dispersal modes (R = 0.13, p = 0.019). No significant differences in species or trait state compositions were found between the Reference Outer Forest and Interior Forest (Fig. 6).

DISCUSSION

We found that the buffer strip at the Malanda Scrub successfully restored the microclimate (soil temperature and canopy cover) and community

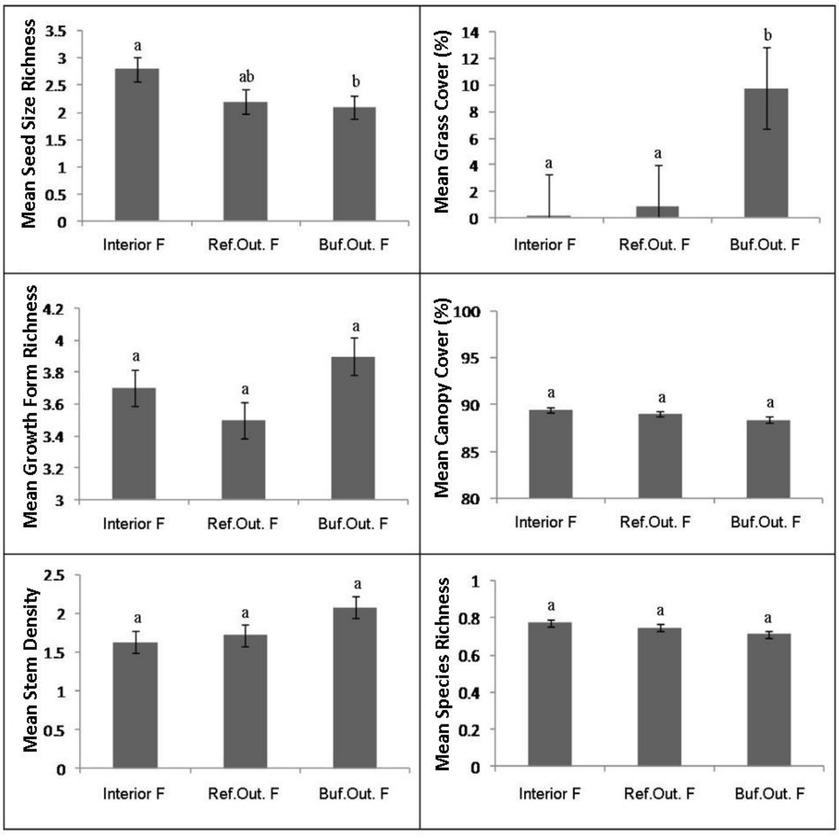

Fig. 5. Mean value of each feature (per m^2 +/- 1 SE) for Forest categories. For categorical trait (seed size, growth form) values are the mean number of trait states per quadrat. Categories that do not share similar letters above error bars are significantly different (p<0.05).

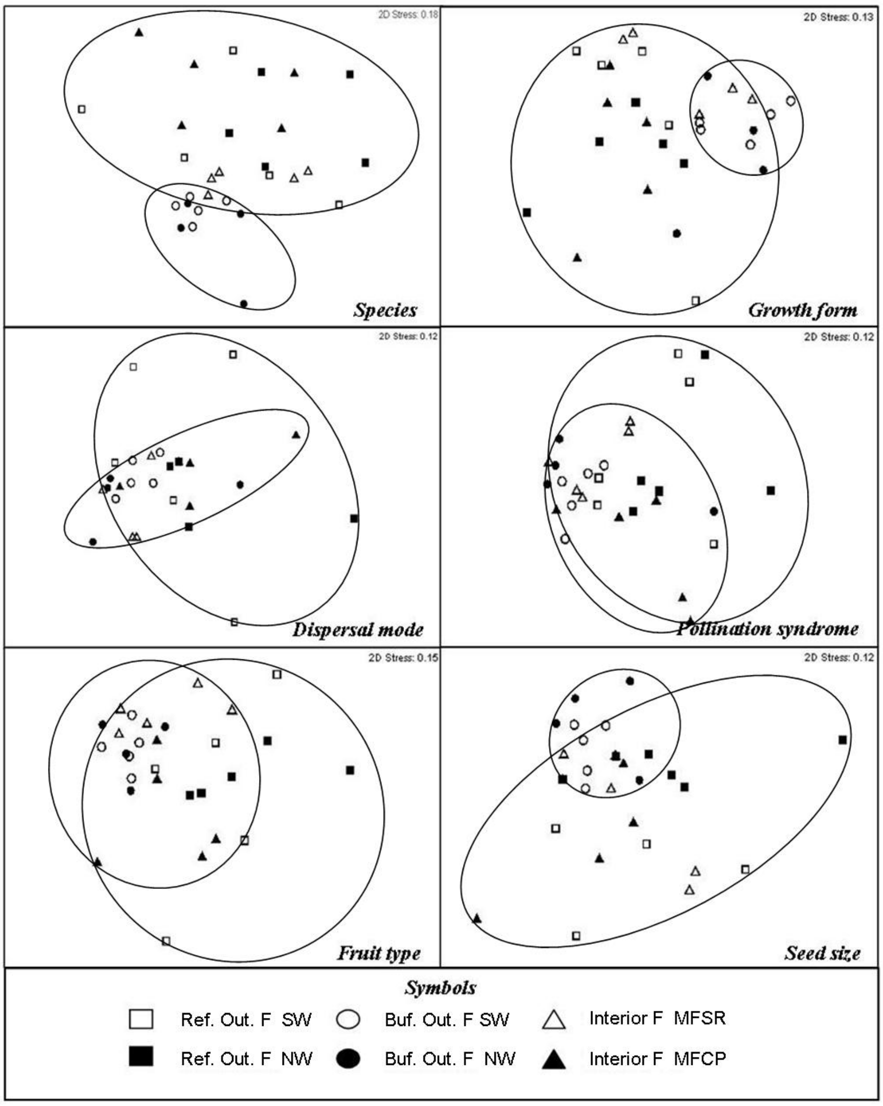

Fig. 6. Multidimensional scaling (MDS) using Bray-Curtis similarity indices for species and functional trait state composition with abundance. The proximity of points in the two-dimensional (2D) plot is proportional to their similarity. The 2D stress value is a measure of how close the 2D configuration of points is to the numerical dissimilarities among Forest categories. Forest categories are marked with different symbols as indicated in the figure. Circles group data points (transects) within Forest categories that are not significantly different (are similar).

structure of the Original Edge to levels consistent with Interior Forest conditions within 14 years of planting. Several ecological features of the Buffered Outer Forest, however, differed significantly from both Reference Outer Forest and Interior Forest conditions. In particular, we found the Buffered Outer Forest contained fewer large seeded species and appeared more vulnerable to structural damage. The distance to which edge effects impacted the forest was less for the Buffered Forest compared to the Reference Forest; and for both forest types, this distance was much less than has been found in other tropical forests (e.g., Laurance 1991). We also found no influence of aspect on microclimate or community structure when sampling NW and SW facing forests at Malanda. This finding is contrary to findings in other forests of this region where aspect has been shown to have an important influence on edge effects (Turton and Frieburgher 1997).

Edge recovery

The similarities in microclimate and community structure features between the Interior Forest and Original Edge suggests the forest recovery rate (transition from a disturbed edge condition to that of an interior forest) at Malanda has been rapid. Although variable, the literature suggests that a transition time for rainforest restoration (natural or aided) of upwards of 40 years is needed to progress from an early to later successional stage (Hopkins 1990; Kariuki and Kooyman 2005). There are several possible explanations for the rapid transition observed at Malanda. First, the

Original Edge may not have passed some key ecological threshold (e.g., edge collapse) prior to planting, which might have prevented its rapid recovery. Alternatively, the Interior Forest may be more ecologically healthy than forests used in other restoration projects, having beneficial characteristics such as extensive soil seed reserves, high plant diversity, and abundant pollination and dispersal agents. It is also possible that this remnant has an unusually favourable history (Stocker 1981) or set of microclimatic conditions (Ewel 1980) for successful restoration. We may never know which features have been so important to this forest's recovery but our findings highlight the need for replicated restoration experiments to help improve our understanding of which features contribute to differences observed across rain-forest restoration projects.

Despite clear evidence that the microclimate and community structure of the Original Edge is recovering, the absence of large seeded species in the buffer strip is concerning. It suggests some ecological functions may not be recovering quickly or may be permanently altered by the fragmented nature of the landscape. Our seed size results are consistent with other studies that found altered seed characteristics in fragmented forests (Wilson and Crome 1989; Hester and Hobbs 1992). The differences in seed sizes between the Original Edge and Interior Forest may be due to higher abundances of earlier successional species, which tend to have smaller seeds (Goosem and Young 1989) in the Buffered Outer Forest. Persistence and dispersal of small seeded species along the Original Edge is expected, as smaller seeds are more readily dispersed and often have more resilient dispersal vectors, such as wind (Foster 1986). Another possibility is that the abundance of large seeded species may have been reduced as the result of altered plant-animal interactions, such as the loss of native seed dispersing animals at Malanda, such as Cassowaries (*Casuarius casuarius johnsonii*) and native marsupials (*Hypsiprimnodon moschatus* and *Pteropus conspicillatus*). The lack of young individuals of large seeded species provides some evidence that certain animal dispersers are not using the forest around the Original Edge and suggests that for remnants like Malanda, focused plantings may be necessary to recover many larger seeded species.

Edge effect penetration distance

Contrary to our predictions, microclimate, community structure and functional diversity were remarkably even along the Buffered and Reference Forest edges. Only four features differed significantly with distance from edge. Of these features, all were indistinguishable from Interior Forest conditions within 5 m, a distance much less than found in previous studies of Australian and other tropical remnants (Laurance 1991; Williams-Linera 1990). Based on previous studies, largely from the Neotropics, we expected tree density (Fox *et al.* 1997), understorey density (Urbina-Cardona *et al.* 2006), leaf litter depth (Didham and Lawton 1999), species richness (Sizer and Tanner 1999), proportion of trees with vines (Viana *et al.* 1997), pollination mode diversity (Aizen and Feinsinger 1994; Brown and Hutchings 1997), and seed dispersal mode diversity (Wilson and Crome 1989) to increase slowly with increasing distance from edge. Our finding that few of these features were negatively impacted by the edge again highlights the variable importance of edge effects acting on fragmented forests in different biogeographic regions and supports the hypothesis that some edge effects do not change monotonically as a function of distance from edge (Didham 1997).

For those features that did show a response to distance from edge, we found they occurred to a greater distance in the Reference Forest than in the Buffered Forest (Fig. 4). This suggests that planted species in the buffer strip were more effective in shielding external conditions and that this vegetation has created an artificially sealed edge (Gascon *et al.* 2000). Edge sealing has been found to naturally occur along other Australian forest edges (Pohlman *et al.* 2007), however, this phenomenon has not before been found in a restoration context.

Our results suggest a buffer strip width of 30 m was more than sufficient to prevent edge effects from seriously impacting this forest remnant and that buffer strips of only a few metres may be sufficient to reduce edge effects in fragments similar to the Malanda Scrub. This is unlikely to be the case, however, for all restoration projects in other tropical locations where edge effects may affect forests to greater distances. This highlights the importance of assessing edge effect conditions prior to undertaking buffer strip plantings.

One curious finding was the change in structural features at mid-point distances along transects throughout the Buffered Forest but not the Reference Forest. One explanation for this pattern is that some areas of the buffer strip may not have developed as extensively as others. Another explanation is that these areas were damaged during recent cyclones (Cyclone Larry in 2006). Cyclones have been shown to cause structural damage up to 30 m into forest remnants on the Atherton Tablelands (Leigh *et al.* 1993). They have also been shown to cause less damage in restoration plantings than in remnant forests (Kanowski *et al.* 2008). Kapos *et al.* (1993) speculated that this pattern may be due to fewer large trees or higher stem densities in restoration plantings. We found the opposite pattern (more damage in the buffer strip), which suggests that despite some similarities to the Interior Forest, the buffer strip vegetation may be in a transitional stage, currently unable to deflect major storm damage. This is of concern given that cyclone damaged canopies are more prone to further storm damage (Thiollay 1992) and cyclones are common in Australia's tropics.

Forest comparisons

The Buffered Outer Forest represents an ecosystem similar to both the Interior Forest and Reference Outer Forest for most measured features (Fig. 5). The floristic and functional composition of the Buffered Outer Forest, however, still significantly differs from both the Interior Forest and Reference Outer Forest (Fig. 6). This pattern creates uncertainty about the longer-term successional trajectory of the planted area. As this restoration project is still relatively young, more time is needed for the buffer strip to develop, but for some functional groups, like animal-dispersed species with large seeds, such a recovery may not occur unaided. The efficiency of restoration projects, like this one, to reduce edge effects may be improved by planting species with particular traits once the reforested area has established. Such species should include those with physiological traits that increase storm resistance (species with low SLA and high wood density) and species dispersed by animals absent from the remnants.

CONCLUSIONS

Our study of the Malanda Scrub demonstrates that buffer strip plantings can be effective for reducing edge effects in at least some fragmented rainforests over short time scales and with relatively small planting efforts. As our study examined only one site, it is still unclear how universally useful this approach is. The evidence we present here, however, adds important information to the limited literature examining the success of rainforest restoration projects in Australia's tropics. What is clear is that the buffer strip at Malanda successfully restored the microclimate and community structure of the Original Edge, as well as many ecological features. Our findings that large seeded plant species are not recolonising the buffer strip and that vulnerability to storm damage is high suggests that not all ecological functions can be quickly or easily restored using this restoration approach alone.

ACKNOWLEDGEMENTS

We are grateful to staff at CSIRO Atherton for project support, to Andrew Ford for plant identification, Kylie Freebody from the Tablelands Regional Council's Community Revegetation Unit for providing valuable information about the Malanda revegetation project and Jessie Wells for providing functional trait data for many of our species. We would also like to acknowledge the Ngadjon-ji people for granting us permission to work on their traditional lands. Funding for DJM was through the Australian Government's Marine & Tropical Sciences Research Facility. Funding for MMM and LJS was provided by The University of Queensland, School of Biological Sciences. Work at Malanda was carried out under EPA permit WITK05057808.

REFERENCES

Aizen, M. A. and Feinsinger, P., 1994. Forest fragmentation, pollination, and plant reproduction in a Chico dry forest, Argentina. *Ecology* **75**: 330–351.

Bierregaard, R. O. J., Lovejoy, T. E., Kapos, V., Augusto dos Santos, A. and Hutchings, R. W., 1992. The biological dynamics of tropical rainforest fragments: a prospective of fragments and continuous forests. *BioScience* **42**: 859–866.

Bostock, P. D. and Holland, A. E., 2007. Census of the Queensland Flora 2007. Queensland Herbarium, Environmental Protection Agency, Brisbane.

Bray, J. R. and Curtis, J. T., 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* **27**: 325–349.

Brown, K. S. and Hutchings, R. W., 1997. Disturbance, fragmentation, and the dynamics of diversity in Amazonian forest butterflies. Pp. 91–110 *in* Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Ed by W. F. Laurance and R. O. J. Bierregaard. University of Chicago Press, Chicago.

Carr, M. R., 1997. Primer User Manual, Plymouth Routines in Multivariate Ecological Research. Plymouth Marine Laboratory, Plymouth.

Cooper, W. and Cooper W. T., 2004. Fruits of the Australian Tropical Rainforest. Nokomis Publications, Clifton Hill, Vic.

DeFries, R., Hansen, A., Newton, A. C. and Hansen, M. C., 2005. Increasing isolation of protected areas in tropical forest over the past twenty years. *Ecological Applications* **15**: 19–26.

Didham, R. K., 1997. The influence of edge effects and forest fragmentation on leaf litter invertebrates in central Amazonia. Pp. 55–70 *in* Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Ed by W. F. Laurance and R. O. J. Bierregaard. University of Chicago Press, Chicago.

Didham, R. K. and Lawton, J. H., 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* **31**: 17–30.

Ewel, J. J., 1980. Tropical succession: manifold routes to maturity. *Biotropica* **12**: 2–9.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics* **34**: 487–515.

Foster, S., 1986. On the adaptive value of large seeds for tropical moist forest trees: A review and synthesis. *The Botanical Review* **52**: 260–299.

Fox, B. J., Taylor, J. E., Fox, M. D. and Williams, C., 1997. Vegetation changes across edges of rainforest remnants. *Biological Conservation* **82**: 1–13.

Freebody, K., 2007. Rainforest revegetation in the uplands of the Australian wet tropics: planting models and monitoring requirements. *Ecological Management & Restoration* **8**: 140–143.

Freeman, A. N. D., 2004. Constraints to community groups monitoring plants and animals in rainforest revegetation sites on the Atherton Tablelands of far north Queensland. *Ecological Management & Restoration* **5**: 199–204.

Gascon, C., Lovejoy, T. E., Bierregaard, R. O., Jr., Malcolm, J. R., Stouffer, P. C., Vasconcelos, H. L., Laurance, W. F., Zimmerman, B., Tocher, M. and Borges, S., 1999. Matrix habitat and species richness in tropical forest remnants. *Biological Conservation* **91**: 223–229.

Gascon, C., Williamson, G. B. and da Fonseca, G. A. B., 2000. Receding forest edges and vanishing reserves. *Science* **288**: 1356–1358.

Grubb, P. J. and Metcalfe, D. J., 1996. Adaption and inertia in the Australian tropical lowland rain-forest flora: contradictory trends in intergeneric and intrageneric comparisons of seed size in relation to light demand. *Functional Ecology* **10**: 512–520.

Grubb, P. J., Metcalfe, D. J., Grubb, E. A. A. and Jones, G. D. 1998. Nitrogen-richness and protection of seeds in Australian tropical rainforest: a test of plant defense theory. *Oikos* 82: 467–482

Hester, A. J. and Hobbs, R. J. 1992. Tropical forest remnants: ecology, management, and conservation of fragmented communities. *Journal of Vegetation Science* **3**: 101–108.

Hopkins, M. S., 1990. Disturbance — the forest transformer. Pp. 40–52 *in* Australian Tropical Rainforests Science — Values — Meaning. Ed by L. J. Webb, Kikkawa, J. CSIRO, Melbourne.

Hurlbert, S. H., 1971. The non-concept of species diversity: a critique and alternative parameters. *Ecology* **52**: 577–586.

Hyland, B. P., Whiffin, T., Christophel, D. C., Gray, B. and Elick, R. W., 2003. Australian Tropical Rain Forest Plants: Trees, Shrubs and Vines. CSIRO, Atherton.

Jordano, P., 1995. Angiosperm fleshy fruits and seed dispersers: A comparative analysis of adaption and constraints in plant-animal interactions. *American Naturalist* **145**: 163–191.

Kanowski, J., Catterall, C. P., Wardell-Johnson, G. W., Proctor, H. and Reis, T., 2003. Development of forest structure on cleared rainforest land in eastern Australia under different styles of reforestation. *Forest Ecology and Management* **183**: 265–280.

Kanowski, J., Catterall, C. P., McKenna, S. G. and Jensen, R., 2008. Impacts of cyclone Larry on the vegetation structure of timber plantations, restoration plantings and rainforest on the Atherton Tableland, Australia. *Austral Ecology* **33**: 485–492.

Kanowski, J. J., Reis, T. M., Catterall, C. P. and Piper, S. D., 2006. Factors affecting the use of reforested sites by reptiles in cleared rainforest landscapes in tropical and subtropical Australia. *Restoration Ecology* **14**: 67–76.

Kapos, V., Ganade, G. M., Matsui, E. and Victoria, R. L., 1993. Partial-derivative-C-13 as an indicator of edge effects in tropical rain-forest reserves. *Journal of Ecology* **81**: 425–432.

Kariuki, M. and Kooyman, R. M., 2005. Floristic changes and regeneration patterns for a 12-year period during the 3rd and 4th decades following selection logging in a subtropical rainforest. *Austral Ecology* **30**: 844–855.

Lamb, D., Erskine, P. D. and Parrotta, J. A., 2005. Restoration of degraded tropical forest landscapes. *Science* **310**: 1628–1632.

Laurance, W. F., 1991. Ecological correlations of extinction proneness in Australian tropical rain forest mammals. *Conservation Biology* **5**: 79–89.

Laurance, W. F., 1997. Hyper-disturbed parks: Edge effects and the ecology of isolated reserves in isolated rainforest reserves in tropical Australia. Pp. 71–84 *in* Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Ed by W. F. Laurance and R. O. J. Bierregaard. University of Chicago Press, Chicago.

Leigh, E. G. J., Wright, S. J., Herre, E. A. and Putz, F. E., 1993. The decline of tree diversity on newly isolated tropical islands: A test of a null hypothesis and some implications. *Evolutionary Ecology* **7**: 1573–8477.

Lindenmayer, D. B. and Fischer, J., 2006. Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis. Island Press, Collingwood.

Magurran, A. E. 1988. Ecological Diversity and Its Measurement. Princeton University Press. Princeton.

Mayfield, M. M., Boni, M. E., Daily, G. C. and Ackerly, D., 2005. Species and functional diversity of native and human-dominated plant communities. *Ecology* **86**: 2365–2372.

Mayfield, M. M. and Daily, G. C., 2005. Countryside biogeography of Neotropical herbaceous and shrubby plants. *Ecological Applications* **15**: 423–439.

McIntyre, S., Diaz, S., Lavorel, S. and Cramer, W., 1999. Plant functional types and disturbance dynamics: Introduction. *Journal of Vegetation Science* **10**: 604–608.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution* **10**: 58–63.

Nicotra, A. B., Chazdon, R. L. and Iriarte, S. V., 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* **80**: 1908–1926.

Parrotta, J. A., Turnbull, J. W. and Jones, N., 1997. Catalyzing native forest regeneration on degraded tropical lands. *Forest Ecology and Management* **99**: 1–7.

Petchey, O. L. and Gaston, K. J., 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* **9**: 741–758.

Pielou, E. C., 1966. The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* **13**: 131–144.

Pielou, E. C., 1975. Ecological Diversity. Wiley, New York.

Pohlman, C. L., Turton, S. M. and Goosem, M., 2007. Edge effects of linear canopy openings on tropical rain forest understory microclimate. *Biotropica* **39**: 62–71.

Putz, F. E., Leigh, E. G. J. and Wright, S. J., 1990. Solitary confinement in Panama. *Garden* **14**: 18–23.

SAS, 2003. JMP: The Discovery Software. SAS Institute, Cary, North Carolina, USA.

Saunders, D. A., Hobbs, R. J. and Margules, C. R., 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5**: 18–32.

Sieving, K. E. and Karr, J. R., 1997. Avian extinction and persistence mechanisms in lowland Panama. Pp. 156–170 *in* Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Ed by W. F. Laurance and R. O. J. Bierregaard. University of Chicago Press, Chicago.

Simpson, E. H., 1949. Measurement of diversity. *Nature* **163**: 688.

Sizer, N. and Tanner, E. V. J., 1999. Responses of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. *Biological Conservation* **91**: 135–142.

Stanley, T. D., 2002. The Flora of South Eastern Queensland. Queensland Department of Primary Industries, Brisbane.

Thiollay, J. M., 1992. Influence of selective logging on bird species diversity in a Guianan rainforest. *Conservation Biology* **6**: 47–63.

Tucker, N. I. J. and Murphy, T. M., 1997. The effects of ecological rehabilitation on vegetation recruitment: some observations from the wet tropics of North Queensland. *Forest Ecology and Management* **99**: 133–152.

Turner, M. G., 1996. Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* **33**: 200–209.

Turton, S. M. and Frieburgher, H. J., 1997. Edge and aspect effects on the microclimate of a small tropical forest remnant on the Atherton Tableland, northeastern Australia. Pp. 45–54 *in* Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Ed by W. F. Laurance and R. O. J. Bierregaard. University of Chicago Press, Chicago.

Urbina-Cardona, J. N., Olivares-Perez, M. and Reynoso, V. H., 2006. Herpetofauna diversity and microenvironment correlates across a pasture-edge-interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. *Biological Conservation* **132**: 61–75.

US Forest Service, 2008. Pacific Island Ecosystems at Risk (PIER). Version 5.4 (7 January 2008). http://www.hear.org/pier/. Accessed 15 August 2008.

Viana, V. M., Tabanez, A. A. J. and Batista, J. L. F., 1997. Dynamics and restoration of forest fragments in the Brazilian Atlantic moist forest. Pp. 351–365 *in* Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Ed by W. F. Laurance and R. O. J. Bierregaard. University of Chicago Press, Chicago.

Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**: 213–227.

Williams-Linera, G., 1990. Origin and early development of forest edge vegetation in Panama. *Biotropica* **22**: 235–241.

Wilson, M. F. and Crome, F. H. J., 1989. Patterns of seed rain at the edge of a tropical Queensland rainforest. *Journal of Tropical Ecology* **5**: 301–0308.

Zar, J. H., 1999. Biostatistical Analysis. Prentice-Hall, Upper Saddle River, New Jersey.

APPENDICES

Appendix A — The Community Revegetation Unit's 1997 Malanda Falls buffer strip project's original planted species list (K. Freebody, Personal Communication). Planting was done in two stages, the first in 1993 (Stage 1) and the second in 1994 (Stage 2). Values listed under each "Stage" are the number of planted individuals of the species listed in that row. Nomenclature and classifications have been updated to follow Bostock and Holland 2007.

Family	Genus	Species	Stage 1 (Nov. 93)	Stage 2 (Nov. 94)	Totals
Anacardiaceae	*Euroschinus*	*falcata*	55	53	108
Apocynaceae	*Alstonia*	*scholaris*	60	48	108
Araucariaceae	*Agathis*	*robusta*	4	48	52
Corynocarpaceae	*Corynocarpus*	*cribbianus*	0	17	17
Cunoniaceae	*Ceratopetalum*	*succirubrum*	12	10	22
Cunoniaceae	*Davidsonia*	*pruriens*	7	20	27
Cunoniaceae	*Geissois*	*biagiana*	53	0	53
Cunoniaceae	*Pullea*	*stutzeri*	6	8	14
Elaeocarpaceae	*Elaeocarpus*	*angustifolius*	105	37	142
Elaeocarpaceae	*Elaeocarpus*	*coorangooloo*	72	32	104
Euphorbiaceae	*Aleurites*	*rockinghamensis*	48	24	72
Euphorbiaceae	*Homolanthus*	*novoguineensis*	15	26	41
Euphorbiaceae	*Mallotus*	*phillippensis*	15	0	15
Fabaceae	*Castanospermum*	*australe*	67	13	80
Flacourtiaceae	*Casaeria*	*dallachii*	19	7	26
Flacourtiaceae	*Scolopia*	*braunii*	19	15	34
Hamamelidaceae	*Ostrearia*	*australiana*	22	0	22
Lauraceae	*Beilschmiedia*	*bancroftii*	0	2	2
Lauraceae	*Beilschmiedia*	*obtusifolia*	0	11	11
Lauraceae	*Beilschmiedia*	*tooram*	0	13	13
Lauraceae	*Cinnamomum*	*laubatii*	31	18	49
Lauraceae	*Cryptocarya*	*hypospodia*	44	0	44
Lauraceae	*Cryptocarya*	*mackinnoniana*	0	37	37
Lauraceae	*Cryptocarya*	*oblata*	0	12	12
Lauraceae	*Cryptocarya*	*triplinervis*	55	19	74
Lauraceae	*Endiandra*	*sankeyana*	49	27	76
Lauraceae	*Litsea*	*leefeana*	87	68	155

Appendix A — *continued*

Family	Genus	Species	Stage 1 (Nov. 93)	Stage 2 (Nov. 94)	Totals
Lauraceae	*Neolitsea*	*dealbata*	52	33	85
Meliaceae	*Dysoxylum*	*mollissimum*	13	0	13
Meliaceae	*Dysoxylum*	*pettigrewianaum*	7	0	7
Meliaceae	*Toona*	*australis*	13	26	39
Mimosaceae	*Acacia*	*celsa*	60	32	92
Mimosaceae	*Acacia*	*cincinnata*	45	0	45
Moraceae	*Ficus*	*destruens*	2	0	2
Moraceae	*Ficus*	*obliqua*	2	3	5
Moraceae	*Ficus*	*pleurocarpa*	2	3	5
Myrtaceae	*Acmena*	*resa*	53	62	115
Myrtaceae	*Pilidiostigma*	*tropicum*	6	12	18
Myrtaceae	*Syzygium*	*canicortex*	50	17	67
Myrtaceae	*Syzygium*	*cormiflorum*	53	0	53
Myrtaceae	*Syzygium*	*endophloium*	61	30	91
Myrtaceae	*Syzygium*	*gustavoides*	37	7	44
Myrtaceae	*Syzygium*	*johnsonii*	0	32	32
Myrtaceae	*Syzygium*	*kuranda*	53	63	116
Myrtaceae	*Syzygium*	*papyraceum*	30	64	94
Myrtaceae	*Syzygium*	*wilsonii*	0	34	34
Myrtaceae	*Xanthostemon*	*whitei*	18	29	47
Proteaceae	*Athertonia*	*diversifolia*	5	2	7
Proteaceae	*Buckinghamia*	*celsissima*	16	51	67
Proteaceae	*Cardwellia*	*sublimis*	13	87	100
Proteaceae	*Carnarvonia*	*araliifolia*	35	40	75
Proteaceae	*Darlingia*	*darlingiana*	30	70	100
Proteaceae	*Darlingia*	*ferruginea*	46	66	112
Proteaceae	*Helicia*	*nortoniana*	31	27	58
Proteaceae	*Stenocarpus*	*sinuatus*	52	62	114
Rhamnaceae	*Alphitonia*	*petriei*	90	15	105
Rhamnaceae	*Emmenosperma*	*alphitoniodies*	4	0	4
Rosaceae	*Prunus*	*turneriana*	4	28	32
Rutaceae	*Acronychia*	*acidula*	68	14	82
Rutaceae	*Flindersia*	*acuminata*	0	14	14
Rutaceae	*Flindersia*	*bourjotiana*	65	48	113
Rutaceae	*Flindersia*	*brayleyana*	51	94	145
Rutaceae	*Flindersia*	*pimenteliana*	37	34	71
Rutaceae	*Halfordia*	*scleroxyla*	0	8	8
Rutaceae	*Melicope*	*elleryana*	57	39	96
Rutaceae	*Melicope*	*xanthoxyloides*	50	28	78
Sapindaceae	*Arytera*	*divaricata*	7	25	32
Sapindaceae	*Castanospora*	*alphandii*	8	38	46
Sapindaceae	*Cupaniopsis*	*foveolata*	15	0	15
Sapindaceae	*Diploglottis*	*smithii*	9	0	9
Sapindaceae	*Guioa*	*lasioneura*	57	52	109
Sapindaceae	*Mischarytera*	*lautererana*	35	42	77
Sapindaceae	*Mischocarpus*	*grandissimus*	0	21	21
Sapindaceae	*Rhysotoechia*	*robertsonii*	20	47	67
Sapindaceae	*Toechima*	*erythrocarpum*	30	16	46
Sterculiaceae	*Argyrodendron*	*peralatum*	52	48	100
Sterculiaceae	*Argyrodendron*	*trifoliolatum*	60	49	109
Sterculiaceae	*Brachychiton*	*acerifolius*	60	18	78
Symplocaceae	*Symplocos*	*cochinchinensis*	20	0	20
Verbenaceae	*Gmelina*	*fasciculiflora*	10	8	18

Appendix B — List of all plant species recorded in this study and their corresponding functional trait states. Species with superscript * are not native to the region. Seed sizes are listed as lengths (mm). For some analyses, seeds were grouped into three size categories: Large (L; >30 mm), Medium (M; 10–30 mm) and Small (S; <10mm). Fruit types follow standard botanical categories. Abbreviations for "Growth Form" are: "Sh", shrub; "V", vine; "T", tree; "H", herb; "St", short tree; and "G", grass. 'Pollination Syndrome' and "Dispersal Mode" are the same as outlined in Table 2 (Notes). Cells are left empty in cases where data were unavailable for a given species. Nomenclature and classifications follow Bostock and Holland 2007. Sources of trait data include: Grubb *et al.* 1998 for seed sizes, Cooper and Cooper 2004 for fruit types and dispersal mechanisms, US Forest Service 2008 for all invasive species trait data, and pollination data and various other trait data came from Stanley 2002 and Hyland *et al.* 2003.

Family	Genus	Species	Growth Form	Seed Size(mm)	Fruit Type	Dispersal Mode	Pollination Syndrome
Acanthaceae	*Hypoestes*	*phyllostachya**	Sh	25	Capsule	Passive	Bee
Acanthaceae	*Pseuderanthemum*	*variabile*	Sh	3	Capsule	Passive	Bee
Amaranthaceae	*Deeringia*	*tournefortia*	V	1	Berry	FlyingEndo	Fly
Anacardiaceae	*Euroschinus*	*falcata*	T		Drupe	FlyingEndo	
Annonaceae	*Haplosticanthus*	*johnsonii*	Sh	9	Berry	FlyingEndo	Moth
Annonaceae	*Melodorum*	*leichhardtii*	V	8	Berry	FlyingEndo	Fly
Apocynaceae	*Melodinus*	*baccellianus*	V	9	Berry	FlyingEndo	Fly
Apocynaceae	*Neisosperma*	*poweri*	St	34	Drupe	GroundEndo	Fly
Araceae	*Alocasia*	*brisbanensis*	H	6	Spike	FlyingEndo	Beetle
Araliaceae	*Polyscias*	*elegans*	T	2	Drupe	FlyingEndo	
Araucariaceae	*Agathis*	*robusta*	T	25	Cone	Wind	
Arecaceae	*Calamus*	*australis*	V	10	Drupe	FlyingEndo	Beetle
Arecaceae	*Calamus*	*moti*	V	10	Drupe	FlyingEndo	Beetle
Asclepiadaceae	*Marsdenia*	*longipedicellata*	V		Follicle		
Asteraceae	*Ageratum*	*conyzoides**	H	1	Nut	Wind	Bee
Asteraceae	*Bidens*	*bipinnata**	H	11	Nut	Wind	Insect
Asteraceae	*Bidens*	*pilosa**	H	7	Nut	Wind	Insect
Asteraceae	*Emilia*	*sonchifolia**	H		Nut	Wind	Insect
Asteraceae	*Synedrella*	*nodiflora**	H	3	Nut	Wind	Bee
Poaceae	*Oplismenus*	*aemulus*	G		Grain	Wind	Wind
Poaceae	*Oplismenus*	*compositus*	G		Grain	Wind	Wind
Poaceae	*Ottochloa*	*nodosa*	G		Grain	Wind	Wind
Poaceae	*Saccharum*	*officinarum**	G		Grain	Wind	Wind
Poaceae	*Gen. indet*	*Sp. indet**	G		Grain	Wind	Wind
Poaceae	*Gen. indet*	*Sp. indet**	G		Grain	Wind	Wind
Poaceae	*Gen. indet*	*Sp. indet**	G		Grain	Wind	Wind
Nephrolepidaceae	*Arthropteris*	*submarginalis*	H				Wind
Proteaceae	*Helicia*	*nortoniana*	St	8	Drupe	FlyingEndo	Bee
Pteridaceae	*Pteris*	*tremula*	H				
Rhamnaceae	*Sageretia*	*hamosa*	V	7	Drupe	FlyingEndo	Fly
Rosaceae	*Prunus*	*turneriana*	T	23	Drupe	FlyingEndo	Fly
Rubiaceae	*Randia*	*tuberculosa*	Sh	4	Drupe	FlyingEndo	
Rutaceae	*Acronychia*	*acidula*	T	4	Drupe	FlyingEndo	
Rutaceae	*Dinosperma*	*erythrococcum*	T	4	Capsule	FlyingEndo	
Rutaceae	*Flindersia*	*acuminata*	T	75	Capsule	Passive	
Rutaceae	*Flindersia*	*brayleyana*	T	65	Capsule	Passive	Bee
Rutaceae	*Flindersia*	*pimenteliana*	T	47	Capsule	Wind	
Sapindaceae	*Arytera*	*pauciflora*	T	12	Capsule	FlyingEndo	
Sapindaceae	*Castanospora*	*alphandii*	T	22	Berry	FlyingEndo	Bee
Sapindaceae	*Guioa*	*acutifolia*	T	7.5	Capsule	FlyingEndo	Bee
Sapindaceae	*Guioa*	*lasioneura*	Sh		Capsule	FlyingEndo	
Sapindaceae	*Harpullia*	*frutescens*	Sh	12	Capsule	FlyingEndo	
Sapindaceae	*Misharytera*	*lautereriana*	T	8	Capsule	FlyingEndo	
Sapindaceae	*Sarcopteryx*	*martyana*	T	8	Capsule	FlyingEndo	Bee
Sapotaceae	*Pouteria*	*brownlessiana*	T	18	Drupe	FlyingEndo	
Smilacaceae	*Ripogonum*	*album*	V	7	Berry	FlyingEndo	
Solanaceae	*Solanum*	*mauritianum**	Sh	2	Berry	FlyingEndo	
Solanaceae	*Solanum*	*seaforthianum**	V	3	Berry	FlyingEndo	
Sterculiaceae	*Argyrodendron*	*peralatum*	T		Samara	Wind	
Symplocaceae	*Symplocos*	*hayesii*	Sh	13	Drupe	FlyingEndo	
Thymelaeaceae	*Wikstroemia*	*indica*	Sh	6	Drupe	FlyingEndo	
Urticaceae	*Dendrocnide*	*moroides*	Sh	1	Nut	FlyingEndo	Wind
Urticaceae	*Urtica*	*incisa*	Sh	1	Nut	FlyingEndo	Wind
Verbenaceae	*Lantana*	*camara**	V	4	Drupe	FlyingEndo	
Vitaceae	*Cayratia*	*japonica*	V	4	Berry	FlyingEndo	
Vitaceae	*Cayratia*	*saponaria*	V	4	Berry	FlyingEndo	Fly
Zamiaceae	*Bowenia*	*spectabilis*	H	30	Cone	Hoarding or caching	
Zingaberaceae	*Alpinia*	*modesta*	H	4	Capsule	FlyingEndo	

Appendix C — Mixed-effects model results of differences in microclimate, community structure and functional diversity across Forest categories. The test effects are calculated from a coefficient of the expected mean square and a denominator synthesized from a linear combination of mean squares in the numerator that do not contain the effect to be tested or other fixed effects. The degree of freedom (*df* in column headings) were constructed using the Satterthwaite method (SAS 2003). The R-square value (*Adjusted R^2 values*) is adjusted to the fit of the data to the model. Values given in the columns labelled "*Model*", "*Forest*" and "*Detail(Forest)*" are the F statistic from the model test. The number of stars denotes the significance of the F statistic as indicated at the bottom of the table.

	Significance of Model and Model Effects (f)			
Measured features	Modeldf:29	Forestdf:2	Detail(Forest) df:3	Adjusted R^2 values
Canopy cover	1.313	0.475	2.162	0.035
Leaf litter depth	2.063**	1.271	2.308	0.110
Soil temperature	15.94***	5.127	0.830	0.655
Species richness (per m^2)	1.309	1.681	0.544	0.035
% Vegetation cover	1.893**	3.630	3.268**	0.094
% Grass cover	3.644****	14.18**	2.563*	0.236
Stem density (per m^2)	1.570**	1.860	1.294	0.062
Understory height	1.549**	0.148	1.481	0.075
Species evenness	3.545**	0.469	4.500**	0.312
Species richness/10 m^2	1.672	1.377	1.452	
Invasive species abundance	3.536**	2.797	2.057*	0.011
Shannon's index	1.708	0.034	2.783*	0.112
Simpson's index	5.698**	0.431	7.395**	0.456
No. of trees	4.495**	3.686	2.167	0.376
Growth form trait richness	0.958	0.068	1.532	0.172
Fruit type trait richness	1.745	0.678	2.093	0.117
Dispersal mode trait richness	0.181	1.347	0.154	0.038
Pollination trait richness	0.401	0.393	0.562	0.080
Mean seed size	1.741	2.684	1.034	0.117
Mean SLA	0.416	0.546	0.513	0.008
Trees with epiphytes	2.101	2.223	1.411	0.160
Buttressed trees	4.729**	4.649	1.923	0.391
Trees with lianas	1.129	1.982	0.810	0.022
Trees with vines	3.946**	3.960	1.807	0.337

Notes: the number of stars denotes the significance level of the F statistic ($p<0.0001$: F****; $p<0.001$: F ***; $p<0.05$: F**; $p<0.1$: F*)