Effects of landscape transformation on bird colonization and extinction patterns: results of a large-scale long-term 'natural experiment'

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Abstract

Conversion of agricultural land to forest plantations is a major driver of global change. Studies on the impact of forest plantations on biodiversity in plantations and in the surrounding native vegetation have been inconclusive. Consequently, it is not known how to best manage the extensive areas of the planet currently covered by plantations. We used a novel, long-term (16 years) and large-scale (30,000 ha) landscape transformation natural experiment (the 'Nanangroe experiment', Australia) to test the effects of land conversion on population dynamics of 64 bird species associated with woodland and forest. A unique aspect of our study is that we focused on the effects of plantations as landscape context (i.e., we investigated what happens to animal populations when the habitat in which they live remains intact but the surrounding matrix changes). Our study design included 56 treatment sites (*Eucalyptus* patches where the surrounding matrix was converted from grazed land to pine plantations), 55 control sites (*Eucalyptus* patches surrounded by grazed land) and 20 matrix sites (sites within the pine plantations and grazed land). Bird populations were studied through point counts and colonization and extinction patterns were inferred through multiple season occupancy models. Large-scale pine plantation establishment affected the colonization or extinction patterns of 89% of studied species and thus lead to a comprehensive turnover in bird communities inhabiting *Eucalyptus* patches embedded within the maturing plantations . Smaller bodied species appeared to respond positively to plantations (i.e. increased colonization and reduced extinction in patches surrounded by plantations)because they were able to use the newly created surrounding matrix. We found that the effects of forest plantations affected the majority of the bird community, and we believe these effects could lead to the artificial selection of one group of species at the expense of another.

Introduction

A substantial body of research shows that the matrix surrounding habitat patches may have drastic effects on patch-dependent species (Gascon et al. 1999; Prevedello & Vieira 2009; Driscoll et al. 2014) because it may affect key processes such as animal movement, dispersal, and resource availability. Although globally the majority of the agricultural matrix is occupied by crops for food production such as wheat (Foley et al. 2005), an increasing amount of agricultural land is being converted to forest plantations. Forest plantations currently cover approximately 200 million ha worldwide (FAO 2010) and are expected to increase due to the pivotal role in carbon sequestration, avoided deforestation, and an increasing demand for wood (FAO 2010; Paquette & Messier 2010).

A fundamental question is, What are the effects of plantations on biodiversity? To date, researchers have found equivocal results (e.g., Allan et al. 1997; Lindenmayer & Hobbs 2004; Brockerhoff et al. 2008), and effects range from negative (e.g,. Wethered & Lawes 2003; Villard & Haché 2012) to positive (e.g. Tomasevic & Estades 2008; Bremer & Farley 2010). Inconsistency of the responses of biodiversity to plantations was confirmed by a meta-analysis of global data (Felton et al. 2010). Furthermore, the mechanisms that drive changes in biodiversity relative to plantations are unknown. Are certain groups of species more sensitive than others? Such knowledge gaps mean it is unclear how to best manage the very large and rapidly increasing areas of plantation-dominated environments worldwide for other values like biodiversity conservation.

Previous studies of plantation-driven landscape transformation have been observational and conducted over short periods and at relatively small scales. However, long-term studies of plantation-derived landscape transformation are critical because of long-term crop rotation length (typically 7-50 years [Pawson et al. 2013]), a time frame that can overlap multiple generations of animal populations. Previous studies have mainly focused on species

occurrence in plantations (e.g., by contrasting assemblages in natural vs. planted forests). Little is known about the effects of plantations as landscape context' (e.g., effects on animals inhabiting habitat patches embedded within a plantation). What happens to animal populations when their habitat remains intact but the surrounding matrix is converted to plantations?

We examined the effect of pine plantations on populations of 64 bird species by conducting one of the largest (131 sites in 30000 haarea) and longest term (16 years) landscape transformation natural experiments. In 1998, in New South Wales (Australia), a series of large pine (*Pinus radiata*) plantations were established on former grazing land characterized by cleared paddocks and remnant native *Eucalyptus* patches. More than 70 *Eucalyptus* patches were progressively surrounded by maturing plantations (Fig. 1). Our experiment provided an opportunity to quantify changes occurring within the *Eucalyptus* patches as the surrounding matrix was transformed from a grazed open environment to closed forest plantation. We selected 'control' *Eucalyptus* patches (which were surrounded by grazed land) that matched the "treatment" *Eucalyptus* patches (which were surrounded by pine plantations) (Fig. 1). Notably, the *Eucalyptus* patches were not modified during the 16-year study period therefore the only difference between treatment and control sites was the surrounding matrix, which was dramatically altered in the case of treatment sites (Fig. 1). The 16-year duration of our investigation permitted us to quantify colonization and extinction patterns - key drivers of animal distribution in fragmented landscapes (Hanski & Gaggiotti 2004)- that have not been explored previously in studies of plantation effects on biodiversity. We sought new insights into the timing of localised colonizations and extinctions following land conversion that have not been previously possible due to the rarity of long-term studies. We studied a set of bird species encompassing a wide range of life history and ecological traits; all our target bird species are associated (for breeding or foraging) with forest and

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woodland. This allowed us to focus on the effects of the matrix on birds inhabiting the woodland patches.

We focused our analyseson the following life-history and ecological traitsbody size, feeding habits, reproductive potential, and matrix and habitat use. We expected that large species would respond negatively to land use change because large body size often correlates with extinction risk (Newbold et al. 2013). Furthermore, we predicted that small species would respond positively to pine plantations because we expected their small size to facilitate their movement through the dense structure of pine plantations and thus to facilitate their exploitation. We expected species with a high reproductive potential (e.g., large clutch size) to be advantaged by the land use change because it would allow them to produce a high number of emigrants, which would in turn enhance the chance of successful colonization of sites (Henle et al. 2004), despite a potentially low landscape permeability (Villard & Haché 2012). We expected frugivorous and nectarivorous species to respond negatively to pine plantations because they are sensitive to land use change (Newbold et al. 2013) and because we did not expect pine plantations to provide extra resources for these species. Conversely, we expected insectivores, omnivorous, and granivores to respond positively (Sekercioglu 2007; Deconchat et al. 2009, Newbold et al. 2013) because pine plantations may provide extra resources for these species. We expected that species responding negatively and positively to plantation establishment would differ in their matrix use (Laurance 1991; Gascon et al. 1999; Sekercioglu et al. 2002). We thus predicted that species responding positively to pine plantations would be significantly more abundant in the pine control sites, whereas species responding negatively were predicted to be significantly more abundant in open areas (Renjifo 2001; Wilson et al. 2013). Finally we explored if the main habitat associations of the species differed between species responding positively versus negatively.

Methods

Study area

Our study was conducted in the Nanangroe area (New South Wales, southeastern Australia [Supporting Information]). The Nanangroe area lies approximately 300 km southwest of Sydney (34°54'-35°4' S and 148°32' - 148°18' E, altitudinal range: 250-750 m asl) and is characterized by hot summers and relatively cool winters. The native vegetation of the treatment and control patches included open woodlands dominated by white box (*Eucalyptus albens*), red box (*E. polyanthemos*), yellow box (*E. melliodora*), red stringybark (*E. macrorhyncha*), and Blakely's red gum (*E. blakleyi*). In the last 2 centuries more than 80% of the original temperate *Eucalyptus* woodland vegetation cover in the Nanangroe area has been cleared for grazing (Lindenmayer et al. 2008).

Experimental design

In the study area, radiata pine (*Pinus radiata*) plantations were established (starting in late 1998) by Forest New South Wales for pulp and timber production and for carbon sequestration purposes (Supporting Information). Over 70 *Eucalyptus* patches of variable sizes were left untouched during the establishment of the plantations which surrounded the *Eucalyptus* patches. The patches formed a progressively emerging and novel matrix (Fig. 1, Supporting Information).

Site selection followed a replicated, random stratified procedure to reduce the potential for bias in the long term experiment. We based the stratification on size of the *Eucalyptus* habitat patches; age cohort of the surrounding pine plantations; and number of boundaries (i.e., shared sides) between patches and surrounding pine stands. There were 56 woodland treatment sites (each site was a *Eucalyptus* woodland patch surrounded by the emerging *Pinus radiata* plantation); 55 woodland control sites (each site was a *Eucalyptus* patch

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surrounded by grazing fields); 10 sites within the *Pinus radiata* plantation; and 10 sites within grazed fields. The overall study area, including treatment and control sites, was approximately 300 km^2.

We randomly selected a number of replicates for each of the following patch size classes: 15 replicates for 0.5-0.9 ha, 20 replicates for 1.0-2.4 ha, 15 replicates for 2.5-4.9 ha, 4 replicates for 5.0-10 ha, and 2 replicates for >10 ha. The *Eucalyptus* patches were surrounded by pines of 2 ages: pines planted in 1998 and pines planted in 2000. Of the 56 woodland treatments, 11 had 1-2 open boundaries with grazed land, whereas the remaining patches were completely surrounded by pines. A synthesis of the design of the Nanangroe study is provided in Supporting Information. The woodland treatment sites were matched with 55 control sites surrounded by grazing land (Supporting Information). Potential confounding effects between treatments and grazing was ruled out by the fact that domestic livestock grazing continued in all sites throughout the study period. We were unable to include an undisturbed woodland area (i.e., non-fragmented and far from plantations) as a reference area because the few existing unfragmented areas were of different vegetation types. Future landscape transformation experiments should, where applicable, include such areas.

Bird surveys

Each site (*n*=131) was surveyed 6 times per year within a 4 day period. Each survey consisted of a 5 –minute point count. We recorded all birds seen or heard in a 50 m radius but did not include birds flying over the site. Eachpoint count was located on a 200 m transect at 0, 100, and 200 m points. The first three out of six point counts were conducted by one observer on the same day, and the last three point counts were conducted by a different observer on a second day.

We completed surveys within four hours after dawn and did not undertake surveys on windy or rainy days. Surveys were conducted in 1998 (prior to the establishment of plantations), 1999, 2000, 2001, 2003, 2005, 2007, 2009, 2011, 2012, and 2013. Surveys were completed in early November, which is the peak breeding season in the study area, by experienced ornithologists from The Australian National University and the Canberra Ornithologists Group.

Data analyses

In addition to treatment and time, we included a subset of predictor variables in data analyses: vegetation type and *Eucalyptus* tree cover surrounding the site. Time was included with the variable year (both as a categorical covariate and as a continuous variable). The variable yearN (numeric) was included to account for potential trends in the population, whereas the variable year (categorical) was included to account for unmeasured year-specific factors. Vegetation type categories (3 categories) were measured in the field and based on the dominant or co-dominant arboreal species in the woodland patch (Supporting Information). *Eucalyptus* tree cover was measured in a circular area (in a 250 m and a 500 m radius) centerd in each sampling site (hereafter buffer area). Tree cover included habitat patches and single scattered trees in the landscape whichwere measured with digitised aerial photographs of the study area in ArcGIS version 10.1. We used tree cover instead of patch size because there is a substantial body of evidence that scattered trees are a crucial element for bird survival in Australian fragmented landscapes (Fischer et al. 2010) and habitat amount has recently been suggested as a single predictor variable (instead of the two variablespatch size and isolation (Fahrig 2013). Because tree cover in the two buffer areas was highly correlated (Spearman Rho=0.79, *p*<0.001), we included these variables separately in the models and selected the buffer that provided a better fit to the data (measured through Akaike information

criteria [AIC]). We used amount of rainfall as a predictor of bird detectability (details in Supporting Information).

False absences (a species was present in a site but not detected) can lead to biased inference (MacKenzie et al. 2006). To account for imperfection in species detection, we fitted multiple season occupancy models (MacKenzie et al. 2003) to detection history data (i.e., the sequence of detection or non detection in each site). In addition to tackling the issue of false absences (by estimating detection probability), the multiple season framework allows the estimation of three other parameters: Ψ_1 , which is the probability of a site being occupied during the first survey, Υ, which is the probability of a site being colonized by the target species between sampling sessions, and ε, which is the probability of the target species becoming locally extinct between sampling sessions. Colonization and extinction are probabilities, not arbitrarily defined events. We estimated them based on detection history data after accounting for the uncertainty in detection; therefore, they were expected to be relatively unbiased (MacKenzie et al. 2003, 2006).

We focused our occupancy analyses on the woodland control and woodland treatment sites (n=111), whereas the 10 agricultural control and 10 pine control sites were retained for separate analyses (see below).

A site (sensu MacKenzie et al. 2003) was defined as a *Eucalyptus* woodland patch (i.e., each of the 111 remnant patches surrounded by pines or grazed fields). Each point count was considered a visit to a site. Therefore, each site had a detection history of 6 visits per year (total of 66 visits throughout the study period). Other parameterisations of multiple season occupancy models were possible (e.g. pooling all point counts conducted per day on each site [MacKenzie et al. 2006]). Because preliminary analyses showed that results were

qualitatively and quantitatively similar with other parameterisations, we chose the one that would provide the largest sample size (in terms of overall visits).

Details on the steps we followed for fitting models are in Supporting Information. We here show all models within 2 ΔAIC (Burnham & Anderson 2002). However, given the limited reliability of model averaging in the presence of interactions (Hegyi & Garamszegi 2010), we limited inferences to the top ranked model. Goodness of fit was measured with Nagelkerke's R^2.

Species richness and diversity

To test whether there was a significant increase or decrease in species richness in each of the four treatment and control sites, we used generalized estimation equations (GEE) with Poisson distribution (log link) (Zuur et al. 2009). The dependent variables were the time series of species richness in each site, and the independent variable was the year of survey. We fitted models with an autoregressive (AR-1) structure to control for non-independence between within-subject (i.e. treatment type) measurements. Significance was evaluated through a Wald test. The value of species richness included all species detected throughout the study. Results were qualitatively similar if they included only the 64 species used for occupancy modeling.

Furthermore, we tested whether species turnover between treatment and control sites varied with time (i.e., β diversity between treatment and control sites). We measured β diversity with the Sorensen index (Magurran 2004) and tested variation over time with a linear regression.

Life history traits analyses

An important aim of our work was to test whether species with the same response to pine plantations were characterized by similar ecological and life-history characteristics (Supporting Information).

We grouped species based on responses to the treatment (i.e., the response variable was a positive or negative response of the species). We considered a species was affected by pine plantations if the variable treatment was included in the top ranking model as a predictor of colonization or extinction parameters. Species that responded positively to pine plantations included species characterized by an increase in colonization rate or a decrease in extinction risk in the treatment sites. Species that responded negatively to pine plantations included species characterized by a decrease in colonization rate or an increase in extinction risk in the treatment sites.

More detailed analyses also were conducted on less broad groupings such as species that responded positively to colonization rate only. We do not report these results here as the outcomes mirrored the results of the broad groupings.

We focused our analyses on the following key life-history and ecological traits: body size, reproductive potential, feeding habit, and matrix and habitat use. Body size was measured as mean body mass (Rising & Somers 1989). We used three proxies of reproductive potential: clutch size, number of broods per season, and reproductive effort (number of broods per year * clutch size). We groupedspecies according to broad feeding habit categories (e.g., insectivores, granivores, etc) (full list of categories in Supporting Information). We quantified the use each species made of the matrix (i.e., the 10 sampling sites in the pine plantations and the 10 sampling sites in the grazed fields) by summing the number of detections for each species in these areas. These values should be considered an index of relative abundance in these sites. We did not fit occupancy models in this case, due to the lower number of sampled sites and due to the fact that some species were never detected in

these areas. We used the Kruskal-Wallis test to compare quantitative variables (body mass, reproductive potential variables, matrix use) , whereas proportions (listed in Supporting Information) were compared using a χ^2 test.

Results

Species richness and β diversity

The average number of species (mean=21.7 [SD 7.7]) in the 56 woodland treatment sites (i.e. the *Eucalyptus* patches surrounded by maturing pine stands) did not increase or decrease significantly throughout the study (Fig. 2 and Table 1), whereas the average number increased significantly in the control sites and in the sites within the pine matrix (Table 1). The Sorensen index decreased significantly over time (F=9.7, $p<0.05$ R^2=0.5). The significant decrease reflects a replacement between species and thus increasing dissimilarity between treatment and control sites over time.

Occupancy models

A full list of top ranking (within 2 ΔAIC) occupancy models is in Table 2. Model fit for the best model was relatively high for all 64 species (median coefficient of determination: R^2=0.57, R^2 range 0.14-0.96).

Pine plantation establishment affected 89% of the target species in the woodland treatment sites (57 of 64 taxa). Approximately 45% of the species responded negatively (i.e., the presence of the pine plantations decreased the probability of a woodland treatment site being colonised or increased the extinction risk) (example provided in Fig. 3). Forty-two percent of the species responded positively (i.e., there was an increase in colonization probability and/or a decrease in the probability of extinction (example is in Fig. 3). In only one case (the Weebill *Smicrornis brevirostris*), we found a contrasting effect of pine plantations (i.e., an increase in colonization and an increase in risk of extinction). Time since the establishment of

plantations surrounding woodland treatment sites was included as a predictor in the top ranking model for 36% of species (Table 2). Several factors affected the probability of a site being occupied in the first season of sampling ($\Psi 1$), including vegetation type (35 species) and tree cover (10 species). In 23 species, the probability of a site being occupied in the first season was equal among patches (Table 2). Patterns of detectability varied strongly between species. The categorical variable year was the main factor affecting detectability in 32 species (Table 2). According to this model, detectability varied in each of the sampling years (example in Supporting Information). The numerical variable year(YN) was the main factor affecting detectability in 10 species. For 6 of these species, we found a positive trend (i.e., detectability increased over time), whereas in 4 cases the trend was negative. Rainfall of the previous year affected detectability in 21 species (example in Supporting Information).

Life-history and ecological traits

Species in the woodland treatment sites that responded negatively to the transformation of the surrounding landscape were characterized by a significantly greater mass than species that responded positively (Kruskal-Wallis $\chi^2 = 7.82$, df 1, $p < 0.01$) (Fig. 4). Separate analyses conducted on the agricultural and pine control sites showed that species that responded negatively were significantly more abundant in grazed fields than species that responded positively (i.e., in the 10 agricultural control sites) (Kruskal-Wallis $\chi^2 = 20.04$, df = 1, $p < 0.001$) (Fig. 4). Conversely, species that responded positively to the transformation of the surrounding landscape were significantly more abundant within the 10 pine control sites than species that responded negatively (Kruskal-Wallis $\chi 2 = 16.13$, df = 1, $p < 0.001$) (Fig. 4). For all the other variables tested, differences between species were not significant ($p > 0.05$ for all variables).

Discussion

Pine plantation establishment led to a comprehensive turnover of the bird communities inhabiting woodland *Eucalyptus* patches: only 7 of the 64 studied bird species were not affected by the newly emerging pine matrix. The realignment occurred without a significant variation in species richness (see also Dornelas et al. 2014): the number of species responding positively to the pine plantations was almost identical to the number of species responding negatively. The turnover between species was confirmed by the significant increase in β diversity with time. Small species were able to better exploit the novel landscape (Hobbs et al. 2006) created by the pine plantations surrounding the *Eucalyptus* patches; thus, their colonization rates increased and/or their extinction risks decreased in the *Eucalyptus* patches. The sensitivity of large species to land use change is well established in the literature (Newbold et al. 2013). However, to the best of our collective knowledge, this study is the first to show that small birds respond positively to plantation establishment.

The magnitude of the effect of time on colonization and extinction patterns was often marked. For example, the extinction risk of the White-plumed Honeyeater (*Lichenostomus penicillatus*) increased from 20% to ~ 70% during 15 years of plantation maturation (Fig. 3). These findings suggest that land managers can expect the effects of pine plantations (whether positive or negative) to increase with plantation maturation. This could occur for several reasons. It may take time for plantations to become accessible to some species. The positive response of small species is a consequence of them using the newly created pine plantation matrix. In a previous study, we found that pine plantations did not increase connectivity (e.g., dispersal) between populations inhabiting *Eucalyptus* patches (Mortelliti et al. 2014), which strongly indicates that the response observed here is a case of matrix supplementation. This implies the matrix may provide additional resources that increase the colonisation or persistence of populations in the *Eucalyptus* patches surrounded by pines. Furthermore, it is possible that the negative response of large species also may release competitive pressure in

Eucalyptus patches and increase niche availability for other species. However, Lindenmayer et al. (2014) found little support for potential competition when examining bird co-occurrence patterns in the Nanangroe area. Previous studies suggest that the ability of species to use the matrix may affect their vulnerability in fragmented landscapes (Gascon et al. 1999). Our findings suggest that smaller species, in particular, may take advantage of pine plantations, rather than being habitat generalists. This is demonstrated by the fact that these species were significantly less abundant in grazed fields. Our findings suggest that their small size facilitates movement throughout the dense structure of pine plantations (see Supporting Information for photographic examples), enabling the exploitation of resources therein. It is possible that plantations may become more accessible to large birds following management interventions such as thinning or with the maturing of pines; thus, we suggest this topic be studied in detail.

The negative response appears to be related to loss of open habitat, which was the case for at least 10 species (e.g., Willie Wagtail [*Rhipidura leucophrys*]), which is a woodland and forest species but may hunt for food in open environments such as native grassland or exotic pastures).

Although plantation-induced edge effects (e.g., increase in insectivorous birds at the boundary between plantations and woodland) have been found elsewhere (Barbaro et al. 2014), we could find no evidence of such in our system (e.g., no significant difference in feeding habits among pecies). Furthermore, the internal habitat structure of patches remained similar between treatments and controls (unpublished data), and our results clearly suggest that matrix use is the key process affecting the system.

Worldwide, grazing land is being converted to forest plantations. Considering the widespread use of pines and of exotic species in plantations, the potential implications of our study

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extend beyond our study region. For example, pines (*Pinus* spp.) are the most widely used species in plantations, accounting for approximately 20% of total worldwide plantation area (Brockerhoff et al. 2008). Nevertheless, replication of our natural experiment in plantations composed of native species and for other taxa should help to further generalise the implications of our findings.

Is there likely to be a general pattern of change with plantations (e.g., change applicable to *Eucalyptus* and palm oil plantations)? This depends on the type of plantation, the habitat replaced, and the pool of species present that could colonise vegetation remnants. However, our results strongly suggest that significant changes in the communities should be expected and that these changes will not be limited to the area affected by the plantations but will affect the adjacent and neighbouring native vegetation.

Previous empirical studies are characterized by strongly contrasting results ranging from forest plantations being considered "biological deserts" to plantations being considered a "lesser evil" relative to other types of matrix (Stephens & Wagner 2007; Brockerhoff et al. 2008). We found that plantations are not biological deserts for birds and do not create deserts in the adjacent *Eucalyptus* patches. Nevertheless, pine plantations substantially affected the turnover of local populations inhabiting habitat patches surrounded by plantations, thereby resulting in a comprehensive realignment of bird communities. Our mechanistic insights suggest that managers should expect the establishment of pine plantations surrounding woodland habitat to positively affect small species and to negatively affect large species and species that use open grazed land. Indeed, the conversion of agricultural land to forest plantations may lead to the artificial selection of one group of species at the expense of another.

Acknowledgments

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Supporting Information

Details on key features of the Nanangroe experiment (Appendix S1), site-level variables (Appendix S2), life-history traits of the target species (Appendix S3), study area map (Appendix S4), photos of the study Area (Appendix S5-7), rainfall estimate methods (Appendix S8), protocols for fitting models (Appendix S9), and detection probability estimates (Appendix S10) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Table 1 Results of the generalized estimation equations with bird species richness as dependent variable and year as predictor variable. A separate model was fitted for each of the separate groups of sites: treatment sites, control sites, sites located within the pine matrix and sites located within the grazed matrix. Study area is located in the Nanangroe landscape (Australia).

use indentation

Treatment

  intercept

  year

  xxx

Sites and predictor variables[a]	β	SE	Wald	*p*
Treatment sites				
intercept	7.187	3.881	3.430	0.064
Year	-0.002	0.002	1.050	0.305
α^b	0.26	0.07		
Control sites				
	-			
Intercept	25.480	5.31	23.0	<0.001
Year	0.014	0.003	28.9	<0.001
α	0.36	0.050		
Pine matrix sites				

-				
Intercept	69.540	18.245	14.5	<0.001
Year	0.036	0.009	15.7	<0.001
α	-0.01	0.090		
Grazed matrix sites				
Intercept	10.202	23.195	0.19	0.660
Year	-0.004	0.012	0.11	0.75
α	0.5	0.160		

[a]Treatment sites= sites surrounded by the pine plantations; control sites=sites surrounded by grazed fields; pine matrix sites= sites located within the pine matrix; grazed matrix sites= sites located within the grazed matrix.

[b]Correlation between two sequential observations.

Table 2 Top ranked single species occupancy models.

Species	ΔAIC[a]	R^{2b}	Model[c]	Response[d]
Australian Magpie	0.00	0.70	Ψ (Veg type) ϒ(T*YN)ε(T*YN)p(Y)	0
	0.62	0.69	Ψ(Veg type) ϒ(T)ε(T*YN)p(Y)	
Australian Raven	0.00	0.48	Ψ(Veg type) ϒ(.)ε(T)p(Y)	1
	1.30	0.47	Ψ(Veg type) ϒ(T)ε(.)p(Y)	
	1.93	0.48	Ψ(Veg type) ϒ(TC250)ε(T)p(Y)	
	1.94	0.48	Ψ(Veg type) ϒ(T)ε(T)p(Y)	
	1.95	0.48	Ψ(Veg type) ϒ(T)ε(TC250)p(Y)	
Black-faced Cuckoo-shrike	0.00	0.41	Ψ(.) ϒ(T)ε(TC250)p(Y)	0
	0.80	0.41	Ψ(.) ϒ(YN)ε(TC250)p(Y)	
Brown Thornbill	0.00	0.96	Ψ(Veg type) ϒ(T*YN)ε(T*YN)p(Y)	1
Brown Treecreeper	0.00	0.73	Ψ(Veg type) ϒ(T)ε(T*YN)p(Y)	0
Buff-rumped Thornbill	0.00	0.19	Ψ(.) ϒ(T)ε(TC250)p(rain)	1
	1.21	0.18	Ψ(.) ϒ(TC250)ε(TC250)p(rain)	
	1.61	0.18	Ψ(.) ϒ(TC250)ε(T)p(rain)	
Common Blackbird	0.00	0.74	Ψ(.) ϒ(T)ε(TC250)p(Y)	1
Common Bronzewing	0.00	0.26	Ψ(.) ϒ(TC250)ε(.)p(Y)	N
	1.29	0.26	Ψ(.) ϒ(TC250)ε(TC250)p(Y)	
	1.99	0.26	Ψ(.) ϒ(TC250)ε(YN)p(Y)	
	2.00	0.26	Ψ(.) ϒ(TC250)ε(T)p(Y)	
Common Starling	0.00	0.61	Ψ(TC500) ϒ(T)ε(TC250)p(Yn)	0
Crescent Honeyeater	0.00	0.89	Ψ(.) ϒ(T)ε(Yn)p(rain)	1
Crested Shrike-tit	0.00	0.43	Ψ(Veg type) ϒ(T)ε(T)p(Yn)	0
	0.50	0.45	Ψ(Veg type) ϒ(T)ε(T*YN)p(Yn)	
	1.77	0.46	Ψ(Veg type) ϒ(T*YN)ε(T*YN)p(Yn)	
Crimson Rosella	0.00	0.37	Ψ(Veg type) ϒ(.)ε(T*YN)p(rain)	0
	1.43	0.37	Ψ(Veg type) ϒ(T)ε(T*YN)p(rain)	
Dusky Woodswallow	0.00	0.62	Ψ(Veg type) ϒ(T*YN)ε(T*YN)p(Y)	0
Eastern Rosella	0.00	0.70	Ψ(Veg type) ϒ(T)ε(.)p(Yn)	0
	0.58	0.71	Ψ(Veg type) ϒ(T)ε(T)p(Yn)	
	0.79	0.71	Ψ(Veg type) ϒ(T)ε(TC250)p(Yn)	
	1.60	0.71	Ψ(Veg type) ϒ(T)ε(Yn)p(Yn)	
Eastern Spinebill	0.00	0.71	Ψ(Veg type) ϒ(T)ε(T*YN)p(Y)	0
Eastern Yellow Robin	0.00	0.59	Ψ(Veg type) ϒ(T)ε(T)p(Y)	1
European Goldfinch	0.00	0.39	Ψ(Veg type) ϒ(T)ε(TC250)p(rain)	1

Galah	0.00	0.40	Ψ(.) Υ(T*YN)ε(.)p(Yn)	0
	0.32	0.39	Ψ(.) Υ(T)ε(TC250)p(Yn)	
	1.05	0.40	Ψ(.) Υ(T*YN)ε(T)p(Yn)	
Gang-gang Cockatoo	0.00	0.30	Ψ(Veg type) Υ(T)ε(.)p(rain)	1
	0.74	0.30	Ψ(Veg type) Υ(T)ε(TC250)p(rain)	
	1.01	0.30	Ψ(Veg type) Υ(T)ε(T)p(rain)	
Golden Whistler	0.00	0.58	Ψ(.) Υ(T*YN)ε(T*YN)p(rain)	1
Grey Fantail[e]	0.00	0.93	Ψ(Veg type) Υ(T*YN)ε(T*YN)p(Y)	1
Grey Shrike-thrush	0.00	0.39	Ψ(TC250) Υ(T*YN)ε(T)p(rain)	1
	0.28	0.38	Ψ(TC250) Υ(T*YN)ε(.)p(rain)	
Jacky Winter	0.00	0.23	Ψ(TC250) Υ(T)ε(.)p(rain)	0
	0.38	0.24	Ψ(TC250) Υ(T)ε(Yn)p(rain)	
	1.27	0.23	Ψ(TC250) Υ(T)ε(TC250)p(rain)	
	1.94	0.23	Ψ(TC250) Υ(T)ε(T)p(rain)	
Laughing Kookaburra	0.00	0.19	Ψ(.) Υ(TC250)ε(.)p(Y)	N
	1.03	0.17	Ψ(.) Υ(.)ε(.)p(Y)	
	1.29	0.20	Ψ(.) Υ(TC250)ε(YN)p(Y)	
	1.44	0.00	Ψ(.) Υ(TC250)ε(YN)p(Y)	
	1.80	0.19	Ψ(.) Υ(.)ε(.)p(Y)	
	2.00	0.19	Ψ(.) Υ(TC250)ε(T)p(Y)	
Leaden Flycatcher	0.00	0.50	Ψ(Veg type) Υ(T)ε(TC250)p(Y)	1
Little Friarbird	0.00	0.38	Ψ(TC250) Υ(TC250)ε(T)p(rain)	0
Little Raven#	0.00	0.52	Ψ(.) Υ(TC250)ε(YN)p(rain)	N
	0.36	0.51	Ψ(.) Υ(.)ε(Yn)p(rain)	
	0.67	0.52	Ψ(.) Υ(T)ε(Yn)p(rain)	
Magpie-lark	0.00	0.71	Ψ(Veg type) Υ(T)ε(.)p(Y)	0
	1.63	0.71	Ψ(Veg type) Υ(T)ε(Yn)p(Y)	
	1.74	0.71	Ψ(Veg type) Υ(T)ε(T)p(Y)	
	1.93	0.71	Ψ(Veg type) Υ(T)ε(TC250)p(Y)	
Mistletoebird	0.00	0.46	Ψ(.) Υ(TC250)ε(YN)p(Y)	N
	1.44	0.44	Ψ(.) Υ(TC250)ε(.)p(Y)	
Noisy Friarbird	0.00	0.85	Ψ(Veg type) Υ(T)ε(TC250)p(Y)	0
	0.39	0.85	Ψ(Veg type) Υ(T*YN)ε(T)p(Y)	
Noisy Miner	0.00	0.80	Ψ(.) Υ(T)ε(T)p(Yn)	0
Peaceful Dove	0.00	0.52	Ψ(Veg type) Υ(T)ε(Yn)p(Y)	0
	0.26	0.54	Ψ(Veg type) Υ(T)ε(T*YN)p(Y)	
Pied Currawong	0.00	0.18	Ψ(.) Υ(T)ε(TC250)p(rain)	1
Rainbow Bee-eater	0.00	0.15	Ψ(.) Υ(Yn)ε(Yn)p(rain)	N
	1.51	0.15	Ψ(.) Υ(.)ε(T*YN)p(rain)	
	1.82	0.12	Ψ(.) Υ(.)ε(Yn)p(rain)	

Red-browed Finch	0.00	0.60	Ψ(.) ϒ(T)ε(.)p(Y)	1
	1.17	0.60	Ψ(.) ϒ(T)ε(TC250)p(Y)	
	1.99	0.60	Ψ(.) ϒ(T)ε(T)p(Y)	
Red-capped Robin	0.00	0.90	Ψ(Veg type) ϒ(T)ε(Yn)p(Y)	1
Red-rumped Parrot	0.00	0.73	Ψ(Veg type) ϒ(T)ε(TC250)p(Y)	0
Red Wattlebird	0.00	0.83	Ψ(.) ϒ(T*YN)ε(T*YN)p(Y)	0
Restless Flycatcher	0.00	0.36	Ψ(Veg type) ϒ(T*YN)ε(T*YN)p(rain)	0
	1.03	0.29	Ψ(Veg type) ϒ(T)ε(.)p(rain)	
	1.45	0.30	Ψ(Veg type) ϒ(T)ε(TC250)p(rain)	
	1.97	0.33	Ψ(.) ϒ(T*YN)ε(T*YN)p(rain)	
Rufous Songlark	0.00	0.93	Ψ(Veg type) ϒ(T*YN)ε(T*YN)p(Y)	0
Rufous Whistler	0.00	0.82	Ψ(Veg type) ϒ(T*YN)ε(T)p(Y)	1
Sacred Kingfisher	0.00	0.41	Ψ(Veg type) ϒ(TC250)ε(T)p(Y)	0
Shining Bronze-Cuckoo	0.00	0.57	Ψ(Veg type) ϒ(T)ε(T)p(rain)	1
	0.03	0.57	Ψ(Veg type) ϒ(T)ε(Yn)p(rain)	
	0.12	0.56	Ψ(Veg type) ϒ(T)ε(.)p(rain)	
	0.14	0.57	Ψ(Veg type) ϒ(T)ε(TC250)p(rain)	
Silvereye	0.00	0.69	Ψ(Veg type) ϒ(T*YN)ε(T)p(Y)	1
Spotted Pardalote	0.00	0.59	Ψ(Veg type) ϒ(T)ε(TC250)p(Y)	1
Striated Pardalote	0.00	0.45	Ψ(.) ϒ(T*YN)ε(T*YN)p(Y)	0
	0.19	0.43	Ψ(.) ϒ(T)ε(T*YN)p(Y)	
Striated Thornbill	0.00	0.75	Ψ(Veg type) ϒ(T*YN)ε(.)p(rain)	1
	0.84	0.76	Ψ(Veg type) ϒ(T*YN)ε(T*YN)p(rain)	
	1.49	0.75	Ψ(Veg type) ϒ(T*YN)ε(T)p(rain)	
Sulphur-crested Cockatoo	0.00	0.37	Ψ(Veg type) ϒ(T)ε(.)p(Y)	0
	0.08	0.38	Ψ(Veg type) ϒ(T)ε(TC250)p(Y)	
	0.49	0.40	Ψ(Veg type) ϒ(T)ε(T*YN)p(Y)	
	1.87	0.37	Ψ(Veg type) ϒ(T)ε(T)p(Y)	
Superb Fairy-wren	0.00	0.74	Ψ(Veg type) ϒ(T*YN)ε(T)p(Y)	1
	1.73	0.75	Ψ(Veg type) ϒ(T*YN)ε(T*YN)p(Y)	
Tree Martin	0.00	0.60	Ψ(TC500) ϒ(T)ε(TC250)p(Yn)	0
	1.86	0.62	Ψ(TC500) ϒ(T*YN)ε(T*YN)p(Yn)	
Varied Sittella	0.00	0.23	Ψ(TC250) ϒ(TC250)ε(YN)p(Yn)	N
	0.34	0.22	Ψ(TC250) ϒ(TC250)ε(T)p(Yn)	
	0.51	0.21	Ψ(TC250) ϒ(TC250)ε(.)p(Yn)	
	0.67	0.21	Ψ(TC250) ϒ(.)ε(T)p(Yn)	
	0.78	0.23	Ψ(TC250) ϒ(.)ε(T*YN)p(Yn)	
	1.69	0.24	Ψ(TC250) ϒ(T)ε(T*YN)p(Yn)	
Weebill	0.00	0.62	Ψ(Veg type) ϒ(T)ε(T)p(Y)	PN
	1.61	0.63	Ψ(Veg type) ϒ(T*YN)ε(T)p(Y)	

	ΔAIC	R²	Model	Response
Welcome Swallow	0.00	0.38	Ψ(TC500) ϒ(T*YN)ε(T*YN)p(rain)	0
Western Gerygone	0.00	0.41	Ψ(.) ϒ(T)ε(TC250)p(Yn)	0
	0.15	0.40	Ψ(.) ϒ(.)ε(TC250)p(Yn)	
	0.51	0.41	Ψ(.) ϒ(TC250)ε(TC250)p(Yn)	
	0.69	0.40	Ψ(.) ϒ(TC250)ε(.)p(Yn)	
White-browed Scrubwren	0.00	0.85	Ψ(Veg type) ϒ(T*YN)ε(T)p(rain)	1
White-eared Honeyeater[e]	0.00	0.87	Ψ(.) ϒ(T)ε(Yn)p(Yn)	1
	1.39	0.88	Ψ(.) ϒ(T*YN)ε(T*YN)p(Yn)	
White-plumed Honeyeater	0.00	0.88	Ψ(Veg type) ϒ(T*YN)ε(T*YN)p(Y)	0
White-throated Gerygone	0.00	0.31	Ψ(TC250) ϒ(T)ε(TC250)p(rain)	1
White-throated Treecreeper[e]	0.00	0.43	Ψ(Veg type) ϒ(TC250)ε(T)p(rain)	1
	0.88	0.40	Ψ(.) ϒ(TC250)ε(T)p(rain)	
White-winged Chough	0.00	0.25	Ψ(TC500) ϒ(TC250)ε(.)p(.)	N
	0.11	0.27	Ψ(TC500) ϒ(TC250)ε(T)p(.)	
	1.82	0.26	Ψ(TC500) ϒ(TC250)ε(YN)p(.)	
	1.89	0.26	Ψ(TC500) ϒ(TC250)ε(TC250)p(.)	
White-winged Triller	0.00	0.38	Ψ(.) ϒ(TC250)ε(T)p(Y)	0
WillieWagtail	0.00	0.77	Ψ(Veg type) ϒ(T)ε(T*YN)p(Yn)	0
	0.85	0.78	Ψ(Veg type) ϒ(T*YN)ε(T*YN)p(Yn)	
Yellow-faced Honeyeater[e]	0.00	0.90	Ψ(Veg type) ϒ(T*YN)ε(T)p(rain)	1
	1.95	0.90	Ψ(Veg type) ϒ(Y*T)ε(.)p(rain)	
Yellow-rumped Thornbill	0.00	0.21	Ψ(TC250) ϒ(T)ε(Yn)p(rain)	1
	0.89	0.26	Ψ(TC250) ϒ(T*YN)ε(T*YN)p(rain)	
	1.25	0.23	Ψ(TC250) ϒ(T)ε(T*YN)p(rain)	

[a] ΔAIC= Delta Akaike Information Criterion (difference between each model and the top ranked model). Only models <2 ΔAIC are shown.[b]Nagelkerke's coefficient of determination.
[c]Key: Ψ, probability of a site being occupied during the first survey; ϒ, probability of colonization; ε ,probability of extinction; p, detection probability; Veg type, vegetation type (categories listed in Appendix S2); T, Treatment; YN , year (numeric covariate); Y, year (categorical covariate); TC250, tree cover in the 250 m buffer; TC500, tree cover in the 500 m buffer; rain, site-specific cumulative rainfall of the previous year; (.), constant model (no covariate).
[d]Response (to pine plantations): 1=positive, 0=negative, N= neutral (Treatment not included in top ranking model), PN = positive to colonization and negative to extinction. [e]Includes spatial autocovariate.

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Fig. 1. (or something like this; as written it was circular). Experimental design of the Nanangroe 'natural experiment' (a) treatment and control sites surrounded by grazed fields, (b) small pines replaced grazed fields in treatment sites, (c) mature plantation surrounds a treatment site while control site is surrounded by grazed fields. Photos of a treatment site show how a *Eucalyptus* patch is progressively surrounded by a maturing pine plantation.

Fig. 2. Average number of species detected each yearin treatment sites (*Eucalyptus* patches surrounded by pine plantations), control sites (*Eucalyptus* patches surrounded by grazed land), matrix sites (sites within the pine plantations and within the grazed fields) (box, defined by the 25th and 75th percentile; whiskers, maximum and minimum value observed excluding outliers [defined as 3/2 the 25th percentile]; line within boxes, median value; circles, outliers)

Fig. 3. Colonization and Extinction probabilities as predicted by the top ranked occupancy model for White-plumed Honeyeater and Superb Fairy-Wren (dashed line, probability of colonization (left) or extinction (right) in the treatment sites [*Eucalyptus* patches surrounded by pine plantations]; black line, probability of colonization (left) or extinction (right) in control sites [*Eucalyptus* patches surrounded by grazed land]; shading, 95% CI; year, year since the start of the study). The first 3 graphs show a time*treatment interaction, whereas the bottom right graph shows a treatment only effect.

Fig. 4. (a) Average body mass of bird species that responded negatively to pine plantations versus species that responded positively (*n*= 56). (b) Bird abundance in the matrix (sampling sites within grazed fields and sampling sites within pine plantations) of species that responded negatively to pine plantations versus species that responded positively (box, defined by the 25th and 75th percentile; whiskers, maximum and minimum value observed excluding outliers [defined as 3/2 the 25th percentile]; line within boxes, median value; circles, outliers)