

Experimental evaluation shows limited influence of pine plantations on the connectivity of highly fragmented bird populations

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Summary

1. Conversion of natural and agricultural areas to conifer plantations is an important element of global change. Despite their widespread distribution and global importance, it is still unclear whether conifer plantations hinder or enhance movement by biota.

2. Population connectivity is difficult to quantify without detailed studies such as those using capture–mark–recapture methods. A novel solution is to quantify the synchrony in abundance between populations over time. Using this approach, more connected populations are expected to display synchrony, whereas disconnected populations are expected to fluctuate asynchronously. Here, we compared the relative effects of spatial proximity and matrix type on the population synchrony of a suite of forest-dependent birds in a long-term, fully controlled, and replicated landscape-scale experiment in south-eastern Australia.

3. Our experiment consisted of comparing bird populations inhabiting remnant eucalypt patches surrounded by *Radiata* pine *Pinus radiata* plantations (50 patches) with bird populations inhabiting remnant eucalypt patches where the surrounding landscapes are grazing fields (55 patches). Our data set encompassed 10 years and included 52 bird species characterized by different life history traits. After controlling for the effects of rainfall and patch characteristics on population dynamics, we found that spatial proximity, not matrix type, was the main driver of population synchrony for 16 species. The effect of the pine plantation matrix was negative (it reduced synchrony). However, the magnitude of its effect was particularly low (being significant only in four species).

4. *Synthesis and applications.* Our results show that pine plantations do not increase connectivity. In fact, they have little effect, with the exception of a few species, for which they may constitute a barrier. The implications of our findings for landscape management are that the conversion of agricultural areas to plantation forestry does not promote substantial movement of individuals (to the extent that would synchronize populations). Therefore, plantation expansion should not be promoted on the belief that it increases connectivity relative to an agricultural matrix.

Key-words: Australia, birds, dispersal, functional connectivity, matrix, pine and conifer plantations, population synchrony

Introduction

Connectivity is defined as the ‘degree to which the landscape facilitates or impedes movement among resource patches’ (Taylor *et al.* 1993); high levels of connectivity

are vital for the persistence of populations in fragmented landscapes (Lindenmayer & Fischer 2006). This is because the characteristics of the matrix surrounding habitat patches are pivotal in determining the connectivity of a given landscape for a given species (Driscoll *et al.* 2013) as they can affect individuals, populations, communities and interactions between species (Crooks & Sanjayan 2006; Prevedello & Vieira 2009).

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Landscape connectivity is assessed by determining how animals move and interact (functional connectivity) within the structural heterogeneity of the landscape (structural connectivity; Taylor *et al.* 1993; Crooks & Sanjayan 2006). Assessing functional connectivity is difficult and often requires behavioural experiments, capture–mark–recapture studies or investigations using landscape genetics (Baguette & Dyck 2007; Lowe & Allendorf 2010), all of which are labour intensive, expensive and difficult to replicate over large spatio-temporal scales. Recently, Powney *et al.* (2011) used the spatial synchrony of populations as an empirical method to assess functional connectivity. Spatial population synchrony is defined as the coincidental changes of population density (or other demographic parameters) over time (Bjørnstad, Ims & Lambin 1999; Liebhold, Koenig & Bjørnstad 2004). The rationale of the method proposed by Powney *et al.* (2011) is that an increase in functional connectivity is expected to increase dispersal between sites and thus increase spatial synchrony (Matter & Roland 2010; Powney, Broaders & Oliver 2012). This is in accordance with the empirical and theoretical understanding of the widespread phenomenon of spatial population synchrony, that is, dispersal between populations as one of the main drivers of spatial population synchrony (Bjørnstad, Ims & Lambin 1999; Lande, Engen & Sæther 1999; Liebhold, Koenig & Bjørnstad 2004). Provided that researchers control for other factors affecting synchrony (e.g. weather), the method proposed by Powney *et al.* (2011) is promising because it targets population-level connectivity – that is, the flow of migrants between patches (a demographic variable) – rather than the movements of single individuals (Lande, Engen & Sæther 1999).

There are many studies dealing with connectivity in the agricultural matrix (Prevedello & Vieira 2009; Driscoll *et al.* 2013), but the effect of forestry plantations on functional connectivity has received limited attention (but see Ricketts 2001; Villard & Haché 2012). However, plantations are an important element of global change (Stephens & Wagner 2007), with planted forests currently covering more than 264 million ha worldwide (7% of total forest area, FAO 2010) and widely distributed throughout all vegetated continents (Brockerhoff *et al.* 2008; FAO 2010). Furthermore, the area of planted forests is increasing annually by 5 million hectares (2000–2010; FAO 2010) and may further increase due to the use of plantations to increase carbon storage (Jackson *et al.* 2005).

Plantations have a negative effect on biodiversity when they replace native forest vegetation (Brockerhoff *et al.* 2008), or where they are used as a means of afforestation of open-ground landscapes of conservation value (e.g. they have negative effects on open-ground species; Reino *et al.* 2009; Wilson *et al.* 2014). The response of forest biodiversity to the afforestation of agricultural land, however, is complex (Felton *et al.* 2010). Previous studies have shown how bird occupancy dynamics in forest remnants may be positively or negatively affected by plantations

(Mitra & Sheldon 1993; Sax 2002; Wethered & Lawes 2003, 2005; Lindenmayer *et al.* 2008; Yamaura *et al.* 2009). Similarly, behavioural studies have shown contrasting results, with the plantation matrix either acting as a strong barrier to individual movements (Villard & Haché 2012) or acting as a ‘soft barrier’ compared with cleared land (Tomasevic & Estades 2008). For these reasons, plantation forestry has been considered a ‘lesser evil’ in fragmented landscapes (if compared to an agricultural matrix), as it may provide a compromise between preserving the economic value of an area and buffering the effect of habitat fragmentation by increasing connectivity (Hampson & Peterken 1998; Norton 1998; Brockerhoff *et al.* 2008). However, we still lack a detailed understanding of the role of plantations in affecting the connectivity of spatially structured populations. This is, in part, because previous research has focused either on individuals or on patch occupancy (presence/absence of a target species). Our goal is to tackle this issue from a new, broader, ecological scale which has not been explored by previous researchers: the synchrony between populations. Our novel approach is expected to lead to a deeper understanding of the mechanisms involved in determining the connectivity in fragmented landscapes because it targets a relatively high level of biological organization (the population level) over a long time frame (15 years, details below).

In this paper, we present the results of a large-scale, longitudinal natural experiment (*sensu* Debinski & Holt 2000) specifically designed to identify the effects of pine plantations on spatially structured populations of birds (Lindenmayer *et al.* 2001). The overarching objective of the study was to contrast populations inhabiting remnant eucalypt patches surrounded by maturing *Radiata* pine *P. radiata* plantations (50 patches, termed ‘woodland treatments’) with populations inhabiting remnant eucalypt patches surrounded by grazing fields (55 patches, termed ‘woodland controls’). The study area supports species-rich bird assemblages (139 species recorded) consisting of a variety of ecological guilds, ranging from granivores to insectivores (Lindenmayer *et al.* 2008). The sites have been monitored 10 times over a 15-year period by expert observers using identical sampling protocols over time. Therefore, our data sets that have been gathered through a long-term, fully controlled and replicated landscape-scale experiment provide an exceptional setting for studying the relative effects of matrix type and spatial proximity on the synchrony of bird populations (Debinski & Holt 2000). Our study differs from previous research conducted in the same study area (Lindenmayer *et al.* 2008) as it targets different ecological parameters (population-level connectivity) and is conducted over a longer time frame (15 vs. 7 years).

Our aim was to compare the relative importance of interpatch distance and matrix type (pine plantations vs. grazed fields) on the synchrony of the population abundance of forest birds. We expected that spatial proximity

would positively influence the degree of synchrony between habitat patches (Bjørnstad, Ims & Lambin 1999; Liebhold, Koenig & Bjørnstad 2004). However, we also expected this effect to be altered by the matrix type (pine plantations vs. grazed fields) since previous studies have shown that pine plantations may increase, decrease or have no effect on the movement of individuals between habitat patches (Ricketts 2001; Brockerhoff *et al.* 2008; Lindenmayer *et al.* 2008).

An empirical assessment of the relative effects of spatial proximity and pine plantations on population synchrony of bird species is crucial given the increasing area of the planet covered by forest plantations (Brockerhoff *et al.* 2008; FAO 2010). Our results are expected to guide managers towards an understanding of the population-level consequences of land use change.

Materials and methods

STUDY AREA

Our study was conducted in the Nanangroe area of New South Wales, south-eastern Australia (Fig. 1). Nanangroe lies *c.* 70 km north-west of Canberra (co-ordinates 34°54'–35°4' and 148°32'–148°18' E, altitudinal range: 250–750 m a.s.l.) and is characterized by a temperate climate (hot summers and relatively cool winters).

The native vegetation of the area includes woodlands dominated by yellow box *Eucalyptus melliodora*, red box *Eucalyptus polyanthemos*, white box *Eucalyptus albens*, red stringybark *Eucalyptus macrorhyncha* and Blakely's red gum *Eucalyptus blakleyi*.

The Nanangroe area is highly modified, and more than 80% of the original temperate eucalypt woodland vegetation cover has been cleared for grazing in the last 150 years. In the past 14 years, large areas have been planted with *P. radiata* for plantation timber and pulp (paper) production (details below). Further details on the study area are provided in Lindenmayer *et al.* (2008) and Lindenmayer (2009).

DESIGN OF THE NANANGROE EXPERIMENT

The Nanangroe study is a large-scale longitudinal experiment in which the biota inhabiting 50 remnant woodland patches surrounded by *P. radiata* plantations (woodland treatments) are contrasted with the biota of 55 remnant woodland patches surrounded by grazed fields (woodland controls). The study began in 1998 before plantations had been established and has continued throughout the subsequent stages of development of the plantation (Lindenmayer *et al.* 2001, 2008).

Patch selection followed a replicated, random stratified procedure to reduce the potential for bias. The three factors considered for stratification were (i) size of the patch, (ii) age cohort of the surrounding pine plantations and (iii) number of boundaries between patches and surrounding pine stands. We selected a number of replicates for each of the following patch size classes: 0.5–0.9 ha (13 replicates), 1.0–2.4 ha (19 replicates), 2.5–4.9 ha (15 replicates), >5.0 ha (three replicates). The woodland patches were surrounded by pines belonging to two age cohorts (cohort 1 = pines planted in 1998 and cohort 2 = pines planted in 2000). Of the 50 woodland treatments, 11 had 1–2 open boundaries with grazed land, whereas the remaining patches were completely surrounded by pines. The design of the Nanangroe study is summarized in Table 1. The woodland treatment sites were matched

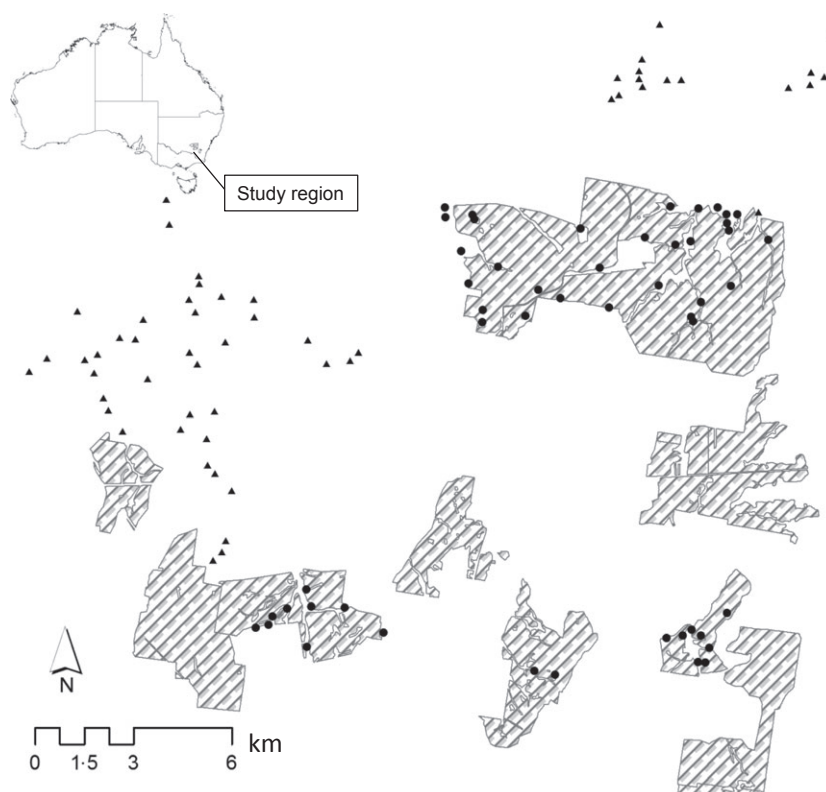


Fig. 1. Map of the Nanangroe experiment study area with sampling sites (triangles = controls; black circles = treatments). The shaded area corresponds to pine plantations, whereas the white area corresponds to grazed field. The Nanangroe area is located in New South Wales, Australia.

Table 1. Number of sites of the Nanangroe study highlighting the factorial study design (Table modified from Lindenmayer *et al.* 2008). We removed six sites used by Lindenmayer *et al.* (2008), due to lack of continuous sampling throughout the 12 study years

Site	Context	Cohort	No. of edges	No. of replicates
Woodland	<i>Pinus radiata</i> plantation	1998	1–2	3
Woodland	<i>P. radiata</i> plantation	1998	3–4	16
Woodland	<i>P. radiata</i> plantation	2000	1–2	6
Woodland	<i>P. radiata</i> plantation	2000	3–4	25
Woodland	Grazed fields			55

with the 55 control sites surrounded by grazing (Table 1). Both treatments and controls occurred in clusters and were separated by comparable distances: average distance between treatments = 7.4 km (SD = 4.2), range = 0.11–16 km; average distance between controls = 8.3 km (SD = 6.1), range = 0.18–21.7 km; and average distance between all sites = 9.3 km (SD = 4.9); Fig. 1.

BIRD SURVEY PROTOCOLS

We surveyed birds along a 200-m transect at each site. We completed 5-min point interval counts at the 0-, 100- and 200-m points along the transect. We recorded all birds seen or heard within a 50 m radius, but did not include birds flying over the site. Each site was surveyed on a different day by a different observer to minimize day effects on detection and to take into account potential bias due to observer heterogeneity (Cunningham *et al.* 1999; Field, Tyre & Possingham 2002). We surveyed for birds at each site on six occasions each sampling session (within 4 days). We completed counts within 4 h from dawn and did not undertake surveys on days of bad weather (e.g. windy or rainy days). Bird surveys were conducted by staff of The Australian National University and the Canberra Ornithologists Group throughout the duration of the 15 years of study (a list of observers is available in Appendix S1, Supporting information). Field sites were surveyed in the following years: 1998, 1999, 2000, 2001, 2003, 2005, 2007, 2009, 2011 and 2012. Surveys were completed during the breeding season for the majority of species (early November) and when summer migrants had arrived.

ABUNDANCE INDEX OF BIRD POPULATIONS

We calculated an index of bird abundance for each site by dividing the total number of detections in the year of sampling by the number of point counts ($N = 6$) in the transect. We followed this approach to minimize variability in counts between observers. This abundance index has been considered a good proxy for the local abundance of birds (Cunningham *et al.* 1999; Cunningham & Olsen 2008).

PREDICTOR VARIABLES

Our dependent variable is a measure of the strength of the association between each pair of sites in our study area (Spearman correlation coefficient of bird abundance). For this reason, where applicable, the predictor variables were measured as similarities between each pair of sites (Haynes *et al.* 2013).

Bird population synchrony may be determined by several factors including spatial proximity, synchrony in weather conditions, characteristics of the habitat (e.g. habitat amount) (Koenig 1998;

Liebhold, Koenig & Bjørnstad 2004). Our main focus here is on spatial proximity (Euclidean distance between sites) and habitat connectivity (amount of pine plantations between each couple of sites). However, in the modelling phase detailed below, we controlled for other possible drivers of population synchrony such as patch size and weather (Powney *et al.* 2011). We acknowledge that other factors such as habitat quality and predation risk also may play a role in driving population synchrony. Measuring habitat quality and predation risk is complex (Mortelliti, Amori & Boitani 2010), particularly over large spatio-temporal scales such as in this study. To further assess potentially confounding effects of non-target variables, we repeated the analyses detailed below by including a proxy measurement of habitat quality (vegetation type) as control variable (categories are listed in Table S2, Supporting information). We recognize that future studies should attempt to include more detailed and direct measurements of habitat quality and predation risk as possible additional drivers of spatial synchrony.

WEATHER DATA

We focused on rainfall because previous research has shown its importance as determinant of bird abundance in eucalypt forest (Maron *et al.* 2005; Mac Nally *et al.* 2009; Stevens & Watson 2013). Rainfall patterns in the study area are shown in Fig. S1 (Supporting information). In this investigation, we utilized the thin-plate smoothing spline method described by Hutchinson (1995) to infer climate variables for each sampling site. This method has been widely applied to estimate monthly and daily climate surfaces (McKenney *et al.* 2011). In particular, these surfaces can be used to calculate accurate spatially explicit, monthly mean climate values at fine spatial scales (Xu & Hutchinson 2013). In Australia, the thin-plate smoothing spline method also has been used to estimate monthly time series surfaces from 1968 by the Australian Greenhouse Office for carbon accounting purposes (Kesteven, Landsberg & Australia 2004). The resulting rainfall surfaces (derived from thousands of site observations by the Australian Bureau of Meteorology as a function of longitude, latitude and elevation, and rigorously tested with cross-validation) were used in this study to calculate point values of precipitation at each site (see Manning *et al.* 2005 for a similar application).

DATA ANALYSIS

The characteristics of the matrix between each pair of sites ($N = 105$) were calculated in the following manner:

We created a shapefile in Arcgis 10.2 of buffers between each combination of sites ($N = 5460$ buffers – i.e. 1 buffer for each couple; width of the buffer = 600 m). We chose a width of 600 m

so that the buffer would be twice the size of the transect (200 m) on both sides. We then calculated the proportion of land covered by pine plantations for each of the buffers.

We analysed data for each bird species separately, following the protocols suggested by Haynes *et al.* (2013). We summarize our analysis protocol below:

1. We excluded species with < 10% of the sites occupied at least once. We selected sites where the average detection probability across the years was higher than 0.01. We followed this procedure because a sequence of zero abundance counts followed by positive values (e.g. site colonization) can inflate synchrony values and therefore increase Type I errors (Powney *et al.* 2010).

2. We detrended the time series by calculating the difference in the log abundances between sequential years: $r = \log N_{(t+1)} - \log N_{(t)}$ (Bjørnstad, Ims & Lambin 1999; Liebhold, Koenig & Bjørnstad 2004). Prior to calculations, we added one to all counts to avoid log-transforming zero counts.

3. We quantified synchrony between populations by calculating the Spearman correlation coefficient between each possible pair of sites ($N = 9$ differences in log abundances for each species examined).

4. We calculated rainfall synchrony among sites through the Spearman correlation coefficient of cumulative rainfall in the previous 2 years between each pair of sites.

5. We calculated the Euclidean distance (in km) between each pair of sites as a measurement of spatial distance.

6. We used the Mahalanobis coefficient to quantify the dissimilarity between the patch size class between each pair of sites (Goslee & Urban 2007). The Mahalanobis coefficient is a scale-invariant measurement that is often used to quantify the dissimilarity of continuous variables (Goslee & Urban 2007).

7. We converted differences in patch size (patch size dissimilarity) and geographical distance to similarities (e.g. spatial distance to proximity) by using the following equation: $1 - (\text{distance from } i \text{ to } j / \text{maximum distance observed})$.

8. We used the Mantel tests to check for collinearity between each predictor variable (listed below). The correlation was low (< 0.2, Table S3, Supporting information), and we therefore introduced variables simultaneously in the modelling phase (see below).

9. To quantify the effect of spatial distance, matrix type, rainfall synchrony and patch size similarity on population synchrony, we used multiple regression of distance matrices (hereafter MRM) with synchrony between populations as the dependent variable and the remaining covariates (spatial proximity + proportion of pine plantations between each pair of sites + patch size similarity + rainfall synchrony) as predictor variables (Lichstein 2006). We fitted the following four types of models based on the combination of predictor covariates: (i) full model (spatial proximity + proportion of pine plantations between each pair of sites + patch size similarity + rainfall synchrony), (ii) space-only model (spatial proximity), (iii) matrix-only model (proportion of pine plantations) and (iv) environment-only model (patch size similarity + rainfall synchrony). The MRM analyses were conducted with 9999 permutations (Legendre, Lapointe & Casgrain 1994).

The MRM analyses allowed us to isolate the influences of spatial proximity, matrix type, rainfall and patch size on the synchrony of bird populations. The MRM approach is conceptually similar to a partial correlation (or a Mantel test) since it allows modelling the partial correlation between distance matrices while controlling for other matrices (Lichstein 2006). In our case, we

were interested in modelling the effects of spatial proximity and matrix type while controlling for the effect of other potentially confounding factors such as rainfall, patch size and vegetation type.

The magnitude of the R^2 (coefficient of determination, a measure of how well the model fits to the data) on distance matrices (e.g. the R^2 for our MRM analyses) does not correspond directly to the magnitude of the R^2 on raw data (e.g. the R^2 of a linear regression, Goslee 2009). Consequently, the maximum possible values for a correlation on distances can be substantially lower than 1, even with a perfect correlation of the raw data. We therefore suggest caution in interpreting the R^2 values that we have provided. This was because low values for the R^2 do not necessarily mean that very small amount of information is explained (Goslee 2009).

Results

We selected 52 species (out of the 139 detected, Table S4, Supporting information) for detailed analysis (following the criteria highlighted in the Materials and methods section).

Results of the MRM analyses are shown in Table 2 (full model), whereas the space model (spatial proximity only), and matrix-only (proportion of pine plantations in the buffer) and environment-only (rainfall synchrony plus similarity in patch size) models are shown in Tables S5–S7 (Supporting information).

We found that 16 species were significantly influenced by spatial proximity ($P \leq 0.05$, Table 2, see Table S4, Supporting information for species names), four species were affected by rainfall synchrony (the Buff-rumped Thornbill, the Laughing Kookaburra, the Peaceful Dove and the Rufous Whistler, $P < 0.05$; Table 2). No species were affected by similarity in patch size. Four species (the Buff-rumped Thornbill, the Noisy Friarbird, the Red Wattlebird and the Yellow-faced Honeyeater) were affected by the proportion of pine plantations between sites. Spatial proximity increased synchrony (closer sites where more synchronous, Table 2), whereas the relationship between the proportion of pine plantations and synchrony was consistently negative: the higher the amount of pine plantations between sites, the lower the synchrony (Table 2). Overall, the effect of spatial proximity was stronger than the effect of matrix type (proportion of pine plantations); the relative effects are shown in Fig. S2 (Supporting information). The effect of rainfall synchrony was mainly positive (with the exception of the Rufous Whistler), that is, an increase of synchrony in rainfall patterns led to an increase in the synchrony of bird population abundance (Table 2).

We re-ran the full model by substituting dissimilarity in vegetation type to patch size similarity to control for potentially confounding effects of patch structure on population synchrony. The effects of spatial proximity and proportion of pine plantations on population synchrony remained unchanged when compared to previous analyses including patch size (Table S8, Supporting information).

Table 2. Results of the multiple regression of distance matrices (MRM) analyses for the Nanangroe study. Full models: the dependent variable was the synchrony between populations, and the independent variables were the spatial proximity, rainfall synchrony, patch size similarity and matrix type (proportion of pine plantations in the buffer). We used 9999 permutations to test for statistical significance (values of $P < 0.05$ are highlighted in bold)

Species	β -Intercept	β -Spatial proximity	P	β -Rainfall synchrony	P	β -Patch size similarity	P	β -Matrix	P	Number of sites
Australian Magpie	-0.006	0.038	0.225	-0.008	0.603	0.022	0.470	-0.017	0.727	94
Australian Raven	-0.048	0.221	0.319	0.021	0.768	-0.126	0.369	0.046	0.764	16
Black-faced Cuckoo-shrike	0.020	-0.002	0.961	-0.007	0.743	0.005	0.868	-0.039	0.464	63
Brown Thornbill	0.099	0.061	0.393	0.007	0.810	-0.001	0.990	-0.078	0.277	49
Brown Treecreeper	-0.075	0.223	0.001	0.026	0.341	-0.048	0.190	0.026	0.804	46
Buff-rumped Thornbill	-0.069	0.150	0.113	0.118	0.013	0.023	0.756	-0.148	0.029	31
Common Blackbird	0.294	0.128	0.550	-0.017	0.809	-0.209	0.262	-0.343	0.099	23
Common Bronzewing	0.108	0.049	0.803	-0.079	0.316	-0.137	0.325	-0.100	0.432	14
Common Starling	0.031	-0.047	0.398	-0.011	0.683	0.030	0.464	-0.017	0.827	49
Crested Shrike-tit	-0.096	0.156	0.047	0.002	0.959	-0.012	0.890	0.039	0.763	27
Crimson Rosella	-0.032	0.063	0.020	-0.015	0.248	-0.009	0.666	0.036	0.173	96
Dusky Woodswallow	0.022	-0.016	0.854	0.069	0.123	-0.014	0.821	-0.049	0.449	29
Eastern Rosella	0.017	0.015	0.718	0.012	0.618	-0.035	0.273	-0.040	0.528	52
Eastern Spinebill	-0.086	0.272	0.037	-0.003	0.964	-0.010	0.973	0.174	0.322	29
Eastern Yellow Robin	-0.084	-0.068	0.809	-0.016	0.910	-0.040	0.908	0.385	0.301	13
European Goldfinch	0.031	-0.055	0.840	0.028	0.754	0.032	0.853	-0.018	0.936	16
Galah	0.003	-0.037	0.496	-0.001	0.973	0.019	0.606	-0.004	0.935	47
Golden Whistler	-0.458	-0.075	0.776	0.219	0.150	0.514	0.077	0.085	0.764	14
Grey Fantail	0.191	0.025	0.643	-0.017	0.409	-0.093	0.208	-0.077	0.205	65
Grey Shrike-thrush	-0.044	0.114	0.002	-0.013	0.353	-0.020	0.427	0.063	0.071	91
Jacky Winter	-0.147	0.238	0.117	0.065	0.339	-0.007	0.943	-0.060	0.704	18
Laughing Kookaburra	0.056	-0.028	0.768	0.122	0.013	-0.054	0.408	-0.036	0.644	29
Leaden Flycatcher	0.285	0.561	0.006	-0.096	0.352	-0.536	0.390	0.398	0.257	14
Magpie-lark	-0.060	0.234	0.016	0.013	0.735	0.001	0.981	-0.288	0.115	37
Mistletoebird	0.217	-0.083	0.333	-0.029	0.405	-0.051	0.570	-0.061	0.527	38
Noisy Friarbird	0.082	0.241	0.000	-0.010	0.537	-0.041	0.359	-0.389	0.000	89
Peaceful Dove	-0.063	0.157	0.235	0.230	0.003	-0.081	0.459	0.452	0.071	21
Pied Currawong	0.114	-0.010	0.948	0.011	0.901	-0.202	0.136	0.111	0.440	15
Red Wattlebird	0.000	0.383	0.000	-0.002	0.906	0.027	0.628	-0.395	0.000	97
Red-browed Finch	0.308	0.304	0.173	-0.038	0.710	-0.159	0.663	-0.400	0.245	15
Red-rumped Parrot	-0.086	0.081	0.100	0.032	0.174	0.076	0.050	-0.033	0.714	54
Restless Flycatcher	-0.077	0.144	0.133	0.047	0.355	-0.010	0.889	-0.020	0.904	25
Rufous Songlark	0.037	0.239	0.000	0.000	0.982	-0.067	0.113	0.026	0.769	66
Rufous Whistler	-0.023	0.012	0.825	-0.045	0.031	0.052	0.455	0.046	0.405	63
Sacred Kingfisher	0.040	-0.010	0.930	-0.027	0.625	0.012	0.905	-0.017	0.938	25
Silvereye	0.026	0.030	0.702	0.058	0.072	-0.075	0.429	0.096	0.270	41
Spotted Pardalote	0.214	-0.012	0.878	0.005	0.887	-0.068	0.667	-0.141	0.245	36
Striated Pardalote	-0.061	0.118	0.003	0.019	0.215	0.028	0.311	-0.011	0.783	82
Striated Thornbill	-0.097	0.066	0.465	0.030	0.435	0.092	0.526	-0.015	0.880	37
Sulphur-crested Cockatoo	0.094	-0.156	0.042	0.073	0.057	0.014	0.820	-0.083	0.397	33
Superb Fairy-wren	-0.010	0.024	0.590	-0.025	0.176	0.001	0.979	0.041	0.325	67
Weebill	0.109	-0.002	0.975	-0.016	0.710	-0.074	0.462	-0.010	0.914	33
Welcome Swallow	-0.236	0.598	0.010	0.058	0.550	-0.185	0.424	0.220	0.483	13
White-browed Scrubwren	0.099	-0.007	0.946	-0.002	0.938	-0.095	0.281	0.158	0.113	40
White-plumed Honeyeater	0.023	0.071	0.158	-0.018	0.337	0.022	0.642	0.050	0.615	73
White-throated Gerygone	-0.083	0.099	0.179	-0.075	0.103	0.009	0.920	-0.014	0.826	30
White-throated Treecreeper	0.083	0.076	0.167	-0.010	0.690	-0.120	0.068	-0.010	0.884	51
White-winged Chough	0.047	0.105	0.529	-0.053	0.584	-0.122	0.338	0.018	0.918	16
White-winged Triller	-0.146	0.140	0.453	0.003	0.975	0.186	0.398	-0.532	0.061	14
Willie Wagtail	-0.075	0.100	0.010	0.019	0.273	0.024	0.420	0.048	0.339	70
Yellow-faced Honeyeater	0.036	0.232	0.001	0.028	0.206	0.006	0.956	-0.173	0.014	62
Yellow-rumped Thornbill	-0.038	0.168	0.040	0.015	0.738	-0.091	0.151	-0.018	0.747	32

Discussion

Our findings challenge existing views on pine plantations as possible tools for increasing connectivity (Hampson & Peterken 1998; Norton 1998; Brockerhoff *et al.* 2008). We

found that spatial proximity, not the proportion of pine plantations between sites, was the main driver of population synchrony for 16 species (of the 52 examined). The magnitude of the effect of matrix type was particularly low, being significant only in four species. These findings

suggest that, at the spatial and temporal scale considered here, spatial proximity was the main driver of population synchrony when compared to matrix type. By approaching the study of highly fragmented populations surrounded by different types of matrix from a novel ecological scale, we have shown how pine plantations do not increase connectivity. Rather, they have no effect, with the noticeable exception of a few species, for which they may constitute a barrier.

Previous studies on the effects of conifer plantations on biodiversity have shown that they act as a barrier to dispersal in some circumstances (Villard & Haché 2012), but facilitate it in others (Wethered & Lawes 2003, 2005; Tomasevic & Estades 2008). Previously in our study area, Lindenmayer *et al.* (2008) observed that bird populations display a range of responses to pine plantations, including negative (decrease), positive (increase) and neutral. Overall, we observed few effects of pine plantations on population synchrony, but there were negative (i.e. barrier) effects on four species, of which two (noisy friarbird and red wattlebird) were highly significant ($P < 0.001$, Table 2). This contrasts with the results of Lindenmayer *et al.* (2008) and suggests that matrix effects have a more marked influence on occupancy patterns than on population synchrony in our study system. We underline that species occupancy (e.g. Lindenmayer *et al.* 2008) and fluctuations in abundance (this study) are two different ecological parameters and thus may not respond identically to a given process such as land use change (Freckleton & Gill 2005). The new insights from this study show how the use of different measurements (e.g. approaching a study from a different ecological scale) may alter management recommendations (see below).

Our results showing the predominant effect of spatial proximity are in accordance with the findings of the observational study conducted by Powney *et al.* (2011) on a butterfly species (speckled wood *Pararge aegeria*) in the UK. These authors found that, at distances < 20 km, the effect of habitat suitability on population synchrony was negligible compared with the effect of spatial proximity. The strength of the experimental approach that we have employed, together with the wide taxonomic scope of our study (> 50 species), allowed us to generalize such findings; in particular, we extend previous knowledge by showing how pine plantations do not modify the predominant effect of spatial proximity.

Our study was focused on a specific spatial scale (< 20 km) which allowed us to work in controlled conditions (i.e. a natural experiment) and thus make direct comparisons between the two types of matrix (grazed land vs. pine plantations). Future studies should assess whether the effect of pine plantations on connectivity becomes more pronounced at larger scales (e.g. hundreds of km, Powney, Broaders & Oliver 2012). However, it will be virtually impossible to answer to such a question (more pronounced effect of connectivity at broader scales) with a

natural experiment; therefore, future studies will have to rely on observational data.

An important additional outcome of our work was the observed lack of significant correlates of synchrony for 32 species of birds. These results may suggest that (i) other factors are affecting synchrony or (ii) the population dynamics of these species are not synchronous in the study area (Koenig 1998, 2001). Nevertheless, we stress that these findings still confirm the lack of a positive (or negative) effect of the pine matrix at the spatio-temporal scale here considered.

Three of the four species for which pine plantations had a negative effect on synchrony (the noisy friarbird, the red wattlebird and yellow-faced honeyeater) are all nectarivorous and belong to the same family (Meliphagidae). The fourth species, the buff-rumped thornbill, belongs to the Pardalotidae and feeds mainly on invertebrates (Ford, Noske & Bridges 1986). Formal statistical analyses on possible effects of life history traits on sensitivity to matrix-driven asynchrony are not warranted due to the fact that we found significant effects on only four species. However, it appears that these four species do not share any other apparent life history or ecological features (Table S3, Supporting information).

MANAGEMENT IMPLICATIONS

Our study focused on the impact of plantations by exotic species on biodiversity (e.g. *P. radiata*). It is possible that the use of native tree species in plantations may reduce their impact on biodiversity but, as highlighted by Brockerhoff *et al.* (2008), more empirical evidence on this topic is needed before we can reach sound conclusions. Nevertheless, we stress that exotic species are an important component of plantations worldwide (Brockerhoff *et al.* 2008; FAO 2010). At the global level, introduced species grow on 25% of the planted forest area with marked differences between regions. As an example, many countries almost exclusively use introduced species (e.g. Kenya, South Africa, New Zealand, Argentina, Brazil; see FAO 2010 for a full list), whereas other nations such as China use introduced species in 28% of their plantations (FAO 2010). *Pinus* species are the most widely used species in native/non-native plantations (ca. 20% of the total plantation area (Brockerhoff *et al.* 2008). In the light of the widespread use of *Pinus* species and of exotic species in plantations, we stress that the potential implications of our study clearly extend well beyond our study region.

The implications of forest plantations for the conservation of biodiversity have been widely debated in the scientific literature (Lindenmayer & Hobbs 2004; Brockerhoff *et al.* 2008) and among environmental organizations (Carrere & Lohman 1996; Cyranoski 2007). Given the rapid rate of plantation expansion worldwide (FAO 2010), landscape managers will be increasingly faced with the issue of converting agricultural land to plantations and will have to mediate between opposing views of

different stakeholders (Cyranoski 2007). An argument for converting agricultural land to plantations has been that plantation forestry may be a 'lesser evil' in fragmented landscapes (when compared to an agricultural matrix; Brockerhoff *et al.* 2008). This is because plantations may provide habitat for some species (Brockerhoff *et al.* 2008; Lindenmayer *et al.* 2008) and function as a soft barrier by increasing connectivity (Hampson & Peterken 1998; Norton 1998; Renjifo 2001; Brockerhoff *et al.* 2008). However, our results show how pine plantations do not increase connectivity of bird populations. Rather, they have relatively little effect, with the noticeable exception of a few species, for which they may constitute a barrier. The implications of our findings for landscape management are that the conversion of agricultural areas to plantation forestry is unlikely to promote substantial movement of individuals (to the extent that would synchronize populations). Therefore, we suggest that plantation expansion should not be promoted in the belief that they may provide increased connectivity for birds compared with an agricultural matrix.

Our results show how the key element for maintaining connectivity in production landscapes is the spatial proximity of remnant vegetation patches. The goal of managers, both in the context of an agricultural matrix or within forest plantations, should be to minimize the distance between patches of native habitat. Such a goal may be achieved by promoting habitat restoration and by enhancing the creation of corridors of native vegetation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Rainfall patterns in the study area.

Figure S2. R^2 of the MRM models.

Table S1. List of observers participating to the Nanangroe study and percentage of point counts conducted by each of them throughout the study.

Table S2. Vegetation type categories used in this study.

Table S3. Results of the Mantel test.

Table S4. Main life history traits of target bird species.

Table S5–S8. Results of the MRM analyses.