Birds as surrogates for mammals and reptiles: are patterns of cross-taxonomic associations stable over time in a human-modified landscape?

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ABSTRACT

Cross-taxonomic surrogates can be feasible alternatives to direct measurements of biodiversity in conservation if validated with robust data and used with explicit goals. However, few studies of cross-taxonomic surrogates have examined how temporal changes in composition or richness in one taxon can drive variation in concordant patterns of diversity in another taxon, particularly in a dynamic and heavily modified landscape. We examined this problem by assessing changes in cross-taxonomic associations over time between the surrogate (birds) and target vertebrate taxa (mammals, reptiles) that demand high sampling effort, in a heterogeneous mosaic landscape comprising pine monoculture, eucalypt woodland remnants and agricultural land. Focussing on four study years (1999, 2001, 2011, 2013) from a dataset spanning 15 years, we: (1) investigated temporal changes in cross-taxonomic congruency among three animal taxa, (2) explored how temporal variation in composition and species richness of each taxon might account for variation in cross-taxonomic congruency, and (3) identified habitat structural variables that are strongly correlated with species composition of each taxon. We found the strength of cross-taxonomic congruency varied between taxa in response to both landscape context and over time. Among the three taxa, overall correlations were weak but were consistently positive and strongest between birds and mammals, while correlations involving reptiles were usually weak and negative. We also found that stronger species richness and composition correlations between birds and mammals were not only more prevalent in woodland remnants in the agricultural matrix, but they also increased in strength over time. Temporal shifts in species composition differed in rate and extent among the taxa even though these changes were significant over time, while important habitat structural correlates were seldom shared across taxa. Our study highlights the role of the landscape matrix and time in shaping animal communities and the resulting cross-taxonomic associations in the woodland remnants, especially after a major perturbation event (i.e. plantation establishment). In such dynamic landscapes, differing and taxon-specific shifts in diversity over time can influence the strength, direction and consistency of cross-taxonomic correlations, therefore posing a ‘temporal’ problem for the use of surrogates like birds in monitoring and assessments of biodiversity, and conservation management practices.

Keywords

Anthropogenic landscapes, conservation, cross-taxonomic surrogates, congruence, indicators of biodiversity, longitudinal study, matrix, time scales

1. Introduction

Land-use change increasingly threatens biodiversity globally by driving habitat loss and degradation (Sala et al. 2000; Reidsma et al. 2006; Sayer et al. 2013). As a result, there is an urgent need to understand how diverse groups of biota respond to land-use modification across various scales (e.g., Mattison & Norris 2005, Haines-Young 2009). Such knowledge is integral to informing decisions on how sites should be conserved and managed (Meir et al. 2004; Vandewalle et al. 2010). However, resource and taxonomic limitations impose enormous difficulties on sampling large suites of taxonomic groups (Lawton et al. 1998; Schulze et al. 2004; Gardner et al. 2008) to understand broad changes in biodiversity patterns. This has resulted in multiple surrogate approaches being developed to act as proxies for components of biodiversity not able to be directly measured (Prendergast & Eversham 1997; Caro 2010; Lindenmayer et al. 2015), or biota that are costly or logistically difficult to survey within time frames available for decision-making (Favreau et al. 2006).

Species-based surrogates of biodiversity are a common type of surrogate (e.g., Caro 2010), and are based on the hypothesis that the occurrence or diversity of a surrogate or indicator taxon reflects the occurrence (i.e. co-occurrence) or diversity (i.e. richness, composition) of other sets of target taxa (Rohr et al. 2006; Rondinini et al. 2006; Gaspar et al. 2010). The best examples of these species surrogates include cross-taxonomic surrogates (e.g., Kati et al. 2004; Gallardo et al. 2011; Gaspar et al. 2010; Fattorini et al. 2012), biodiversity indicator species or species groups (e.g., Nally & Fleishman 2002; Roberge & Angelstam 2004; Branton & Richardson 2011), and higher-taxonomic groups (e.g., Báldi 2003; Heino & Soininen 2007).

Species surrogates of diversity in conservation have several empirical and conceptual shortcomings (e.g., Andelman & Fagan 2000; Heink & Kowarik 2010). First, studies of cross-taxonomic relationships have yielded mixed results in terms of the strength and direction of congruency across different taxa, often varying with the analytical approaches used (Gioria et al. 2011), even when landscape contexts and scales are broadly similar (Wolters et al. 2006; Lewandowski et al. 2009). At small to intermediate spatial scales of study, cross-taxonomic congruency of species richness was found to be weak in some studies (e.g., Kati et al. 2004; Lovell et al. 2007) but strong in others (e.g., Negi & Gadgil 2002). Such divergent findings are further exacerbated by the fact that these surrogates are often used to predict occurrence and diversity of target taxa with different ecological attributes (e.g. dispersal ability, habitat requirements, life histories) (e.g., Ricketts et al. 1999). Second, many studies testing surrogacy relationships with respect to a biodiversity target are not clearly defined within a theoretical framework, thus weakening the ecological basis for using a surrogate (Belovsky *et al*. 2004; Lindenmayer & Likens 2010). Many studies emphasise the identification of cross-taxonomic surrogate associations, but fail to define the surrogate relationships clearly, or under a robust framework that incorporate cause-effect relationships and predictive strength (Barton et al. 2015). Others like Hunter et al. (2016) has pointed out controversies arising from surrogate concept as a result of differing goals of surrogate application in conservation. Third, many studies of surrogates are 'snapshot' investigations and fail to tackle the problem of how species surrogates perform over time, or with respect to temporal variability in ecological processes (Anderson 2001; Favreau et al. 2006; Magurran et al. 2010). For any biodiversity surrogate to function as a useful tool for conservation, it should consistently predict diversity patterns or responses of other species over time (Rodrigues et al. 2000). Understanding of how biodiversity surrogates perform over time (Favreau et al. 2006) is constrained by the paucity of long-term datasets, with the result that few studies (e.g., Thomson et al. 2007) have examined how long-term shifts in the composition of animal communities associated with landscape modification may affect cross-taxonomic congruency (see Table 1 for definitions).

Biodiversity patterns in general, and individual species in particular, respond to the extent of landscape modification in different and diverse ways (Fischer & Lindenmayer 2007). Typically, modification of a landscape leads to changes in habitat spatial configuration and structure (e.g., patch size, matrix quality, edge effects), which impact animal communities differently, depending on individual species' ecological needs and their ability to disperse across the wider landscape (Dormann et al. 2007; Driscoll et al. 2013). Over time, species composition in a biotic community can be affected by dynamic changes in landscape configuration and vegetation structure or habitat recovery post-disturbance (e.g., Guedo & Lamb 2013). While it remains unclear how shifts in community composition of one taxon changes relative to other taxa, a taxonomic group can act as a good surrogate for others if it undergoes turnover (see Table 1 for definition) in species richness or compositional patterns that are consistent and congruent with other taxa over space and time. For instance, strong patterns of congruency between turnover of invertebrate and macroalgal diversity highlight the potential of macroalgae assemblages to act as biodiversity surrogates for fish and invertebrates (Thomson et al. 2014)

In this study, we investigated temporal variation in cross-taxonomic congruency (see Table 1 for definitions) of diversity between pairs of three taxa, and explored how, (a) temporal shifts in diversity and, (b) habitat correlates specific to each animal taxon can drive variation in the extent of cross-taxonomic congruency. We used a large dataset that has been collected over a period of 15 years in a dynamic, human-modified landscape that has undergone rapid transformation from a woodland-agriculture mosaic to large tracts of pine monoculture (Lindenmayer et al. 2001; Lindenmayer et al. 2008). We focussed on birds, mammals and reptiles as these taxa are not only frequently used in conservation assessments (e.g., Westgate et al. 2014), but are also species-rich in our study landscape (See Table A6, A7, A8 for list of species). In addition, sampling these three taxa demands very different amounts of effort and resources given the nature of field surveys. For instance, birds can be easily surveyed and have found to be popular and cost-effective surrogates in inventories of biodiversity (e.g., Lawton et al. 1998; Gardner et al. 2008) whereas sampling reptile diversity not only involves a very different methodology, but also demands specialist knowledge (e.g., McDiarmid et al. 2011). For mammals, the nocturnal habits and cryptic behaviour of many species (e.g., Suter *et al*. 2000) means effort-intensive night surveys and baited traps are needed to survey them. Differences in natural history across taxa, and disparate sampling effort to be invested in different taxonomic groups underscores the need for viable biodiversity surrogates, which could facilitate more optimal use of resources in inventorying biodiversity.

The aim of our study was to evaluate congruence in diversity and species composition measures between birds, mammals and reptiles over time, and thus uncover evidence for consistent cross-taxonomic surrogacy (Table 1 for definitions), as the quantification of cross-taxonomic congruency is a critical step in identifying surrogates (Gioria et al. 2011) . To quantify cross-taxonomic congruency, we used metrics of correlation between species richness and species composition, as both measures are frequently adopted in studies of cross-taxon surrogates (e.g., Kati et al. 2004; Sauberer et al. 2004; Gaspar et al. 2010; Cabra-García et al. 2012) and collectively can offer a comprehensive evaluation of cross-taxonomic congruency (Su et al. 2004; Gioria et al. 2011). To address our study aims, we posed three questions:

1. Based on the strength and direction of associations between pairs of taxa, what is the extent of variation in cross-taxonomic congruence patterns at the species richness and composition levels over 15 years?

Given the limited vagility of reptiles, small spatial requirements (Stow et al. 2014) and the limited effect posed by habitat fragmentation on lizard communities (e.g., Jellinek et al. 2004) compared to birds or mammals, we predicted that reptiles were likely to show low congruency in diversity patterns with either mammals or birds.

Cross-taxonomic congruency patterns are often derived from measures of diversity and thus determined by temporal shifts in the diversity of different taxonomic groups relative to each other. To, (a) explore the extent of temporal variation in diversity across the taxonomic groups and, (b) determine how different habitat structural variables in remnant woodlands can influence each taxon in our study, we asked:

2. In terms of species richness, abundance and composition, what is the extent of temporal change in three animal taxa over 15 years?

3. Are the habitat structure variables that best predict patterns of species composition common to all three taxa?

Based on our findings, we discuss how variation in the predictive strength of surrogates for other aspects of biodiversity (e.g., other taxonomic groups) can be influenced by taxon-specific temporal shifts and habitat conditions, as well as implications for the use of cross-taxonomic surrogates in conservation assessments, inventorying and monitoring.

2. Materials and methods

2.1. Study region

Our study was conducted in the Nanangroe region (34°57'54"S, 148°28'46"E) near Jugiong and Gundagai, Central New South Wales, Australia. Nanangroe is a dynamic landscape spanning c. 30,000 ha of agricultural (i.e., grazing) land and exotic tree plantations. Nanangroe was established as a long-term natural experiment to understand how animal communities respond to differing landscape treatments over time (Lindenmayer et al. 2008). Much of the original *Eucalyptus*-dominated, box-gum grassy woodland landscape has been cleared for agriculture in the past two centuries (Yates & Hobbs 1997), leaving what is best described as a variegated landscape consisting of distinct patches and strips of remnant woodlands of varying tree densities (McIntyre & Barrett 1992) surrounded by a larger matrix of pastures grazed by livestock. These woodland remnants are dominated by five *Eucalyptus* species: white box (*E. albens*), red box (*E. polyanthemos*), yellow box (*E. melliodora*), red stringybark (*E. macrorhyncha*) and Blakely's red gum (*E. blakelyi*), while the understorey supports a diverse community of native and introduced grasses and forbs.

Prior to the commencement of the Nanangroe Natural Experiment in 1999, 52 Eucalypt-woodland remnants were identified using two landscape contexts and four patch sizes classes (0.5-0.9 ha; 1.0-2.4 ha; 2.5-4.9 ha; 5.0-10 ha). In 1998, the agricultural matrix landscape surrounding these 52 woodland remnants was transformed by the establishment of dense plantations of the exotic Monterey Pine *Pinus radiata* (hereafter these remnants are referred to as “woodland remnants in pine matrix”). In addition, sampling points in 56 patches of Eucalypt-woodland remnants of broadly similar vegetation classes and areas were established in surrounding agricultural land (hereafter these remnants are referred to as “woodland remnants in agricultural matrix”), mostly on farms under private ownership (see Table A1 in the supplementary material for definitions on landscape contexts). Additionally, 10 sites in cleared and grazed paddocks and 10 sites in pine plantations were established as “controls”. Inclusive of these two sets of control sites, there were a total of four landscape contexts examined in our study.

2.2. Animal sampling

Permanent transects were marked and established at all 128 study sites prior to the commencement of the study in 1999. In woodland remnants exceeding one hectare in area, a straight 200m long transect was established. For a few small remnants less than one hectare in area, a ‘dog-legged’ 200m or 150m transect was established.

We sampled bird diversity and abundance at each site using three, five-minute point counts along each transect, which were conducted between 05:00–10:00hrs during early-middle spring (October-November). At each point count, observers recorded the numbers of individual species heard or seen within a 50m radius. Each point was re-sampled by a different observer on another day during the survey period to minimize bias as a result of weather and variable detection skills by different observers. Bird surveys were conducted in the years, 1999, 2000, 2001, 2003, 2005, 2007, 2009, 2011, 2012 and 2013.

To survey reptile abundance and diversity, we conducted standardised, area-constrained searches at two points along each transect once a year between late winter to early spring (October–November). During the establishment of the transects, artificial substrates consisting of corrugated metal sheets (c. 1.0m x 1.0m), hardwood timber sleepers (c. 1.0m long, 0.2m thick) and roof tiles (c. 0.3m x 0.3m) were placed at the 0m and 100m points along each transect to simulate microhabitats for small terrestrial reptiles like snakes, skinks and other lizards. Active searches for reptiles were completed by turning over logs, rocks and the artificial substrates throughout the sites. Standardised reptile surveys were conducted in the years: 1999, 2000, 2001, 2003, 2006, 2011 and 2013.

Finally, we surveyed mammal diversity and abundance using standardised, nocturnal spotlighting searches along each transect, on nights of good weather (i.e. no rain, storms). Mammal spotlight surveys were conducted in the years: 1999, 2001, 2004, 2005, 2009, 2011 and 2013. Additional details on our mammal and reptile surveys have been described in Lindenmayer et al. (2001) and (2008).

2.3. Vegetation sampling

To describe the habitat structure at each study site, we conducted vegetation surveys at all study sites once every four years. A total of 34 vegetation variables was measured at each site to capture the variation in vegetation structure from the ground to the canopy. We averaged measures taken from each of three sampling points to obtain mean values for all habitat structure variables at every site. A full list of the vegetation variables is available in the supplementary information section (Table A2).

2.4. Data analysis

2.4.1. Data selection

We used species data from surveys of birds, mammals and reptiles completed in 1999, 2001, 2011 and 2013. Each of these years were selected for our analysis as they included data where all three taxonomic groups were simultaneously surveyed in the same year and season, and therefore minimized the influence of temporal effects on our dataset.

2.4.2. Tests for correlations of species richness between different taxa over time (Question 1)

We used Spearman's rank correlations to test for cross-taxonomic congruence in species richness patterns over time between pair-wise combinations of the three taxa for each of four study years and each landscape context class (including both control sites). The strength of correlation of species richness between two taxa is often used as a proxy of cross-taxonomic associations (e.g., Hess et al. 2006; Wolters et al. 2006). Spearman's correlation was chosen over Pearson's correlation as the metric of correlation strength as species richness was relatively low across sites, particularly for mammals, and is thus likely to be distributed non-normally. We also calculated correlations between birds, and pooled species richness of mammals and reptiles combined. Using 1,000 bootstrap replicates, we calculated the 95% confidence interval for all Spearman's correlations. The strength of the Spearman's correlation coefficient (ρ), which is used as a measure of congruency of species richness between two taxa was interpreted as follows: correlation values of ≥ 0·50 were considered to be strong, between 0.10 to 0·30 to be moderate, and correlations ≤ 0·10 to be weak (see Lamoreux et al. 2006).

2.4.3. Test for correlations of species composition over time (Question 1)

We used partial Mantel tests to investigate the strength of cross-taxonomic congruence in species composition between pair-wise combinations of animal taxa for each year of four study years. Partial Mantel tests were used because the data were not independent and Mantel tests are able to address the problem of partial dependence in dissimilarity matrices (Legendre & Legendre 1998), and have previously been used to identify correlations between pairs of taxa (e.g., Su et al. 2004; Gioria et al. 2011; Gaspar et al. 2012). Abundance values for all species were square-root transformed to reduce the potential over-influence of highly abundant species on among-site dissimilarity values. We quantified species composition using Bray-Curtis dissimilarity metric between pairs of sites for all landscapes contexts. The advantage of partial Mantel tests over simple Mantel tests is that they can measure the correlation between two matrices (Paszkowski & Tonn 2000; Su et al. 2004) after considering variation associated with a matrix of spatial (Euclidean) distances, thus accounting for potential problems of spatial autocorrelation. Significance of all partial Mantel tests was assessed using a Monte Carlo procedure with 999 permutations. Mantel and Spearman's correlations were implemented using the 'ecodist' package in R version 1.2.9, while confidence intervals for Spearman's correlations were estimated using 1,000 bootstraps in the 'RVAideMemoire' package (R Development Core Team 2013).

2.4.4. Test of species composition of two taxa as predictors over time (Question 1)

We completed multiple regressions on distance matrices (MRM) (Lichstein 2007) to test if species composition of two taxa based on dissimilarity matrices can collectively better predict composition of a target taxa selected *a priori*. Unlike partial Mantel tests which are limited to comparing pairs of taxa, this approach allows multiple taxa to be used as predictor variables. MRM involves regressing the response matrix using more than one explanatory matrix, while each matrix contains all combinations of pair-wise distances between *n* number of sample units. We chose not to use bird data as the response variable in any of our MRM models. This was because birds are usually *the* surrogate taxon in conservation of other components of biodiversity (e.g., Blair 1999; Sauberer et al. 2004; Larsen et al. 2012) given the relative ease of collecting bird data compared to data of other taxa. Additionally, we factored geographic distance into our models as a predictor matrix, since spatial data derived from geographic coordinates are often available along with species datasets and can be used to reveal ecologically meaningful effects (e.g., strong spatial influences on composition may reveal dispersal limitations imposed by space).

We constructed a set of candidate models using all possible combinations of bird, reptile and mammal composition and spatial distances as predictor variables, while only mammal or reptile composition was treated as the response. MRM analysis was completed only for species data collected from woodland remnant sites in pine and agricultural sites as there were too few data for analysis in the control sites due to low species abundance and richness. As with our partial Mantel tests, we square-root transformed the animal count data, and used the Bray-Curtis metric to calculate pair-wise species dissimilarity. The statistical significance of each MRM model was assessed with 999 permutations.

2.4.5. Analysis of shifts in animal communities over time (Question 2)

We plotted site-level, mean species richness and mean abundance for each taxon in both landscape contexts and control sites to assess temporal changes in species richness and abundance over the four study years. To visualise changes in community composition between the four landscape contexts over the four study years, we first performed non-metric multidimensional scaling (NMDS) analysis using the R function 'metaMDS' to ordinate site counts in species space for all three groups and the two main landscape contexts (woodland remnants in agriculture and pine). For each landscape context, all ordinations of each taxon were presented together in each plot, but separated by year using coloured polygons. We then used the multiple response permutation procedure (MRPP) as a non-parametric test for significant differences in species compositional changes over time. MRPP generates the effect size statistic A, which provides a measure of within-group heterogeneity, and a measure of significance P. The significance of the effect size A was assessed using 999 permutations. Bray-Curtis dissimilarity was used as the measure for species composition in both the NMDS and MRPP analyses.

To explore how different habitat structural variables influenced each of the three taxa in ordination space, we fitted vectors for all habitat variables measured in each ordination, to identify those that were significantly correlated to the two NMDS axes for each taxon. The R function 'envfit' available in the vegan package computes vectors or factor averages of environmental variables fitted to the ordination matrix. The significance of these fitted vectors was then assessed using 999 permutations. Habitat correlates that were significant at $P < 0.05$, and marginally significant $0.05 < P \leq 0.1$ were retained for further consideration.

2.4.6. Evaluating the influence(s) of habitat structural correlates on animal communities (Question 3)

We were interested in identifying habitat structural variables consistently associated with species composition among the three taxa in the Eucalypt-woodland remnants. We constructed a series of candidate ‘global’ models using multiple regressions on distance matrices for each taxa, and using the full set of habitat structural variables to explore how the different variables influenced each taxon. Only habitat variables not strongly correlated with others (Pearson’s $r < 0.5$) were retained in the MRM analysis after an initial screening of the full set of variables in a correlogram matrix. NMDS and MRPP analyses were completed using the ‘vegan’ package in R version 2.2-1 (R Development Core Team 2013) while MRM analysis was carried out using the ‘ecodist’ package in R version 1.2.9 (R Development Core Team 2013)

3. Results

3.1. What is the extent of variation in cross-taxonomic congruence patterns at the richness and composition over 15 years (Question 1)?

3.1.1. Change in correlations of species richness over 15 years

We found that correlations of species richness varied between different pairs of taxa and across landscape contexts, but increased in strength and significance over the 15 years (Figure 1, Table A3). In woodland remnants in the agricultural matrix, species richness was weakly and negatively correlated between reptiles and birds, but none of these correlations were significant (see supplementary material). Mammal species richness was weakly and negatively correlated with that of birds in 1999, but the correlations became positive and strengthened over time, with mammal species richness being significantly correlated with bird species richness in 2011 and 2013 (Spearman's $\rho = 0.306$ with $P = 0.022$; Spearman's $\rho = 0.350$ with $P = 0.01$) but not in 1999 and 2001. Additionally, a linear model relating year to correlations of species richness for bird–mammal congruency was significant (model adjusted R-square = 0.998, coefficient estimate = 0.0297, $P = 0.0007$). Species richness correlations between birds and reptiles, and pooled mammal and reptile richness were weak and insignificant for all years except in 2011 (Spearman's $\rho = 0.308$ with $P = 0.022$).

In woodland remnants in the pine plantation matrix, bird species richness was consistently and positively correlated with that of mammals, and the strength of these correlations increased with time, with correlations in 2013 being marginally significant (Spearman's $\rho = 0.277$ with $P = 0.065$). In addition, bird species richness was positively correlated with pooled mammal and reptile species richness in later years, being significantly so in 2013 (Spearman's $\rho = 0.300$ with $P = 0.04$).

3.1.2. Change in correlations of species composition over 15 years

We found that partial Mantel correlations between distance matrices of animal groups were often weak and insignificant (Table 2, Figure 2). For instance, in woodland remnants in the agricultural matrix, bird and reptile composition was negatively correlated in all study years except in 2001. Bird and mammal composition were mostly positively correlated over the four study years, although only correlations in later years – 2011 and 2013 were moderately strong and significant (Mantel $R = 0.306$ with $P = 0.002$; Mantel $R = 0.168$ with $P = 0.008$). None of the correlations between reptile and mammal composition were strong or significant, and fluctuated between being weakly positive and negative over time.

In woodland remnants in the pine plantation matrix, bird and reptile composition were positively correlated only in 1999 (Mantel $R = 0.1912$ with $P = 0.035$), but negatively correlated in all other years. Although consistently positive, we found that correlations of bird and mammal composition were weak and insignificant across all study years except 2001 (Mantel $R = 0.279$ with $P = 0.012$). None of the correlations between mammals and reptiles were significant, and were mostly negative. Overall, we found that while correlations involving reptiles were usually negative and weak (Figure 2), correlations between mammal and bird species composition were consistently positive, and appeared to have strengthened over time, at least for woodland remnants in the agricultural matrix (2011 Mantel $R = 0.306$ with $P = 0.002$). Such a trend did not apply for woodland remnants in the pine matrix, as correlation strength peaked in 2001, but declined thereafter.

3.1.3. Change in predictive strength of two taxa for a single target animal group over 15 years

We found that MRM models incorporating distance matrices of birds, reptiles and spatial distances were able to predict mammalian composition, albeit weakly for woodland remnants sites in the agricultural matrix, but relationships declined in predictive strength between 2011 ($R^2 = 0.182$) and 2013 ($R^2 = 0.0565$) (Table 3). Of three explanatory variables including reptile composition and spatial distances, bird species composition explained 85.9% of the variation in mammal species composition in 2011 but only 42.5% in 2013, although bird composition remained significant as a predictor in both years. Reptile composition and spatial distance were weak and non-significant predictors in all candidate models explaining mammal composition in 2011 and 2013. For candidate models using birds, mammals and spatial distance to predict reptile composition, bird and mammal composition never emerged as significant predictor, being weakly but positively correlated in most years. However, spatial distance appeared to be a significant and relatively important predictor of reptile composition, explaining 48.3%

and 55.9% of the variation of reptile composition in 2011 and 2013 respectively (Table 3).

All candidate models incorporating species compositional and spatial distances for woodland remnants in the pine matrix explained very little variation in either reptile or mammal composition. Although bird species composition explained 31.0% of the variation in mammalian composition in 2013, it was not a significant predictor in other years, and in fact was negatively correlated in 2011. Neither mammal nor bird species composition with spatial distances were useful predictors of reptile species composition in woodland remnants in the pine matrix, although mammal species composition was marginally significant as a predictor in 2011 and 2013 ($0.05 < P < 0.1$).

3.2. What is the extent of temporal changes in three animal communities over 15 years (Question 2)?

3.2.1. Changes in species richness and abundance of three taxa over 15 years

Across the study landscape, we found that mammal and reptile species richness showed clear increases over the four study years, while bird species richness increased marginally between 1999 and 2011, but declined in 2013 (Figure 3, Supplementary Tables A6, A7, A8). Species richness and abundance, and their change over 15 years in both pine and agricultural control sites were limited especially for mammals and reptiles, and consistently lower than corresponding woodland sites in either landscape contexts. At a site level, we found weak and insignificant patterns of change in bird species richness for woodland remnants in the pine matrix over time (Figure 3) while mean site abundance increased from 57.7 to 68.9 individuals (Mann-Whitney $U = 693$, $Z = 1.65$, $P > 0.05$). By comparison, bird species richness in woodland remnants in the agricultural matrix increased more rapidly over time, from 12.1 species in 1999 to 15.0 species per site (Mann-Whitney $U = 971$, $Z = -3.231$, $P < 0.05$) in 2013. The trends in reptile richness and abundance over time for woodland remnants in the pine matrix were less clear compared to those in the agricultural matrix, but changed somewhat faster, and were significant. For example, mean reptile species richness in woodland remnants in agriculture increased from 0.357 species per site in 1999 to 2.52 species in 2013 (Mann-Whitney $U = 244$, $Z = 5.771$, $P < 0.001$) while mean reptile richness in woodland remnants in pine increased from 0.54 to 2.33 species over the same period (Mann-Whitney $U = 971$, $Z = -3.231$, $P < 0.001$). Unlike birds or reptiles, both mammal species richness and abundance showed consistent increases in the two landscape contexts over the study period. For example, mean mammal species richness for woodland remnants in the pine matrix increased from 0.475 to 1.27 species in 2013 (Mann-Whitney $U = 517$, $Z = 3.368$, $P < 0.001$), while mean abundance increased from 0.775 individuals in 1999 to 2.4 individuals (Mann-Whitney $U = 531$, $Z = 3.245$, $P < 0.05$). Likewise, mean mammal richness for woodland remnants in the agricultural matrix doubled over the same period, from 0.518 species in 1999 to 1.03 species per site in 2013 (Mann-Whitney $U = 1076.5$, $Z = -2.6009$, $P < 0.01$).

3.2.2. Changes in community composition of three taxa over 15 years

In woodland remnants in the pine matrix, we found that points representing mammal species composition in ordination space clustered towards the negative end of NMDS axis 1 in 1999, but became less clustered in subsequent years, and shifted positively along the axis (Figure 4a). The MRPP results indicated that mammal assemblages differed over the four years ($A = 0.0464$, $P < 0.01$). Points representing reptiles were well spread in ordination space in 1999 (Figure 4b), but became increasingly clustered towards the positive end of NMDS axis 1 in later years, with these changes in species assemblage being significantly different over time ($A = 0.0504$, $P < 0.01$). Similarly, points representing birds were sparsely clustered in 1999, but subsequently clustered closely towards the negative end of NMDS axis 1 in 2011 and 2013 (Figure 4c). Such a change in the bird assemblage over time was also found to be significant in our MRPP analysis ($A = 0.0741$, $P < 0.01$) and suggests that bird composition in these woodland remnants were become increasingly similar over the 15 years.

For woodland remnants in the agriculture matrix, points representing mammal species were sparsely clustered in ordination space, and appeared to be even less so in 2013 and 2011 than in 1999 and 2001 (Figure 4d). Although changes in the mammal assemblage over time were significant, they were weaker than the species compositional changes observed for the other two groups ($A = 0.0193$, $P < 0.05$), and for all animal groups in woodland remnants in the pine matrix.

We did not plot the ordinations for reptiles due to the very large scatter of points. However, we noted that reptile assemblages in woodland remnants in the agricultural matrix changed significantly over 15 years ($A = 0.103$ $P < 0.001$) (see also Figure A2 in the supplementary material for cluster dendrograms representing differences in Bray-Curtis dissimilarity across the study years). Likewise, the bird assemblage in these woodland remnants differed significantly over 15 years ($A = 0.0222$, $P < 0.001$). The change in bird species composition is shown in the positive shift in clusters of points representing bird species composition in ordination space along NMDS axis 1 (Figure 4e).

3.3. Are the habitat variables that drive shifts in species composition over time shared among the three taxa (Question 3)?

3.3.1. Significant habitat structure variables correlated with each taxonomic group

We found that the habitat variables strongly correlated with species communities differed among taxa and between woodland remnants in the two key landscape contexts (Table 4, see also Table A5), and few variables were shared. Bird species composition was correlated with more habitat structure variables than either reptiles or mammals for woodland remnants in both landscape contexts. ‘Blackberry cover’ was a recurrent explanatory variable for birds and reptiles, correlating strongly with at least one NMDS axis for each group. In woodland remnants surrounded by pine, ‘crown structure’ ($R^2 = 0.163$, $P < 0.05$) and ‘basal count’ ($R^2 = 0.272$, $P < 0.01$) were moderately and significantly correlated with both NMDS axes for birds, while ‘blackberry cover’ and ‘woodland strata’ appeared only weakly correlated. While ‘blackberry cover’ ($R^2 = 0.292$, $P < 0.01$), ‘dominant cover’ ($R^2 = 0.226$, $P < 0.05$) and ‘shrub stem count’ ($R^2 = 0.154$, $P < 0.05$) appeared to be important correlates for reptile species composition in woodland remnants surrounded by pine, we found that no habitat variables were strongly and significantly correlated to either NMDS axes for mammals.

Bird species composition in the woodland remnants in the agricultural matrix was significantly correlated with eight habitat structure variables, with two of these variables shared with mammals (‘exposed rock’, ‘blackberry cover’). While reptiles were found not to be significantly correlated with any habitat variables in the landscape contexts, we found that mammal species composition in woodland remnants in the agricultural matrix was strongly correlated with four variables, with ‘blackberry cover’ ($R^2 = 1.00$, $P < 0.05$) again being very strongly and positively correlated with NMDS axis 1, and negatively with NMDS axis 2.

4. Discussion

4.1. Overview

We assessed the strength and direction of cross-taxonomic correlations in species richness and composition between three vertebrate taxa that feature frequently in conservation assessments (e.g., Lawton et al. 1998; Schulze et al. 2004; Westgate et al. 2014). We then compared these associations over each of four study years spread over 15 years to assess whether cross-taxonomic congruency was consistent over time, a requisite of a good biodiversity surrogate. Below, we discuss our key findings and outline some of the implications of our research for the use of cross-taxonomic surrogates in dynamic landscapes undergoing rapid transformation.

4.2. Variation in cross-taxonomic congruency patterns over time

Whether based on a species richness or a species composition approach, we found that the strength of congruency between pairs of animal taxa varied with the taxon examined, landscape context, and over time (Question 1). Between pairs of taxa, we found that correlations from both approaches ranged from being very weak to moderate, and that correlations in either species richness or composition tended to be positive and stronger between birds and mammals than between either group and reptiles. We also found that species richness and composition correlations increased in strength over time for woodland remnants in both agricultural and pine matrixes. The prevalence of stronger and significant associations between taxa in woodland remnants in the agricultural matrix in the later years compared to woodland remnants in the pine matrix underscores the role played by the matrix in shaping animal communities in remnant woodland patches (e.g., Ricketts 2001), possibly by influencing the dispersal of different species (e.g., Dormann et al. 2007; Driscoll et al. 2013). For instance, the stronger cross-taxonomic associations may arise from greater dispersal into, and out of these woodland patches by species in all three taxa through the comparatively more open agricultural matrix. Additionally, the effects of the pine plantation matrix on animal communities in the Eucalypt-woodland patches embedded within may be further accentuated by the limited food resources available (e.g. flowering plants, arthropods) and a different set of microclimatic conditions resulting from the dense pine cover.

4.3. Change in species richness and composition of animal communities over time

We found that species richness and abundances of mammals and reptiles showed larger shifts than birds over time for woodland remnants in both pine and agricultural matrixes. We also found that the extent of temporal change in species composition differed with taxa, and between the two major landscape contexts (Question 2). Our findings of taxa-specific shifts in diversity and abundance here mirror the variation in congruency across taxa described earlier, and add yet another line of evidence to the influences exerted by the landscape matrix on shaping the animal communities occurring within these habitat patches. It is likely that woodland remnants in the pine matrix showed lower cross-taxonomic congruence a decade after the initial disturbance period (when pine monoculture was established) because the dense pine plantation matrix may have acted as a barrier to the dispersing reptiles and mammals (Mortelliti et al. 2014), thus influencing species richness and composition of both taxa over time. Our finding here highlights the problem posed by differential turnover in species diversity across taxonomic groups to cross-taxonomic surrogacy because it compromises the temporal consistency required if these surrogates are to be used in conservation monitoring and biodiversity assessments.

4.4. Differing habitat structure variables correlated with animal taxa

Our analyses of the influence of habitat structure variables on animal taxa indicated that the explanatory variables that fit best with the NMDS axes were different for each group (Table 3) at the landscape scale, although one variable was frequently shared (blackberry index). When an MRM approach was used to evaluate the relative influence of habitat structure correlates, we again found that there were few or no shared correlates between any two taxa. Other studies of cross-taxonomic surrogates have also reported such differences of explanatory variables across taxa (e.g., Dauber et al. 2003). Blackberry (*Rubus fruticosus* sp. agg.) is widely recognized as one of the most invasive plant species across Australia (Dehaan et al. 2013) and has increasingly spread across our study sites. Blackberry forms dense patches in woodland remnants along creeks in our study sites and is likely to have modified habitats and microclimatic conditions for many terrestrial species. This may account for its strong correlation with the composition of all three animal taxa as revealed in our ordination analysis (Figure 4).

We hypothesize that the broadly differing set of correlated habitat structure variables identified in our analyses is the outcome of divergent habitat requirements of birds, reptiles and mammals at the landscape scale. Bird species composition was predicted by more habitat variables than reptiles or mammals in both landscape contexts. This pattern is likely due to the fact that while the majority of reptile species (e.g. skinks) and mammal species are more affected by habitat structural variables on the ground, bird species composition are more strongly affected by a larger set of habitat variables associated with trees (e.g. stand height, number of trees, number of strata), due to the arboreal behaviour of many species (Barton et al. 2014). The differential associations of each taxa with specific sets of habitat attributes and their changing relationship over time, may explain the weak cross-taxonomic congruency observed in our study, and has also been highlighted by other studies of cross-taxonomic associations (e.g., Dauber et al. 2003; Azeria et al. 2009; Heino et al. 2009).

4.5. Implications for the use of cross-taxonomic surrogates in conservation

Our findings have several key implications for the use of some vertebrate taxa, particularly birds, as surrogates or broad indicators for the diversity of other taxa in conservation. First, variation in species richness and composition over time and among the taxa studied suggests that species richness and compositional approaches to quantifying surrogates of species diversity should be applied cautiously. Our finding that stronger cross-taxonomic associations in composition and species richness occurred in woodland remnants in the agricultural matrix alludes to the role played by the landscape matrix in shaping animal communities, either by limiting or promoting species dispersal (e.g., Driscoll *et al*. 2013). Differences in dispersal ability and spatial requirements may have influenced cross-taxonomic associations at the landscape scale, and may explain why both birds and mammals were better correlated with each other, but were often weakly and negatively correlated with reptiles, which are not only predominantly terrestrial but less vagile, and thus have smaller spatial requirements (e.g. Stow et al. 2014).

Second, our finding of stronger and more positive associations between bird and mammal diversity in both landscape contexts over time suggests that animal communities can become increasingly similar and more stable, possibly in response to changes in vegetation structure as woodland remnants regenerate and mature in the years following initial disturbance (e.g., change of the landscape matrix when pines were planted). Strengthening of these cross-taxonomic relationships may be also paralleled by increases in mean species richness at the site level for both taxa (Figure 3). Communities in heavily modified landscapes are likely to show lower community stability and higher temporal turnover in species composition. However these communities can become more stable with time post-disturbance (Leibold 2009) and with increased overall species diversity (van Ruijven & Berendse 2007). We hypothesise that increased community stability and higher diversity at the landscape scale may have a role in driving stronger cross-taxonomic congruency at the species richness and composition levels observed in our study in 2011 and 2013, and suggest that cross-taxonomic surrogates may not be very useful for assessing biodiversity in landscapes that have recently been subject to heavy anthropogenic disturbance.

Third, our findings suggest that high rates of taxa-specific turnover and among-group differences in habitat correlates, can affect the degree of congruency in diversity patterns between different taxa. For example, birds showed significant shifts in species composition over time, but with little increase in richness or abundance. By contrast, the reptile communities showed significant temporal turnover, and increases in overall diversity and abundance (Figure 3). Differing rates of temporal turnover shown by change in Bray-Curtis dissimilarity over the study period may account for the large variation in the Mantel correlations over time. While many studies have explored cross-taxonomic congruency using large sets of species data (e.g., Schulze et al. 2004; Grenyer et al. 2006; Stoch et al. 2009), we note that few have examined congruency patterns in relation to temporal changes in species richness, abundance and composition. This temporal problem continues to persist because most surrogate studies are based on short-termed datasets (Favreau et al. 2006). Therefore, we suggest that strong congruencies observed between two taxonomic groups at one point in time may be ephemeral, especially in highly disturbed landscapes undergoing change. Our results thus offer some support to the predictions by Prendergast & Eversham (1997) that differential responses to the environment (in this case, habitat structure variables), may be responsible for driving weakly congruent patterns of diversity. From a conservation standpoint, the use of one or few taxa as cross-taxonomic surrogates, especially birds, is likely to be problematic since it could inherently fail to represent diversity patterns of other taxa (e.g., Dauber et al. 2003) and their responses to changing habitat structure (e.g., Barton et al. 2014).

4.6. Ecological basis of surrogacy relationships and scope for future research

Snapshot-type studies of cross-taxonomic surrogates are ubiquitous in the literature but lack a temporal dimension, thus failing to take into consideration ecological processes that take time to manifest (e.g. Bond 2001, Favreau et al. 2006). Since many ecological patterns and processes are highly dynamic in time and space (Morgan et al. 1994), short-term studies will inherently fail to capture the temporal variability of communities and their effects on cross-taxonomic comparisons. Moreover, many such surrogate studies are also conducted at scales too large for surrogacy patterns to be meaningful for conservation (Westgate et al. 2014), often at a continental to global scale. However, Grenyer et al. (2006) and others (e.g. Weibull et al. 2003) have noted that congruency between taxa tends to be highly scale dependent; levels of congruency may be particularly low if these patterns are measured at the fine spatial resolutions relevant to conservation. There is thus a need for more studies of cross-taxonomic surrogacy at these fine spatial scales which these surrogates are to be applied.

Our findings of stronger associations at the species richness and composition level between mammals and birds, both which are known to be better dispersers and have larger spatial requirements than reptiles, underscores the role of dispersal and spatial scale in shaping animal communities (e.g., Howeth & Leibold 2010). These ecological factors needs to be considered when identifying species surrogates for conservation application in dynamic landscapes. Our findings also raise problems for the efficacy of using biodiversity surrogates in dynamic, human-modified landscapes because cross-taxonomic congruency changes over time with temporal shifts in diversity (e.g., Wolters et al. 2006).

Finally, an immediate goal for ecologists studying indicators of biodiversity should be to identify clearer links between different taxonomic groups and in relation to underlying ecological processes, to ensure that taxa used as surrogates are grounded within a more robust, science-driven framework that considers causal links that allows for validation across spatial and temporal contexts (e.g., Lindenmayer & Likens 2011; Barton et al. 2015). Identifying shared responses and relationships to landscape and habitat structure variables between species, and between different taxa could be a first step in understanding these associations in a mechanistic manner. This, in turn, needs to be coupled with a better understanding of how temporal processes may alter these relationships, although doing so will demand greater investments into collecting long-term data.

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Figure and table annotations

Figures

Figure 1. Plots showing variation in Spearman's ρ (congruency of species richness) over the four study years. Error bars represent 95% confidence intervals after 1,000 bootstraps. Diamond-shaped points represent woodland remnants in pine (treatment) while circle-shaped points represent woodland remnants in the agricultural matrix. Only the relationship between year and congruency of species richness for bird-mammal congruency was found to be significant (model adjusted R-square = 0.998, coefficient estimate = 0.0297, $P = 0.0007$)

Figure 2. Plots showing variation in partial Mantel R (congruency of species composition) over the study period. Error bars represent the 95% confidence intervals after 999 permutations. Diamond shaped points represent woodland remnants in the pine matrix (treatment) while circle-shaped points represent woodland remnants in the agricultural matrix.

Figure 3. Scatterplots showing shifts in mean site species richness and abundance for birds, reptiles and mammals over the study years spanning 1999 and 2013. (Legend: shaded diamond-shaped points represent woodland remnants in pine (treatment) while shaded circle-shaped points represent remnants in agriculture; unshaded diamond- and circle-shaped points represent the control sites in the respective pine and agricultural matrix)

Figure 4. NMDS ordination plots for (a) mammal, (b) reptile and (c) bird communities in woodland remnants surrounded in the pine (treatment) matrix, and (d) mammals and (e) birds in woodland remnants in the agricultural matrix. The ordination plot for reptiles in agricultural woodland remnants is not shown

due to its wide scatter of point clusters. Number of dimensions and stress values for all NMDS ordinations are shown on each plot. (Legend: black diamond – 1999, purple triangle – 2001, blue circle – 2011, red square – 2013)

Table 1. Glossary of selected important terms in the concept of cross-taxonomic surrogacy and their definitions.

Table 2. Results of partial Mantel correlations of species composition for three taxa over the study period. Results for pine control (PIN) sites are not presented as there was only adequate species data for one site.

Table 3. Multiple regression in matrix (MRM) models and summary statistics for predictor variables. Predictor variables included bird, mammal and reptile composition, and geographic space. See Table A4 for model attributes for years 1999 and 2001.

Table 4. Significant habitat structure correlates of bird, reptile and mammals in two different landscape contexts, identified with non-metric multidimensional scaling.

Figure 1

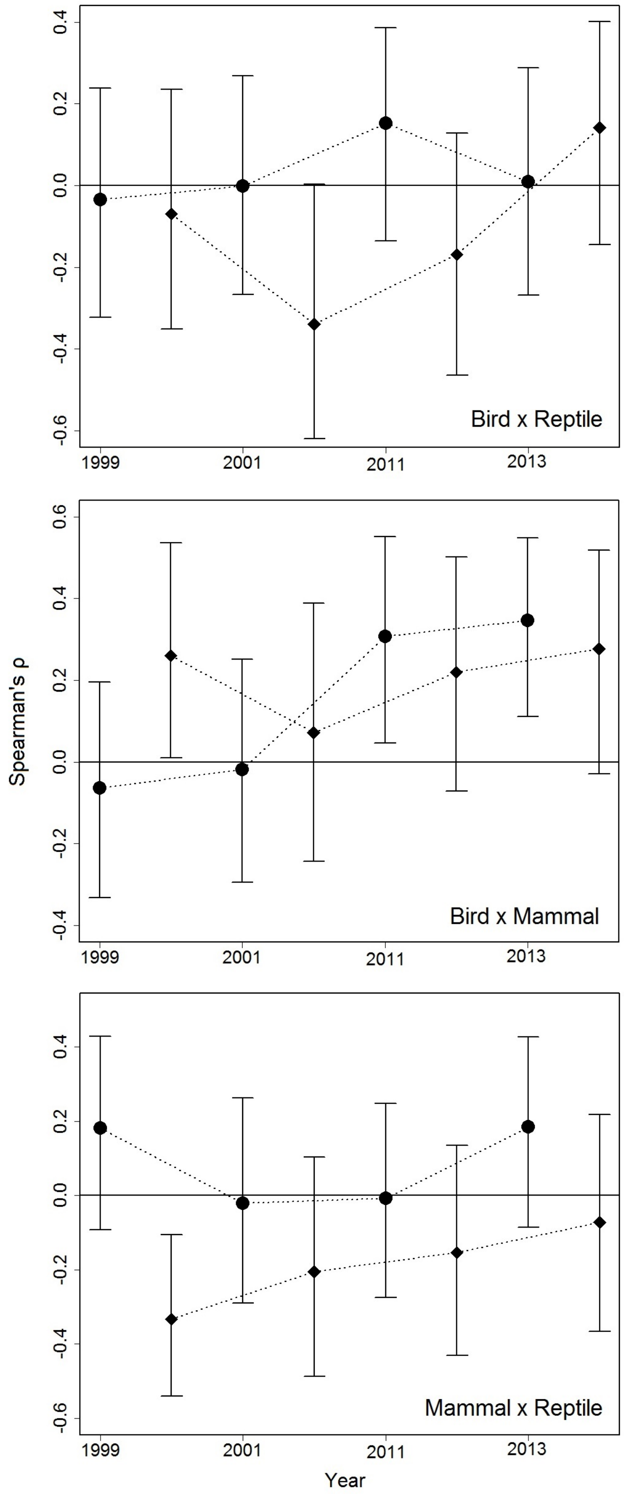
0.4
0.2
0.0
-0.2
-0.4
-0.6
Bird x Reptile
1999
2001
2011
2013
0.6
0.4
0.2
0.0
-0.2
-0.4
Spearman's ρ
Bird x Mammal
1999
2001
2011
2013
0.4
0.2
0.0
-0.2
-0.4
-0.6
Mammal x Reptile
1999
2001
2011
2013
Year

Figure 2

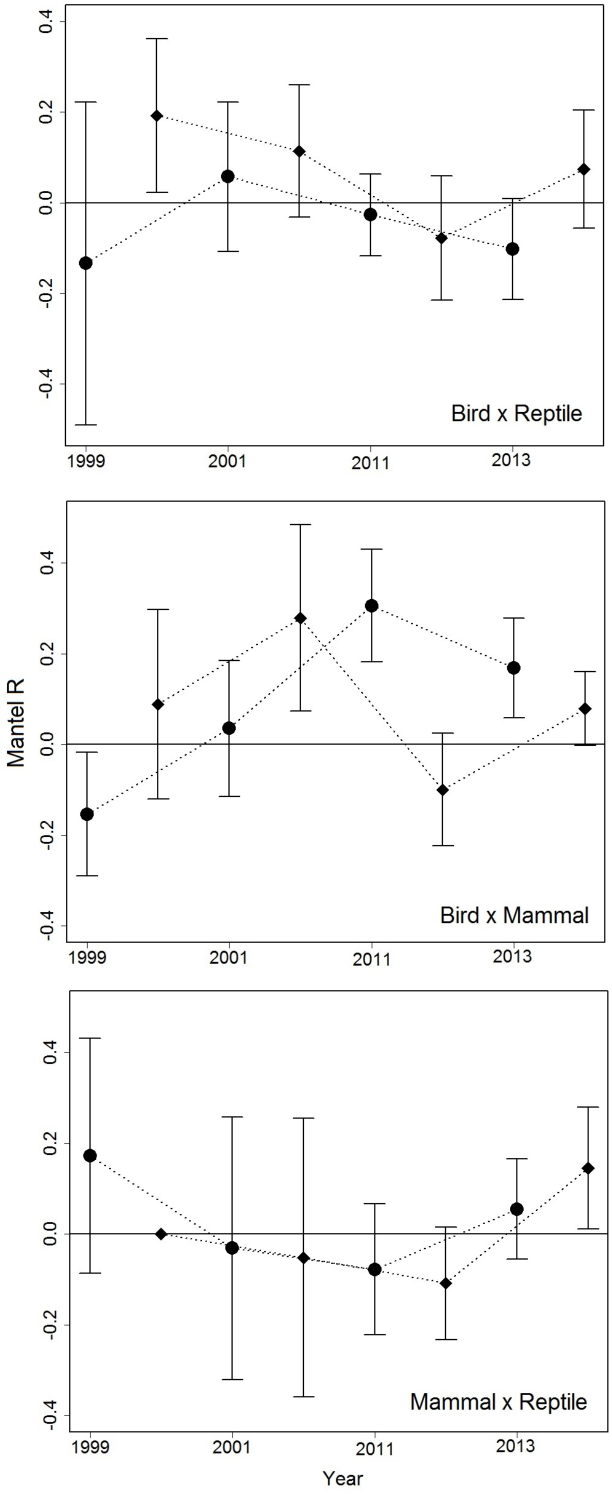
0.4
0.2
0.0
-0.2
-0.4
Bird x Reptile
1999
2001
2011
2013
0.4
0.2
0.0
-0.2
-0.4
Mantel R
Bird x Mammal
1999
2001
2011
2013
0.4
0.2
0.0
-0.2
-0.4
Mammal x Reptile
1999
2001
2011
2013
Year

Figure 3

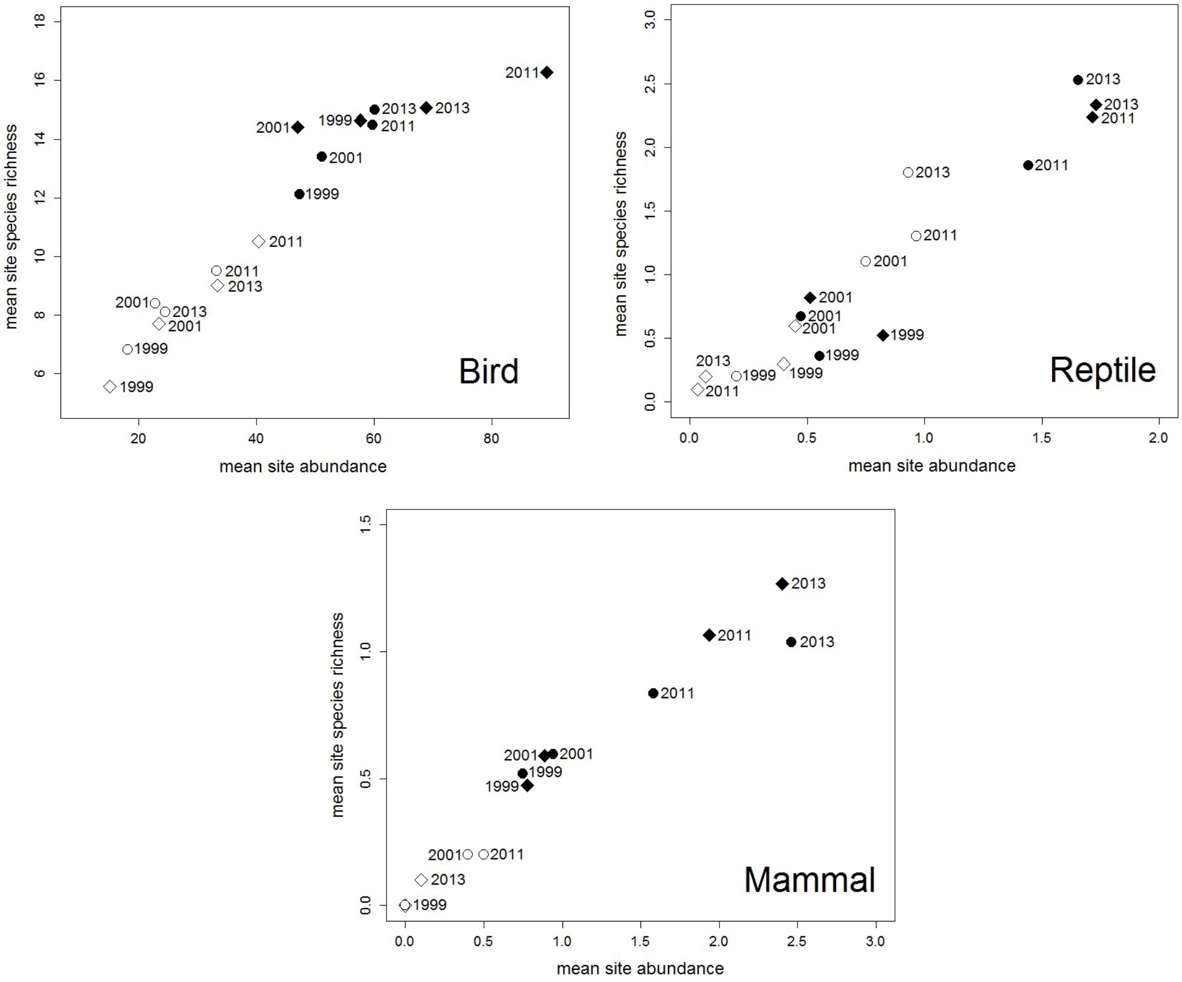
Bird
mean site species richness
mean site abundance
6
8
10
12
14
16
18
20
40
60
80
2011
1999
2013
2001
2013
2011
2001
1999
2011
2011
2013
2001
2013
2001
1999
1999
Reptile
mean site species richness
mean site abundance
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0.0
0.5
1.0
1.5
2.0
2013
2013
2011
2013
2011
2011
2001
2001
2001
2001
1999
1999
2013
1999
1999
2011
Mammal
mean site species richness
mean site abundance
0.0
0.5
1.0
1.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
2013
2011
2013
2011
2001
2001
1999
1999
2001
2011
2013
1999

Figure 4

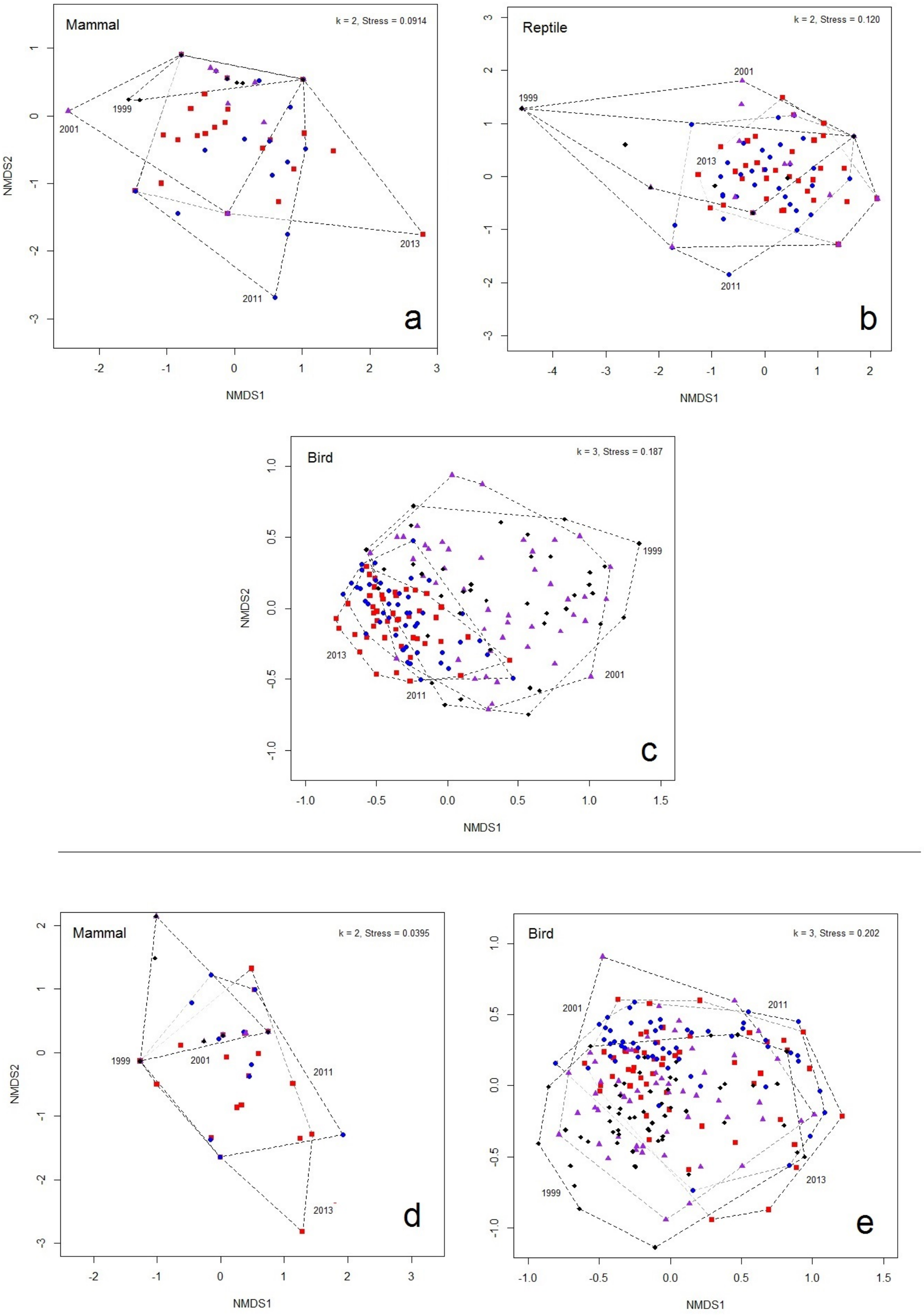
Mammal
k = 2, Stress = 0.0914
1999
2001
2011
2013
a
NMDS1
NMDS2
Reptile
k = 2, Stress = 0.120
1999
2001
2011
2013
b
Bird
k = 3, Stress = 0.187
1999
2001
2011
2013
c
Mammal
k = 2, Stress = 0.0395
1999
2001
2011
2013
d
Bird
k = 3, Stress = 0.202
1999
2001
2011
2013
e

Table 1

Term	Definition
Cross-taxonomic surrogacy	The hypothesis that changes in the diversity or composition in a defined taxon (the surrogate) reflects a similar and commensurate change in another taxon (the target).
Congruence	The degree of concordance between measures of two defined taxonomic units (e.g. Fattorini et al. 2012; Westgate et al. 2014). Often measured by the level of correlation between diversity metrics of the defined taxonomic groups (e.g. Su et al. 2004), and is an important requisite in identifying cross-taxonomic surrogates (Gioria et al. 2011)
Indicator species	A species that can be used as a surrogate or proxy measure for the distribution and occurrence of other species, species groups (Ricketts et al 1999) and environmental conditions.
Species-based surrogate	A surrogate approach based on data of individual species, defined groups of species or measures of species diversity.
Species richness	The total number of species in a defined biotic community; also a commonly used metric in measures of biodiversity.
Species composition	A metric of a biodiversity that considers the identity and relative abundance of species in a defined biotic community.
Species temporal turnover	Change in species composition in a biotic community over time.

Table 2

Taxa correlated	**Mantel *R***	***n***	**Mantel *R***	***n***	**Mantel *R***	***n***	**Mantel *R***	***n***
Agriculture control (AGR)		1999		2001		2011		2013
Bird vs Reptile	-	-	-0.403	4	0.424*	7	0.0531	9
Bird vs Mammal	-	-	-	-	-	-	-	-
Reptile vs Mammal	-	-	-	-	-	-	-	-
Woodland remnants in agricultural matrix								
Bird vs Reptile	-0.134	17	0.0576	20	-0.0271	45	-0.102	50
Bird vs Mammal	-0.154	7	0.0350	11	0.306**	25	0.168*	50
Reptile vs Mammal	0.173	25	-0.0314	25	-0.0779	32	0.0548	33
Woodland remnants in pine matrix								
Bird vs Reptile	0.191*	17	0.114	21	-0.0780	41	0.0739	42
Bird vs Mammal	0.0880	13	0.279**	9	-0.0996	28	0.0791	29
Reptile vs Mammal	-	-	-0.0521	17	-0.109	32	0.145	32

Significance $P < 0.001$ **, $P <\leq 0.05$ *, $0.05 < P \leq 0.1$ •

Table 3

Predictor variable	***2013***		***2011***	
	Coefficient	***P***	**Coefficient**	***P***
Woodland remnants in pine matrix				
Mammal ~ Bird + Reptile + Space		$R^2 = 0.0309$		$R^2 = 0.0254$
Bird	0.312	0.157	-0.385	0.0911
Reptile	0.150	0.0650	-0.144	0.0731
Space	-0.0500	0.915	0.475	0.184
Reptile ~ Bird + Mammal + Space		$R^2 = 0.0309$		$R^2 = 0.0285$
Bird	0.312	0.167	-0.321	0.285
Mammal	0.150	0.0771	-0.100	0.098
Space	-0.0500	0.924	0.555	0.165
Woodland remnants in agricultural matrix				
Mammal ~ Bird + Reptile + Space		$R^2 = 0.0565$*		$R^2 = 0.182$*
Bird	0.425	0.00400*	0.859	0.00100*
Reptile	0.0979	0.258	-0.0870	0.376
Space	0.195	0.429	-0.0420	0.881
Reptile ~ Bird + Mammal + Space		$R^2 = 0.0287$		$R^2 = 0.0176$
Bird	-0.225	0.131	0.00942	0.955
Mammal	0.0582	0.280	-0.0620	0.343
Space	0.559	0.0130*	0.483	0.0450*

Significance $P < 0.001$ **, $P <\leq 0.05$ *, $0.05 < P \leq 0.1$ ·

Table 4

Variable	*NMDS*1	*NMDS*2	R^2	Variable	*NMDS*1	*NMDS*2	R^2
Woodland remnants in pine matrix				**Woodland remnants in agricultural matrix**			
Bird species composition				*Bird species composition*			
% crown affected	0.581	-0.814	0.163*	Blackberry	0.463	-0.886	0.104·
Basal count	0.907	-0.420	0.272**	Dead trees	0.777	0.629	0.265**
Blackberry	-0.997	-0.0793	0.149·	Exposed rock	0.900	-0.436	0.162**
Logs 10-20cm	0.961	-0.276	0.114·	Ground cover	0.377	0.926	0.137*
Number of strata	-0.762	-0.647	0.129·	Number of strata	0.801	0.599	0.190**
Reptile species composition				Number of trees	0.543	0.840	0.214**
Blackberry	0.989	-0.149	0.292**	Shrub cover	0.941	0.339	0.236**
Dominant cover	-0.487	0.874	0.226*	Stand height	-0.566	0.825	0.119*
Number of strata	0.999	0.0545	0.145·	Subdominant cover	0.522	0.853	0.119*
Stem count 11-20cm	0.846	-0.534	0.154*	*Reptile species composition*			
Mammal species composition				Foliage depth	0.486	-0.874	0.116·
Logs >50cm	0.336	0.942	0.181·	*Mammal species composition*			
				Blackberry	0.957	-0.290	1.000*
				Exposed rock	0.00146	1.000	0.241*
				Foliage depth	-0.00110	1.000	0.190*
				Stand height	-0.00122	1.000	0.168*

Significance $P < 0.001$ **, $P <\leq 0.05$ *, $0.05 < P \leq 0.1$ ·