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Use of restored habitat by rainforest birds is limited by spatial context and species' functional traits but not by their predicted climate sensitivity

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ABSTRACT

Active restoration of biodiverse forest uses significant resource investment to produce rapid partial recovery of biodiversity, but with unknown longer term outcomes. Here we test the capacity of intensive high diversity rainforest restoration plantings to develop forest-like bird communities beyond their first decade of growth. Across a network comprising 16 such plantings aged 10–24 years and eight old growth rainforest reference sites, spread across about 700 km^2 in the Australian Wet Tropics, we measured bird community composition and 18 attributes related to the sites' local and landscape vegetation cover and other spatial properties. We compiled additional information on the bird species' habitat use, movement patterns, responses to edges between forest and cleared land, and expected climate sensitivities. Data analyses showed that bird communities in restoration plantings did not become more similar to those of reference rainforest during their second decade of development. Across replanted sites, occupancy by bird species was significantly predicted by their functional traits, being least among rainforest-dependent species that were also either endemic or sedentary edge-avoiders. Occupancy by rainforest-dependent species was least when nearby remnant rainforest cover (within 200 m) was lowest. Species predicted to be climate-sensitive occupied restored habitat at similar rates to other species. These findings provide a foundation for better spatial planning for both habitat-focused and species-focused restoration, and show that expectations based on promising early outcomes of intensive forest restoration projects must be tempered with awareness of likely longer term limitations, highlighting the need to set realistic restoration goals.

1. Introduction

Strategic reforestation is an emerging tool for averting or mitigating the biodiversity impacts of past tropical deforestation (Chazdon et al., 2009; Holl and Aide, 2011; Rodrigues et al., 2011) and to facilitate species' adaptation to climate change (Shoo et al., 2011). Following extensive land clearing for agricultural development, species which depend on forest habitats have become locally, regionally or globally extinct because of the loss of habitat area, followed by additional impacts due to the fragmentation of remaining habitat, and its interactions with other threats such as hunting, altered disturbance regimes and climate change (Gardner et al., 2007). Logically, restoration of forest habitat could be expected to reduce the extirpation rates of forest-dependent species by increasing the size of at-risk populations, and their opportunities for dispersal. Implicit in this expectation is a "field of dreams" hypothesis, which assumes that actions to reinstate vegetation will catalyse the subsequent occupancy of restored sites by desired species of fauna (Hilderbrand et al., 2005).

However, forest restoration will be unable to mitigate or reverse biodiversity loss unless two criteria are met: (1) adequacy – restored habitat must be suitable for at-risk species; and (2) accessibility – sufficient individuals must disperse from remnant populations to restored sites. Successful colonisation by forest-dependent fauna thus depends on the interaction between habitat quality in the reforested areas, the characteristics of the surrounding landscape and the functional characteristics of species. Existing evidence is inadequate to support either the assumption that reforested areas can, within the timeframe needed by management, develop the necessary habitat elements to support the diversity of species that typically occur in older growth forest; or that individuals will disperse across open agricultural land between

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source populations and restored forest (Chazdon et al., 2009; Gardner et al., 2007; Gibson et al., 2011). Furthermore, reforestation occurs through a range of pathways, including unassisted secondary forest regrowth, various plantation styles, and other types of intervention, while these different pathways also vary in their capacity to acquire the biodiversity characteristics of intact old growth forest (Catterall et al., 2008; Shoo et al., 2013). Within this spectrum, biodiverse ecological restoration plantings provide a special and extreme case, since this method has been devised to invest significant resources in order to maximise both the speed and quality of ecosystem recovery (Catterall et al. 2008; Rodrigues et al. 2011).

Research into how well reforestation promotes recovery of animal communities has often focused on aggregate species richness, a superficial metric which provides a poor indicator of recovery, because it allows rapid colonisation of reforested sites by generalist or open-country species to mask much slower responses among forest-dependent species (Dunn, 2004; Bowen et al., 2007; Reid et al., 2014). For example, Catterall et al. (2012) found that by around 10 years of growth, biodiverse rainforest restoration plantings had recovered about half the species richness of rainforest-dependent birds that characterised old growth forest, whilst the richness of species that typically use more open habitats greatly exceeded that of reference rainforest. More generally, habitat specialisation and endemism are increasingly being recognised as likely factors associated with limited use of reforested sites by many of the species that are targeted by restoration efforts (Bowen et al., 2007; Chazdon et al., 2009). Measurements that account for functional differences among species are needed to provide meaningful tests of biodiversity recovery in reforested sites.

The present study tests what factors limit ecological recovery of bird communities in biodiverse rainforest restoration planting sites beyond their first decade of growth. We consider both species' functional traits and sites' spatial attributes. Using a network of 24 replanted and forest reference sites we address the following questions (1) Does community composition develop further towards that of reference rainforest after the first decade? (2) Is variation in species' occupancy of replanted sites related to their degree of rainforest habitat specialisation and their predicted recolonization capacities, based on independent information about their ecology and behaviour? (3) Is variation among sites in their rate of occupancy by rainforest-dependent bird species related to patch size, landscape context or other spatial characteristics? (4) What is the value of habitat restoration to climate-sensitive species?

We find that avifaunal recovery showed no progress in the second decade after site establishment, and that species' functional attributes (but not their climate sensitivities) and restored sites' landscape context are both significant predictors of community composition. These findings provide a foundation for improved realism of restoration goals, and better spatial restoration planning for both habitat-focused and species-focused forest restoration.

2. Methods

2.1. Study region and survey sites

Sixteen replanted sites with "established rainforest revegetation" (ERR), aged 10–24 years, and eight old growth rainforest reference (FO) sites, were surveyed for birds and landscape context. The sites were distributed across the southern Atherton Tablelands region of the Australian Wet Tropics, an upland plateau around 35 km inland. Original rainforest cover on the plateau was extensively cleared for agriculture early in the twentieth century, and the remaining small scattered patches of old growth forest together with more extensive tracts on the adjacent steep slopes acquired legislative protection from clearing and logging during the 1990s (Stork et al., 2008). From the late 1980s, community groups, government agencies and private individuals undertook a series of restoration projects, using biodiverse ecological restoration plantings of small saplings. These plantings were often configured as small (<5 ha) linear riparian patches, and used a diverse mix of mainly locally-native tree species at high density (20–50 or more species, typically >30, with spacing up to 2 m), together with periodic maintenance in the first 3–4 years to suppress competitive grasses and herbs (Freeman, 2004; Freebody, 2007; Catterall et al., 2008). The ERR sites selected for this study met these criteria and had experienced minimal damage during a cyclone in 2006. Hunting pressure in the region is negligible.

This study's FO sites had a closed canopy (foliage cover >70%, mean 79%), with mean tree height 29 m, and a high diversity of structural features (e.g., presence of buttresses, variety of stem diameters), life-forms (e.g., vines, epiphytes, terrestrial ferns) and tree species. Trees and shrubs within the families Euphorbiaceae, Lauraceae, Myrtaceae, Rutaceae and Sapindaceae were strongly represented (as both species and stems). The ERR and FO sites were interspersed across an area about 39 km by 22 km (latitude 17°S with ERR at 11–32′ and FO at 11–30′; longitude 145°E with ERR at 32–39′ and FO at 31–44′), on similar soil (15 of 16 ERR sites and all FO sites were on basaltic soils) and at similar elevations (ERR mean 750 m, range 680–870 m, FO mean 771 m, range 685–865 m).

2.2. Bird data

Birds were surveyed at all sites in 2008, and prior surveys had also been made at five of the FO sites and seven of the ERR sites in 2001 (when these were aged 6–17 years). In both years there were six repeat 30-min survey visits to an area of 0.3 ha, by 2–3 different observers. Wherever possible the survey area's dimensions were 100×30 m; however in about one-third of sites its shape was modified to fit within the replanted area. A single observer progressed in a wandering path, varied to negotiate obstacles such as dense vegetation. Whenever a species was encountered, an estimate was made of the number of individuals. Surveys avoided heavy rain, strong wind and the hottest part of the day. In 2008 surveys were at approximately monthly intervals between May and December; in 2001 four surveys were conducted in different months during April–August and two during the previous October–November. Records were analysed only if birds were seen on-transect within 10 m above the tree canopy (or if identified from calls were clearly localised to points within-transect). Data analyses used either species-specific abundance (number of individuals) totalled across all six surveys at a site or species' presence (recorded on one or more of these surveys).

2.3. Analysis of development towards a rainforest-like bird species composition

To assess the extent to which the full bird community composition became more rainforest-like as ERR sites grew older, we conducted two ordination analyses. These used abundances of all species at each site, with inter-site differences quantified using the Bray–Curtis metric and graphically visualised using nonmetric multidimensional scaling (MDS) ordination in two dimensions. First we ordinated all the 2008 bird data, with sites in three categories: younger ERR (10–13 years, $N = 8$), older ERR (14–24 years, $N = 8$) and FO ($N = 8$). Second we ordinated both the 2001 and 2008 data for the 12 sites that were surveyed in both years (five FO, seven ERR; the latter aged 6–17 and 13–24 years respectively).