

TEMPORAL CHANGES IN VERTEBRATES DURING LANDSCAPE TRANSFORMATION: A LARGE-SCALE “NATURAL EXPERIMENT”

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Abstract. Plantation development is a significant form of landscape change worldwide. We report findings from a large-scale longitudinal natural experiment that quantified changes in Australian vertebrates as a former grazing landscape was transformed to one dominated by a radiata pine (*Pinus radiata*) plantation. The study included four main “treatments”: woodland remnants surrounded by emerging radiata pine (52 sites, termed “woodland treatments”), stands of radiata pine (10 sites, “pine controls”), woodland remnants where the surrounding landscape remained unchanged (56 sites, “woodland controls”), and paddocks with scattered woodland trees that surrounded the 56 woodland remnants (10 sites, “paddock controls”). In our study region, woodland is distinguished from forest by differences in tree height, tree spacing, bole length, and canopy development.

Between 1998 and 2006, occupancy rates of “woodland treatments” by most mammals and reptiles increased linearly. Similar trends occurred in the “woodland controls,” suggesting that species had increased landscape-wide, rather than displaying year \times treatment interaction effects. We cross-classified birds according to the statistical significance and nature of time trajectories. Groups included those that: (1) declined in woodland treatments in comparison with woodland controls, (2) decreased within woodland treatments but increased in woodland controls, (3) declined across the entire study area, (4) increased within woodland treatments in comparison with woodland controls, (5) increased within woodland treatments but declined in woodland controls, and (6) increased across the entire study area.

Attributes of woodland treatments significantly associated with temporal changes in bird occupancy included: (1) age of surrounding pine stands; (2) number of boundaries with surrounding pines; (3) size of the woodland patches; (4) dominant vegetation type of woodland patches; and (5) temporal changes in vegetation structure in the woodland treatments.

Bird species associated with open country and woodland environments were disadvantaged by landscape transformation, whereas those that benefited were forest taxa and/or habitat generalists capable of inhabiting pine stands and adjacent woodland patches. Beyond this generalization, an unanticipated finding was a lack of association between life history attributes and landscape transformation. We suggest that several key processes are likely drivers of change at multiple spatial scales. Recognition of such processes is important for conservation in landscapes transformed by plantation expansion.

Key words: *landscape context; landscape transformation; longitudinal study; Pinus radiata; plantation establishment; southeastern Australia; temporal change mechanisms; woodland remnants; vertebrates.*

INTRODUCTION

Around the world, large-scale landscape change resulting from human land use (UNEP 1999) is a major driver of altered ecosystem processes (McIntyre and Hobbs 1999, Foley et al. 2005, Millennium Ecosystem Assessment 2005) and biodiversity loss (Sala et al. 2000, Lindenmayer and Fischer 2006). Plantation expansion is a significant form of landscape transformation worldwide (Jackson et al. 2005, Food and Agriculture Organization of the United Nations 2007) and it is an increasingly common land use in places such as South

America (Estades and Temple 1999), North America (Haskell et al. 2006), Europe (Shakesby et al. 1996, Martínez-Sánchez et al. 1999), Asia (Cubbage et al. 1996), Japan (Yamaura et al. 2006), Australia (Burns et al. 1999, Salt et al. 2004), New Zealand (Clout and Gaze 1984, Allen et al. 1995, Dyck 2000), and Africa (Wethered and Lawes 2003). In 1996, the global area of plantations exceeded 130 million ha (Cubbage et al. 1996), and in 2001 it was more than 187 million ha (Food and Agriculture Organization of the United Nations 2001). Indeed, there is a worldwide trend toward a greater reliance on wood sourced from plantations (Food and Agriculture Organization of the United Nations 2007), with an increasing emphasis on “industrialized” plantation forestry in the southern

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hemisphere (Franklin 2003). Increasingly, arguments are being made that plantation establishment can help to offset net greenhouse gas emissions through carbon sequestration (Jackson and Schlesinger 2004).

A better understanding of the responses of biota to landscape transformation, including large-scale plantation establishment and expansion, is pivotal to the development of effective natural resource management strategies (Peterken and Ratcliffe 1995, Moore and Allen 1999, Lindenmayer and Hobbs 2004). Attempts to improve such understanding have resulted in an enormous and rapidly growing literature on the effects of landscape change on biodiversity (reviewed by McGarigal and Cushman 2002, Fahrig 2003, Lindenmayer and Fischer 2006). Many of these studies have noted that an important determinant of the biota that occupies patches of native vegetation in modified landscapes is landscape context, or the condition of the matrix surrounding them (sensu Laurance 1991, Gascon et al. 1999, Renjifo 2001, Ricketts 2001, Lindenmayer et al. 2002, Viveiros de Castro and Fernandez 2004). For the purposes of this paper, we define the matrix from a conservation biology perspective and consider it to be areas dominated by nonnative vegetation used primarily for commodity production (see Lindenmayer and Franklin 2002:7).

Conditions in the matrix can influence the occupancy of patches of remnant native vegetation in several ways. These include: (1) influencing inter-patch movement, patch colonization, and rescue effects (Hanski 1999, Revilla et al. 2004, Bender and Fahrig 2005, Haynes et al. 2006); (2) providing suitable places to forage (Loman and von Schantz 1991, Rodenhouse and Best 1994), which can increase the sizes of populations within patches (McCarthy et al. 2000, Tubelis et al. 2004); (3) altering regional populations of species (Askins et al. 1987, Gascon et al. 1999) and in turn providing a source of colonists, which then invade patches from surrounding areas (Tocher et al. 1997, Ås 1999, Davies et al. 2001); and (4) altering boundary conditions and influencing edge effects (Bayne and Hobson 1997, Harper et al. 2005), including increased levels of predation and parasitism of animals within patches (Murcia 1995, Ries et al. 2004).

There is a large literature on the biological attributes of species that are associated with their risk of decline or chance of increase in response to landscape transformation (Thomas and Kunin 1999, reviewed by McKinney 1997, O'Grady et al. 2004, Lindenmayer and Fischer 2006). Among these biological attributes are: (1) the degree of habitat and niche specialization or generalization (Johns and Skorupa 1987, Koh et al. 2004); (2) mobility (including dispersal ability) (Angermeier 1995, Lindenmayer et al. 2002, Driscoll and Weir 2005, Kotiaho et al. 2005) and home range size (Woodroffe and Ginsberg 1998); (3) body size (Johns and Skorupa 1987, Lindenmayer et al. 2002); (4) mating system and the complexity of behavior (McKinney 1997, Brashares

2003); and (5) edge sensitivity (Lehtinen et al. 2003). These biological attributes can be associated with a species being able to use the matrix (Laurance 1991, Davies et al. 2001) and tolerate disturbance (Blake 1983, Balmford 1996, Ricketts 2001, Sekercioglu et al. 2002).

Most studies on the effects of matrix conditions on patches of native vegetation have been "snapshot" cross-sectional or observational investigations (sensu Diamond 1986) (reviewed by McGarigal and Cushman 2002, Fahrig 2003, Lindenmayer and Fischer 2006). In contrast, large-scale experiments and longitudinal natural experiments (sensu Lindenmayer et al. 2001) of temporal effects of matrix transformation on patches are rare (reviewed by Debinski and Holt 2000). A clear advantage of longitudinal studies over cross-sectional studies is that they enable relationships between explanatory variables and a response arising from covariation between sites to be distinguished from those arising from covariation within sites.

In 1997, we commenced a large-scale longitudinal natural experiment to directly quantify changes in woodland patch occupancy by vertebrates as the surrounding landscape was transformed from a semi-cleared grazing landscape to one dominated by an exotic softwood plantation (Lindenmayer et al. 2001). Our longitudinal "natural experiment," known as the Nanangroe study, involved gathering data on vertebrates inhabiting 52 woodland remnants (termed "woodland treatments") before the transformation of the surrounding landscape and then gathering data repeatedly after the surrounding areas supporting scattered paddock trees were cleared and stands of exotic plantation radiata pine (*Pinus radiata*) established. We matched these 52 woodland treatments with a set of 56 woodland remnants (which we term "woodland controls") where the immediate surrounding landscape was not transformed and remained dominated by scattered paddock trees and grazing paddocks. Notably, in Australia, forest and woodland are considered distinctly different vegetation types characterized by marked differences in tree height, tree spacing, length of boles, canopy development, and spacing, as well as several other features (Specht and Specht 1999).

In this paper, we quantify longitudinal changes in vertebrate occupancy of woodland remnants over nine years as surrounding radiata pine plantation stands matured. We sought to cross-classify species by their responses to the different treatments in our natural experiment, and in particular to temporal changes in surrounding landscape context. We also attempt to elucidate some of the processes that have given rise to the emergent patterns of vertebrate occurrence that we observed. As part of quantifying vertebrate responses to landscape transformation, we also sought to determine if broad sets of responses could be associated with particular functional groups or species with particular kinds of life history attributes. Hence, we sought to determine if biological attributes found to be associated

TABLE 1. Postulated responses to experimental landscape transformation from grazing to woodland dominated by an exotic plantation, broad drivers of response, and characteristics of taxa exhibiting particular kinds of responses.

Response	Possible driver(s)	Possible characteristics of taxa
a) Negative response to landscape transformation		
Decline in woodland treatments, increase in woodland controls	displacement	high mobility, inability to use matrix
Decline in woodland treatments, static in woodland controls	local extinction, altered connectivity	limited mobility, inability to use matrix, sensitive to woodland/pine boundaries
Overall decline across study area	reduced foraging area, altered connectivity	woodland specialists, requirement for large woodland areas
b) Positive response to landscape transformation		
Addition of new species	addition of new (pine) environment, altered connectivity	taxa typical of forest environments, ability to use matrix
Increase in woodland treatments, stable in woodland controls	increased foraging area because of pine stands, altered connectivity, positive response to woodland/pine boundaries	high mobility, ability to use matrix, habitat generalists: "spillover" from pine stands to adjacent woodland patches
Overall increase across the study area	increased foraging area, altered connectivity	high mobility, habitat generalists

with species change in other studies (reviewed by McKinney 1997, Lindenmayer and Fischer 2006) also were found in this study. Some of our postulated responses to landscape transformation are outlined in Table 1.

Much of the recent ecological literature emphasizes species extinctions resulting from landscape transformation (Sala et al. 2000, Primack 2001, Groombridge and Jenkins 2002). However, as implied in Table 1, landscape transformations may not only produce declines but also allow some new species to become established and other formerly rare taxa may become more abundant (Hobbs et al. 2006, Olden and Rooney 2006). Such changes in species occurrence are a substantial component of this study and enable us to better understand the response of biota to landscape change. Our findings are important for elucidating the potential impacts on biodiversity of large-scale plantation establishment.

METHODS

Study area

The Nanangroe area is 10–20 km southeast of the town of Jugiong in southern New South Wales, southeastern Australia (Fig. 1). The original vegetation cover in the study area included several woodland vegetation types, particularly those dominated by yellow box (*Eucalyptus melliodora*), red box (*E. polyanthemus*), white box (*E. albens*), red stringybark (*E. macro-rhyncha*), and Blakely's red gum (*E. blakleyi*). The vegetation structure of patches of these woodland tree species can generally be categorized as old-growth woodland, coppice regrowth woodland, or seedling regrowth woodland. Coppice regrowth refers to (multi-stemmed) regrowth from existing living trees recovering after disturbance by fire, clearing, or both. Seedling regrowth is natural regrowth originating from seeds germinating after being dropped by overstory trees. Old-

growth woodland is woodland dominated by large, old trees, typically ≥ 200 years old. Prolonged periods of livestock grazing in the region meant that understorey vegetation of *Acacia* spp. and other plants was largely absent from all areas of woodland in the study area.

More than 80% of the original vegetation cover in the Nanangroe area has been cleared over the past 150 years, primarily for domestic stock grazing (Bungongo Centenary Committee 1986). Vegetation in these heavily cleared areas was paddocks dominated by exotic pasture grasses and isolated single trees that were the remnants of past woodland vegetation cover.

In several parts of the region, an emerging pine plantation now surrounds patches of remnant woodland that escaped earlier waves of land clearing. Further details of the study area can be found in Lindenmayer et al. (2001).

The design of the Nanangroe study

The Nanangroe study is a large-scale (20 000-ha) longitudinal investigation in which changes over time within sites (period effects) can be distinguished from differences among sites in their baseline levels (cohort effects) prior to the application of treatments.

In 1997, we established a set of foundation sites for the study and characterized all 70 patches of remnant native vegetation that occurred on land broadly designated for subsequent pine plantation establishment. Patches were mapped from aerial photographs and then were ground-thruthed on foot. In 1998, prior to the commencement of landscape transformation to a pine-dominated system, we randomly selected 52 of the 70 woodland remnants from strata defined by vegetation class and woodland patch area. These woodland remnants were exempt from clearing during plantation establishment and are hereafter referred to as the "woodland treatments." We considered four patch size classes within these woodland treatments, and our site

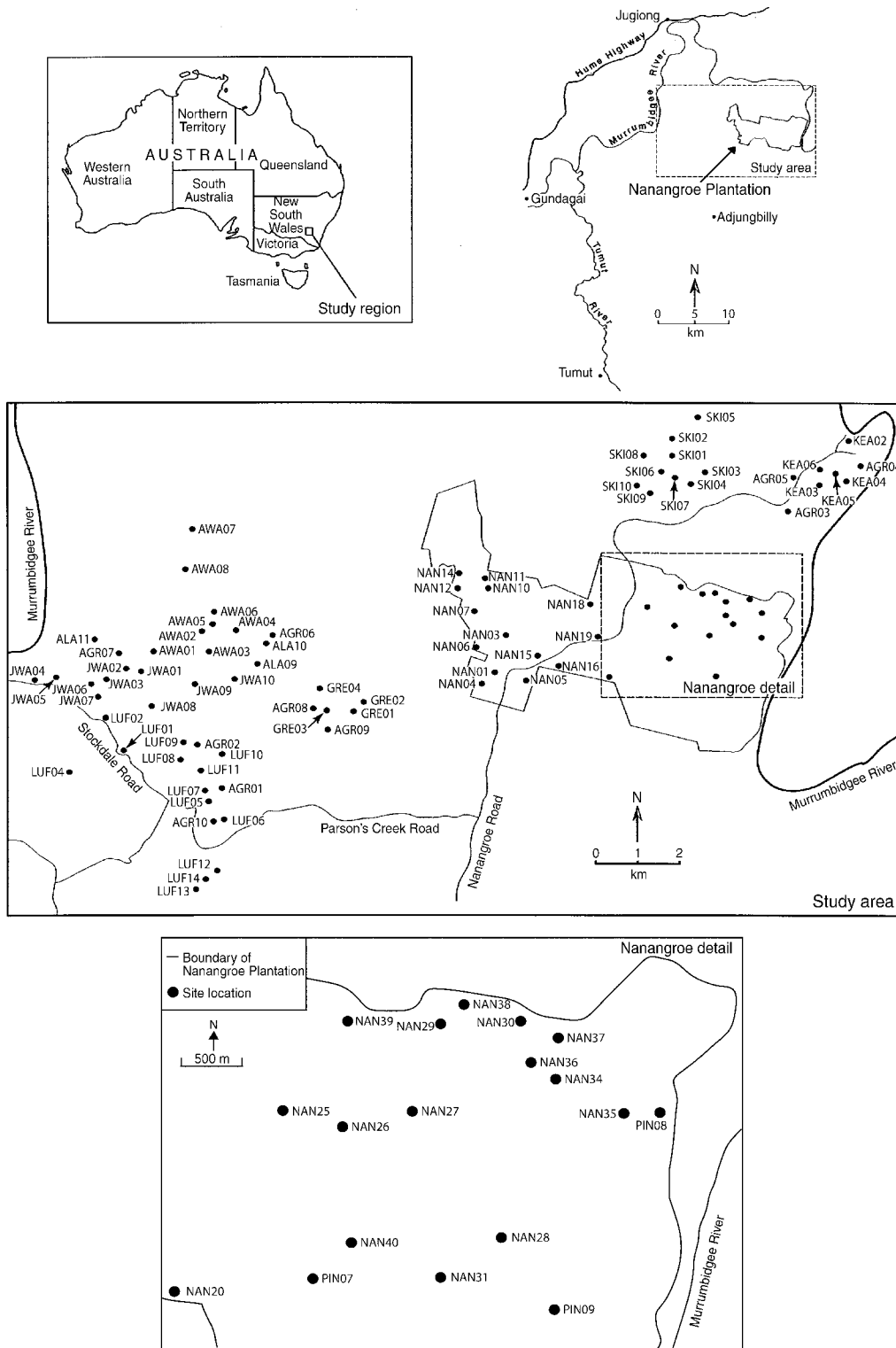


FIG. 1. General location of the Nanangroe study area, New South Wales, Australia. Sites with the prefix “NAN” are woodland remnants surrounded by maturing stands of radiata pine (*Pinus radiata*). Sites with the prefix “PIN” are stands of radiata pine planted between 1998 and 2000. Sites with the prefix “AGR” are grazing paddocks on grazing properties. All other sites are woodland remnants on grazing properties.

selection procedures yielded 13 remnants in the 0.5–0.9 ha class, 20 remnants in the 1.0–2.4 ha size class, 17 remnants in the 2.5–4.9 ha class, and two remnants in the 5.0–10.0 ha class. Few large remnants were available for selection because of the extent of previous clearing for livestock grazing. We recognized three broad woodland vegetation classes within the woodland treatments: (1) red box and red stringybark (codominant) with apple box (*E. bridgesiana*), long-leaf box (*E. goniocalyx*), and broad-leaved peppermint (*E. dives*) (19 sites); (2) yellow box, white box, red stringybark (codominant), and Blakely's red gum (23 sites); and (3) mountain swamp gum (*E. camphora*) and other kinds of vegetation (e.g., river oak *Allocausarina cunninghamiana*) (10 sites).

We commenced surveys of vertebrates before stands of radiata pine were planted and then surveyed different landscape treatments repeatedly after plantation establishment. Clearing to plant radiata pine in the areas surrounding the woodland remnants involved the felling and burning of isolated paddock trees and other shrubby vegetation (Fig. 2). Native vegetation clearing controls applied by the former Department of Land and Water Conservation meant that nine of the 18 woodland remnants that were not included in our study remained uncleared. Most of the nine remnants that were cleared were 1 ha or smaller and the total area of woodland removed was 16.9 ha. The total area of woodland remnants remaining after clearing in the Nanangroe study area was 157.7 ha. Distances between remaining woodland remnants ranged from 300 m to 4 km.

Site preparation for pine plantation establishment involved deep-ripping and mounding of the soil with a bulldozer. This created exposed mineral soil into which radiata pine seedlings were planted. The total area of pine established in the study area was 5500 ha. We defined two age cohorts of recently planted pine stands. These were trees established in 1998 (cohort 1) and trees established in 2000 (cohort 2). Of the 52 woodland treatments, 11 had 1–2 open boundaries with adjacent agricultural areas. Radiata pine stands completely surrounded the remaining 41 woodland remnants. We distinguished between these two kinds of woodland remnants in our analyses.

In addition to the 52 woodland treatments, we also established a set of “natural control” sites. These included: 10 sites in the newly planted stands of radiata pine trees (hereafter referred to as “pine controls”); 56 woodland remnants on semi-cleared private grazing properties surrounded by areas of scattered paddock trees and located adjacent to the new plantation estate (hereafter referred to as “woodland controls”); and 10 permanent sites in grazing paddocks that surrounded the 56 woodland remnants on grazing properties (hereafter referred to as “paddock controls”).

Domestic livestock grazing continued in all woodland remnants in the study and the maturing radiata pine stands, thus preventing potential confounding between

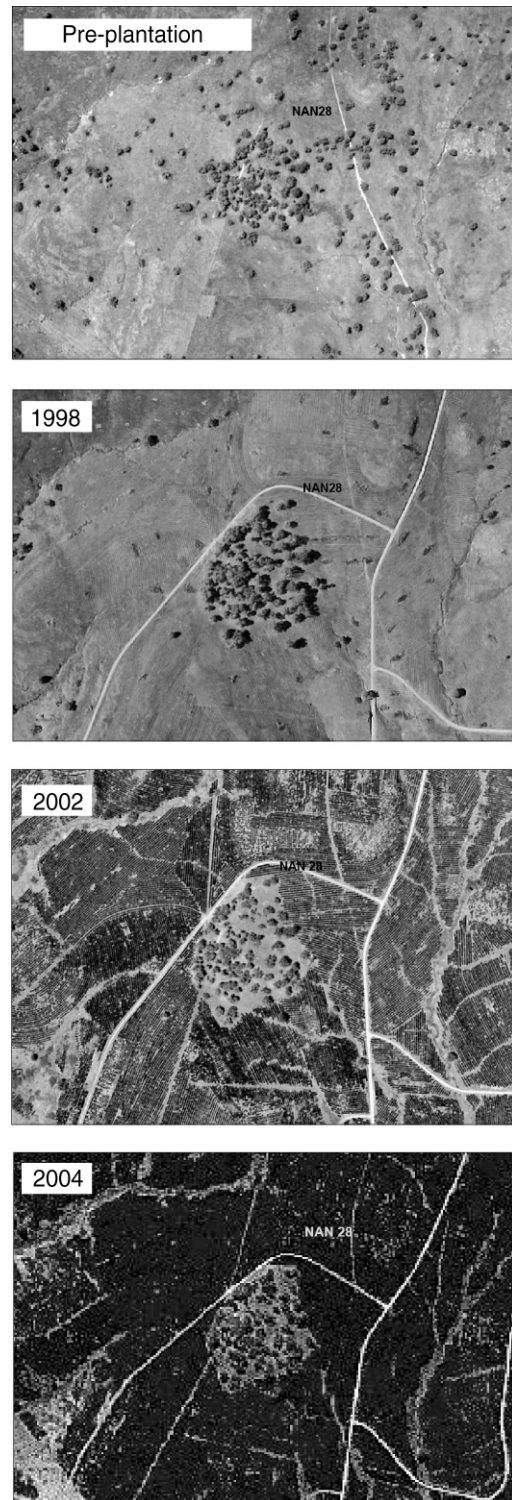


FIG. 2. Landscape changes on the Nanangroe property between 1997 and 2005 (photos showing landscape context changes around site NAN28 (photos courtesy of Forests NSW, Tumut Office).

TABLE 2. Number of sites cross-classified by various parameters, highlighting the factorial structure of the design of the Nanangroe study, New South Wales, Australia.

Site type	Surrounding vegetation	Cohort	No. edges	1998 planting	2005 planting
Woodland	pine	1	1–2	3	3
Woodland	pine	1	3–4	16	15
Woodland	pine	2	1–2	8	5
Woodland	pine	2	3–4	25	29
Woodland	paddock			56	55
Pine	pine			10	10
Paddock	paddock			10	10

Note: We present counts of sites for the first (1998) and eighth (2005) years of the study to show minor losses or additions of sites as plantation establishment proceeded.

treatments and grazing effects. Table 2 summarizes the treatment design and number of sites in each category.

In summary, six key features characterized the design of the Nanangroe study. These were as follows: (1) quantification of animal abundance prior to landscape treatments being applied, with each site becoming its own control, making the investigation more powerful for studying temporal change than cross-sectional studies; (2) the use of a randomized and replicated patch selection procedure to reduce the potential for bias and to average over random factors; (3) the establishment of a set of “natural external control” sites to quantify natural year-to-year fluctuation in animal occupancy of sites and to provide additional contrasts helping to quantify patterns of change; (4) the repeated measurement of biophysical attributes at the site level to link changes in them to changes in biota; (5) repeated field surveys over a prolonged period to better quantify species response trajectories to landscape transformation; and (6) the implementation of the study at a large spatial scale to make it appropriate for mobile groups such as birds (Wiens 1999), which can be difficult to investigate with small-scale studies (Debinksi and Holt 2000, Lindenmayer and Fischer 2006).

Vertebrate surveys

Mammal and reptiles.—We established a permanent 200 m long transect at each of the 128 sites in our study. We counted arboreal marsupials and macropods by spotlighting along each transect in the spring of 1997, 1999, 2000, 2001, 2004, and 2006. We used a 50-W handheld spotlight and a single observer walked each transect at a speed of ~3 km/h. We commenced spotlighting one hour after dusk to ensure that arboreal marsupials had emerged from their den or nesting sites (see Lindenmayer et al. 1991). We halted surveys after three hours to avoid the risk of observer fatigue leading to failure to detect animals. No spotlighting surveys were conducted on windy nights or during rain or fog to limit the risks of weather conditions leading to animals being overlooked. We recorded the number of individuals of each species of arboreal marsupial and macropod seen.

We gathered data on reptiles by searching under artificial substrates established at 0-, 100-, and 200-m plot points along each transect. We established three types of substrates at each point: (1) three overlaid sheets of corrugated iron, each measuring 1 × 1 m, (2) a pile of hardwood timber offcuts composed of four pieces of timber each measuring 1 m long × 15 cm wide × 3 cm deep, and (3) a set of four standard (420 × 245 mm) roof tiles. For each year, we aggregated our data to the site level for statistical analysis of both mammals and reptiles.

Birds.—We recorded bird data at the 0-, 100-, and 200-m plot points along the 128 transects. We completed repeated 5-minute point interval counts (sensu Pyke and Recher 1983) at these three stations in early November in 1998, 1999, 2000, 2001, 2003, and 2005. Early November is the peak breeding season in the study region, when most summer migrants are present and birds have established territories and exhibit strong patterns of site fidelity. For each point count, observers recorded birds within 50 m of the plot point and that also were within the woodland remnant. Counts were completed between 05:30 and 09:30 hours and were not undertaken on days of poor weather (rain, high wind, fog, or heavy cloud cover).

Ten bird observers from the Canberra Ornithologists Group participated in the bird surveys. Although observers were highly experienced, they varied in their ability to detect some groups of birds. Cunningham et al. (1999) showed that averaging the counts of two or more observers at the same site could compensate for extra variability due to observer heterogeneity. Field et al. (2002) showed that weather and other conditions on any given day can influence bird detectability. Thus, in each survey year, each of the 128 sites was surveyed by two different observers on different days.

Vegetation measures and other covariates

We established vegetation plots measuring 10 × 10 m at the 0-, 50-, 100-, 150-, and 200-m points along the marked transect at each site. We measured site-based and other broader-scaled covariates at the start of the study (1998) and again in 2005 (see Appendix A).

Data structures and statistical methods

Mammal and reptile analyses.—We modeled mammal and reptile data using generalized linear mixed modeling (McCulloch and Searle 2001). The response variable for our analyses was binary: the presence or absence of a given species of mammal or reptile at a site in a given year. We modeled the probability p of occupancy by an animal as a function of year, treatment (i.e., “woodland treatments” vs. “woodland controls”), and year \times treatment interaction, while taking account of the repeated-measures structure of the study design via the inclusion of appropriate random effects. There are compelling statistical reasons for using the logistic transformation to transform p from $[0, 1]$ to take values on the real line. Among other things, this prevents the model from producing nonsensical probabilities above 1. The logistic function $\text{logit}(p) = \log\{p/(1 - p)\}$ achieves this end and can often be modeled on a linear scale. The resulting model was a mixed linear logistic model with fixed effects for treatment, year, and their interaction and random effects for site and site \times year to account for possible dependence in our data. We assume because we have repeat observations at the same site, that detection rates are high (non-detection is low) and hereafter we use the term occupancy rate or the probability of occupancy at a site.

Bird analyses.—We aggregated our data to give the number of detections of a given species out of the number of plots by observer combinations. Hence, data were expressed as a proportion or detection rate (e.g., two detections recorded by two observers each surveying three plots = $2/(2 \times 3) = 1/3$). Previous work has shown a strong relationship between detection rate and the number of birds counted (Lindenmayer et al. 2002) and that over six point counts, non-detection is low for the vast majority of bird species. As in the case of mammal and reptile data, we assumed, because we gathered repeat observations at the same site, that detection rates for birds are high (and non-detection is low); hence we refer to occupancy rates or the probability of occupancy at a site.

We characterized sites by treatment, environmental, landscape, and other variables as well as temporal effects by year (or age of the pine). Our primary focus was on temporal changes in bird occupancy sites defined by the seven treatment classes listed in Table 2 (i.e., temporal changes in mean values over all sites within a group). Hence, our thinking was in terms of a “typical” longitudinal site profile for a given treatment class. That is, we focused our inference for bird taxa on broad landscape “treatment” effects by considering sites having the same treatment classification as a group. As for mammals and reptiles, we used logistic linear mixed models to model the probability of occupancy and hence determine the significance and nature of species response to landscape change. These results provided a formal basis for classifying birds according to the statistical significance and nature of time trajectories to woodland treatments.

Animal life history attributes.—We collated extensive data on life history and other attributes of each vertebrate species from the literature. As an example, for birds, the data we gathered included body mass, group type (solitary, pairs, or flock), social system (monogamous, polygamous, and so on), nest type (hollow, cup, mud bowl, and so on), nest placement (horizontal fork, ground, and so on), nesting height, clutch size, broods per year, movement behavior (resident vs. migrant, latitudinal or altitudinal migrant), and foraging guild. The data we assembled from the literature for reptiles and mammals included body mass, mode of locomotion, nesting behavior (e.g., cavity-using or log-dependent), social organization, and diet.

We used contingency tables, ANOVA, and canonical variate analysis to conduct formal statistical analyses of associations between animal life history attributes (e.g., body size, diet, or foraging guild) and responses to landscape transformation. Further we engaged 12 expert ornithologists to informally assess associations between life history attributes and our classification of birds.

RESULTS

Mammals

Because mammals were virtually absent from the 10 pine controls and the 10 paddock controls, we excluded these sites from subsequent analyses. Hence, the results we present focus on tracking changes in the woodland controls and woodland treatments (Table 3). We particularly emphasize time trajectories in species’ probabilities of occupancy of woodland treatment sites.

We recorded three species of arboreal marsupials. The common brushtail possum (*Trichosurus vulpecula*) exhibited a significant ($P = 0.03$) linear increase in probability of occupancy over all woodland remnants, with a suggestion ($P = 0.10$) of a greater increase in woodland treatments (Fig. 3a). Similar patterns were observed for the sugar glider (*Petaurus breviceps*), but were not statistically significant (Fig. 3b). There was weak evidence ($P = 0.11$) of an overall decline in the probability of occupancy of the common ringtail possum (*Pseudocheirus peregrinus*) in both types of woodland remnants (Fig. 3c).

We found that the probabilities of occupancy for the terrestrial marsupial, the eastern gray kangaroo (*Macropus giganteus*), increased significantly over time in both the woodland treatments and the woodland controls ($P < 0.001$). Although this linear year effect was strongest for woodland treatments (Fig. 3d), there was no evidence of a year \times treatment interaction effect. We identified a similar pattern for the swamp wallaby (*Wallabia bicolor*), but the statistical evidence for the linear effect was weaker ($P = 0.03$; Fig. 3e).

We explored for the effects of covariates such as pine cohort, woodland patch size, and dominant species of woodland tree. There was no evidence that linear changes in occupancy probabilities for any species of arboreal marsupial or macropod were responding to

TABLE 3. Occupancy rates (percentage of detections) for arboreal marsupials and macropods, by treatment, in the Nanangroe study.

Species	Treatment	Detections (% occupied)			
		1999	2001	2004	2006
<i>Petauroides volans</i>	woodland controls	0	0	0	0
	woodland treatments	0	1.9	0	1.8
<i>Petaurus breviceps</i>	woodland controls	3.6	1.9	2.2	1.8
	woodland treatments	4	1.9	7.1	8.9
<i>Pseudocheirus peregrinus</i>	woodland controls	16.1	21.2	13.3	10.9
	woodland treatments	18	13	17.9	7.1
<i>Trichosurus vulpecula</i>	woodland controls	21.4	23.1	26.7	23.6
	woodland treatments	12	27.8	28.6	35.7
<i>Macropus giganteus</i>	woodland controls	0	1.9	13.3	12.7
	woodland treatments	0	3.7	39.3	28.6
<i>Macropus robustus</i>	woodland controls	0	0	2.2	3.6
	woodland treatments	0	0	1.8	3.6
<i>Macropus rufogriseus</i>	woodland controls	0	0	0	0
	woodland treatments	0	1.9	7.1	0
<i>Wallabia bicolor</i>	woodland controls	0	0	2.2	0
	woodland treatments	0	1.9	5.4	7.1

Notes: Percentages are calculated by dividing the number of sites occupied by the total number of sites in each treatment group and multiplying by 100. Totals for woodland surrounded by paddock (woodland controls) and woodland surrounded by pine (woodland treatments) were 56 and 52, respectively.

measured attributes characterizing the woodland remnants. However, there was evidence ($P = 0.02$) of a strong, linear increase in the sugar glider in high-altitude remnants, but a slight decline in low-altitude remnants.

There were too few mammal taxa (five) for which we had good data on responses to landscape context and other effects to undertake formal statistical analyses of associations between functional groups or life history attributes and landscape transformation.

Reptiles

Reptiles were virtually absent from the 10 pine controls (see Table 4) and we excluded them from subsequent analyses. Thirteen of the 17 recorded species of reptiles were rare (Table 4), making formal statistical analyses possible only for four species. We found evidence of significant temporal linear increases in the probability of detection for southern rainbow skink *Carlia tetradactyla* ($P = 0.009$; Fig. 4a), marbled gecko

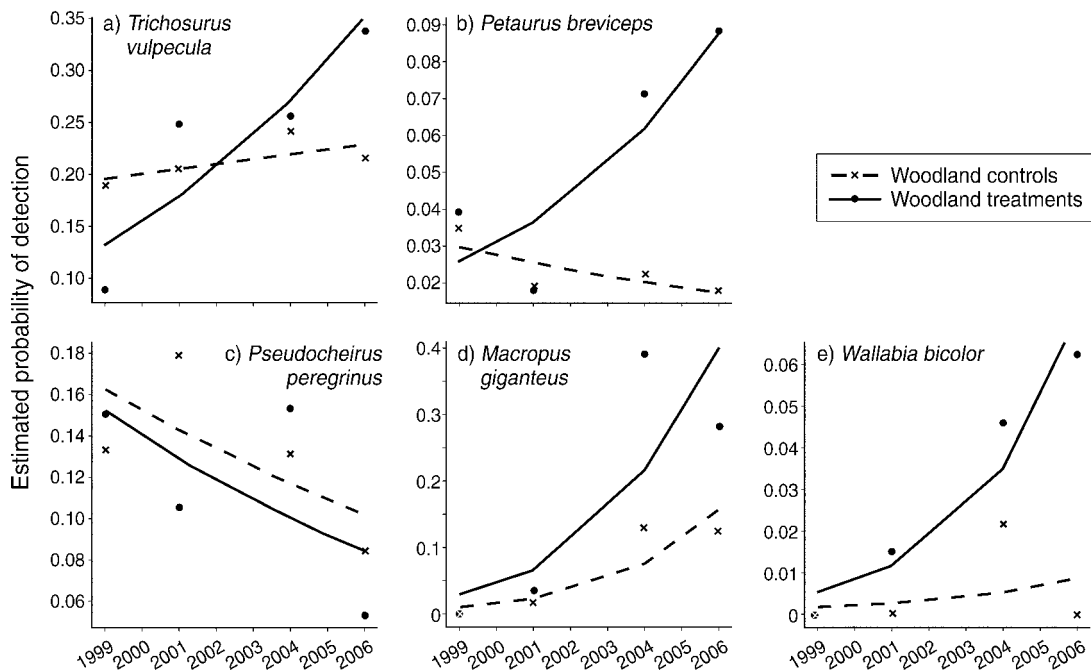


FIG. 3. Linear trends for mammals showing evidence of changed detection rates in woodland treatments and woodland controls.

TABLE 4. Occupancy rates for reptiles, by treatment, in the Nanangroo study.

Species and treatment	Detections (% occupied)				
	2000–2001	2000–2002	2001	2003	2006
<i>Acritoscincus platynotum</i>					
Paddock controls	0	0	0	0	0
Woodland controls	0	0	0	0	0
Pine controls	0	0	0	0	0
Woodland treatments	0	5.7	0	5.4	3.6
<i>Carlia tetradactyla</i>					
Paddock controls	0	20	10	10	22.2
Woodland controls	10	13.8	12.7	43.4	20.8
Pine controls	0	0	0	10	0
Woodland treatments	0	8.6	6.1	12.5	16.1
<i>Christinus marmoratus</i>					
Paddock controls	0	0	0	10	22.2
Woodland controls	0	0	25.5	24.5	37.7
Pine controls	0	0	0	0	0
Woodland treatments	5	2.9	14.3	8.9	19.6
<i>Ctenotus robustus</i>					
Paddock controls	40	0	10	0	55.6
Woodland controls	0	0	0	7.5	17
Pine controls	0	0	0	0	0
Woodland treatments	0	2.9	0	1.8	1.8
<i>Ctenotus taeniolatus</i>					
Paddock controls	0	0	0	0	0
Woodland controls	0	0	3.6	0	0
Pine controls	0	0	0	0	0
Woodland treatments	0	2.9	2	3.6	3.6
<i>Egernia striolata</i>					
Paddock controls	0	0	0	10	0
Woodland controls	0	0	0	0	1.9
<i>Egernia striolata</i>					
Pine controls	0	0	0	0	0
Woodland treatments	0	0	0	0	1.8
<i>Eulamprus heatwolei</i>					
Paddock controls	0	0	0	0	0
Woodland controls	0	0	0	0	0
Pine controls	0	0	0	0	0
Woodland treatments	0	0	2	5.4	3.6
<i>Hemiergis decresiensis</i>					
Paddock controls	0	20	30	10	33.3
Woodland controls	5	17.2	20	34	20.8
Pine controls	20	20	30	30	10
Woodland treatments	20	31.4	24.5	39.3	51.8
<i>Lampropholis delicata</i>					
Paddock controls	0	0	0	0	0
Woodland controls	5	0	0	0	0
Pine controls	20	0	0	0	0
Woodland treatments	0	5.7	10.2	3.6	1.8
<i>Lampropholis guichenoti</i>					
Paddock controls	0	0	0	0	11.1
Woodland controls	0	0	0	0	0
Pine controls	0	0	0	0	0
Woodland treatments	5	2.9	2	7.1	3.6
<i>Leiopisma duperreyi</i>					
Paddock controls	0	0	0	0	0
Woodland controls	0	0	0	0	0
Pine controls	0	20	0	0	0
Woodland treatments	0	2.9	0	7.1	1.8

TABLE 4. Continued.

Species and treatment	Detections (% occupied)				
	2000–2001	2000–2002	2001	2003	2006
<i>Morethia boulengeri</i>					
Paddock controls	20	0	10	20	11.1
Woodland controls	0	0	0	17	9.4
Pine controls	20	0	0	0	0
Woodland treatments	5	11.4	4.1	8.9	7.1
<i>Niveoscincus coventryi</i>					
Paddock controls	0	0	0	0	0
Woodland controls	0	0	0	0	0
Pine controls	0	0	0	0	0
Woodland treatments	0	0	0	0	1.8
<i>Pogona barbata</i>					
Paddock controls	0	0	0	0	0
Woodland controls	0	0	0	1.9	1.9
Pine controls	0	0	0	0	0
Woodland treatments	0	0	0	1.8	0
<i>Pseudechis porphyiacus</i>					
Paddock controls	0	0	0	0	0
Woodland controls	0	0	0	0	1.9
Pine controls	0	0	0	0	0
Woodland treatments	0	0	0	0	0
<i>Pseudonaja textilis</i>					
Paddock controls	0	0	0	0	0
Woodland controls	0	0	0	1.9	0
Pine controls	0	0	0	0	0
Woodland treatments	0	0	0	0	0
<i>Tiliqua scinicoides scinicoides</i>					
Paddock controls	0	0	0	0	0
Woodland controls	0	0	0	0	1.9
Pine controls	0	0	0	0	0
Woodland treatments	0	0	2	0	1.8

Note: Occupancy percentages were calculated as described in Table 3.

Christinus marmoratus ($P < 0.001$; Fig. 4b), three-toed skink *Hemiergis decresiensis* (Fig. 4c; $P = 0.008$), and Boulenger's skink *Morethia boulengeri* ($P = 0.017$; data not shown). For all four species of reptiles, this trend was consistent across three of the four broad classes of sites (woodland treatments, woodland controls, paddock controls). That is, there was no evidence of interaction between year and treatment (Fig. 4a–c).

We found no evidence that linear changes in the probability of occupancy for any reptiles were responding to other characteristics of woodland remnants. Again we had insufficient data on responses of reptiles (four species) to undertake meaningful analyses of associations between life history attributes and landscape transformation.

Birds

Species richness.—We recorded a total of 119 different species of birds during seven surveys completed between 1998 and 2005. Latin names for all species detected can be found in Appendix B. Overall, the total number of species in the landscape remained approximately constant (averaging 93–95 species). We found strong

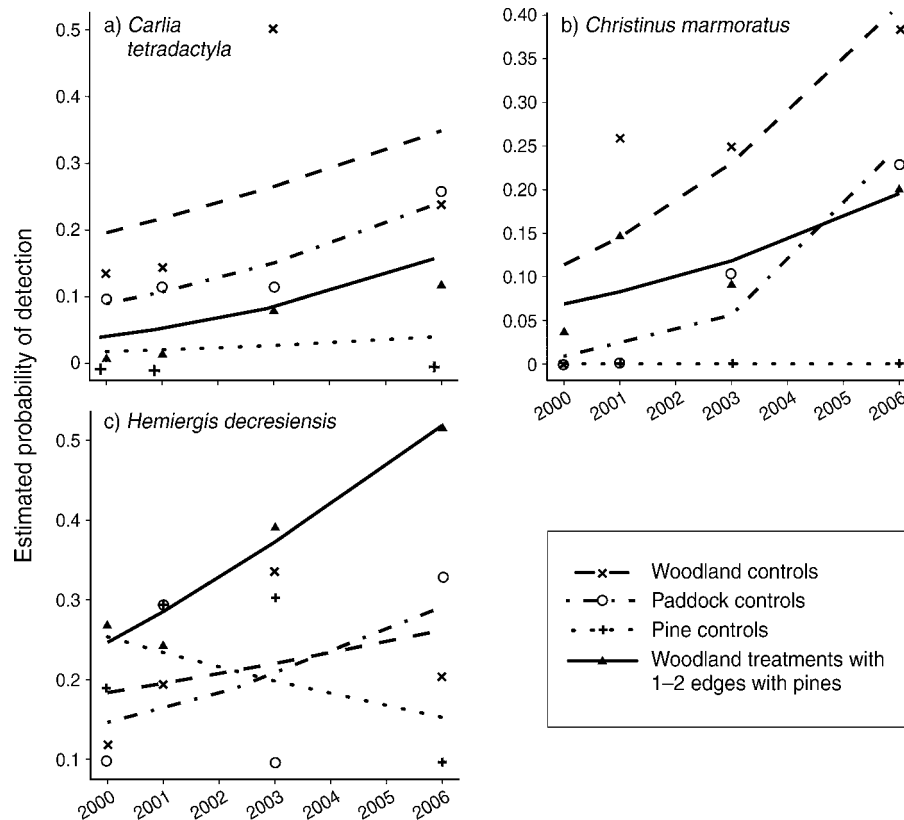


FIG. 4. Linear trends for a selection of reptiles in four treatments: paddock controls, woodland controls, pine controls, and woodland treatments with 1–2 open boundaries with agricultural areas and 1–2 edges with pines.

evidence ($P < 0.001$) of a temporal increase in species richness in the 10 pine controls, and a trend showing an increase in the woodland control sites (Fig. 5). There was no evidence of differences in the trajectory of species richness for the other treatments over the eight years of the study. Because there was no evidence of a difference between pine cohorts (based on year planted), we averaged over them for the graphical representation of the species richness results (Fig. 5).

Individual bird species responses.—We considered 96 species with an occupancy rate of $>1\%$ for detailed analysis. We were principally interested in the longitudinal occupancy rate profiles of species within the woodland treatments and woodland controls. Hence, we estimated the linear trend (and associated standard error) by modeling variation in the response as a linear function of year. We inferred the response to be significant if the trend estimate/SE (trend) exceeded ± 2 .

Study-area-wide changes.—Several species of birds showed significant changes in occupancy rates across the entire study area. Examples of study-wide decliners were the Black-faced Cuckoo-shrike and Sulphur-crested Cockatoo. Examples of increasers included the Yellow-faced Honeyeater (Fig. 6c) and the Common Bronzewing (Fig. 6a).

Changes in pine controls.—We found strong evidence that occupancy rates increased throughout the eight years in the pine controls for species such as the Gray Fantail (Fig. 7a), White-browed Scrub-wren (data not shown), and Rufous Whistler (Fig. 7b). Others, such as the Superb Fairy-wren, initially increased but then showed evidence of a temporal decline (data not shown).

Changes in woodland treatments vs. woodland controls.—We classified birds according to response groups based on comparisons of occupancy rates in woodland treatments and woodland controls (Table 5).

Overall, our data indicate that more species in our study respond positively than negatively. However, four notable species (Black-faced Cuckoo-shrike, Dusky Woodswallow, Common Starling, and Sulphur-crested Cockatoo) showed negative changes in detection rates both in the woodland treatments and the woodland controls. They also declined across the entire landscape (see also Fig. 6). Two others, the Brown Treecreeper (Fig. 8) and the Red-rumped Parrot (data not shown), showed evidence of more complex effects in that they exhibited a negative response to woodland treatments, but a positive one to woodland controls.

Five bird species, including the Gray Shrike-thrush (Fig. 8a) and Weebill (data not shown), responded

positively both to the woodland treatments and woodland controls (Table 5). They also increased across the whole study area, as did many of the other species that responded positively to woodland treatments. We identified no birds that exhibited a positive response to the woodland treatments but a negative one to the woodland controls (Table 5).

The largest groups of birds that we identified were those showing neutral responses to at least one of the two major experimental treatments. These were: (1) those that increased in the woodland controls but showed no evidence of change in the woodland treatments; (2) those that increased in the woodland treatments but showed no evidence of change in the woodland controls; and (3) those that showed no evidence of change in either kind of woodland remnant (Table 5). Many of the birds in these neutral response categories showed increases in occupancy rates across the landscape, and only one (the Galah) exhibited a decrease. We highlight examples of the varying longitudinal profiles in Fig. 8.

Factors contributing to changes in longitudinal landscape context effects for birds in woodland treatments.—We examined factors relating to changes in longitudinal profiles for individual bird species within woodland treatments.

1. *Pine boundary effects.*—Fig. 9 shows contrasting pine boundary effects for individual bird species within woodland treatments. The Gray Shrike-thrush (Fig. 9b) increased significantly over time within woodland treatments having 3–4 boundaries with radiata pine forest. The Magpie Lark (Fig. 9a) and Eastern Rosella (data not shown) showed the reverse trend and probabilities of occupancy were greater in woodland treatments with 1–2 boundaries with agricultural areas than in remnants where 3–4 of the patch boundaries were with the radiata pine forest.

2. *Pine cohort effects.*—The probabilities of occupancy for several species within the woodland treatments varied in response to the cohort (year planted) of the surrounding radiata pine stands (Fig. 10). As an example, probability of occupancy by the Rufous Songlark (Fig. 10a) showed a clear decline in woodland treatments where pine was planted in 1998 (cohort 1), but there was no evidence of change in woodland treatments surrounded by pine planted two years later (cohort 2). In the case of the Yellow-rumped Thornbill (Fig. 10d), the probability of occupancy declined over time for both age cohorts, but was more prominent in cohort 1. The White-naped Honeyeater (data not shown) and White-throated Treecreeper (Fig. 10b) displayed upward overall increases in the probability of occupancy for both age cohorts, but the trend was more pronounced in cohort 1. There was evidence of convergence in the trend curves for the two pine cohorts of woodland treatments for the Brown Thornbill (Fig. 10c).

3. *Woodland remnant area effects.*—A number of bird species showed changing occupancy rates in relation to

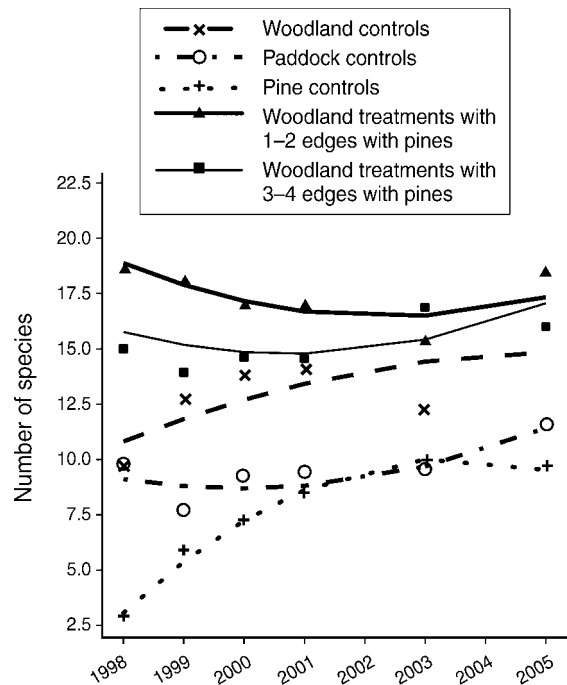


FIG. 5. Smoothed (second-order polynomial) temporal profiles (shown by lines) in the number of species detected in four treatments. Birds detected on fewer than four occasions have been excluded.

the area of woodland remnants surrounded by radiata pine stands. As an example, occupancy rates for the Spotted Pardalote (Fig. 11a) and Weebill (Fig. 11b) increased faster in the larger remnants than in the medium and small ones. The decline of the White-plumed Honeyeater (Fig. 11c) was fastest in the large woodland treatment sites, whereas the decline of the Yellow-rumped Thornbill (Fig. 11d) was fastest in the small remnants but slowest in the medium-sized woodland treatment sites (Fig. 11). In contrast, the Dusky Woodswallow (data not shown) declined most rapidly in the medium-sized patches.

4. *Woodland vegetation type effects.*—We identified significant vegetation effects for several species of birds in woodland treatments. For example, the probability of occupancy by the White-throated Treecreeper increased significantly ($P = 0.004$) over the eight years of the study in the vegetation class comprising red box, red stringybark, broad-leaved peppermint, and apple box, but remained unchanged in mountain swamp gum and yellow box/white box (Fig. 12d). In contrast, the Superb Fairy-Wren declined significantly in mountain swamp gum but occupancy rates increased significantly in the other two vegetation classes ($P < 0.001$) (Fig. 12c). Other examples of significant vegetation type effects include those for the Noisy Friarbird (Fig. 12a), Brown Thornbill (data not shown), and Red Wattlebird (Fig. 12b).

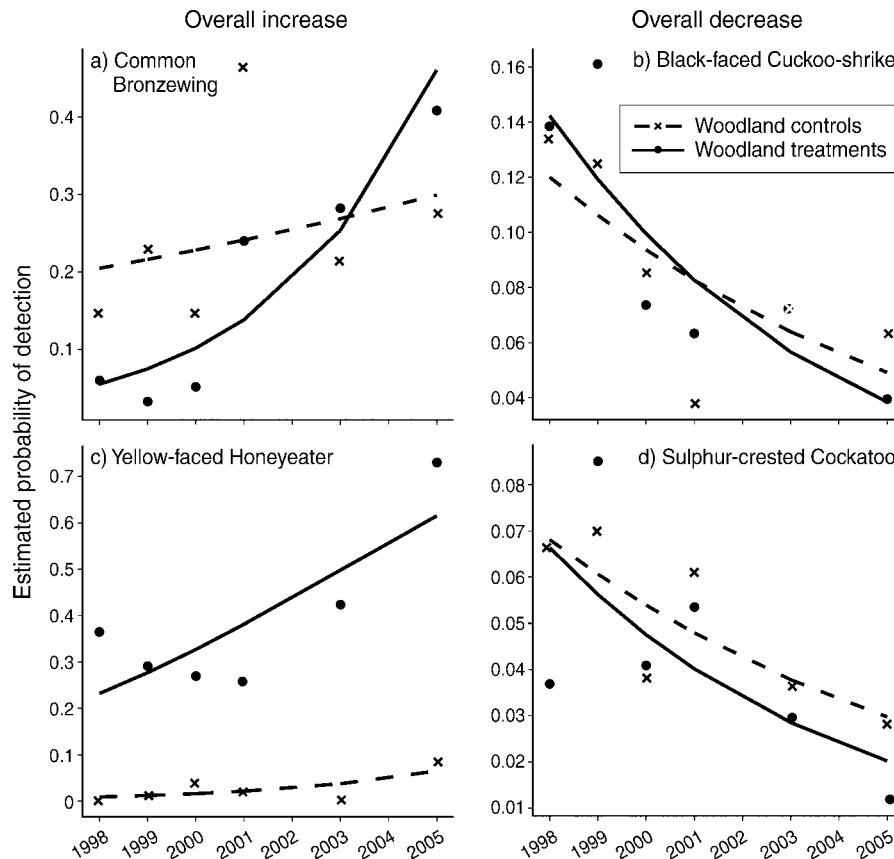


FIG. 6. Linear trends and predicted detection rates for a selection of individual bird species that showed temporal changes across the entire study area under the two major treatments in the study: woodland controls and woodland treatments.

5. *Temporal changes in habitat covariates and effects on longitudinal profiles.*—A clear advantage of our longitudinal study was that it was possible to directly estimate the association between changing habitat covariates within woodland remnants. We examined habitat covariates measured both in 1998 and 2005 (see Appendix A) and identified covariates significantly ($P < 0.05$) associated with changes in bird occupancy rates (Fig. 13). Significant covariates for several species included ground cover, shrub cover, and litter layer. As an example, Fig. 13 shows a significant within-site association (pooled over sites) between the occupancy rate of the Brown Treecreeper and percent ground cover over the period 1998–2005.

Overview.—Based on our results, we were able to identify five distinct patterns of change. First was an added environment response pattern across the entire study area. We believe this is plausible for those species that increased (e.g., Yellow-faced Honeyeater, eastern gray kangaroo, common brushtail possum) or decreased (e.g., Black-faced Cuckoo-shrike, common ringtail possum) across the entire study area. Second, we observed a landscape-scale displacement response pattern in which a species decreased within woodland remnants surrounded by radiata pine stands but, at the

same time, increased in woodland remnants in grazing lands adjacent to the Nanangroe property (where no landscape transformation had taken place) (e.g., Red-rumped Parrot). Third, we found an added-environment response pattern in the pine stands in which animals were recruited into recently established areas of pine (e.g., European Blackbird). Fourth, our data suggested a spillover response pattern in which animals were recruited to newly established stands of radiata pine and then apparently “spilled over” into the woodland remnants surrounded by pine (e.g., Gray Fantail). Finally, we found a landscape-context response pattern in which the probabilities of occupancy showed a temporal increase or decrease in woodland treatment sites. Covariates that helped to explain these effects included: (1) patch boundary number (e.g., Eastern Rosella); (2) age of surrounding pine (e.g., White-throated Treecreeper); (3) woodland patch size (e.g., Spotted Pardalote); (4) woodland vegetation type (e.g., Noisy Friarbird); and (5) habitat attributes within woodland patches (e.g., Brown Treecreeper).

These response patterns and covariate effects can be crudely classified in terms of their spatial scale. At the largest scale, there were overall study-wide changes in animal occupancy rates that were positive for some taxa

and negative for others. At a patch scale, an array of species was influenced by changes in the landscape context of woodland remnants when the surrounding landscape was transformed to pine stands. At the smallest spatial scale, localized changes in habitat attributes within woodland patches surrounded by maturing pines had a significant influence on some species.

Links with life history and other attributes.—Contingency tables, ANOVA, and canonical variate analysis of associations between bird life history attributes (e.g., body size, diet, or foraging guild) and our classification of birds (see Table 5) showed no evidence of statistically significant associations or even near-significant associations. Further, our panel of experts could not identify any clear patterns in our data. We note that failure to find significant associations does not mean that they do not exist; such associations may be present but are obscured by variability in our data.

DISCUSSION

Large-scale landscape transformation is a global phenomenon (Foley et al. 2005, Millennium Ecosystem Assessment 2005) with significant impacts on biodiversity and ecosystem processes (UNEP 1999, Sala et al. 2000). Plantation development is a major form of landscape transformation in all parts of the world (Estades and Temple 1999, Lindenmayer and Hobbs 2004, Jackson et al. 2005). We have implemented a large-scale longitudinal natural experiment to generate high-quality data to better elucidate the mechanisms underpinning temporal changes in biota that accompany plantation development. A better understanding of the possible mechanisms for change increases opportunities for moving away from species- or landscape-specific outcomes to facilitate a more general translation of findings to other species and landscapes (Fahrig 2003).

We discuss the response patterns we observed, beginning with an outline of study-area-wide changes, then changes within radiata pine stands, and finally landscape-context effects. Because mammals and reptiles exhibited few significant treatment or woodland patch covariate effects (Figs. 3 and 4), much of our discussion relates to findings for birds and it is largely based on our cross-classification of individual species' responses (see Table 5). Our study produced a number of novel effects not anticipated at the commencement of our work, and an outline of these effects precedes the final part of the paper, where we summarize some of the key implications of our research for landscape management. These general implications also may apply to other landscapes and regions around the world where plantations are being established on agricultural land (e.g., Peterken and Ratcliffe 1995, Dyck 2000).

Study-area-wide changes

Although the transformation treatment was applied at the landscape level in this study, we observed changes across the entire study area for many species. That is,

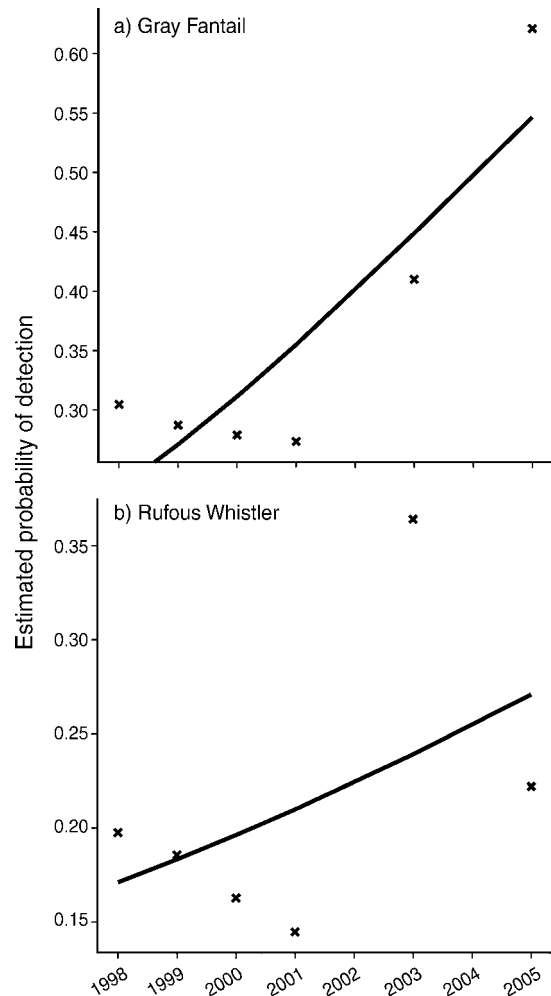


FIG. 7. Linear trends and predicted detection rates of the Gray Fantail and the Rufous Whistler in radiata pine stands per se. Symbols represent the data for a given year, and the line is fitted.

landscape context was altered for 52 woodland remnants surrounded by pine stands (the woodland treatments), but changes in detection rates also were recorded across the entire study area, including the 56 woodland remnants where no change in landscape context had occurred (the woodland controls). Such changes in species assemblages highlight the magnitude of change that the global trend in plantation expansion (Franklin 2003) may trigger. We suggest that different processes are likely to be driving the responses of different species.

Prior to the commencement of our investigation, we postulated that the birds that were likely to increase across the study area would be wide-ranging forest generalists that use pine stands. In contrast, woodland species that need large foraging areas would be likely to decline (Table 1). The creation of a new environment of densely spaced radiata pine trees in the Nanangroe study does appear to have made the entire study area more suitable for some typical forest bird species (e.g.,

TABLE 5. Birds cross-classified according to the nature of the significance of linear changes in detection rates in woodland treatments and woodland controls.

Birds grouped by response to woodland treatments		
Positive	Neutral	Negative
a) Species with positive response to woodland controls		
Positive for treatments surrounded by pines and controls with no change in landscape context; overall landscape "increasers"	Static in treatments, increasing in controls (with many increasing in the landscape)	Declining in treatments, increasing in controls
Gray Shrike-thrush, Spotted Pardalote, Weebill, White-throated Treecreeper, Yellow-faced Honeyeater	Australian Magpie, Little Friarbird, Magpie Lark, Peaceful Dove, Red Wattlebird, Striated Pardalote, Noisy Friarbird, Australian Raven, Buff-rumped Thornbill, Fan-tailed Cuckoo, [Richard's Pipit], [Little Lorikeet]	Brown Treecreeper, Red-rumped Parrot
b) Species with neutral response to woodland controls		
Increasing in treatments, static in controls (with many increasing in the landscape)	No change for both key groups of woodland sites	Declining in treatments, static in controls
Common Bronzewing, Gang-gang Cockatoo, Laughing Kookaburra, Silvereeye, Superb Fairy-wren, Blackbird, Noisy Miner, Rufous Whistler, Shining Bronze-cuckoo, Golden Whistler, White-winged Chough, Crescent Honeyeater, Gray Fantail	Crimson Rosella, Striated Thornbill, White-winged Triller, Brown-headed Honeyeater, Brown Thornbill, Crested Shrike-tit, Eastern Rosella, European Goldfinch, Horsfields Bronze-Cuckoo, Nankeen Kestrel, Olive-backed Oriole, Pacific Black Duck, Pied Currawong, Stubble Quail, Tree Martin, Welcome Swallow, Western Gerygone, White-browed Scrubwren	[Galah], Gray Butcherbird, Rufous Songlark, White-plumed Honeyeater, Willie Wagtail, Yellow-rumped Thornbill
c) Species with negative response to woodland controls		
Declining in controls, increasing in treatments	No change in treatments, decreasing in controls	Negative for both key groups of sites; overall landscape "decliners"
No species	Restless Flycatcher	[Black-faced Cuckoo-shrike], [Common Starling], [Dusky Woodswallow], [Sacred Kingfisher], [Sulphur-Crested Cockatoo]

Notes: Species in boldface show a significant ($P < 0.05$) increase in the region overall. For birds shown in italics in a given type of woodland remnant, there were insufficient data (<1% detections) to estimate the linear trends for the other type of remnants. Birds in brackets (e.g., the Galah) show a significant ($P < 0.05$) decline in the overall region. For birds in lightface, the trend was not significant. Responses are presented for all bird species with detection rates exceeding 1%.

Common Bronzewing and Spotted Pardalote; Figs. 6a and 8b). This is consistent with the outcomes of other studies that suggest that altering regional populations will provide a source of colonists to invade patches from surrounding areas (Askins et al. 1987, Gascon et al. 1999, Bender and Fahrig 2005). It is also congruent with the findings of our earlier cross-sectional study in the neighboring Tumut region in which typical forest species such as the Yellow-faced Honeyeater and White-throated Treecreeper were common both in stands of radiata pine and in the eucalypt forests remnants adjacent to plantation trees (Lindenmayer et al. 2002). We found evidence of an overall study-area-wide decline for several species. These were predominately open-country and native-woodland taxa such as the Black-faced Cuckoo-shrike (Table 5). In earlier studies in the nearby Tumut region, we found that this species was uncommon in many eucalypt forest remnants surrounded by 10–70 year old radiata pine (Lindenmayer et al. 2002).

In Table 1 we postulated the existence of a "displacement" mechanism (e.g., Darveau et al. 1995) at

Nanangroe in which birds may vacate an area made increasingly unsuitable by changes in the matrix, but colonize suitable ones nearby where landscape transformation is not occurring. We found strong evidence for two species that declined in the woodland treatments but increased in the woodland controls (Fig. 8). We forecast that these species would be mobile species and strongly woodland-associated (and hence sensitive to matrix conversion to densely spaced stands of radiata pine trees). This appears to be true for one of the species (the Red-rumped Parrot), but only partly true for the other, the Brown Treecreeper, which is found predominately in woodland and rangeland areas but is known to be dispersal-limited (Walters et al. 1999, Cooper et al. 2002). We did not record the reverse "displacement" pattern, in which species that declined in the woodland controls increased in the woodland treatments. Thus, the factors that made the woodland controls unsuitable appeared to result in birds declining across the entire study area (e.g., Black-faced Cuckoo-shrike) rather than such effects being offset by an increase in woodland treatments. Three of the four species that declined in

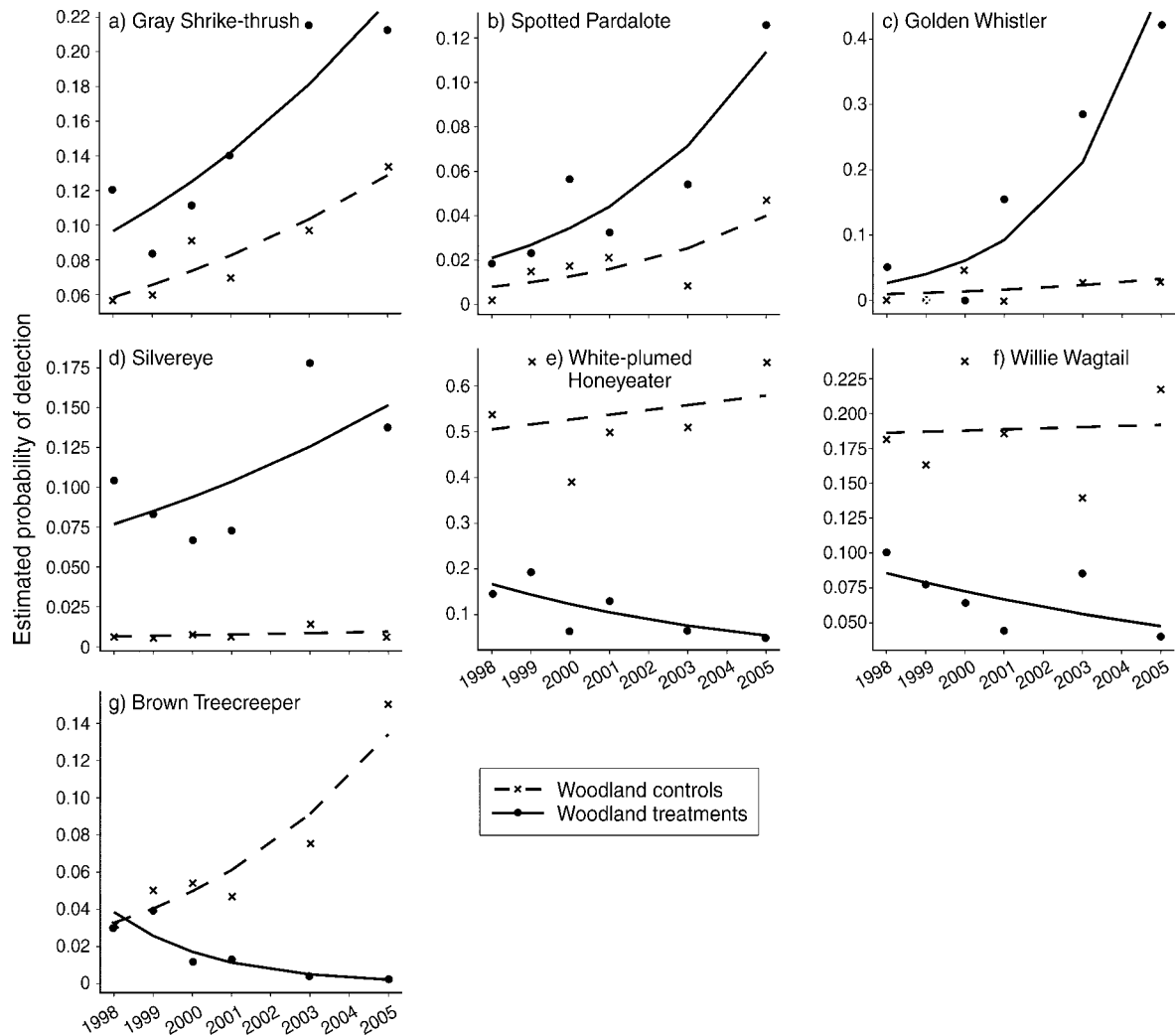


FIG. 8. Linear trends for birds showing evidence of changed detection rates in woodland treatments and/or woodland controls. (a, b) Increase in woodland treatments and in woodland controls. (c, d) Increase in woodland treatments but not in woodland controls. (e, f) Decrease in woodland treatments but not in woodland controls. (g) Decrease in woodland treatments and increase in woodland controls.

woodland controls are typical open-country birds that range over large areas (Table 5). As previously discussed, stands of radiata pine may be unsuitable habitat for them and also may impair their movement.

We identified a number of species that declined in the woodland treatments but remained unchanged in the woodland controls (e.g., Rufous Songlark and White-plumed Honeyeater; Table 5). A possible explanation for this effect might be the removal of nine woodland patches during the establishment of the pine plantations. However, the total area of woodland vegetation that was removed as part of the implementation of our experiment was limited to 16.9 ha or 9.7% of the woodland area. The majority of taxa in our study have territories 1–3 ha in size and processes other than the removal of patches are likely to be more important for them. We

discuss these processes in the section on landscape context effects on woodland treatments.

Our postulate that wide-ranging, mobile, and habitat-generalist species would be among those likely to exhibit increases across the entire study area (Table 1) appeared to hold for two species of macropod (Fig. 3d, e) and the common brushtail possum (Fig. 3a). Animals from populations increasing in woodland treatments (where increases were greatest) may have dispersed into neighboring areas where no plantation expansion has occurred. However, an exception to this pattern occurred among the mammals that we surveyed. The common ringtail possum declined both in woodland patches surrounded by pine stands (the woodland treatments) and in the matched set of woodland controls (Fig. 3c). This species is not a woodland specialist, but is widespread and occurs in many kinds of environments

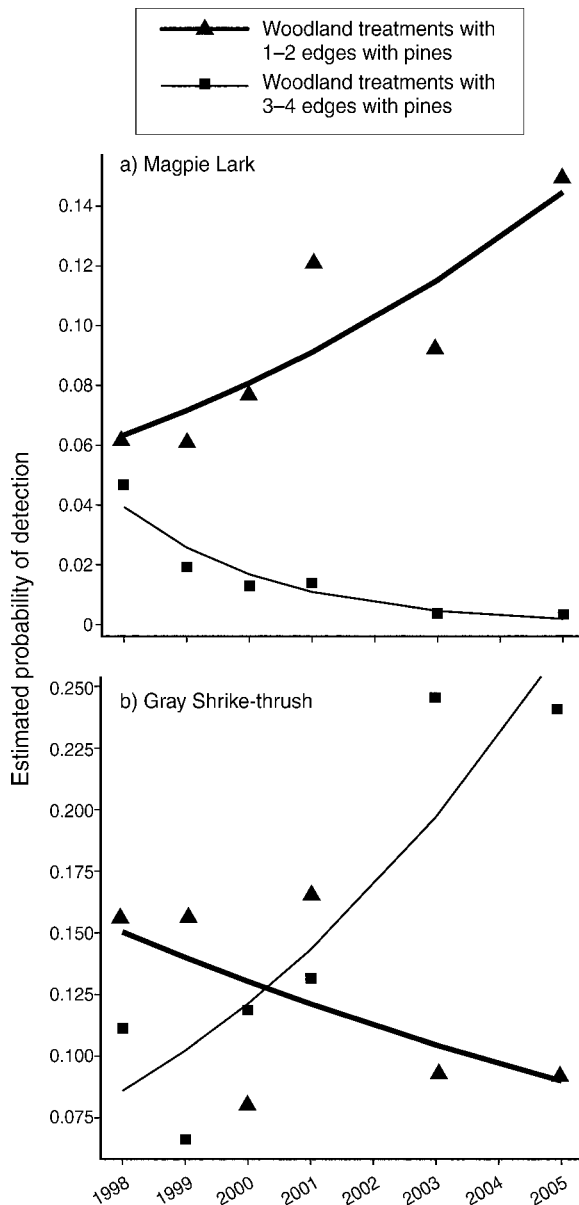


FIG. 9. Linear profiles for detection rates of selected individual bird species for woodland treatments with 1–2 patch boundaries with radiata pine forest and woodland treatments where 3–4 patch boundaries are radiata pine forest.

in eastern Australia (Kavanagh 2004), including stands of radiata pine (which composed the matrix in this study). The species was common at the start of the Nanangroe study (Lindenmayer et al. 2001). We have anecdotal evidence of an increasing number of large forest owls in the region over the past few years. We speculate that the establishment of pine stands may have attracted these wide-ranging avian predators of the common ringtail possum. This may explain the decline in occupancy rates for the species across the entire study area. Although plausible, climatic conditions appear

unlikely to be a driver of change for mammals in our investigation. This is because our nine-year study has spanned both dry and wet periods.

At the start of this investigation, we anticipated that most species of reptiles would decline across large parts of the study area because of changes in the temperature and ground cover conditions associated with plantation establishment (Gepp 1979), particularly in young pine stands (Fischer et al. 2005). However, we identified increases in occupancy rates in both the woodland treatments and the woodland controls. A possible explanation for this is that the artificial substrates we established became increasingly suitable for reptiles over time. Hence, the patterns for reptiles may have been an artifact of our survey methodology. However, the paucity of reptiles under the artificial substrates that we established in our 10 pine controls suggests the effects of other important factors. The lack of potentially suitable environments for reptiles such as logs that were removed during plantation establishment may explain their absence from the 10 pine control sites.

Changes in the pine controls

The establishment of pine stands in the Nanangroe study added a new environment composed of relatively densely spaced trees that previously did not occur in the landscape. At the commencement of this study, we forecast that this would trigger the recruitment of additional species (Table 1), particularly for typical forest-associated taxa. We observed such trends for birds and we documented a highly significant ($P < 0.001$) temporal increase in species richness within pine stands (Fig. 5).

The extent of canopy closure, light penetration, size and interconnectivity of lateral branches, and amount of bark development are among the range of features known to change as pine stands mature (Gepp 1979). These, in turn, alter the suitability of foraging and/or nesting resources for many bird species; favoring some taxa such as those strongly associated with dense forests (e.g., the European Blackbird; see also Suckling et al. 1976, reviewed by Lindenmayer and Hobbs 2004). Several of the new species that colonized the pine stands were of conservation significance, including known declining woodland birds such as the Eastern Yellow Robin and the Rufous Whistler (see Barrett et al. 2003). However, other woodland species that are currently experiencing regional declines, such as the Brown Treecreeper, disappeared from areas where pine stands were established.

The patterns that we quantified for birds in the pine controls were not replicated for arboreal marsupials and reptiles. We were unable to conduct formal statistical analyses for either group because of the paucity of animals in the 10 pine control sites.

It will be important to continue to track changes in the vertebrate fauna occupying the 10 sites in pine stands as trees mature and a range of structural and other

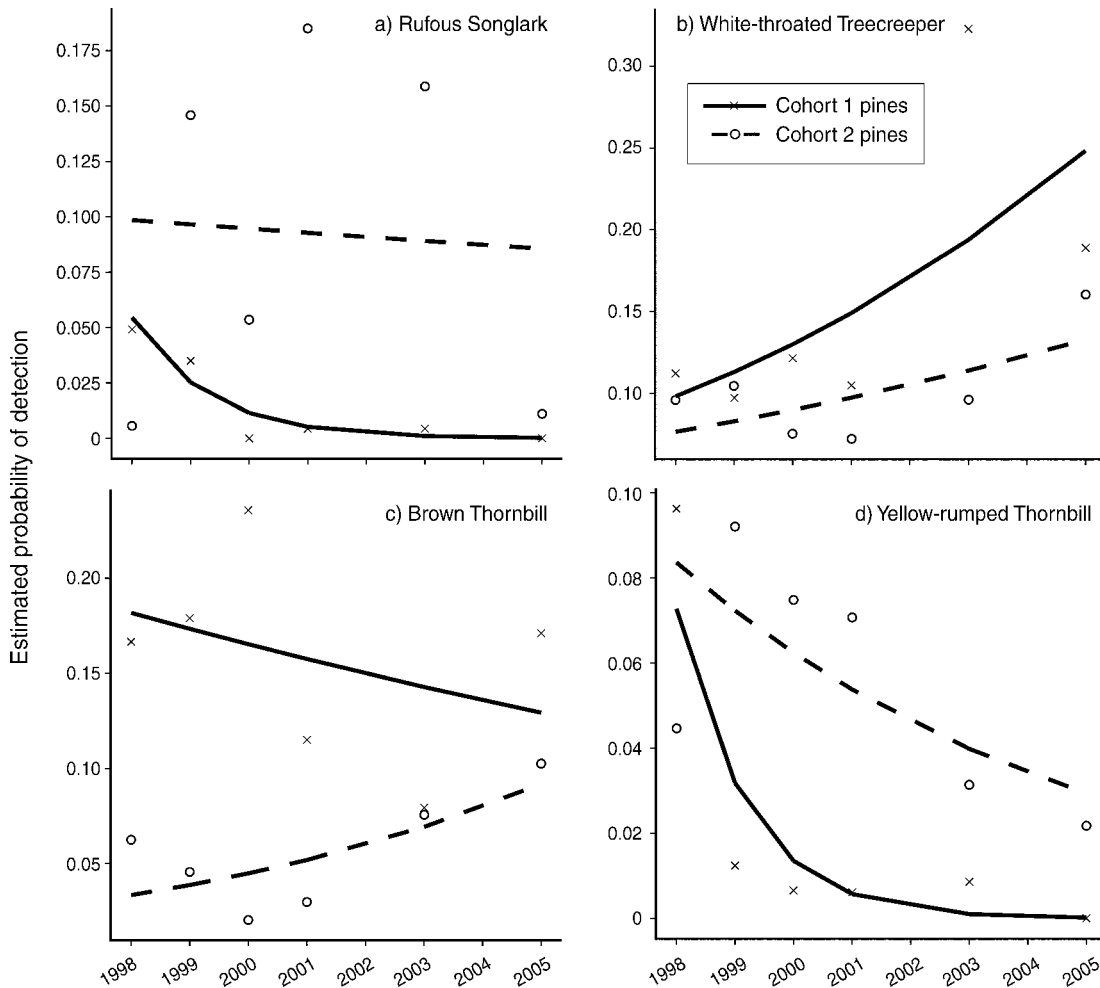


FIG. 10. Linear trends for the detection rates of selected individual bird species for woodland remnants where the surrounding stands of radiata pine were planted in 1998 (cohort 1) and woodland remnants where the surrounding stands of radiata pine were planted in 1999/2000.

characteristics of these stands change. Ongoing maturation of these stands may increase their value as habitat for some species (Gepp 1979, Lindenmayer and Hobbs 2004, Tubelis et al. 2004, Fischer et al. 2005) and increase the time available for additional colonization of these areas.

Woodland patch-level (context) effects

Several studies have demonstrated that changes in the matrix can have a marked influence on the abundance and persistence of biota in patches of remnant native vegetation (Laurance 1991, Renjifo 2001, Lindenmayer and Franklin 2002). A range of positive and negative biotic responses can manifest (Table 1); in this investigation we found marked differences in longitudinal profiles between vertebrate groups and among species within groups. Table 5 shows nine broad kinds of response of birds to combinations of the two woodland treatments in our study. Densely spaced trees characteristic of pine plantations may favor the colonization of woodland remnants by forest birds, but may

disadvantage species typical of more open woodland environments. This is consistent with the fact that many of the species increasing in the pine stands (e.g., see Figs. 6 and 7) and the woodland remnants they surrounded (e.g., Spotted Pardalote; Fig. 8) also were common in long-established native forest remnant/pine plantation mosaic in the nearby Tumut area (Lindenmayer et al. 2002). As we will briefly outline, five attributes of woodland patches surrounded by pine helped to explain the landscape context effects.

1. *Pine cohort effects.*—Time since landscape change is known to be an important factor influencing the occurrence of biota in patches (Tilman et al. 1994, Berglund and Jonsson 2005). We demonstrated that changes in the structure and composition of pine stands took some time to influence the occupancy of the woodland patches that they surrounded. Negative cohort effects, which were more apparent for the earlier plantings, were observed for taxa more typical of open agricultural country or woodland areas.

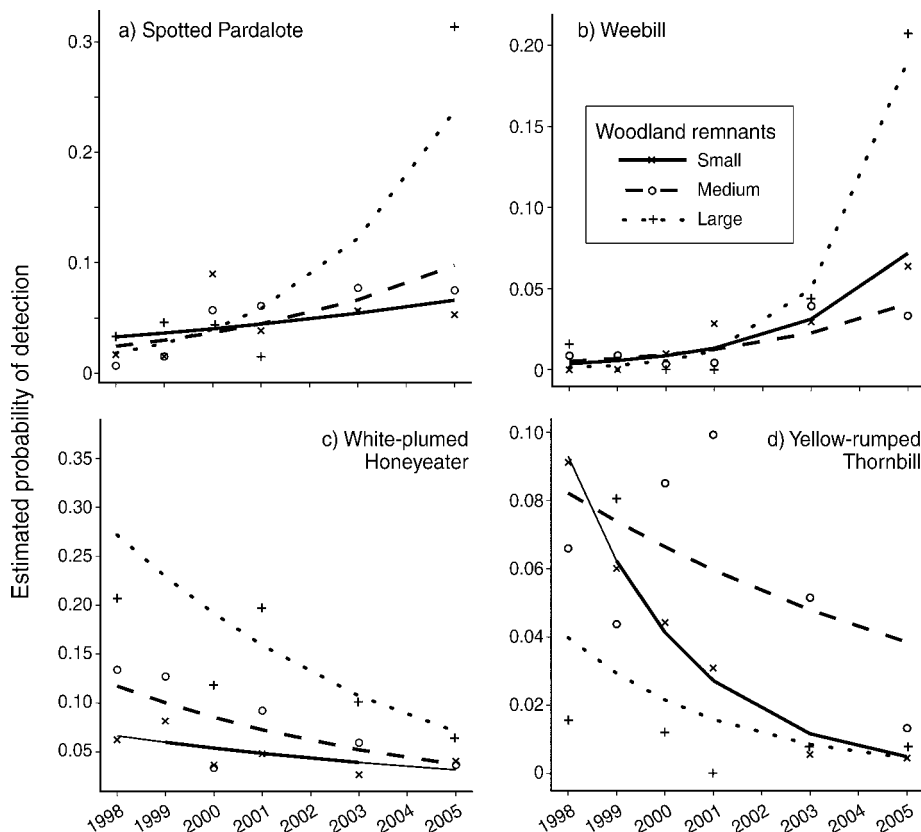


FIG. 11. Linear trends in the detection rates of selected individual bird species for woodland remnants of different sizes surrounded by stands of radiata pine. Data are shown for the Spotted Pardalote, Weebill, White-plumed Honeyeater, and Yellow-rumped Thornbill in large (>3.5 ha), medium (2–3.5 ha), and small (<2 ha) woodland remnants.

We found positive cohort effects for primarily forest birds such as the White-throated Treecreeper, which has been shown to forage further from eucalypt patches, and into surrounding pine stands as pine trees mature (Tubelis et al. 2004). In addition, birds attracted to pine stands may then “spill over” into the adjacent woodland patches they surround. Such findings were consistent with our postulate (see Table 1) that matrix-using species will have limited negative sensitivity to landscape transformation (see also Blake 1983, Laurance 1991, Ricketts 2001) and that species that can use the matrix will often be those also found in remnant patches of native vegetation (Tocher et al. 1997, Ås 1999).

The woodland treatment and pine plantation system at Nanangroe is dynamic and we anticipate further temporal changes in vertebrate assemblages as we continue to monitor the study area over the coming decades. The plantation will be clear-felled once pine trees reach ~30 years of age and it will be important to determine if, for example, such management practices facilitate recolonization by open-country species of woodland treatment sites surrounded by harvested forest.

2. Boundary effects.—Changes in landscape context previously have been shown to influence edge effects

and, in turn, occupancy of patches of remnant native vegetation (e.g., Bayne and Hobson 1997, 1998, Harper et al. 2005). We found that some bird species responded significantly to the number of boundaries with the surrounding plantation (see also Fletcher 2005). Open-country birds were more likely to be recorded in remnants with 1–2 open boundaries with agricultural land than in remnants fully enclosed by pine. One possible explanation for this is that densely spaced plantation trees may create barriers to movement, thereby limiting their use of completely surrounded woodland patches.

3. Woodland patch size effects.—An enormous and rapidly expanding literature has documented many kinds of biotic relationships with patch size (Hanski 1994, Rosenzweig 1995, reviewed by Lindenmayer and Fischer 2006). We found that landscape context effects varied among patches of remnant woodland of different sizes. For some bird species, rates of decline in occupancy rates were slower in the larger woodland remnants. Large patches will have larger interior areas and should support higher populations of animals typical of agricultural and woodland areas. In contrast, smaller patches may rapidly lose birds typical of woodlands after the conversion of the surrounding areas

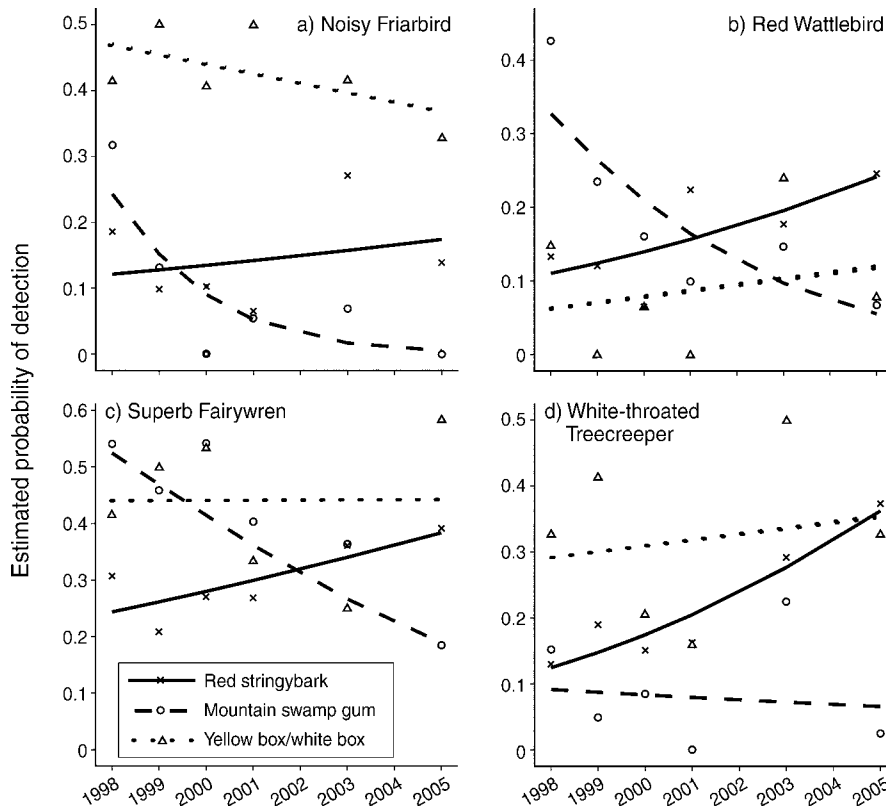


FIG. 12. Linear trends in the detection rates of selected individual bird species for woodland remnants in different vegetation types (red stringybark, mountain swamp gum, yellow box/white box) that were surrounded by stands of radiata pine.

to pine plantations. The Yellow-rumped Thornbill exhibited this response.

Not all of the patch size effects that we quantified have straightforward explanations. Birds typical of forests may benefit from altered landscape-context effects and might be expected to increase faster in smaller remnants because of the higher edge to area ratio. However, the opposite was observed for some forest species such as the Spotted Pardalote (Fig. 11b). Similarly, the Dusky Woodswallow (data not shown) declined most rapidly in the medium-sized patches. These unexpected findings suggest that other unidentified processes are driving the responses of some species.

4. *Vegetation type effects within woodland patches.*—Vegetation composition within patches may significantly affect patch occupancy (Zanette et al. 2000, Lindenmayer et al. 2003). We found that landscape-context effects for some bird species were influenced by the dominant vegetation type that characterized woodland patches surrounded by maturing pine stands. Two examples were the White-throated Treecreeper and the Noisy Friarbird. Populations of invertebrate prey vary markedly between vegetation types (e.g., Majer et al. 1994) and this may have contributed to the effects that we quantified for a range of primarily or partially insectivorous bird species. For example, the White-throated Treecreeper is primarily a forest bird and

exhibited the greatest temporal increases in woodland patches that were dominated by red stringybark and red box eucalypts. The White-throated Treecreeper preferentially forages on these kinds of trees (Noske 1982, Lindenmayer et al. 2007) and this may explain why occupancy rates increased most rapidly in those woodland treatments where stringybark eucalypts was dominant (Fig. 12).

5. *Changes in within-woodland patch habitat covariates.*—Landscape context may combine with variations in habitat quality to influence patch occupancy (e.g., Yamaura et al. 2006). We found that temporal changes in covariates within woodland patches surrounded by pines (such as percentage of ground cover) were significantly associated with temporal changes in occupancy rates of some bird species (e.g., the Brown Treecreeper; Fig. 13).

Unanticipated findings

We identified several important and unanticipated effects. At the beginning of this study, we developed postulates about the attributes of species that might characterize broad groups of species that respond in different ways to landscape transformation (see Table 1). We found that species associated with open country and woodland environments were often those disadvantaged by landscape transformation whereas those that

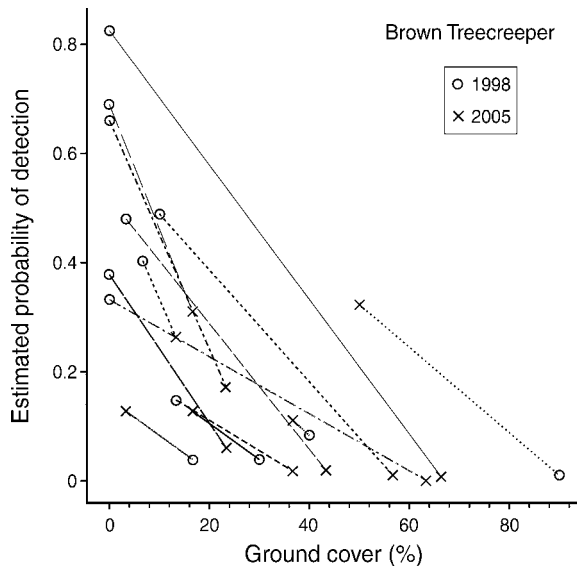


FIG. 13. Predictions from statistical models for the Brown Treecreeper showing an association between bird detection rates in 1998 and 2005 and the ground cover.

benefited included forest taxa and/or those with generalist habitat requirements capable of inhabiting recently established pine stands (the matrix; Fig. 5) and adjacent woodland patches. However, beyond these broad generalizations, an unanticipated finding of our investigation was that we did not find any significant (or even near-significant) relationships between life history attributes and landscape transformation. This contrasts markedly with other studies from around the world in which relationships have been found between landscape alteration and life history attributes such as foraging guild, body size, diet, social organization, and breeding system (e.g., Terborgh 1974, Koh et al. 2004, Cardillo et al. 2005; reviewed by McKinney 1997, Lindenmayer and Fischer 2006). Although our results for mammals and reptiles may be associated with the small number of species for which we had sufficient data, this was not the case for the species-rich assemblage of birds; there were 63 bird species with sufficient data suitable for analysis. An interesting outcome was that the paucity of life history relationships contrasts with the results of our large-scale cross-sectional study of vertebrates in eucalypt forest patches surrounded by pines in the neighboring Tumut region. In that case, attributes of birds such as body size, foraging guild, migratory behavior, clutch size, and nesting height were significantly associated with contrasts in site occupancy between eucalypt patches and the pine matrix and between eucalypt patches of different shape (Lindenmayer et al. 2002). The reasons for the paucity of functional group effects at Nanangroe remains unclear, but it may be associated with the marked differences in responses to

the treatments exhibited by different taxa, even closely related ones with similar life history attributes.

A second unexpected finding, which is loosely related to the first one, corresponds to predictability between landscapes, not for groups of species with common life history attributes, but for individual species. We found that key results for particular vertebrate species from a large study of remnant forest patches surrounded by pine stands in a nearby area at Tumut (Lindenmayer et al. 1999, 2002) could not be readily transferred to the Nanangroe ecosystem. For example, the common ringtail possum was abundant at Tumut, and at the start of this project we anticipated that the species would increase in the woodland remnants as areas of surrounding pine matured. However, the reverse trend occurred and the species declined across the entire study area (Fig. 3). Similarly, the Sulphur-crested Cockatoo and Sacred Kingfisher were common birds in the remnant forest patch system at Tumut (Lindenmayer et al. 1996, 2002), but exhibited study-area-wide declines at Nanangroe (Table 5).

A third unexpected finding was that after nine years of our study, we found some highly unusual combinations of native birds in the woodland treatments. For example, the bird species that increased in these woodland patches included a unique blend of primarily forest birds (e.g., White-eared Honeyeater) and primarily open-woodland birds (e.g., Peaceful Dove, Weebill, and Rufous Songlark). This blend of species was new at Nanangroe and was not found in the tall forest ecosystems in the nearby Tumut area (Cunningham et al. 1999, Lindenmayer et al. 2002) or in an extensive study of woodland birds in the neighboring South West Slopes region (Cunningham et al. 2008). In cases where species "occur in combinations and relative abundances that have not occurred previously in a given biome," Hobbs et al. (2006) considered that a novel ecosystem had developed. Hence, some years after landscape transformation at Nanangroe, the bird assemblages appear to be consistent with the development of a novel ecosystem.

Fourth, although losses and gains of species from small and large patches are well documented (Hanski 1994, Forman 1995, Rosenzweig 1995, Lindenmayer and Fischer 2006), we found effects for medium-sized patches that have seldom been observed previously. An example was the Dusky Woodswallow, which declined most rapidly in the medium-sized woodland treatment sites. Other workers have suggested that medium-sized patches of native vegetation can be important (Turner 1996) but the mechanisms underpinning their importance for particular species of birds in this study remain unclear.

Our findings from the Nanangroe study highlight the potential difficulties in using the results from a given landscape to make forecasts about the effects of landscape transformation on the biota in another landscape, even one relatively nearby and for compar-

atively well-known groups such as birds and mammals. This emphasizes the fact that the impacts of landscape transformation on biodiversity may not always be readily predictable. This is important because landscape transformation resulting from broad-acre plantation expansion is a widespread phenomenon worldwide and may well yield “surprises” in other jurisdictions (e.g., see Estades and Temple 1999, Wethered and Lawes 2003). Despite the fact that the responses of some elements of the biota were unanticipated, the approach that we have taken nevertheless allowed us to identify some general response patterns displayed by various taxa.

Implications for landscape management

Our study has produced a range of important insights that have broad implications, particularly for other regions in the world that are undergoing landscape transformation through land use change such as plantation expansion. The impacts of plantation establishment on natural resources such as water quality and quantity are now well documented (Jackson et al. 2005). Based on our empirical study, together with previous reviews (e.g., Peterken and Radcliffe 1995, Lindenmayer and Hobbs 2004), it is clear that the responses of biodiversity are more complex. They vary markedly among species, among groups of species, and are dependent on both the spatial and temporal scale considered. Our results also emphasize the critical importance of well-informed plantation design when the conservation of biodiversity is also a consideration, which we discuss further in the remainder of this paper.

A key consideration for plantation design that was highlighted by our study was the importance of patches of remnant native vegetation embedded within the plantation. We found that a range of bird, mammal, and reptile species used these remnants. The value of native vegetation for biota within plantations is a result consistent across studies from around the world (e.g., Peterken and Radcliffe 1995, Zanuncio et al. 1998, Estades and Temple 1999, Lindenmayer and Hobbs 2004). Thus, the biodiversity found in plantations that contain areas of remnant native vegetation will be different from a plantation monoculture. This emphasizes the critical importance of creating heterogeneous landscape mosaics (*sensu* Bennett et al. 2006) as part of integrating conservation into plantation design.

A second finding from our investigation was that even relatively small areas of remnant native vegetation supported a wide range of species. For example, all but two of our woodland patches surrounded maturing pine stands were 5 ha or smaller but supported ~15–17 bird species per site throughout the nine years of our study (Fig. 5). The case for conserving large patches is well established from conservation theory (Rosenzweig 1995). However, our data suggest that protocols for establishing plantations on semi-cleared land should ensure that even small patches of remnant native vegetation should be retained and not always be targets

for clearing simply because they are small. This recommendation is consistent with studies in other parts of the world that have highlighted the conservation significance of small patches of remnant native vegetation (e.g., Semlitsch and Bodie 1998, McCoy and Mushinsky 1999).

A third key consideration for plantation design is that landscape context matters (Ricketts 2001, Lindenmayer and Franklin 2002). The transformation of the landscape surrounding patches of remnant native vegetation will significantly alter species presence and abundance in those patches. Thus, even if patches of remnant native vegetation are retained, some representatives of initial faunal assemblages may be lost and some new species may be gained. In general, it appears that species typical of forest environments are likely to be favored, but those more characteristic of open environments such as woodlands will be disadvantaged. Such changes need to be considered in terms of the taxa likely to be of conservation concern in a given landscape or region. In the Nanangroe natural experiment, some woodland species, including several of conservation concern (such as the Brown Treecreeper) declined and appeared to be replaced by other more widespread species, a change that has been termed “biotic homogenization” (Olden and Rooney 2006). However, not all species of conservation concern declined as a result of plantation establishment. An example of an increasing species was the Rufous Whistler, a species thought to be declining elsewhere, particularly in woodland environments in southeastern Australia (Barrett et al. 2003). It is notable that studies elsewhere in the world have found that plantations and the areas of native vegetation they contain can be important for a range of threatened species (e.g., Polmares et al. 2000, Grez et al. 2006).

A fourth consideration for plantation design is that landscape transformation can influence biodiversity responses at several spatial scales. For example, we observed species increases and declines across the entire study area as well as species displacements between woodland treatments and woodland controls. This means that for some species, such as those that are displaced, negative plantation establishment effects may be offset by increases elsewhere. For others where there was no displacement effect or for which large-scale declines occur, regional conservation issues may arise. The appropriateness of plantation establishment might be questioned in these cases, or additional conservation efforts may be required to secure populations in other locations.

Land use changes such as plantation establishment are becoming increasingly widespread, particularly as carbon offsets to combat greenhouse gas emissions (Jackson and Schlesinger 2004). The effects of these rapid landscape transformations can be substantial, multi-scaled, dynamic, and sometimes unexpected. This highlights the importance of establishing longitudinal experiments to better quantify their impacts.

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APPENDIX A

Measure of vegetation structure and plant species composition recorded at each five vegetation plots established at each site in the study (*Ecological Archives* M078-023-A1).

APPENDIX B

Bird species recorded in the study (*Ecological Archives* M078-023-A2).