

Ecological and spatial drivers of population synchrony in bird assemblages



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Abstract

Spatial population synchrony is defined as the coincidental changes of population density or other demographic parameters over time. Synchrony between local populations is believed to be widespread in nature because it has been found across a range of ecological guilds and across large spatial scales. However, a detailed understanding is still lacking of the extent of synchronous patterns in population parameters across animal communities, and of the relative importance of the several potential causes of population synchrony.

This study aimed to contribute to the understanding of how widespread spatial synchrony is in bird communities and to identify the main ecological drivers of synchrony. To achieve this we examined patterns of synchrony among bird populations inhabiting two contrasting areas of southeast Australia: the Victoria Central Highlands and Booderee National Park. Bird populations were studied through yearly point counts spanning 2004–2012 in Victoria and 2003–2012 in Booderee National Park.

Our empirical assessment showed that spatial proximity, synchrony in weather (cumulative rainfall) and habitat type influenced the level of spatial synchrony in 11 out of the 38 species examined (i.e. 29% of the species). Synchrony was primarily driven by spatial proximity, followed by synchrony in rainfall; habitat similarity played a small role as driver of synchrony in both areas.

Zusammenfassung

Räumliche Synchronität von Populationen ist definiert als das zeitliche Zusammenfallen von Änderungen der Populationsdichte oder anderer demographischer Parameter. Synchronität zwischen lokalen Populationen gilt als in der Natur weit verbreitet, denn sie wurde bei einer Reihe von ökologischen Gilden und über weite räumliche Skalen gefunden. Indessen mangelt es immer noch an detaillierten Kenntnissen zum Ausmaß synchroner Muster bei den Populationsparametern vieler Tiergemeinschaften und zur relativen Bedeutung der vielen potentiellen Ursachen für Synchronität. Ziel unserer Studie war es, einen Beitrag zum Verständnis davon zu leisten, wie weit verbreitet räumliche Synchronität bei Vogelpopulationen ist, sowie die wichtigsten bestimmenden Faktoren der Synchronität zu identifizieren. Hierzu untersuchten wir Synchronitätsmuster von Vogelpopulationen, die zwei unterschiedliche Gebiete Südostaustraliens bewohnen: das Hochland von Zentral-Viktoria und den Booderee-Nationalpark.

Die Vogelpopulationen wurden mit jährlichen point counts erfasst, von 2004–2012 in Victoria und von 2003 bis 2012 im Booderee-Nationalpark. Unsere Analysen zeigten, dass räumliche Nähe, Synchronität des Wetters (kumulativer Niederschlag)

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und Habitattyp den Grad der räumlichen Synchronität bei 11 von 38 untersuchten Arten (d.h. 29%) beeinflusste. Die Synchronität wurde hauptsächlich durch räumliche Nähe gesteuert, danach durch Synchronität der Niederschläge. Ähnlichkeit des Habitats spielte in beiden Gebieten eine geringe Rolle als Steuergröße der Synchronität.

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Introduction

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). Synchrony between local populations is believed to be a pervasive phenomenon because it has been found across a range of ecological guilds, in many taxa, and across large spatial scales (e.g. thousands of kilometres; Koenig 2002; Liebhold et al. 2004). Synchrony among populations arises mainly through two classes of mechanisms: climate which acts over broad scales (Ranta, Kaitala, Lindström, & Helle 1997; Koenig 2002) – and dispersal – a more local effect caused by individuals dispersing between neighbouring populations (Ripa 2000; Peltonen, Liebhold, Bjørnstad, & Williams 2002). Recent application of advanced statistical modelling to long-term large-scale datasets on population dynamics has helped to increase our understanding of spatial and ecological drivers of population synchrony (e.g. Gouhier, Guichard, & Menge 2010; Haynes, Bjørnstad, Allstadt, & Liebhold 2013). However, we still lack a detailed understanding of the prevalence of synchronous patterns across animal communities, and of the relative importance of the several potential causes of population synchrony (Liebhold et al. 2004).

Several issues have hampered a detailed understanding of patterns of spatial synchrony, in particular: (a) *The lack of data*. The study of synchrony requires large-scale datasets encompassing several years. (b) *Restricted taxonomic scope*. Synchrony is often studied in single species or small portions of the community (e.g. Bellamy, Rothery, & Hinsley 2003). (c) *Sampling bias*. Observer and sampling variability may mask or bias patterns of synchrony (Thomas 1991), leading to underestimation of the nature and extent of synchrony.

In this paper, we present a study designed to explore patterns of synchrony in the abundance of bird populations inhabiting two contrasting areas of south-eastern Australia: the Victoria Central Highlands (VCH), an area characterised by continuous areas of tall wet *Eucalyptus* forest belonging to several different forest types; and Booderee National Park (BNP), an extremely heterogeneous coastal area characterised by highly contrasting vegetation types. Both areas support species-rich bird assemblages (77 species recorded in VCH and 128 in BNP) consisting of a variety

of ecological guilds, ranging from consumers of nectar to insectivores.

Our study was developed around two broad and exploratory questions:

How widespread is synchrony in bird communities?

We tested for spatial synchrony among the most frequently recorded birds occurring in the study areas (22 species in VCH and 30 in BNP). We expected relatively high levels of synchrony due to the relatively high level of connectivity existing in both areas (Powney, Broaders, & Oliver 2012) and due to the relatively high dispersal capabilities of many species of birds (Paradis, Baillie, Sutherland, & Gregory 1999). However, we predicted that synchrony would be lower in BNP due to the high levels of vegetation heterogeneity (e.g. different vegetation types characterised by different bird communities, Appendix A: Tables 1 and 2).

Which are the main drivers of spatial synchrony in bird populations?

At the scale considered here (3281 km² VCH and 110 km² BNP), dispersal should be expected to prevail over weather factors because differences in weather should be small and dispersal between local populations should be high (Lande, Engen, & Sæther 1999; Kendall, Bjørnstad, Bascompte, Keitt, & Fagan 2000). We also expected that habitat type would play a major role in determining synchrony in the highly heterogeneous BNP due to reduced connectivity between local populations (Bellamy et al. 2003; Powney, Roy, Chapman, Brereton, & Oliver 2011).

Materials and methods

Study areas

The Victoria Central Highlands region (Fig. 1) lies approximately 120 km north-east of Melbourne (coordinates 37°20'–37°55'S and 145°30'–146°20'E, altitudinal range: 303–1225 m asl; area covered by convex polygon encompassing sites: 3281 km²) and is characterised by mild, humid winters with occasional periods of snow. The study area consists mainly of Mountain ash (*Eucalyptus regnans*), Alpine ash (*Eucalyptus delegatensis*) and eucalypt forest (Appendix A: Table 1).

Booderee National Park (Fig. 1) is located ~200 km south of Sydney on the southern coast of New South Wales (coordinates 35°7'–35°11'S and 150°45'–150°35'E, altitudinal

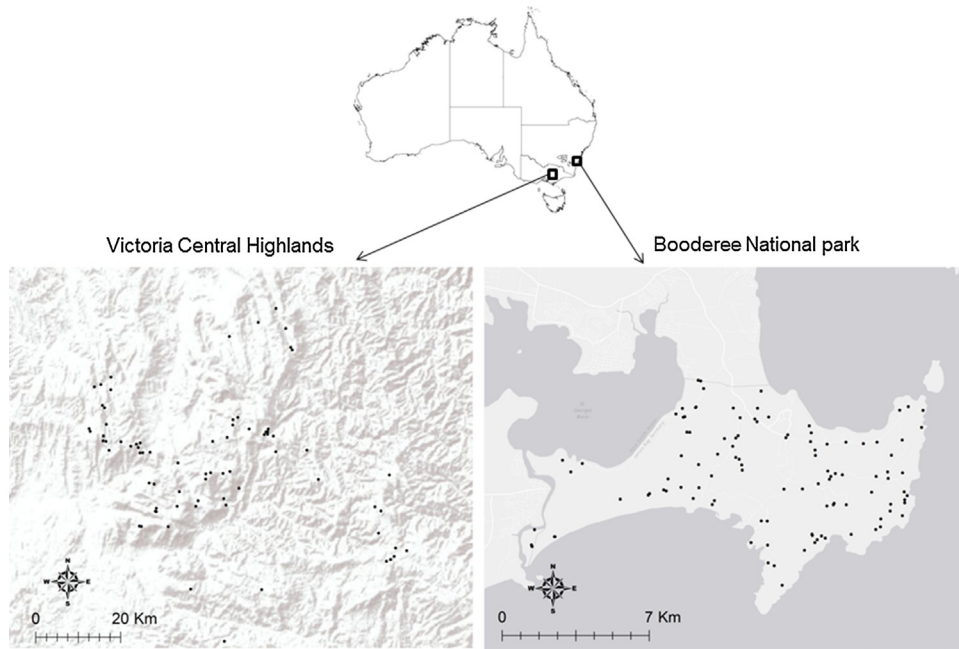


Fig. 1. Study areas. Study areas (Victoria Central Highlands, Booderee National Park) in south east Australia. Black circles are study sites (each site = 1 survey transect).

range: 0–154 m asl; area covered by convex polygon encompassing sites: 110 km²). The area is characterised by a temperate maritime climate with rainfall spread relatively evenly over the year. The area supports a high degree of patchiness and heterogeneity in vegetation types, ranging from dry heathland to warm temperate rain forest. For this study, we recognised 10 broad categories of native vegetation cover (Appendix A: Table 2).

Selection of sampling sites

We used permanent sampling sites to provide a comprehensive coverage of the main habitat types occurring in the two study areas, and of factors such as stand age, aspect and years since last fire. Our site selection process ensured that (1) samples occurred in each habitat type, (2) there was replication of sites within each category (e.g. stand age cohort within a habitat type), (3) sites were well distributed throughout the study area to eliminate geographical bias, and (4) the total number of samples was generally proportional to the total area occupied by each category. Within each category, site locations were randomly selected.

We identified three main habitat types in the VCH region: (1) forest dominated by Mountain ash, (2) forest dominated by the Alpine Ash, (3) mixed forest type (shared dominance between Alpine and Mountain ash). Sites varied in age, aspect and years since last fire. A total of 75 sites was selected for this study (average distance between sites = 25.19 km; range: 0.19–65.97 km; Appendix A: Table 1).

In the BNP area, we identified 10 vegetation types (Appendix A: Table 2). Sites varied according to years

since the last fire. Vegetation types were extremely heterogeneous ranging from dry heathland to rainforest and thus support different bird communities. We selected a total of 110 sites (average distance between sites = 5.18 km; range: 0.18–16.14 km; Appendix A: Table 2).

Bird survey protocols

Each site was surveyed with a 100 m (VCH) and 60 m (BNP) transect. In the VCH, 5 min point interval counts were completed at the 0 m, 50 m and 100 m points along the transect, whereas in BNP 5 min point interval counts were conducted at the start and end point of the transect. We recorded all birds seen or heard in a 50 m radius, excluding birds flying over our sites. Each site was surveyed on a different day by a different observer to minimise day effects on detection and to tackle potential bias due to observer heterogeneity. A total of 6 visits per site were carried out in VCH and 4 visits per site in BNP. We completed counts between 5.30 and 9.30 am and did not undertake surveys on days of poor weather. Bird surveys were conducted by the same observers in both areas throughout the duration of the decade-long sampling periods.

In the VCH, field sites were surveyed annually from 2004 to 2012 with the exception of 2006 and 2008, whereas in BNP sites were surveyed annually from 2003 to 2012 with the exception of 2008. Surveys were completed during the breeding season for the majority of species (September in BNP and late November in VCH) and when summer migrants have arrived.

Abundance index

We calculated an abundance index for each site by dividing the total number of detections in a given year by the number of point counts in the transect. We followed this approach to minimise variability in counts between observers. This abundance index has been considered a good proxy for the local abundance of birds (Cunningham, Lindenmayer, Nix, & Lindenmayer 1999; Cunningham & Olsen 2008). In addition, we further checked for the correlation (Spearman correlation coefficient) between the absolute number of birds estimated by the same observer (D.B.L.) and the abundance index, finding a reasonable fidelity (VCH: average = 0.54, range = 0.38–0.73; BNP: average = 0.63, range = 0.47–0.81). We are therefore confident that our index provides a good representation of the abundance of the local populations in both areas.

As the amount of sampling variation strongly affects researchers' capability of detecting synchrony, to explore sampling variation in more detail (i.e. to quantify variance within and between sample times) we fitted generalised linear mixed effects models (glmm) on the point count data (i.e. including the actual number of birds estimated by observers) using the lme4 package in R (release 2.15.2, R Core Team 2012).

Weather data

We focused on rainfall because previous research has shown its importance as determinant of bird abundance in Australia (Mac Nally et al. 2009; Stevens & Watson 2013). To infer climate variables for each sampling site in this work we have utilised the thin-plate smoothing spline method (Hutchinson 1995). 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 (Xu & Hutchinson 2013). In Australia the thin plate smoothing splines have 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 latitude, longitude and elevation, and rigorously tested with cross-validation, Hutchinson 1995) have been used in this study to calculate point values of precipitation at each site. Rainfall patterns are shown in Appendix A: Fig. 1.

Data analysis

We analysed data for each species and study area separately, following the steps summarised below (see also Haynes et al. 2009, 2013).

We excluded species with less than 10% of the sites occupied at least once. We selected sites where the average detection rate across the years was higher than 0.1. This was

done because a sequence of zero abundance counts followed by positive values (e.g. site colonisation) can inflate synchrony values and therefore increase Type I errors (Sutcliffe, Thomas, & Moss 1996).

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 et al. 1999). We added one to all counts prior to the calculations to avoid the issue of logging zero counts.

The synchrony between populations was quantified by calculating the Spearman correlation coefficient between each pair of sites (Bjørnstad et al. 1999; Liebhold et al. 2004).

The rainfall synchrony among sites was quantified by calculating the Spearman correlation coefficient of cumulative rainfall in each site in the previous two years between each pair of sites (e.g. correlation between cumulative rainfall in site i the two years before each sampling and cumulative rainfall in site j the two years before each sampling).

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

We used the Gower measurement to quantify the dissimilarity between habitat types and the Mahalanobis coefficient to quantify the dissimilarity between age and fire intensity for each pair of sites (Goslee & Urban 2007). The Gower measurement is a dissimilarity measurement used for mixed (continuous and categorical) variables, whereas the Mahalanobis measurement is a scale-invariant measurement that can be used for continuous variables (Goslee & Urban 2007).

Vegetation type and geographic distance were converted to similarities (or proximity) by calculating: $1 - \text{distance from } i \text{ to } j / \text{maximum distance observed}$.

We checked for collinearity between the rainfall measurement, spatial distance and habitat dissimilarity using a Mantel test. The correlation was ≤ 0.6 (Appendix A: Table 3) and we therefore introduced variables simultaneously in the modelling phase detailed below.

To quantify the effect of spatial distance, weather synchrony and habitat dissimilarity on population synchrony, we used multiple regression of distance matrices (hereafter MRM) with synchrony between populations as a dependent variable and the remaining covariates as predictor variables (Lichstein 2006). We fitted the following three types of models based on the combination of predictor covariates: full model (spatial distance + habitat dissimilarity + weather dissimilarity), space-only model (spatial distance) and environment-only model (habitat dissimilarity + weather dissimilarity). The analyses using the MRM were conducted with 9999 permutations.

We measured the "pure" effect of each predictor by following the variance partitioning approach (Borcard, Legendre, & Drapeau 1992). We stress that spatially structured variation in environmental characteristics that is not described by the environmental predictors (e.g. habitat type, age) will be attributed to spatial effects (Lichstein 2006), which implies that spatial effects may not necessarily be driven by dispersal only.

The magnitude of the R^2 on distance matrices (e.g. an R^2 for MRM analyses) does not correspond directly to the magnitude of the R^2 on raw data (Goslee 2009). It follows that the maximum possible values for a correlation on distances can be substantially lower than 1, even with a perfect correlation of the raw data. Consequently, we suggest caution in interpreting the provided R^2 values: low values do not necessarily mean that a very small amount of information is explained. Furthermore, we emphasise that confidence intervals of parameter estimates are currently not available within the ‘ecodist’ package used to fit MRM models, therefore additional caution should be exerted in interpreting results.

To simplify tables we elected to present results only for similarity of habitat type as measurement of ecological distance (rather than including also similarity in age and time since last fire) because the final results were qualitatively similar. All analyses were conducted using R software (release 2.15.2, R Core Team 2012).

Results

We selected a total of 22 species from the VCH and 30 species from BNP for detailed analysis. Local populations showed strong variations in abundance throughout the years (examples are provided in Appendix A: Figs. 2 and 3).

The level of synchrony varied substantially between sites and between species, ranging from no synchrony (i.e. minimum of the Spearman correlation coefficient = 0.00, $p > 0.05$) to almost perfect synchrony (i.e. maximum of the Spearman correlation coefficient = 0.99, $p < 0.001$). However, the average synchrony between sites was low for all the species examined (e.g. range of the average Spearman correlation coefficient for all sites and species = 0.00–0.23). Results on the GLMM’s fitted on the point count data are shown in Appendix A: Table 4. These results show how the within-site and between-observer variation was relatively high.

Results of the MRM analyses are shown in Tables 1 and 2 (full model including spatial proximity, rainfall synchrony and habitat type), whereas the space model (spatial proximity only) and environment only model (rainfall synchrony plus habitat type) are shown in Appendix A: Tables 5–8. In the VCH, we found that four species were significantly influenced by spatial proximity only (the Eastern Spinebill, the Golden Whistler, the Striated Thornbill and the Striated Pardalote, Table 1), two species were affected by rainfall synchrony (the Silvereye and White-browed Scrubwren; Table 1), one species was affected by rainfall synchrony and habitat type (the Grey Fantail) and one species (the Crescent Honeyeater) was affected by habitat type only. We found no significant effects on synchrony for the remaining 15 species (Table 1). The “pure effect” of spatial proximity vs environment (rainfall and habitat type) for each species is shown

in Fig. 2A. As can be seen, both factors (spatial proximity and environment) have comparable “pure effects”, however, the effect of spatial proximity was slightly stronger, particularly for species with significant spatial synchrony between populations.

In the BNP, we found that three species were significantly influenced by spatial proximity only (the Eastern Spinebill, the Silvereye and the Little Wattlebird, Table 2), two species were affected by spatial proximity and by rainfall synchrony (the Golden Whistler and Noisy Friarbird; Table 2), one species (the Eastern Bristlebird) was affected by rainfall synchrony only, whereas two species (the New Holland Honeyeater and the Spotted Pardalote) were affected by habitat type only. We found no significant effects on synchrony for the remaining 21 species (Table 2). The “pure effect” of spatial proximity vs environment (rainfall and habitat type) for each species is shown in Fig. 2B. As can be seen both factors (spatial proximity and environment) have comparable “pure effects”, however, the effect of environment is slightly stronger. Nevertheless, species with significant spatial synchrony between populations are characterised by a stronger effect of spatial proximity.

Discussion

Our empirical assessment encompassed a total of 38 individual species in two study areas in south-east Australia, and showed that spatial proximity, synchrony in weather conditions (cumulative rainfall) and habitat type influenced the level of spatial synchrony in 11 of the 38 species examined (i.e. approximately 29% of the species). These results are in line with the study of Koenig (2001) who found a similar proportion of synchronous species in his study conducted over a much large spatial scale (e.g. 10^6 km²) than our study. Interestingly, the spatial scale at which Koenig (2001) found most of the evidence for synchrony was comparable to ours (i.e. <100 km).

The overall level of synchrony that we have measured is relatively weak (range of the average Spearman correlation coefficient = 0.00–0.23). Our results may suggest that, at the spatial and temporal scale that we considered, more than half the species display asynchronous patterns, which could suggest that local factors may be the driving force of local population dynamics. Nevertheless, caution is warranted since the observed patterns may be driven by several factors, such as methodological issues as well as genuine lack of synchrony in the target community. These factors are difficult to disentangle in empirical data therefore limited inference may be made in the presence of asynchrony. Possibly, for this reason, synchronous patterns are reported more often than a-synchronous patterns (but see Sutcliffe et al. 1996; Koenig 2001).

A factor that may have affected our conclusion is differences in abundance and/or detectability between synchronous vs non-synchronous species (e.g. the ready detection of some

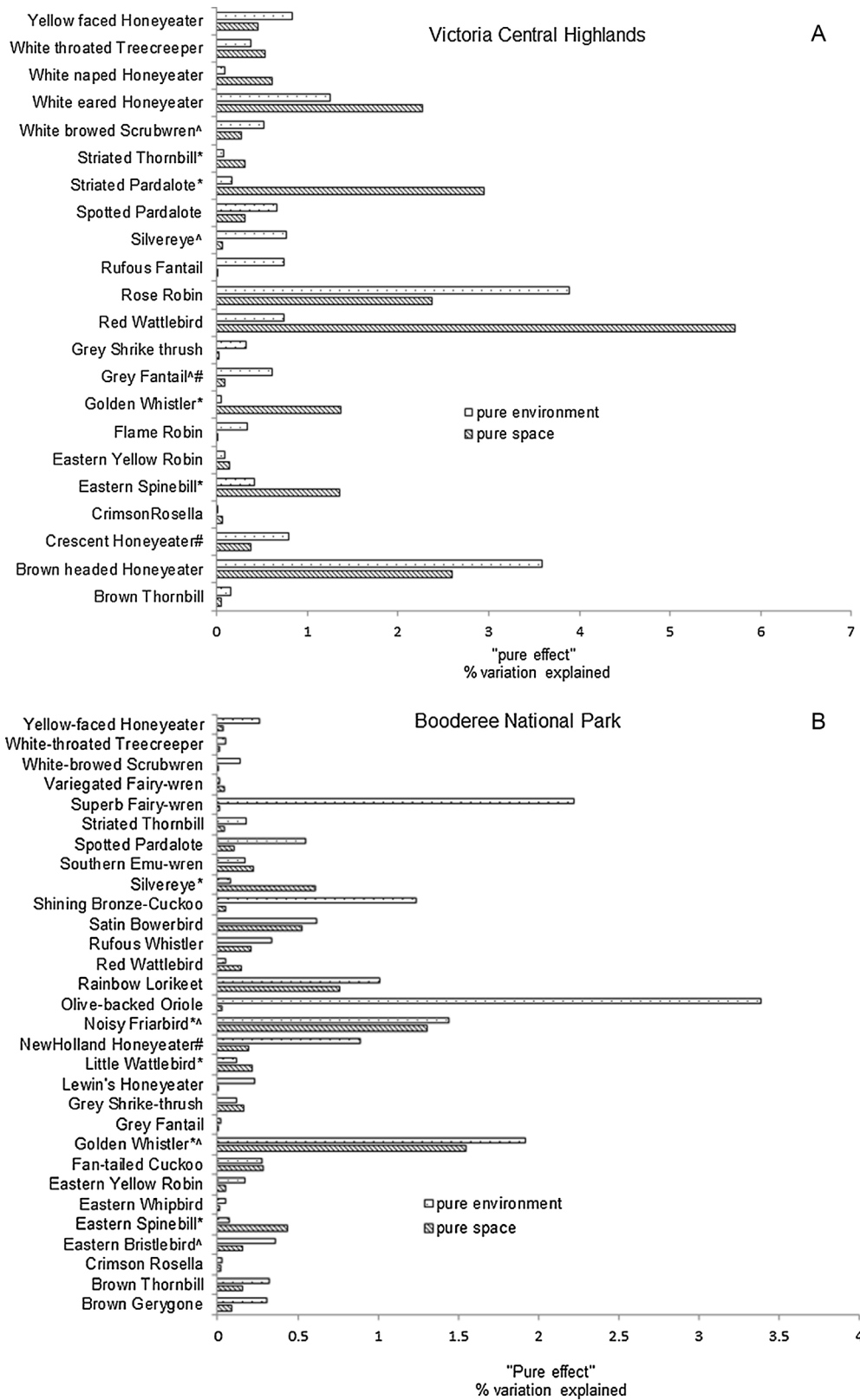


Fig. 2. Relative effects of spatial and environmental predictors “Pure effects” of spatial (euclidean distance between sites) and environmental (synchrony in rainfall and similarity of habitat types) drivers of local population synchrony in bird communities of the Victoria Central Highlands (panel A) and the Booderee national park (panel B), south-east Australia. * Significant effect of spatial proximity; [^] significant effect of rainfall synchrony; # significant effect of the similarity of habitat type.

Table 1. Results of the MRM (multiple regression of distance matrices) analyses for the Victoria Central Highlands. Full models: the dependent variable was the synchrony between populations and the independent variables were spatial proximity, the weather synchrony (cumulative rainfall) and similarity of habitat types (ecological similarity). We used 9999 permutations to test for statistical significance (when $p < 0.05$ values are highlighted in bold).

Species	β intercept	β spatial proximity	p	β rainfall synchrony	p	β ecological similarity	p	R^2	p
Brown Thornbill	−0.024	0.065	0.388	0.007	0.983	0.038	0.152	0.003	0.239
Brown headed Honeyeater	1.327	0.668	0.244	−1.967	0.138	0.077	0.644	0.047	0.344
Crescent Honeyeater	−0.272	0.171	0.113	0.287	0.498	−0.093	0.032	0.014	0.059
Crimson Rosella	0.054	−0.078	0.341	−0.001	0.996	0.000	0.999	0.001	0.714
Eastern Spinebill	−1.116	0.382	0.018	0.975	0.248	−0.043	0.576	0.047	0.006
Eastern Yellow Robin	0.036	0.109	0.177	−0.111	0.666	−0.029	0.204	0.002	0.297
Flame Robin	−0.166	−0.038	0.779	0.242	0.688	−0.062	0.137	0.003	0.586
Golden Whistler	−0.316	0.328	0.000	0.143	0.592	−0.020	0.418	0.026	0.000
Grey Fantail	−0.661	0.086	0.209	0.706	0.009	−0.055	0.037	0.013	0.003
Grey Shrike thrush	−0.573	0.042	0.709	0.598	0.175	−0.016	0.733	0.006	0.312
Red Wattlebird	0.649	0.675	0.052	−1.086	0.467	−0.034	0.779	0.073	0.149
Rose Robin	0.560	0.522	0.083	−0.825	0.514	−0.172	0.152	0.045	0.184
Rufous Fantail	0.393	−0.010	0.964	−0.529	0.343	0.122	0.347	0.007	0.669
Silvereye	−0.623	−0.076	0.462	0.816	0.041	−0.062	0.090	0.008	0.118
Spotted Pardalote	−0.560	−0.147	0.192	0.670	0.078	0.013	0.768	0.007	0.265
Striated Pardalote	0.266	0.476	0.016	−0.358	0.685	−0.018	0.773	0.031	0.118
Striated Thornbill	−0.250	0.150	0.010	0.181	0.349	−0.025	0.199	0.007	0.007
White browed Scrubwren	0.653	0.144	0.074	−0.722	0.029	0.039	0.174	0.006	0.100
White eared Honeyeater	1.189	0.375	0.066	−1.482	0.177	−0.004	0.964	0.023	0.272
White naped Honeyeater	0.194	0.257	0.547	−0.408	0.809	0.002	0.995	0.007	0.956
White throated Treecreeper	0.443	0.210	0.102	−0.541	0.252	−0.007	0.895	0.006	0.464
Yellow faced Honeyeater	−0.492	−0.197	0.432	0.720	0.440	−0.084	0.339	0.011	0.697

species may have increased the statistical power of analyses e.g. number of sites included in the analyses). However, several readily detectable and abundant species (e.g. the Crimson Rosella, the Brown Thornbill and the Grey fantail) did not display significant synchronous patterns which suggests that, for several of the species that we have examined, this was not an issue. Furthermore, repeating analyses with a higher cutoff in detection rate (e.g. 0.5 rather than 0.1, see methods) led to a similar proportion of synchronous/non-synchronous species, further suggesting that differences in abundance and detectability were not major factors affecting inference on synchrony.

The main methodological issue that may mask patterns of synchrony is sampling error (Thomas 1991). Our sampling protocol was designed to take into account sampling error. Each sampling transect covered a relatively large sampling area (e.g. 2.35 ha per transect in VCH and 1.56 ha per transect in BNP) and was composed of multiple detection points surveyed by different observers on different days. Detections at the multiple points were then averaged across a transect, thus reducing spatiotemporal variability. The transect was likely to cover the home ranges of many individuals because most of the target species were small (median body weight = 18 g) and therefore have small territories. Moreover field surveys were conducted during the breeding period, when territoriality is high. Ideally, an additional averaging of data over

several transects would have further helped to reduce the potential masking effect of sampling error. However, this approach would have substantially reduced our sample size (and thus the power of our analyses) and would have forced us to group transects falling in different habitat types (e.g. in the highly heterogeneous Booderee national park). For these reasons, we chose to keep analyses focused at the transect scale.

Results from the generalised mixed effects models analyses suggest that the amount of sampling variation in the raw data was relatively high and therefore our efforts to control it (e.g. averaging across point counts) may have not been sufficient and this may have affected our power to detect synchronous patterns in some species. Similarly, the average Spearman correlation coefficient between point counts in the same site was relatively low (Appendix A: Table 4). Finally, we emphasise that our parameter estimates do not include confidence intervals (see methods) therefore we suggest additional caution in interpreting the results and the ecological meaning of p values in our models (Ellison, Gotelli, Inouye & Strong 2014). Given the dominance of measurement error and its impacts on characterisation of spatial patterns (Dungan et al. 2002), caution is mandatory on these issues, therefore further broad scale multi-species studies are required to confirm our findings on the prevalence of synchrony in bird communities.

Table 2. Results of the MRM (multiple regression of distance matrices) analyses for the Booderee national park. Full models: the dependent variable was the synchrony between populations and the independent variables were spatial proximity, the weather synchrony (cumulative rainfall) and similarity of habitat types (ecological similarity). We used 9999 permutations to test for statistical significance (when $p < 0.05$ values are highlighted in bold).

Species	β intercept	β spatial proximity	p	β rainfall synchrony	p	β ecological similarity	p	R^2	p
Brown Gerygone	−8.079	−0.117	0.790	8.266	0.628	0.010	0.905	0.0050	0.942
Brown Thornbill	0.378	0.086	0.097	−0.418	0.172	0.033	0.102	0.0039	0.142
Crimson Rosella	−4.157	−0.081	0.567	4.236	0.461	−0.001	0.976	0.0003	0.889
Eastern Bristlebird	−15.051	−0.235	0.154	15.294	0.046	0.005	0.865	0.0053	0.119
Eastern Spinebill	0.114	0.158	0.001	−0.211	0.325	0.017	0.341	0.0045	0.018
Eastern Whipbird	−0.175	0.022	0.609	0.148	0.388	0.013	0.600	0.0007	0.665
Eastern Yellow Robin	−7.778	−0.123	0.460	7.937	0.284	−0.023	0.453	0.0022	0.531
Fan-tailed Cuckoo	13.726	0.360	0.267	−14.081	0.426	0.035	0.505	0.0046	0.539
Golden Whistler	31.963	0.743	0.001	−32.609	0.000	0.005	0.893	0.0193	0.005
Grey Fantail	0.154	−0.004	0.919	−0.107	0.655	−0.004	0.848	0.0002	0.930
Grey Shrike-thrush	7.466	0.221	0.214	−7.651	0.293	0.003	0.933	0.0017	0.653
Lewin's Honeyeater	0.200	0.012	0.912	−0.096	0.788	−0.058	0.277	0.0024	0.876
Little Wattlebird	7.382	0.249	0.041	−7.549	0.163	−0.016	0.565	0.0030	0.132
NewHolland Honeyeater	−0.476	0.092	0.119	0.557	0.063	−0.072	0.005	0.0145	0.002
Noisy Friarbird	28.515	0.661	0.022	−28.931	0.047	−0.060	0.188	0.0165	0.095
Olive-backed Oriole	16.389	0.111	0.888	−16.464	0.708	0.142	0.166	0.0384	0.403
Rainbow Lorikeet	10.594	0.541	0.193	−11.017	0.595	0.095	0.153	0.0316	0.119
Red Wattlebird	3.279	0.213	0.361	−3.329	0.748	0.019	0.677	0.0051	0.447
Rufous Whistler	15.126	0.274	0.314	−15.169	0.271	0.017	0.745	0.0035	0.771
Satin Bowerbird	15.461	0.358	0.322	−15.793	0.301	−0.004	0.962	0.0062	0.763
Shining Bronze-Cuckoo	10.054	0.146	0.752	−10.082	0.646	−0.112	0.129	0.0125	0.514
Silvereye	−0.131	0.170	0.005	0.083	0.790	−0.033	0.243	0.0082	0.021
Southern Emu-wren	4.892	0.317	0.624	−5.113	0.906	0.033	0.693	0.0066	0.895
Spotted Pardalote	−11.132	−0.182	0.242	11.386	0.112	−0.057	0.038	0.0063	0.061
Striated Thornbill	6.545	0.108	0.673	−6.529	0.535	−0.028	0.498	0.0021	0.819
Superb Fairy-wren	0.730	−0.025	0.894	−0.563	0.234	−0.071	0.505	0.0226	0.422
Variagated Fairy-wren	0.132	0.049	0.523	−0.092	0.866	−0.001	0.971	0.0005	0.954
White-browed Scrubwren	0.299	0.017	0.722	−0.287	0.282	0.022	0.235	0.0014	0.420
White-throated Treecreeper	4.510	0.059	0.743	−4.545	0.566	0.007	0.828	0.0008	0.881
Yellow-faced Honeyeater	0.421	0.040	0.469	−0.377	0.274	0.011	0.649	0.0027	0.466

What are the main drivers of spatial synchrony in bird populations?

Spatial proximity was the strongest predictor of population synchrony, followed by synchrony in rainfall and ecological similarity, which is in accordance with theoretical predictions and with empirical findings (Ranta et al. 1997; Bjørnstad et al. 1999; Liebhold et al. 2004). Previous research, however, has focused on the similarity between population synchrony and weather conditions, rather than including an actual measurement of weather synchrony (as done in this study: synchrony of rainfall as predictor of synchrony of populations). As underlined by Haynes et al. (2013), the fundamental property of an environmental synchronising agent is that it should fluctuate synchronously. Rainfall-driven synchrony was lower than spatial proximity-driven synchrony in both areas (Fig. 2A and B). Although weather and microclimatic conditions are known to be important at both large and

small spatial scales (Vanwallegheem & Meentemeyer 2009; Ashcroft & Gollan 2013) and despite some degree of variation in rainfall between sites (Appendix A: Fig. 1) our results suggest that at the small spatial scale examined rainfall-driven synchrony does not play a major role.

Contrary to our predictions, despite the high level of habitat heterogeneity in BNP compared to VCH, the effect of ecological (habitat) similarity on population synchrony was similar in both areas (2 species in each area, Tables 1 and 2). These results suggest a weak effect of ecological dissimilarity as a factor dampening population synchrony, as suggested by previous studies (Haynes et al. 2013).

Conclusions

Our study considered a wide range of ecological conditions, which included an extremely heterogeneous range

of species belonging to different guilds (encompassing consumers of nectar to insectivores) and a variety of habitats, ranging from dry coastal heathland to alpine-type vegetation. Through our empirical assessment we found evidence of synchrony in approximately 29% of the species examined which is in line with previous studies conducted in North America (Koenig 2001). Synchrony was primarily driven by spatial proximity, followed by synchrony in rainfall. Despite the extremely high level of vegetation heterogeneity of BNP, habitat similarity played a small role as driver of synchrony in both areas.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2015.01.008>.

References

- Ashcroft, M. B., & Gollan, J. R. (2013). Moisture, thermal inertia, and the spatial distributions of near-surface soil and air temperatures: Understanding factors that promote microrefugia. *Agricultural and Forest Meteorology*, *176*, 77–89.
- Bellamy, P., Rothery, P., & Hinsley, S. (2003). Synchrony of woodland bird populations: The effect of landscape structure. *Ecography*, *3*, 338–348.
- Bjørnstad, O., Ims, R., & Lambin, X. (1999). Spatial population dynamics: Analyzing patterns and processes of population synchrony. *Trends in Ecology & Evolution*, *14*, 427–432.
- Borcard, D., Legendre, P., & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, *73*, 1045–1055.
- Cunningham, R. B., Lindenmayer, D. B., Nix, H. A., & Lindenmayer, B. D. (1999). Quantifying observer heterogeneity in bird counts. *Austral Ecology*, *24*, 270–277.
- Cunningham, R., & Olsen, P. (2008). A statistical methodology for tracking long-term change in reporting rates of birds from volunteer-collected presence–absence data. *Biodiversity and Conservation*, *18*, 1305–1327.
- Dungan, J. L., Perry, J. N., Dale, M. R. T., Legendre, P., Citron-Pousty, S., Fortin, M., et al. (2002). A balanced view of scale in spatial statistical analysis. *Ecography*, *5*, 626–640.
- Ellison, A. M., Gotelli, N. J., Inouye, B. D., & Strong, D. R. (2014). P values, hypothesis testing, and model selection: It's déjà vu all over again. *Ecology*, *95*, 609–610.
- Goslee, S. C. (2009). Correlation analysis of dissimilarity matrices. *Plant Ecology*, *206*, 279–286.
- Goslee, S., & Urban, D. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, *22*, 1–19.
- Gouhier, T. C., Guichard, F., & Menge, B. A. (2010). Ecological processes can synchronize marine population dynamics over continental scales. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 8281–8286.
- Haynes, K. J., Bjørnstad, O. N., Allstadt, A. J., & Liebhold, A. M. (2013). Geographical variation in the spatial synchrony of a forest-defoliating insect: isolation of environmental and spatial drivers. *Proceedings of Biological Sciences/The Royal Society*, *280*, 2012–2373.
- Haynes, K. J., Liebhold, A. M., Fearer, T. M., Wang, G., Norman, G. W., & Johnson, D. M. (2009). Spatial synchrony propagates through a forest food web via consumer–resource interactions. *Ecology*, *90*, 2974–2983.
- Hutchinson, M. F. (1995). Interpolating mean rainfall using thin plate smoothing splines. *International Journal of Geographical Information Systems*, *9*, 385–403.
- Kendall, B., Bjørnstad, O., Bascompte, J., Keitt, T., & Fagan, W. (2000). Dispersal, environmental correlation, and spatial synchrony in population dynamics. *The American Naturalist*, *155*, 628–636.
- Kesteven, J., Landsberg, J., & Australia, U. (2004). *Developing a national forest productivity model* (pp. 1–65). Canberra.
- Koenig, W. (2002). Global patterns of environmental synchrony and the Moran effect. *Ecography*, *25*, 283–288.
- Koenig, W. (2001). Spatial autocorrelation and local disappearances in wintering North American birds. *Ecology*, *82*, 2636–2644.
- Lande, R., Engen, S., & Sæther, B. (1999). Spatial scale of population synchrony: Environmental correlation versus dispersal and density regulation. *The American Naturalist*, *154*, 271–281.
- Lichstein, J. W. (2006). Multiple regression on distance matrices: A multivariate spatial analysis tool. *Plant Ecology*, *188*, 117–131.
- Liebhold, A., Koenig, W. D., & Bjørnstad, O. N. (2004). Spatial synchrony in population dynamics. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 467–490.
- McKenney, D., Hutchinson, M. F., Papadopol, P., Lawrence, K., Pedlar, J., Campbell, K., et al. (2011). Customized spatial climate models for North America. *Bulletin of the American Meteorological Society Meteorological Society*, *92*, 1611–1622.
- Mac Nally, R., Bennett, A. F., Thomson, J. R., Radford, J. Q., Unmack, G., Horrocks, G., et al. (2009). Collapse of an avifauna: Climate change appears to exacerbate habitat loss and degradation. *Diversity and Distributions*, *15*, 720–730.
- Paradis, E., Baillie, S. R., Sutherland, W. J., & Gregory, R. D. (1999). Dispersal and spatial scale affect synchrony in spatial population dynamics. *Ecology Letters*, *2*, 114–120.
- Peltonen, M., Liebhold, A., Bjørnstad, O., & Williams, D. (2002). Spatial synchrony in forest insect outbreaks: Roles of regional stochasticity and dispersal. *Ecology*, *83*, 3120–3129.
- Powney, G. D., Broaders, L. K., & Oliver, T. H. (2012). Towards a measure of functional connectivity: Local synchrony matches small scale movements in a woodland edge butterfly. *Landscape Ecology*, *27*, 1109–1120.
- Powney, G. D., Roy, D. B., Chapman, D., Brereton, T., & Oliver, T. H. (2011). Measuring functional connectivity using long-term monitoring data. *Methods in Ecology and Evolution*, *2*, 527–533.
- Ranta, E., Kaitala, V., Lindström, J., & Helle, E. (1997). The Moran effect and synchrony in population dynamics. *Oikos*, *78*, 136–142.
- Ripa, J. (2000). Analysing the Moran effect and dispersal: Their significance and interaction in synchronous population dynamics. *Oikos*, *89*, 175–187.

- Stevens, H., & Watson, D. (2013). Reduced rainfall explains avian declines in an unfragmented landscape: Incremental steps toward an empty forest? *Emu*, *113*, 112.
- Sutcliffe, O., Thomas, C., & Moss, D. (1996). Spatial synchrony and asynchrony in butterfly population dynamics. *Journal of Animal Ecology*, *65*, 85–95.
- Thomas, C. D. (1991). Spatial and temporal variability in a butterfly population. *Oecologia*, *87*, 577–580.
- Vanwalleghem, T., & Meentemeyer, R. K. (2009). Predicting forest microclimate in heterogeneous landscapes. *Ecosystems*, *12*, 1158–1172.
- Xu, T., & Hutchinson, M. F. (2013). New developments and applications in the ANUCLIM spatial climatic and bioclimatic modelling package. *Environmental Modelling & Software*, *40*, 267–279.

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