Biological Conservation 146 (2012) 53–61

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Can active restoration of tropical rainforest rescue biodiversity? A case with bird community indicators

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ARTICLE INFO

Article history:
Received 1 July 2011
Received in revised form 11 October 2011
Accepted 18 October 2011
Available online 23 December 2011

Keywords:
Endemic species
Functional group
Forest
Pasture
Plantation
Developmental trajectory

ABSTRACT

There is vigorous debate about the potential for reforestation to offset losses in biodiversity associated with tropical deforestation, but a scarcity of good data. We quantified developmental trajectories following active restoration (replanting) of deforested pasture land to tropical Australian rainforest, using 20 different bird community indicators within chronosequences of multiple sites. Bird species composition in restored sites (1–24 years old) was intermediate between that of reference sites in pasture and primary rainforest. Total species richness was much less sensitive to land cover change than composition indicators, because of contrasting species-specific response patterns. For example, open-country (grassland/wetland) bird species declined in richness and abundance with increasing site age, while rainforest-dependent species increased. Results from two different landscapes (uplands and lowlands) were remarkably consistent, despite differing bird assemblages. After 10 years, restored sites averaged about half the number of rainforest-dependent bird species typical of rainforest. Mean values at around 20 years overlapped with the "poorest" rainforest reference sites, but projections suggest that >150 years are required to reach mean rainforest levels, and high variability among sites means that many were not on track towards ever achieving a rainforest-like bird community. Regional rainforest endemics were half as likely to occupy older revegetated sites as non-endemic rainforest-dependent species. Between-site variability and slow colonisation by regional endemics strongly constrain the potential of rainforest restoration to offset the biodiversity impacts of tropical deforestation. The results also mean that ongoing monitoring of biodiversity is an essential part of restoration management.

1. Introduction

Extensive clearing of tropical forests worldwide has been a major driver of biodiversity loss and decline, and the large area of habitat lost means that a conservation reserve system based only on remnant older-growth forest will be insufficient to sustain biodiversity into the future (Dent and Wright, 2009; Gardner et al., 2009). A major challenge for the future prospects of tropical biodiversity is the management of land cover outside of conserved remnant forest in a manner that will help forest-dependent species to persist or recover. Reforestation offers the hope of biodiversity recovery (Chazdon, 2008; Lamb et al., 2005), and there is increasing interest in its possible use as compensatory habitat to offset biodiversity losses from future land development (e.g., Moilanen et al., 2009). However, the idea that contemporary reforestation could perhaps compensate for past or future deforestation depends on an assumption that revegetated areas can rapidly develop the capacity to support species that depend on native forest. This assumption is a subject of vigorous recent debate but a scarcity of good data (Chazdon et al., 2009; Dent and Wright, 2009; Gardner et al., 2007). Conservation planners urgently need a better quantitative knowledge of the rates and modifiers of biodiversity development during reforestation (Chazdon et al., 2009; Gardner et al., 2009).

Tropical reforestation may commence through a wide variety of pathways, including plantation forestry, ecological restoration and unassisted regrowth (Catterall et al., 2008; Erskine et al., 2007; Lamb et al., 2005). Regrowth forests are especially widespread but recent reviews agree that knowledge of their capacity to support forest-dependent fauna is inadequate, especially given a very high observed variability in case-specific outcomes (Bowen et al., 2007; Chazdon et al., 2009; Dent and Wright, 2009; Gardner et al., 2007). Furthermore, the measured outcome of reforestation may also vary greatly depending on the type of biodiversity indicator in use (Dent and Wright, 2009; Dunn, 2004). In particular, there may be a predictably slowest-returning subset of species that are either specialists on slow-developing resources such as large decaying wood or endemics of special conservation concern,

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doi:10.1016/j.biocon.2011.10.033

however this has rarely been explicitly tested (Bowen et al., 2007; Chazdon et al., 2009; Dent and Wright, 2009; Gardner et al., 2007).

Active revegetation of tropical rainforest through ecological restoration aims to accelerate the recovery of biodiversity by overcoming obstacles to plant regeneration, such as those associated with depleted soil seed banks, limited plant dispersal and suppression of seedling regeneration by competition with oldfield grasses and herbs (Catterall et al., 2008; Erskine et al., 2007; Holl, 2007). Tree-planting projects are a well-developed form of ecological restoration, and in some regions there is an established technology of using a highly diverse mix of native plant species which are selected to recover floristic and functional diversity and attract vertebrate seed-dispersers, as well as overcoming initial dispersal constraints by directly establishing dispersal-limited plant species (Freebody, 2007; Tucker, 2008; Rodrigues et al., 2009, 2011). Such interventions have typically involved a "field of dreams" expectation that plantings of this type will catalyse colonisation by forest-dependent fauna, but this assumption remains inadequately tested, both in tropical forest restoration (Catterall et al., 2008; Tucker, 2000; Rodrigues et al., 2009) and elsewhere (Hilderbrand et al., 2005; Munro et al., 2007; Young, 2000). Tests of the capacity of reforested areas to develop on a trajectory towards native forest require designs which incorporate both reference ecosystems and restored sites of varying age (SER, 2004). However, this is difficult to achieve in many landscapes due to scarcity or inaccessibility of sites (Catterall et al., 2004; Rodrigues et al., 2009).

Here we quantify the development of bird communities in two different landscapes following active restoration of deforested pasture land to tropical rainforest. The design uses a chronosequence of multiple sites in each landscape. Biodiversity is indicated by 20 different types of bird community measurement within four categories: (1) total species richness and abundance; (2) indices of abundance and species richness within *a priori* functional groups of species based on their use of uncleared habitat; (3) species richness and abundance within response guilds based on measured species-specific use of reference rainforest and pasture in this study; and (4) community composition from multivariate analyses. The study's results support the hypotheses that different biodiversity indicators will show differing developmental trajectories, and that regional endemics will be slow colonisers. Our findings quantify variability amongst different sites, which demonstrates both the potential and the limitations of "best practice" restoration activities.

2. Methods

2.1. Study region

The study took place in the Wet Tropics bioregion of north-east Australia (approximately 15–19°S; 145–146°30′E). This biologically diverse region contains 50% of Australia's bird species and has high levels of endemism in its fauna (Williams et al., 1996). This study was focused on two extensively-cleared subregions ("landscapes"), which occupy two different bioclimatic zones: the coastal lowlands, a narrow strip within which sites were located in an area around 133 km by 40 km at elevation 10–26 m; and the Atherton Tableland (henceforth termed "uplands"), a plateau around 35 km inland within which sites were placed in an area about 40 km by 22 km, at 640–870 m elevation, separated from the lowlands by steep forested ranges. Cleared land in these landscapes at the time of the study included large areas of livestock pasture, various croplands (especially sugar cane in the lowlands) and urban settlements. Both landscapes also contained small patches of remnant rainforest.

Since the late 1980s, there have been increasing efforts to restore rainforest vegetation in these landscapes (Catterall and Harrison, 2006; Freeman, 2004). Ecological restoration has typically involved the planting of advanced seedlings of mainly native species, established at high density and diversity in order to develop a closed forest canopy as rapidly as possible (Catterall et al., 2008; Erskine et al., 2007; Freebody, 2007; Tucker, 2008). Plantings have comprised small (mainly <5 ha) linear patches, typically in narrow riparian strips. Grasses and herbaceous plants were controlled using herbicide until suppressed by the shade of the developing tree canopy at around three to 5 years.

2.2. Study design

Networks of replicate survey sites were established to investigate the development of bird communities in the two study landscapes. The restored sites varied in age, and had been independently established with previous support from community-based and/or government-funded revegetation initiatives. They were located through previous inventories (Catterall and Harrison, 2006) and local knowledge. There were 16 revegetated sites in the lowlands (age 1–13 years since planting) and 25 in the uplands (1–24 years). To provide context for interpreting the bird community composition in restored sites, we selected reference sites comprising five pasture and eight rainforest sites in each landscape, resulting in a total of 29 lowland and 38 upland sites. Reference sites were similar to the replanted sites in soil type, elevation, rainfall, and geographical location. All reference rainforest sites had a closed canopy (foliage cover >70%, average about 80%), with tree height >25 m, and a high diversity of structural features (e.g., presence of buttresses, variety of stem diameters), lifeforms (e.g., vines, epiphytes, terrestrial ferns), and tree species. Trees and shrubs within the families Euphorbiaceae, Lauraceae, Myrtaceae, Rutaceae and Sapindaceae were strongly represented by numbers of species and individuals in reference rainforest of both landscapes. Revegetated sites varied in landscape context from small isolated patches to buffer plantings adjacent to mature rainforest. Pasture sites in the lowlands were on average 0.4 km from the nearest remnant rainforest (patch >1 ha), compared with 1.2 km for uplands (range 0.05–1.2 km lowlands, 0.5–1.9 uplands), and at least 50 m from the nearest area of revegetation (average 0.7 km lowlands, 0.2 km uplands).

Replanted sites were selected only if they were readily accessible, physically similar (see above) and met the following criteria:

- planted with a diverse mix (20–50 or more species; >30 in most sites) of mainly locally-native tree species at high density (typical spacing up to 2 m);
- area at least 0.3 ha (range of areas planted in the focal year 0.3–5.8 ha, median 1.4 ha, with 60% of sites at least 1.0 ha); most sites were part of larger forest patches comprising other-aged plantings and/or remnant forest such that the total forest patch area ranged from 0.7 to >1000 ha (median 17 ha with 95% >1 ha), and the range of patch widths at the study sites was 15–230 m (median 35 m);
- adequate previous maintenance to enable survival of planted trees, and minimal damage from a cyclone that traversed the region in 2006 (Kanowski et al., 2008);
- distance from another site of the same age at least 500 m, and different ages spatially interspersed as far as possible within each study landscape.

2.3. Bird surveys

An area of 0.3 ha at each site was surveyed six times (by 2–3 different observers) at approximately monthly intervals between May and December 2008. Wherever possible the survey area's dimensions were 100 × 30 m; however in about one-third of sites its shape was altered to fit within a small or narrow replanted area. Each survey was a 30-min area search, in which a single observer progressed in a wandering path, which varied to negotiate obstacles such as dense vegetation. Surveys avoided weather conditions likely to depress bird activity (heavy rain, strong wind or hottest part of the day). Whenever a species was encountered, a count or estimate was made of the number of individuals; these encounters are termed "records". Bird species were named according to Christidis and Boles (2008). Records were analysed only if birds were seen or heard on-transect, and were located not more than 10 m above the tree canopy in forest and replanted sites or 20 m above the ground in pasture sites. At two lowland replanted sites, difficulties with access meant that only five and three of six planned surveys were conducted, respectively. The missing data were simulated for these sites by averaging and rounding to integers the abundances of each species recorded during the available surveys.

Analyses used sites as replicates and, following initial data exploration, were based on either numbers of records or numbers of species, both accumulated across all six surveys at a site. Records rather than individuals were chosen for relative abundance comparisons across sites, to reduce variability such as that associated with occasional high numbers in some flocking species. This also reduced the potential effects of inter-observer variability, which was further minimised by the small transect area relative to the survey time (ensuring that virtually all birds present were recorded), and by systematically stratifying different site-types and replanting ages across different observers.

2.4. Functional classifications of species

Bird species were classified into *a priori* functional "habitat" groups based primarily on published descriptions (see Kanowski et al., 2010 and Catterall et al., 2004 for list of sources) of their use of uncleared vegetation types within the study region. One category (MF) was also further subdivided on the basis of data from this study.

Rainforest-dependent (RF) species are largely confined to, or dependent on, rainforest. *Rainforest Wet Tropics* (RWT) are a subset comprising endemic species whose Australian distribution is completely within the Wet Tropics and its northern vicinity.

Mixed Forest (MF) species occur mainly in a range of forested habitats from rainforest to more open-canopied eucalypt communities. The following two subsets with differing preferences for rainforest, were also identified (being landscape-specific for each species):

Mixed Forest a (MFa) species (also termed "mixed to RF") were those recorded in at least four of the eight rainforest reference sites in this study.

Mixed Forest b (MFb) species were those recorded in less than four rainforest reference sites.

Eucalypt Forest (EF) species are typically found in eucalypt communities (which typically have canopy foliage cover <70%), and only occasionally occur in denser forest (including rainforest), or less wooded habitats.

Grassland/Wetland (GW) species occur mainly in grassland, wetland or water, although they may also occur within lightly-timbered open habitat, or be dependent on dense swampy vegetation; includes aerial feeding species.

Non-native (XX) species are introduced species which have established free-living populations since European settlement.

2.5. Analyses of community similarity and developmental trajectories

Patterns of multivariate avifaunal similarity among sites were quantified using Sorensen's dissimilarity index (based on the presence of shared species between site-pairs) and graphically visualised using nonmetric multidimensional scaling ordination in two dimensions (MDS; Clarke, 1993) in the Community Analysis Package 3.0 (Seaby and Henderson, 2004); based on all species in each landscape. Differences in bird species composition among pasture, rainforest and revegetated sites in each of three age categories 1–5, 6–10 and >10 years) were statistically tested using Analysis of Similarity (ANOSIM, in PRIMER, Version 6.1.10; Plymouth Marine Laboratory, 2006).

Twenty univariate bird community attributes were also obtained for each site. Sixteen of these attributes comprised either the number of records or the number of species within eight categories: all species, RF, MFa, MFb, EF, GW, XX and RWT species as defined above. Two other attributes were based on species' rainforest-association estimated from this study's data on their occurrence in reference sites (in each landscape separately): "species of reference forest" were those recorded from any rainforest reference site, and "specialists of reference forest" were species recorded from any rainforest reference site but not recorded from any pasture site. For some analyses, the site-specific values of these bird attributes were divided by their mean values across all rainforest sites, to give a standardised measurement relative to rainforest (=1.0), thus providing directly-comparable measurements across the two study landscapes in spite of intrinsic differences in their numbers of species. The final two bird attributes were derived from observed multivariate patterning across all species in each landscape. First, the "Sorensen's distance to forest" for each site was its average dissimilarity from the eight relevant rainforest reference sites. Second, the "trajectory distance to forest" was the standardised distance of each site along a trajectory between pasture and forest in the two-dimensional space obtained from multispecies ordination (see above). The trajectory was the line passing through the two centroids representing pasture and rainforest reference sites in the ordination plot (each derived from mean x- and y-coordinates); the pasture centroid was assigned a value of zero units along the line, the forest centroid had a value of 1.0, sites whose projection fell on the non-forest side of the pasture centroid had negative values, a site midway between pasture and forest would have a value of 0.5, and sites on the non-pasture side of forest had values >1.0.

Developmental trajectories of bird communities in revegetated sites were quantified using parametric linear regressions between the log-transformed age of each site and each of the 20 bird community attributes. For the attributes significantly correlated with revegetation age (also termed "indicators"), we modelled the time that would be required for a replanted site to reach the mean attribute value of rainforest reference sites, and its 95% confidence limits, using the values of the regression intercept, slope, and the slope's standard error.

We also conducted two analyses relating species-specific specialisation to the use of restored sites. First, we tested the strength of association between the degree of intrinsic rainforest specialisation in each *a priori* bird habitat group ($N = 5$) and its pattern of change in species richness over time during revegetation, using Spearman's rank correlation (assigning specialisation ranks 1–5 in the order GW, EF, MFb, MFa, RF, and quantifying each group's pattern of change over time as the Pearson's correlation between the number of species and log of site age). Second, we tested whether older revegetated sites (>10 years) were occupied by fewer endemic than non-endemic rainforest-dependent species by comparing site-specific relative species richnesses between RWT and other RF species, using Wilcoxon matched-pairs signed-ranks tests, in each landscape separately (lowland $N = 6$ revegetated sites, upland $N = 15$). In these analyses relative richness is the value in a revegetated site divided by the mean value in forest reference sites.

3. Results

Across all 67 study sites we obtained 3494 records of 141 species, of which 55 species were present in both lowlands and uplands (Supplementary Table S1). There were 1504 records of 92 species from 29 lowland sites and 1990 records of 104 species from 38 upland sites. Providing a context for the target of restoration, 45 species were recorded in lowland and 56 in upland rainforest reference (henceforth termed "forest") sites. In the lowlands 20 (44%) species in forest sites were classified as RF, as were 32 (57%) species in upland forest (Supplementary Table S1). Site-level species richness was substantially lower in pasture than in forest in both landscapes, and mean species richness within forest was slightly higher in uplands (25) than lowlands (20), whereas in pasture it was higher in the lowlands (14) than uplands (6) (Supplementary Table S1). In both forest and pasture there were different dominant species in lowlands and uplands (Supplementary Table S2), although cross-landscape overlap was greater in pasture.

Revegetated sites of differing ages showed similar patterns of bird species composition relative to pasture and forest reference sites in both landscapes (Table 1, Fig. 1). All revegetated sites were intermediate between pasture and forest, with only 1–5 year old revegetation not differing significantly from pasture, while all revegetation ages differed significantly from forest (Table 1). The 1–5 year old revegetation differed less from 6 to 10 year revegetation than from >10 year revegetation (Fig. 1, Table 1), the latter having progressed a substantial distance through the ordination space separating pasture from forest (Fig. 1).

Across all bird species, both total richness and total abundance in revegetated sites had reached levels similar to those of forest within about 5 years after trees were planted (Fig. 2), and both were significantly correlated with revegetation age in the uplands (Table 2), but not in the lowlands (where baseline differences between pasture and forest were low). Subdivision of the total species richness into categories based on species' differing *a priori* habitat associations yielded substantially stronger correlations with revegetation age in spite of a high level of among-site variability (Fig. 3; Table 2). RF and MFa species increased significantly towards forest levels with age, whereas GW species decreased. MFb and EF species (typically found in open-forest habitats) tended to be more diverse and abundant in revegetated sites than in either forest or pasture (Fig. 2), with no significant response to revegetation age (Table 2). Across the five *a priori* habitat associations, the degree of intrinsic rainforest specialisation was significantly correlated with the tendency for increase in richness with site age (Spearman's r between specialisation ranks and age-richness correlations (from Table 2): lowland 1.0, $P < 0.01$; upland 0.90, $P = 0.04$).

Richness and abundance of rainforest-associated species as defined on the basis of this study's data increased significantly with site age, appearing to approach forest levels in older sites, as did the two indices of progress towards a forest-like whole-community species composition (Table 2, Fig. 4). Non-native (XX) species declined. Regionally-endemic rainforest-dependent (RWT) species increased in richness and abundance with site age, but with marginal significance, and did not approach forest levels even in the oldest revegetated sites (>20 year; Table 2, Fig. 4). Furthermore, the RWT species used older (>10 year) revegetated sites significantly less frequently than did other RF species; for example, richness of endemics in upland restored forest was 36% of that seen in reference forest, compared with 71% for other RF species (Table 3).

Table 1
Tests of difference in bird species composition among rainforest, pasture and revegetation (Reveg) in three age categories, for two landscapes (lowlands, uplands): ANOSIM P; R statistics in brackets. Global ANOSIM $R = 0.59$ in lowlands, 0.57 in uplands, $P < 0.001$ for both). Bracketed numbers in headings are sample sizes (no. of sites).

	Pasture (5)	Reveg. 1–5 year[a]	Reveg. 6–10 year	Reveg. > 10 year
(a) Lowlands				
Reveg. 1–5 year (5)[a]	0.13 (0.14)			
Reveg. 6–10 year (5)	0.008 (0.67)	0.05 (0.18)		
Reveg. > 10 year (6)	0.002 (0.73)	0.004 (0.34)	0.17 (0.12)	
Rainforest (8)	<0.001 (0.97)	<0.001 (0.77)	<0.001 (0.88)	<0.001 (0.78)
(b) Uplands				
Reveg. 1–5 year (4)[a]	0.33 (0.08)			
Reveg. 6–10 year (6)	0.002 (0.64)	0.01 (0.41)		
Reveg. > 10 year (15)	<0.001 (0.94)	0.002 (0.72)	0.09 (0.17)	
Rainforest (8)	<0.001 (0.84)	0.002 (0.81)	<0.001 (0.86)	0.003 (0.33)

[a] *Note*: High heterogeneity of 1–5 year revegetated sites means that R values (ratio of dissimilarity between-treatment to within-treatment) between them and other site-types are lowered (and should be interpreted with caution); P-values are unaffected by this.

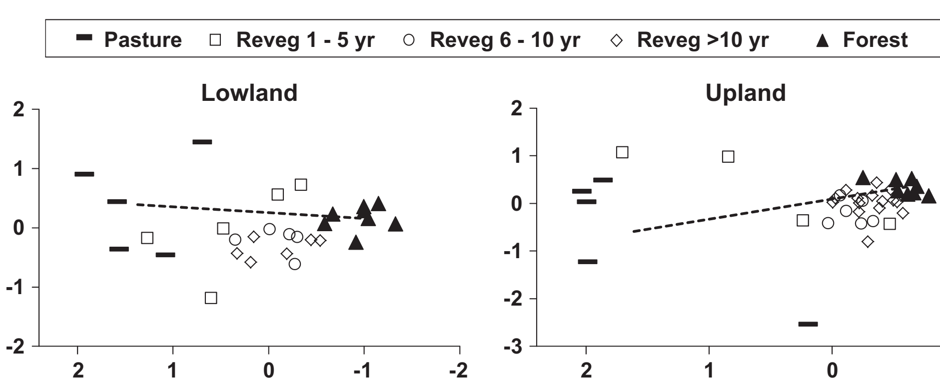

Fig. 1. Ordination by bird species composition of sites in rainforest (Forest), pasture and revegetated (Reveg., in three age categories), for two landscapes. The dotted line shows the trajectory linking the pasture and forest centroids. Lowlands (MDS stress = 0.14) had 92 species in 29 sites (pasture 5, Reveg. 16, forest 8); Uplands (MDS stress = 0.14) had 102 species in 38 sites (pasture 5, Reveg. 25, forest 8).

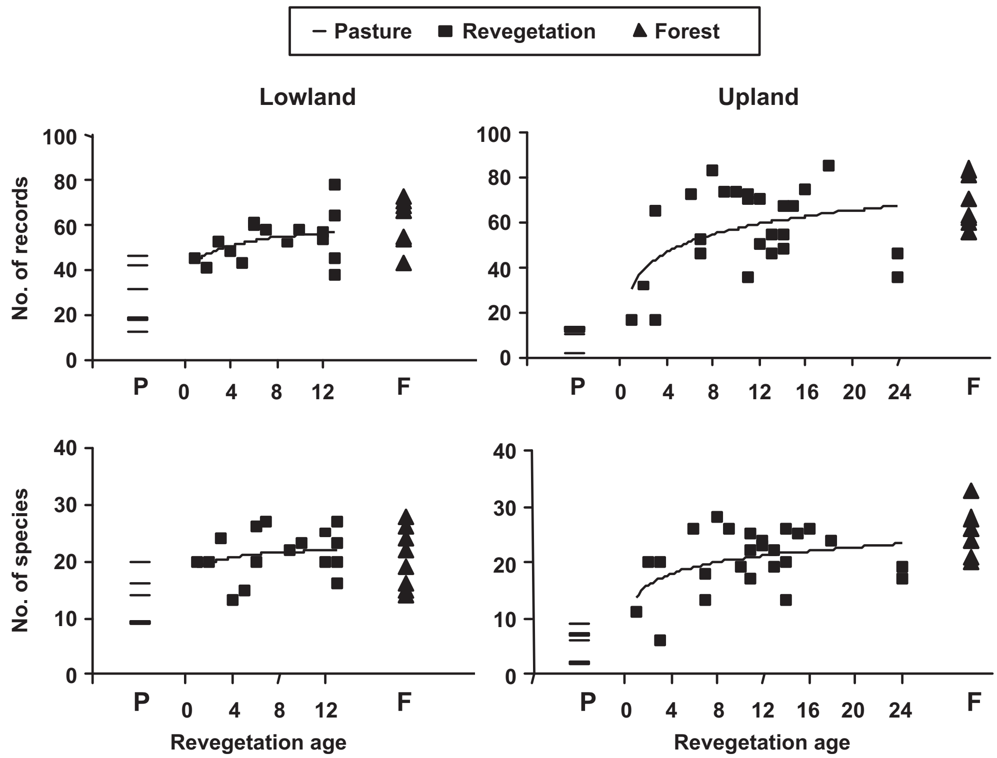

Fig. 2. Bird abundance (no. of records) and richness (no. of species) in pasture (P), rainforest (F) and revegetated sites aged 1–24 years in two landscapes (Lowlands, Uplands). Fitted lines are logarithmic. Sample sizes (P, Reveg., F): Lowland 5,16,8; Upland 5,25,8.

Table 2
The strength of relationship between age of revegetated sites and different indicators of bird community change. Numbers are Pearson's r using log-transformed site ages; N = 41 sites across two landscapes, 16 Lowland, 25 Upland. Bird indicators obtained from six, 30-min surveys in 0.3 ha.

Type of indicator	Metrics using species' presence			Metrics using abundance[a]		
	Lowland	Upland	Both	Lowland	Upland	Both
All species	0.22	0.42*	0.19	0.40	0.46*	0.42**
A priori species categories[b]						
Rainforest-dependent (RF)	0.64**	0.50*	0.54***	0.62*	0.56**	0.57***
Mixed to RF (MFa)	0.63**	0.60**	0.62***	0.53*	0.47*	0.49**
Mixed Forest (MFb)	0.35	0.02	0.07	0.17	0.03	0.02
Eucalypt Forest (EF)	−0.25	−0.16	−0.18	−0.25	−0.26	−0.28+
Grassland/wetland (GW)	−0.66**	−0.29	−0.36*	−0.75**	−0.36+	−0.47**
Endemic RF species (RWT)	0.36	0.29	0.34*	0.34	0.42*	0.41*
Non-native species (XX)	−0.44+	−0.32	−0.38*	−0.50*	−0.32	−0.41**
Forest association from data						
Species of reference F[c]	0.67**	0.51**	0.51***	0.63**	0.55**	0.59***
Specialists of reference F[d]	0.67**	0.54**	0.61***	0.60*	0.57**	0.61***
Community composition						
Sorensen's distance to F[e]	0.71**	0.64**	0.67***	–	–	–
Trajectory distance to F[f]	0.74**	0.61**	0.66***	–	–	–

[a] Abundance is no. of records (encounters with a single bird or group of conspecifics).
[b] Number of species or abundance within *a priori* categories of either habitat association in uncleared landscapes or geographical distribution (RWT, XX).
[c] Recorded from any rainforest reference site.
[d] Recorded from any rainforest reference site but not in any pasture site.
[e] Average Sorensen's similarity between each revegetated site and the eight relevant rainforest reference sites.
[f] Standardised distance of each site along a trajectory from pasture to forest in the multispecies ordination space (see Section 2).
+ $P < 0.10$.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

The power of this test for similar patterns in the lowlands was limited by smaller sample sizes and low numbers of endemic species (Table 3).

Modelled predictions of the time that would be needed for restored sites to acquire an avifauna similar to the average seen in reference forest varied considerably among significant indicators

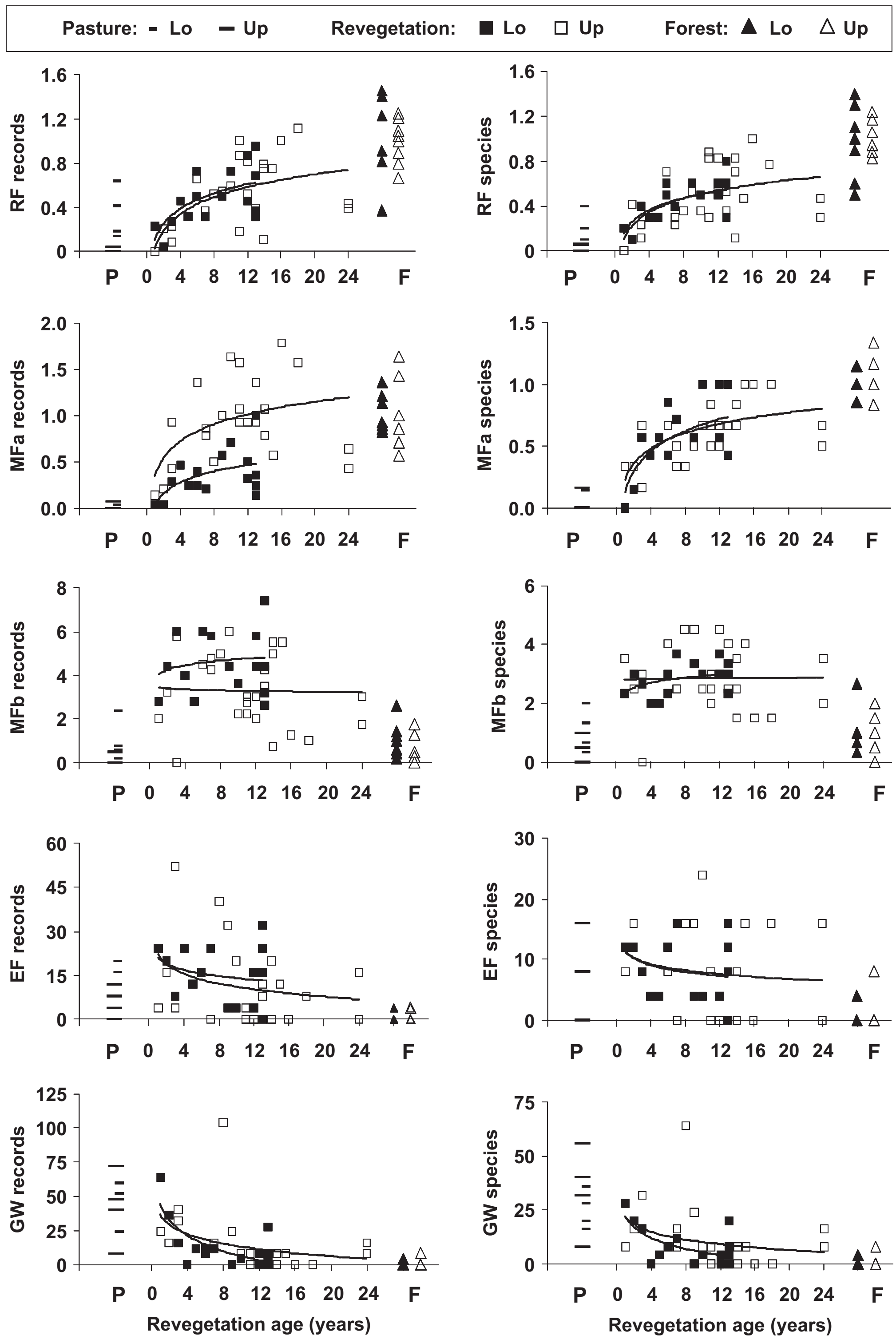

Fig. 3. Changes in bird abundance (records) and richness (species) within *a priori* habitat-based groupings in relation to age of revegetated (Reveg.) sites and within reference ecosystems (pasture P, rainforest F). Two landscapes (Lowland Lo; Upland Up) are shown on each graph, with separate fitted logarithmic curves. Bird categories: RF rainforest-dependent; MFa Mixed to RF; MFb Mixed Forest; EF Eucalypt Forest; GW Grassland/Wetland (see Table 2), with values standardised relative to averages in rainforest sites (mean $F = 1.0$). Species' intrinsic dependence on rainforest decreases from top to bottom. Sample sizes (P, Reveg., F): Lowland 5, 16, 8; Upland 5, 25, 8; some graphed points coincide.

(Supplementary Table S3). The mean projected time to forest levels was consistently longest for RF species (>150 years in both landscapes) whereas for other groupings (including species' categorisations based on this study's data) it was mostly in the range 30–70 years. Additionally, the lower 95% confidence projections of the time needed for many indicators to reach average forest levels were <20 years (26 years for upland RF species), whereas upper 95% projections were >1000 years.

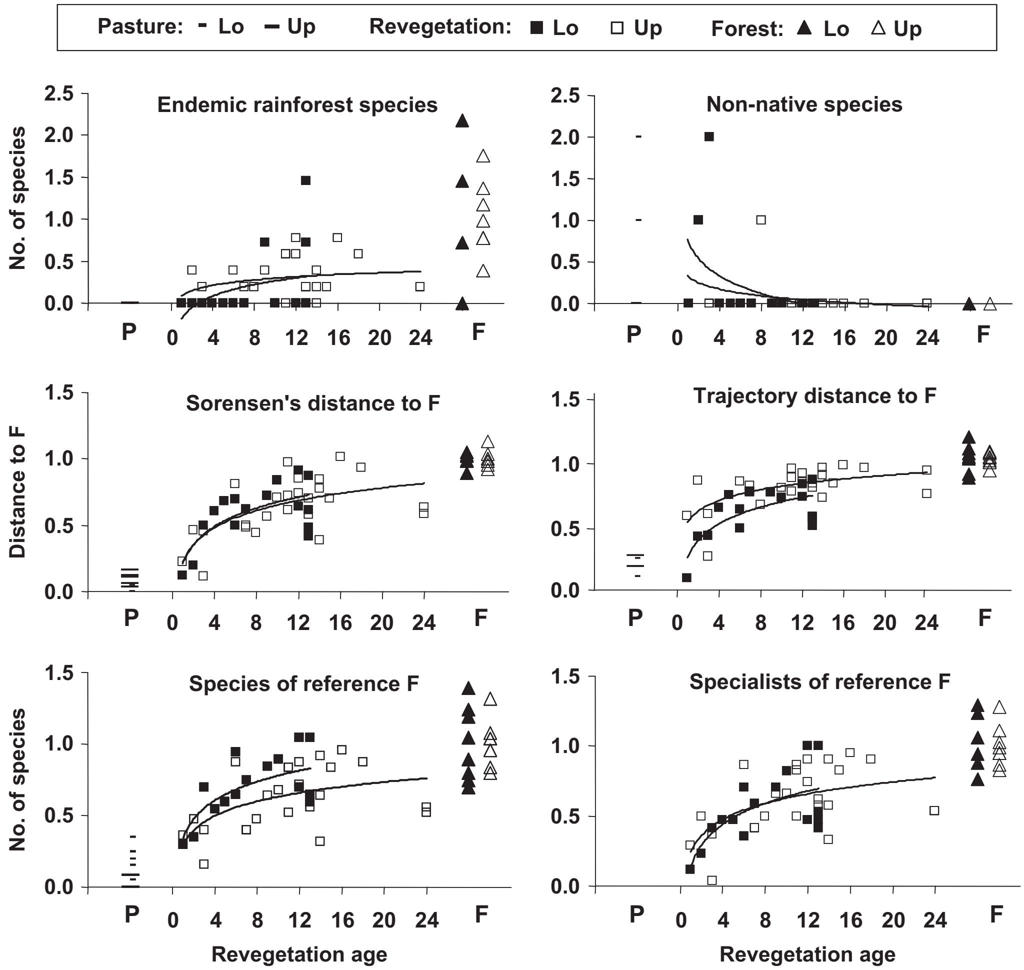

Fig. 4. Changes in species richness of endemic species and non-native species, and in four community indicators, in relation to age of revegetated sites, and within reference ecosystems (pasture P, rainforest F). Two landscapes (Lowland Lo; Upland Up) are shown on each graph, with separate fitted logarithmic curves. See also Table 2. Values for numbers of endemic rainforest species are standardised relative to averages in rainforest sites but this was not done for non-native species. Sample sizes (P, Reveg., F): Lowland 5, 16, 8; Upland 5, 25, 8; some graphed points coincide.

Table 3
Use of older revegetated sites (11–24 years) by rainforest-dependent birds that are regionally-endemic compared with other rainforest-dependent species. Bird variables are mean values from *N* sites in each region. *P* shows the results of testing whether endemics show lower occupancy, using 1-tailed Wilcoxon matched-pairs signed-ranks tests.

Bird variable[a]	Lowland (N = 6 sites)			Upland (N = 15 sites)		
	Endemics[b]	Others	P	Endemics[b]	Others	P
Species per site	0.36	0.55	0.23	0.36	0.71	<0.001
Records per site	0.28	0.65	0.04	0.36	0.73	<0.001

[a] Accumulated number of species or total records from six, 30-min surveys in 0.3 ha, where a record is an encounter with a single bird or group of conspecifics. Values have also been standardised relative to the average in rainforest reference sites in each landscape (i.e., mean rainforest value = 1.0).

[b] Species that are both rainforest-dependent and endemic to the Australian Wet Tropics (four in total recorded from lowland rainforest sites; 11 in the uplands).

4. Discussion

4.1. Biodiversity responses to deforestation and early phases of ecological restoration

In spite of underlying ecological differences in bird and plant assemblages and land-uses between upland and lowland forests in the Wet Tropics, the two study landscapes showed remarkable consistency in developmental trajectories of bird community composition within replanted rainforest, for any particular indicator. There was rapid development towards a more rainforest-like state in the first decade after planting. Previous work in this study's uplands has also reported rapid early development of the bird community in ecological restoration (Catterall et al., 2004; Freeman et al., 2009; Jansen, 2005) – after around 10 years of growth, restored sites contain on average about half the number of rainforest-dependent species seen in forest reference sites. The birds have responded to the fast development of vegetation structure which follows the tailored high-diversity and high-density tree-planting and early maintenance considered to be best-practice in ecological restoration within the Australian Wet Tropics (Catterall et al., 2008; Freebody, 2007; Kanowski et al., 2003; Tucker, 2008). When these techniques are used, many aspects of vegetation structure recover within a decade to a level resembling reference forest (including the closed canopy, high stem densities and ground litter layer), although other structural attributes (such as large-diameter trees and vines, and diversity of structural life-forms) have only partly developed (Kanowski et al., 2003). However this outcome requires considerable investment; initial establishment of ecological restoration at sites in the Wet Tropics had an average cost in 1997–2002 of about AUD$25,000/ha (Catterall and Harrison, 2006).

Changes in bird communities during this study's chronosequences included an increase in rainforest-associated species and a decrease in open-country species. Bird species whose typical habitat was open eucalypt forest tended to be more diverse in young revegetated sites than in either pasture or rainforest; they moved in as the planted trees started to grow, but with canopy coalescence and increased foliage volume, habitat suitability for these birds decreases. A broadly-similar temporary influx of open-country bird species was reported by Raman et al. (1998) for a forest regeneration chronosequence in India.

4.2. Selecting effective indicators of biodiversity recovery

Understanding biodiversity development requires meaningful quantitative indicators of the state of multispecies faunal communities. Recent debate has focused on the capacity of reforested areas to regain a forest-like species composition (Chazdon et al., 2009; Dent and Wright, 2009; Gardner et al., 2009). In contrast, total species richness has been the most frequently used measure of recovery (Dunn, 2004), even though adding species numbers without recognition of their ecological differences obscures contrasting species-specific response patterns, and can thereby lead to misleading conclusions about trends in biodiversity (Dunn, 2004; Bowen et al., 2007; Waltert et al., 2005). In the present study, total bird species richness was a relatively insensitive measure of both forest–pasture differences and community development during restoration.

We also compared developmental trajectories as revealed by differing measurements of species composition, obtained either by partitioning species into categories of different habitat preference or by calculating indices based on multivariate analyses of composition in restored sites relative to reference sites. Different specific indicators showed differing sensitivities to site development. Informative results that were very consistent across landscapes were obtained from indices of multispecies similarity to reference habitats and also from the sampled richness of rainforest-associated species (whether derived from *a priori* literature descriptions of species' habitat preference or from their patterns of occurrence in this study's reference sites). These all gave fitted developmental trajectories in which the mean value in older revegetated sites (around 20 years) overlapped in value with the "poorest" forest reference sites. While some of the abundance-based metrics also gave comparable results, we consider that indices based on species' presence are preferable as they are simpler and less vulnerable to observer effects.

4.3. Developmental trajectories and their implications

Most previous work on developmental trajectories in tropical reforestation has focused on spontaneous regrowth. Dunn (2004) concluded from a meta-analysis of 10 bird datasets that total species richness in forest regrowth reached a level similar to that in reference old-growth forest after 20–40 years, but with recovery of species composition being much slower. In contrast, Dent and Wright's (2009) meta-analysis of 65 studies spanning various higher taxa suggested that moderate levels of similarity in species composition to old growth forest can be reached after a few decades of regrowth. After reviewing 37 vertebrate studies (15 using birds), Gardner et al. (2007) were unable to reach firm conclusions, but argued qualitatively that many species of old-growth forest may be unable to use regrowth forest, and that development of specific resources for many species is slow. Chazdon et al. (2009) reviewed 31 sources of data on the proportion of old-growth-associated species found in regrowth, and concluded that few general inferences could be made, due to limitations in study designs and measurements and also to large between-study variability stemming from variation in landscape-scale forest cover, and variation in the presence of seed-dispersing fauna.

There has been limited previous multi-site research into the trajectories of biodiversity development following active ecological restoration (as distinct from passive regrowth) of tropical forest. Our results confirm that there is a predictably slower-returning subset of species during forest restoration (cf Dent and Wright, 2009; Chazdon et al., 2009; Gardner et al., 2007, 2009), even when replanting is used to accelerate vegetation development. The slow-returners comprised species of special conservation concern – the rainforest-dependent Wet Tropics endemic (RWT) species, whose occupancy rate in older revegetated upland sites was about half that seen in the other (non-endemic) rainforest-dependent species. Nine of the 13 rainforest specialists that are regionally-endemic to the Wet Tropics are confined to higher elevations (Williams et al., 1996). Their endemism in this region is probably in itself a consequence of a high level of habitat specialisation, as they are considered relicts of past contractions of rainforest habitat during Pleistocene periods of climatic dryness, when the Wet Tropics was the only part of Australia to retain substantial rainforest (Williams and Pearson, 1997). Therefore, it is logical that these specialised WT endemics would also be slow to colonise modern-day rainforest habitat that is redeveloping after clearing. There is an emerging global pattern that range-restricted tropical forest bird species are less tolerant of habitat disturbance than are other species in their regional pool, as reported by Dunn and Romdal (2005, Americas), Raman (2001; India), Waltert et al. (2004; Indonesia), and Waltert et al. (2005; 2011; Africa). Thus, the restored rainforest is least effective in providing habitat for the species that need it most (see also Gardner et al., 2007).

Extrapolating the relationship between site ages and bird community indicators gave a very wide range of projected time-spans needed for revegetated sites to reach typical reference rainforest values. Such extrapolations well beyond the timeframe of data collection cannot be relied upon as predictions, but it is noteworthy that projected recovery times were greatest for rainforest-associated species, compared with the other indicator groups. Furthermore, the wide confidence limits of projections (1–2 decades to >1000 years) caused by the large scatter of sites around the mean trajectories demonstrates that it would be wrong to assume that undertaking "best practice" restoration activities for a few years can reliably set any area on track towards the biodiversity of intact native forest. Landscape context is likely to contribute to this uncertainty (Bowen et al., 2007; Chazdon et al., 2009; Gardner et al., 2009). This study's restored sites included small isolated patches (<5 ha) surrounded by agricultural land, which would not be expected to ever reach a fully rainforest-like bird community as they could not supply the quality and quantity of habitat needed by even one or two individuals of many species. At the other extreme were buffer plantings adjacent to remnant rainforest, from which rainforest-dependent birds could readily extend their home ranges to make use of the revegetation, even if it did not meet all their habitat requirements. Moreover, any site's developmental trajectory may change in the future. For example, instead of the planted trees being progressively replaced by the desired recruits, they may be overcome by smothering vines as is known to occur in small remnants of native rainforest (Laurance, 1997), and paradoxically these vines are often dispersed by birds (Catterall et al., 2008).

Such a high level of variability and uncertainty places strong constraints on the potential usefulness of rainforest restoration as a tool to compensate for biodiversity loss from land development. This variability means that very large offset ratios (Moilanen et al., 2009) would be required if the creation of compensatory habitat by replanting were to be attempted. It also means that ongoing monitoring of biodiversity outcomes is an essential part of restoration activities, to confirm whether sites are developing on-track and to signal if and when further management intervention is needed. Like the bird communities dependent on them, the developmental trajectories of plant communities in actively-restored rainforest are poorly understood because of the short history of replanting (Freebody, 2007). To enable better planning and design of future restoration investments for cost-effective biodiversity outcomes, larger-scale and longer-term research and experimental management are needed.

Acknowledgements

Funds and support were provided by the Australian government's MTSRF and NERP programs (via Reef and Rainforest Research Centre) and the Griffith University Environmental Futures Centre. We thank Will Goulding, Debra Harrison, Anna Koetz, Stephen McKenna, Ian Northcott, Terry Reis, Terrain NRM staff and members of the GU Wildlife Ecology Discussion Group for assistance and/or discussions. Thanks to many landholders for property access and information. Queensland Parks and Wildlife Service provided Scientific Purposes Permit F1/000365/00/SAA.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.10.033.

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