OIKOS 106: 433–444, 2004

Can the biotic nestedness matrix be used predictively?

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Maron, M., Mac Nally, R., Watson, D. M. and Lill, A. 2004. Can the biotic nestedness matrix be used predictively? – Oikos 106: 433–444.

The biotas of a suite of neighboring patches of remnant vegetation often form a series of nested sub-sets, in which the species present in species-poor patches are non-random sub-sets of those present in richer patches. There has been recent interest in ways in which this knowledge may be used to aid conservation. We focus here on whether nested patterns can be used predictively. If nestedness in a fragmented system increases over time through biotic relaxation, locations where particular species may become extinct or are likely to colonize might be predictable and this could be useful in threatened-species management. We used the Temperature Calculator of Atmar and Patterson (1995) to arrange a matrix of bird species' occurrences in a series of buloke *Allocasuarina leuhmannii* woodland remnants so that nestedness was maximized. Probability bands generated by the calculator were used to predict possible colonization and extinction events. We then re-surveyed the avifauna of the fragments after a seven-year interval to test these predictions. Although nestedness increased between the two survey periods, there was no linear relationship between the generated probability of extinctions or colonizations and the accuracy of the predictions. The predictions derived from the calculator were no more accurate than a second set of predictions generated by use of a simple non-nested model. Despite the increase in nestedness, the arrangement of sites in each of the two maximally packed matrices was substantially different. For the nestedness matrix to generate accurate predictions, an increase in nestedness must be due to a minimization of unexpected species presences and absences rather than an extensive redistribution of species among remnants, as we found. The potential utility of nested patterns in predicting systematic colonization and extinction events should be further evaluated in other, less dynamic, fragmented systems such as those undergoing biotic relaxation.

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Biotic nestedness (or nested sub-sets) occurs when the biotas of species-poor sites comprise non-random subsets of the biotas of richer sites (Patterson and Atmar 1986). A perfectly nested system is one in which the species present in a given site are a sub-set of those present in the next most species-rich site. Various degrees of nestedness have been recorded within systems of islands (Patterson and Atmar 1986, Conroy et al. 1999), anthropogenically generated habitat patches (McCoy and Mushinsky 1994, Mac Nally et al. 2002), natural fragments (e.g. mountain tops, Brown and Kodric-Brown 1977, Watson 2003) and ponds (Hecnar and McCloskey 1997). There is a growing literature documenting nested patterns in a range of landscapes and for many taxa. While some examples in certain taxonomic groups seem not to be nested or even 'anti-nested' (Worthen and Rohde 1996, Rohde et al. 1998), biotic nestedness appears to be a widespread

Accepted 16 January 2004

ISSN 0030-1299

ecological and biogeographic phenomenon (Wright et al. 1998).

An emphasis in nestedness studies has been on comparing strengths and weaknesses of alternative measures of nestedness (Cook and Quinn 1998, Wright et al. 1998). Although this matter remains unresolved, there nevertheless has been more recent focus on two issues: (1) mechanisms responsible for nested-sub-set patterns (Cutler 1994, Lomolino 1996, Worthen 1996, Loo et al. 2002) and (2) use of the nested patterns in biodiversity management and conservation (Patterson 1987, Boecklen 1997, Fleishman and Mac Nally 2002). Here we address the second of these topics. We ask: can nestedness be used in a practical fashion to move beyond the mere representation of nested biota and applied as a tool with which predictions of likely species extinction from and colonization of particular locations can be made?

The Temperature Calculator

Patterson and Atmar (2000) used the incidence matrix, which is an arrangement of species' occurrences among habitat patches of a system, to identify species in particular patches (mountain ranges in their example) that would be poor candidates for conservation efforts or good candidates for reintroduction programs. Their approach was to order the incidence matrix into a state of 'maximum packing', which means that the rows (species) and columns (patches or sites) are arranged such that there is minimum 'unexpectedness' in the distribution of species among patches (Atmar and Patterson 1993). The matrix is initially arranged so that the most species-rich (or hospitable, Patterson and Atmar 2000) patch is placed at the left of the incidence matrix and columns are ordered by decreasing species richness. The most widespread species is positioned in the top row, and more restricted species (i.e. fewer patches occupied) are positioned lower in the matrix. However, there is a unique arrangement of sites and species (columns and rows) in which there are fewest 'holes' (unexpected absences) in the upper left part of the incidence matrix and, simultaneously, fewest 'outliers' (unexpected presences) in the lower right of the matrix (Patterson and Atmar 2000). This arrangement can be derived from the initial matrix and is termed the maximally packed incidence matrix.

Patterson and Atmar (2000) suggested that the maximally packed incidence matrix may be useful for identifying locations where re-introductions of a particular species might be expected to have high success rates (good candidates) and those where conservation efforts would be wasted (poor candidates). They equated the former with holes and the latter with outliers in the incidence matrix. In a 'relaxing' system, outliers can be thought of as (sub)populations that are ultimately destined for local extinction. The populations may have 'hung on' in a given patch or remnant by chance (given their fate in other, similar remnants), but are not expected to continue to do so for long due to effects of demographic or environmental stochasticity (Lande 1993, Caughley 1994) or more deterministic mechanisms (e.g. Allee effect, Fischer and Matthies 1998, Foley 2000).

Similarly, the 'holes' in the incidence matrix can be regarded as locations at which particular species might be expected to recolonize successfully and the matrix probabilities can be used similarly to make predictions about which species might appear in particular patches with a greater probability. For example, species that were not recorded from the upper-left part of the incidence matrix (typically widespread species missing from species-rich patches) might be expected to recolonize those patches, especially if their widespread occurrence is related to mobility and other factors enhancing capacities for colonization.

The software made publicly available by Atmar and Patterson, the 'Temperature Calculator' (Atmar and Patterson 1995), allows the computation of maximum packing of any incidence matrix. Here we utilize the software's capacity to calculate the probability of any species' occurrence in or absence from a particular site, given the position of the corresponding cell within the matrix. This is called the matrix-position probability.

The Temperature Calculator provides percentile 'bands' (0–10%, . . ., 80–90%, 90–97%, 97–100%) that we use here to group incidences of species in particular fragments into sets with different projected probabilities of extinction. Thus, a species that occurs in a given patch with a low matrix-position probability (P) (i.e. an unexpected presence or outlier), say $\leq 10\%$, is interpreted as having a high probability of being lost from that patch over time. However, an outlier position with a matrix-position probability of $10\% < P \leq 20\%$ is expected to be less likely to be lost through time, and so forth. We expect that there should be a generally monotonic relationship between the proportion of incidences that eventually disappear from within probability bands and the probability level of the band. For example, we might expect perhaps 75% of incidences in the $\leq 10\%$ probability band to be lost over some time period, 50% in the $10\% < P \leq 20\%$, 35% in the $20\% < P \leq 30\%$, and so on.

The current study

A test of the usefulness of the Temperature Calculator for predicting changes in species incidences requires measurements of species occurrence in the one system of patches over at least two separate time periods, preferably many years apart. To minimize confounding of differences in time with differences in method, the survey methodology needs to be identical at both survey times. The study we describe here involves an exact emulation of the bird-survey program conducted in the fragmented buloke *Allocasuarina leuhmannii* woodlands of western Victoria, Australia, in 1994–95 (Watson et al. 2000). The current surveys were conducted seven years later in 2001–02. While this is not a very long period of time, it exceeds the average lifetimes of individuals of most species involved (Poiani and Jermiin 1994, Bennett and Owens 2002) and so is likely to be a reasonable test duration. We used the Temperature Calculator to derive a series of predictions of colonizations and extinctions on the basis of data from the first survey period. We also assessed the success rate of these predictions by comparing the rate with that of a separate set of predictions produced by a simple, non-nested model, which does not take nestedness into account.

Methods

Study areas

The study region is in western Victoria adjoining South Australia, and is dominated by the extensive Wimmera plains. Primarily of aeolian origin, this landform comprises low, elongated sand-ridges or linear dunes with sandy clay soils (Land Conservation Council 1985). The climate is temperate with hot, dry summers and mild winters. About 60% of the rainfall occurs during the winter months (Land Conservation Council 1985). Frosts are common during winter.

The Wimmera plains were originally covered with open woodlands dominated by grey box *Eucalyptus microcarpa*, yellow gum *E. leucoxylon*, black box *E. largiflorens* and buloke, interspersed with expanses of native grassland (Connor 1966, Land Conservation Council 1985). Virtually all of the grasslands were subjected to grazing by sheep during early european settlement and approximately 95% of the woodlands was subsequently cleared. Cereal, legume and oilseed cropping are now the major land uses in the region. Remaining buloke woodlands occur on freehold farmland, roadside strips and in small reserves. Most are degraded to various degrees. In severely degraded remnants, floristic richness is low and there is little regeneration of buloke, with most trees being of similar age and size. The understorey of some remnants is dominated by exotic grasses whilst that of other, heavily grazed remnants is comprised largely of bare, compacted soil. While the main agent of degradation appears to be grazing and soil disturbance by domestic stock, additional contributing factors include other introduced herbivores (e.g. European rabbit *Oryctolagus cuniculus*), timber removal and the spread of weed species (Land Conservation Council 1985).

Twenty-six remnants of buloke woodland were selected for study (remnant 4 of Watson et al. 2000 appears to have been cleared in the intervening period). For each remnant, the area, canopy composition, tree density, understorey characteristics and management status (intensity of sheep grazing) were recorded. All remnants were on the same landform (Land Conservation Council 1985) and were located within an area of 3200 km^2 (Watson et al. 2000: Fig. 1). Twenty-two remnants were on freehold land while the others were flora and fauna reserves (remnants 1, 5 and 15) or small blocks of public land (remnant 2). Most remnants were isolated from other stands of native vegetation by large expanses of cropping land; the distance from each remnant studied to the nearest patch of remnant native vegetation ≥ 10 ha averaged 1457 m (range: 221–5206 m).

Bird surveys

Birds were surveyed by using transect counts (Recher 1989). Fixed transect dimensions were used, 200×50 m, yielding a sampling area of 1 ha. For consistency, transects were located >20 m from the edge of the remnant, the maximum value possible in the smallest remnant. Transects were randomly located in remnants apart from this restriction. Survey time was standardized to 20 min, with 5 min taken to traverse each 50 m section following a path down the centre of the transect. All birds observed within a transect were recorded.

In both sets of surveys, each remnant was surveyed nine times at approximately 6-week intervals. The first set was conducted between April 20, 1994 and March 22, 1995 by DMW. The second set of surveys was conducted between June 30, 2001 and June 14, 2002 by MM. Surveys were conducted in the early morning (beginning more than 30 min after sunrise) and the late afternoon (completed more than 30 min before sunset), with at least four morning surveys being carried out in each remnant. Surveys were conducted only in still, dry conditions. A constrained randomization technique was developed to determine the order in which remnants were surveyed. The 26 remnants were grouped into five sectors according to their geographic proximity. The order in which these sectors were visited was randomized, and the order in which the remnants in each sector were surveyed was also randomized.

Analyses

Each of the two resulting incidence matrices was maximally packed using the Temperature Calculator of Atmar and Patterson (1995). The rank orders of sites in

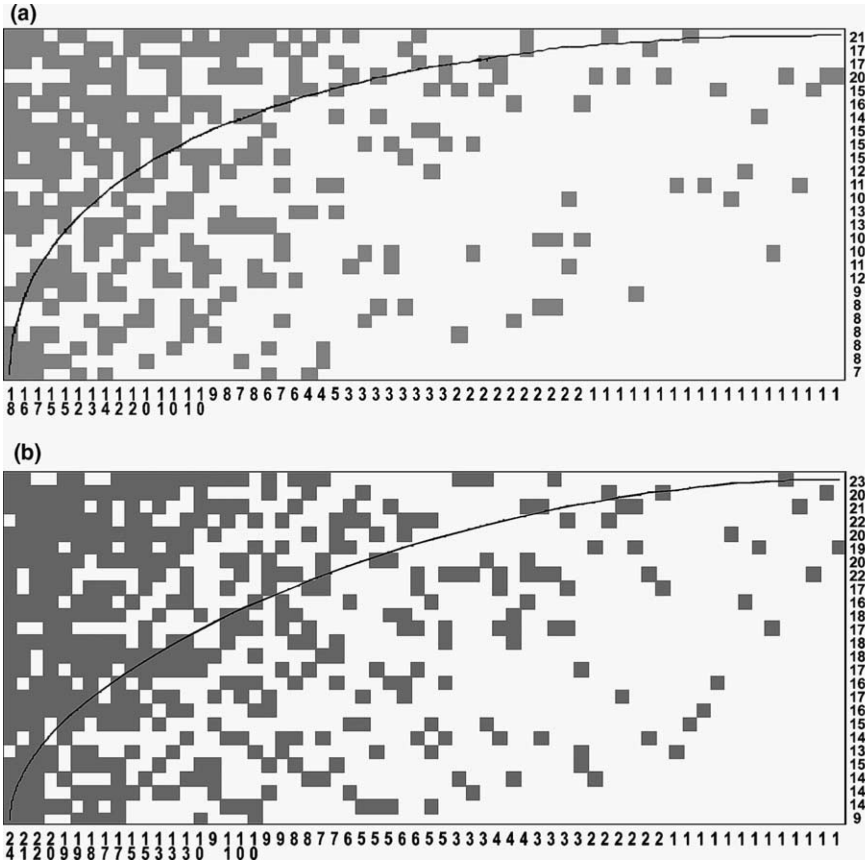

Fig. 1. Incidence matrices for the buloke remnant system in western Victoria, Australia in the (a) 1994–95 surveys and (b) 2001–02 surveys. Sites are on the vertical axis and species are on the horizontal axis. Row totals represent each site's species richness, and column totals give the total number of sites in which each species occurred.

the maximally packed matrices were compared between years by calculating Spearman's rank correlation coefficient. We then generated sets of predictions based on the maximally packed configuration of the matrix of 1994–95 data. 'Outliers', unexpected presences of individual species in particular remnants of buloke woodlands, were identified with the matrix-probability band given by the Temperature Calculator. These are colour-coded in the program's output. Five bands were used for outliers, ranging in 10% intervals from 0–10% (matrix-position probability) through to 40–50%.

For all absences in the matrix, there are no probabilities provided in the output of the Temperature Calculator. Therefore, we cannot obtain directly the probability values of 'holes' where species are expected to be present but were not recorded. While holes do not have probabilities associated with them, surrounding presences within the matrix are probability coded. Therefore, matrix probability bands for holes were interpolated from surrounding presences. We chose to consider for holes only the three high matrix probability bands (80–90%, 90–97%, 97–100%) because interpolation was difficult to make for holes within lower probability bands, especially in the long upper-right tail of the maximally packed matrix (Fig. 1a, b).

We hypothesized that there should be an inverse relationship between the probability of occurrence and the success rates of predictions of species extinctions (Atmar and Patterson 1995). Thus, for the 0–10% band (mid-point 5%), the success rate of predictions of local extinctions should be highest. With increasing probability of occurrence (15%, 25%, 35%, 45%), success rates should be lower (fewer successfully predicted extinctions). Similarly, we would expect a direct relationship between the probability of occurrence and the success rates of predictions of species colonizations. We validated the generated predictions against the presence/absence data from 2001–02, and calculated the proportion of correct predictions for each probability band.

In order to determine whether the expected relationships between prediction success and probability of occurrence were evident, we fitted a Bayesian binomial regression to the data for the local extinctions. The model was:

$$\mathrm{logit}(\pi_i) = \alpha + \beta_1(m_i\text{-}\bar{m}) + \beta_2(m_i\text{-}\bar{m})^2/100 + \sigma_\varepsilon, r_i \mathrm{Binomial}(\pi_i, n_i).$$

In this model, the π_i are the unknown binomial population success rates (proportions) of predictions from which the observed numbers of successes, r_i, were obtained from the n_i predictions. The m_i are the means of the five probability bands (5, 15, ...) and are centred to accelerate convergence of model calculations. The possibility of non-linear relationships is allowed for by including the squares of the m_i, which are scaled by division by 100 to make the regression coefficients (β_i) more similar to one another. The σ_ε represent probability-band random effects.

We used the WinBUGS Bayesian analysis program (version 1.3, Spielgelhalter et al. 2000). "Non-specific" normal priors were used for the β and α coefficients. This means that we do not have any prior information for the probability distributions for these model coefficients, so we use a Normal prior distribution with mean $\mu = 0$ and high standard deviation (typically $\sigma = 100$). WinBUGS combines the model, the stated prior distributions (which have virtually no influence given their high standard deviations) and the data to compute the posterior probability distributions for all model parameters. In all analyses, means and medians of posterior distributions (PPMs) of parameters were similar, indicating symmetric posterior probability distributions. We avoided formal significance tests based on the null hypothesis and P-values as is appropriate for a Bayesian analysis but used a decision rule (Hilborn and Mangel 1997). We regarded "important" differences to be those in which $\geq 90\%$ of the posterior probability mass for an estimated quantity (e.g. regression coefficient, population probability value, π_i) exceeded 0, or 90% of the mass was less than zero if the coefficient were negative. Means and standard deviations are provided so that other decision criteria can be used if the reader so desires. The flexibility of the WinBUGS programming environment allowed us to compute posterior probability distributions of differences (i.e. post hoc comparisons) in the π-coefficients for all pairs of values ($^5C_2 = 10$ in all). From these comparisons we can estimate which coefficients are substantially different from one another.

Non-nested model

A non-nested modeling approach was used to assess whether the empirical spatial pattern of occurrences that is represented by the maximally packed matrix is necessary to make successful predictions. In other words, can a simpler model predict equally well? We made a second set of predictions using such a non-nested model. This model was based only upon the frequency of occurrence of each species without reference to the specific distributional data explicitly encapsulated by the maximally packed occurrence matrix. First, bird species were ranked in order of decreasing occurrence. The most commonly occurring species was considered to have a 100% chance of being present in every site. This was done for consistency with the 'probability bands' generated by the Temperature Calculator (i.e. $< 10\%$, 10–20%,..., 97–100%), so that success rates of the non-nested model could be compared directly with those of the Temperature Calculator. Note that the actual maximum occurrence frequency was 69% (i.e. 18 sites, yellow-rumped thornbill *Acanthiza chrysorrhoa*). Therefore, this species was predicted to colonize each site from which it was initially absent. The non-nested-model 'probability bands' were calculated by expressing the number of sites at which each species occurred as a percentage of the maximum number of sites at which a single species occurred (i.e. 18 sites). Each species was assigned the same probability of occurrence for each site in which it was initially recorded. For example, the white-browed babbler *Pomatostomus superciliosus* was recorded from only one site so this occurrence was placed in the $< 10\%$ probability band. The brown treecreeper *Climacteris picumnus* was recorded in seven sites, and so was assigned a 39% probability of occurrence in each of those sites (i.e. each occurrence therefore fell within the 30–40% probability band). Predictions again were made for 'outliers' (rarely occurring species) and 'holes' (Table 5, 6).

Results

Matrix fill

The presence matrix consists of a sites by species array. The matrix fill is equal to the observed number of presences divided by the total number of cells in the matrix (species × sites). For the 1994–95 data, matrix fill was 0.20 (i.e. 323 of the 62 species × 26 sites = 1612 matrix cells were presences). For the 2001–02 data, the matrix fill was 0.30 (486 presences in 1612 cells).

Nestedness statistics

The 1994–95 incidence matrix had a 'temperature' of $T = 32$ (compared to a mean $T \pm SD$ for 50 matrix randomizations $= 54 \pm 4$; lower temperatures indicate greater nestedness), which indicated a highly nested arrangement (Fig. 1a). Similarly, the 2001–02 incidence matrix was also more highly nested than expected for a random arrangement with $T = 39$ (mean $T \pm$ SD for 50 matrix randomizations $= 65 \pm 3$, Fig. 1b). Although both matrices were nested, the ordering of sites in the maximally packed configurations was markedly different, as reflected in the lack of correlation between the site order ranks ($r_s^2 = 0.0001$).

To test whether degrees of nestedness differed between the matrices for the two time periods, we used the Z-statistic of Wright and Reeves (1992). Unlike the Temperature Calculator, the Wright-Reeves method does not force maximal packing of the incidence matrices. Instead, sites were placed in order of decreasing richness, and species in order of decreasing frequency of occurrence. We used the standardized Wright-Reeves C statistic to characterize nestedness for the two time periods. This statistic is useful because it constrains the nestedness value to between 0 and 1, and also is used in statistical comparisons between any two values, such as for the 1994–95 and 2001–02 matrices. The value for the 1994–95 data was $C = 0.257$, while the nestedness value for the 2001–02 data-set was $C = 0.324$. The system was substantially more nested in the later period (standardized normal variate, $Z = 5.539$).

Success of predictions: 'outliers'

Details of predicted species losses from particular buloke remnants are presented in Table 1. Success rates for predicted extinctions were highest for the 0–10% probability band (60% correct), decreasing for bands with higher probabilities (Table 1). The decline in success rate with increasing probability of occurrence was not linear as we had expected, but had a substantial quadratic component (Table 2). This was driven largely by a higher prediction success rate for the 40–50% band (47% correct) than for the 10–20%, 20–30% and 30–40% bands (Table 2). Prediction success rates were substantially greater for the 0–10% band than for all other bands (PPM $\geq$ 90%, Table 2). The only other important difference was between bands 40–50% and 30–40%, with the latter having a lower success rate than the former. In summary, there seemed to be higher success rates for predictions for the band in which outliers (unexpected presences) were least likely to occur (0–10%) but the pattern of decline of success rates as a function of the probability band was not linear.

There was much heterogeneity among species of birds vis-à-vis predictive success (Table 1). Success rates of extinction predictions for several species were high across all probability bands (e.g. dusky woodswallow *Artamus cyanopterus*, 5 of 7; jacky winter *Microeca fascinans*, 5 of 6; black honeyeater *Certhionyx niger*, 5 of 5). Success rates for some other species were low or zero (e.g. yellow thornbill *Acanthiza nana*, 0 of 6; red-rumped parrot *Psephotus haematonotus*, 0 of 5; varied sittella *Daphoenositta chrysoptera*, 0 of 6; brown treecreeper, 0 of 5).

Success of predictions: 'holes'

Information on predicted species colonizations in particular buloke remnants is presented in Table 3. The table is arranged as species in rows and remnant numbers in one of three columns, which refer to the nominal matrix probability bands.

Given that we used only three probability bands (97–100%, mid-point 98.5%; 90–97%, mid-point 93.5%; 80–90%, mid-point 85%), the quadratic component could not be used in the Bayesian binomial regression because one needs at least four points to estimate the quadratic curve. There was no evidence of a linear relationship between prediction success rates and mid-points of probability bands (Table 4, $\beta_1 \sim 0$). None of the pair-wise comparisons of π-values differed greatly from zero (Table 4).

Although based on many fewer predictions than for the extinctions, success rates of predicted colonizations for some species were high. All predictions for the hooded robin *Melanodryas cucullata* and red-rumped parrot (three each) were found to be correct, as were three of four for the Australian magpie *Gymnorhina tibicen* (Table 3).

Overall success of predictions

When success rates for predicted outliers and holes were combined, sets of predictions for some remnants were remarkably accurate. For example, all nine predictions for remnant 13 were correct, while 13 of 17 were correct for remnant 1. Predictions for two remnants were poor, namely, remnant 5 (three correct of eleven) and remnant 15 (two correct of ten). No species' fate was predicted well by both sets of predictions (i.e. extinctions and colonizations).

Success of predictions based on the non-nested model

Success rates of the non-nested model set of predictions of species losses in each 'probability band' are shown in Table 5. The success rate of extinction predictions for the < 10% occurrence band again was greater than that of the higher probability bands and at 84% was considerably higher than that achieved by the < 10% band predictions of the Temperature Calculator (i.e. 59%). The pattern of success rates again was not linear. While success rate declined through the 10–20% and 20–30% bands, it increased again for the 30–40% and 40–50% bands. Across all five bands, the success rate (from 118 predictions) was 56%, 12% higher than the predictions of the Temperature Calculator.

Only eight and nine predictions of species colonizations were made for the 97–100% and 90–97% bands, respectively (Table 6); these were the numbers of sites from which the two most common species were absent during survey period 1. There was no evidence of a linear relationship; the higher success rate (66%) was for

Table 1. Predicted species losses from specific buloke remnants as a function of probability bands derived from the Temperature Calculator. Numbers in columns refer to individual remnants. Correct predictions are in bold type.

Bird species	Probability classes				
	≤ 10%	10–20%	20–30%	30–40%	40–50%
Red-capped robin *Petroica goodenovii*	–	7	11	8	–
Yellow thornbill *Acanthiza nana*	7	11	8	18	16,22
Australian magpie *Gymnorhina tibicen*	–	11	–	–	16,20,**22**
Willie wagtail *Rhipidura leucophrys*	–	11	3,18	–	20,22
White-plumed honeyeater *Lichenostomus penicillatus*	–	–	23	25	15,**17**
White-fronted honeyeater *Phylidonyris albifrons*	**7**	8	–	**16,20**	10
Hooded robin *Melanodryas cucullata*	**7**	**8**,18	16,25	20	17
Red-rumped parrot *Psephotus haematonotu*s	–	23	25	15	5,12
Crested pigeon *Ocyphaps lophotes*	11	3,23	25	–	5
Chestnut-rumped thornbill *Acanthiza uropygialis*	–	18	16,22	17	**10**
Galah *Cacatua roseicapilla*	–	3,18,23,**25**	–	**10**,12,15	**27**
Mistletoebird *Dicaeum hirundinaceum*	8	–	20	10,12	–
Varied sittella *Daphoenositta chrysoptera*	–	–	20,22	12,17	21,27
Striated pardalote *Pardalotus striatus*	**18**	3	**17,22**	–	27
Dusky woodswallow *Artamus cyanopterus*	–	**23**	**15,20,22**	5,21	**27**
Rufous whistler *Pachycephala rufiventris*	**11**	–	17	–	**2**,27
Grey fantail *Rhipidura fuliginosa*	–	16	**12,17**	21	–
Brown treecreeper *Climacteris picumnus*	23	25	15	5,27	–
Jacky winter *Microeca fascinans*	–	**20,22**	**17**	27	**2,9**
Black honeyeater *Certhionyx niger*	**7,8**	**20**	**17**	–	**19**
Eastern rosella *Platycercus eximius*	8,11	–	–	5	–
Singing honeyeater *Lichenostomus virescens*	–	20	12	–	–
Southern boobook *Ninox novaeseelandiae*	7	–	**12**	–	–
Spiny-cheeked honeyeater *Acanthagenys rufogularis*	–	–	5,12	–	2
Noisy miner *Manorina melanocephala*	18	–	–	–	**13**
Grey shrike-thrush *Colluricincla harmonica*	–	**22**	–	–	–
Restless flycatcher *Myiagra inquieta*	**3**	–	–	**27**	–
Variegated fairy-wren *Malurus lamberti*	3	–	–	2	–
Laughing kookaburra *Dacelo novaeguineae*	–	**15**,22	–	9	–
White-browed woodswallow *Artamus superciliosus*	**23**	15	–	**9**	–
Blue bonnet *Northiella haematogaster*	–	–	–	**19**	–
Australian raven *Corvus coronoides*	–	–	**19,21**	–	–
Brown falcon *Falco berigora*	–	–	–	9	**1**
Black-faced cuckoo-shrike *Coracina novaehollandiae*	**3**	**25**	—	–	–
Purple-crowned lorikeet *Glossopsitta porphyrocephala*	–	15	–	**9**	–
Brown-headed honeyeater *Melithreptus brevirostris*	–	–	–	–	**1,14**
Nankeen kestrel *Falco cenchroides*	–	–	–	**13**	**14**
Rufous song-lark *Cinclorhamphus mathewsi*	23	–	24	–	–
Australian magpie-lark *Grallina cyanoleuca*	**25**	–	**24**	–	–
Welcome swallow *Hirundo neoxena*	**3**,25	–	–	–	–
Silvereye *Zosterops lateralis*	–	**10,22**	–	–	–
Weebill *Smicrornis brevirostris*	–	–	–	**1**	–
Gilbert's whistler *Pachycephala inornata*	–	–	–	**1**	–
Barn owl *Tyto alba*	–	**16**	–	–	–
White-browed babbler *Pomatostomus superciliosus*	–	–	–	–	**26**
Tree martin *Hirundo nigricans*	15	–	–	–	–
Black-shouldered kite *Elanus axillaris*	–	**13**	–	–	–
Horsfield's bronze-cuckoo *Chrysococcyx basalis*	**5**	–	–	–	–
Golden whistler *Pachycephala pectoralis*	–	**1**	–	–	–
White-faced heron *Egretta novaehollandiae*	**21**	–	–	–	–
Fan-tailed cuckoo *Cacomantis flabelliformis*	**10**	–	–	–	–
Common bronzewing *Phaps chalcoptera*	–	**1**	–	–	–
Long-billed corella *Cacatua tenuirostris*	**1**	–	–	–	–
Black-eared cuckoo *Chrysococcyx osculans*	**5**	–	–	–	–
Red wattlebird *Anthochaera carunculata*	**13**	–	–	–	–
Yellow-plumed honeyeater *Lichenostomus ornatus*	**5**	–	–	–	–
White-eared honeyeater *Lichenostomus leucotis*	1	–	–	–	–
Fuscous honeyeater *Lichenostomus fuscus*	**1**	–	–	–	–
Total predictions	32	35	33	32	32
Correct predictions	19	15	13	10	15
Percent correct	59	43	39	31	47

predictions of colonization in the 80–90% band. The success rate of predictions of species colonizations across all three bands was 54%, which was 7% lower than that of the predictions of the Temperature Calculator.

Although there was no linear pattern in success rates with respect to probability bands, the predictions made on the basis of species-occurrence frequency (the non-nested model) achieved an average success rate of 55%,

Table 2. Critical parameter details for the Bayesian analysis of success rates of local extinction predictions (see text). Data are presented as posterior probability distributions. "Posterior probability mass" (PPM) indicates how much of the posterior probability mass for a parameter exceeds 0 (positive differences) or is less than 0 (negative differences).

Parameter	Description	Mean ± SD	PPM (%)	95% credible interval
Model parameters				
α	Intercept	−0.26±0.19	...	−0.64, 0.10
β_1	Linear coefficient	−0.10±0.05	97†	−0.21, 0.004
β_2	Quadratic coefficient	0.18±0.11	95†	−0.04, 0.39
σ_ε	Band random effects	0.18±0.19	...	0.26, 0.70
π_5	5% band probability	0.61±0.08	...	0.44, 0.76
π_{15}	15% band probability	0.42±0.06	...	0.30, 0.56
π_{25}	25% band probability	0.35±0.07	...	0.23, 0.50
π_{35}	35% band probability	0.33±0.06	...	0.21, 0.46
π_{45}	45% band probability	0.47±0.09	...	0.30, 0.64
Band comparisons				
$\pi_5-\pi_{15}$	5% band vs 15% band	0.17±0.08	98†	0.01, 0.32
$\pi_5-\pi_{25}$	5% band vs 25% band	0.24±0.11	99†	0.03, 0.44
$\pi_5-\pi_{35}$	5% band vs 35% band	0.25±0.11	99†	0.04, 0.45
$\pi_5-\pi_{45}$	5% band vs 45% band	0.15±0.11	90†	−0.07, 0.36
$\pi_{15}-\pi_{25}$	15% band vs 25% band	0.07±0.06	89	−0.06, 0.19
$\pi_{15}-\pi_{35}$	15% band vs 35% band	0.08±0.07	89	−0.05, 0.23
$\pi_{15}-\pi_{45}$	15% band vs 45% band	−0.02±0.11	60	−0.23, 0.19
$\pi_{25}-\pi_{35}$	25% band vs 35% band	0.01±0.06	54	−0.10, 0.16
$\pi_{25}-\pi_{45}$	25% band vs 45% band	−0.09±0.11	81	−0.30, 0.11
$\pi_{35}-\pi_{45}$	35% band vs 45% band	−0.11±0.08	91†	−0.26, 0.05

†Deemed a substantial effect ($\geq 90\%$).

compared with 50% for the predictions of the Temperature Calculator.

Discussion

The predictions of species colonization and extinction based on the probability bands generated by the Temperature Calculator did not have a high success rate, with an average of 44% for species extinctions, and 61% for colonizations. However, absolute success rates are likely to be sensitive to the amount of time elapsed since the initial survey period. More informative is the absence of the expected linear relationship between probability and success rate. Although the 0–10% probability band produced more accurate predictions of extinction than did higher probability bands, the relationship was not linear. The predictions of the Temperature Calculator also were less successful overall than predictions based on the simpler non-nested model of species-occurrence frequencies. It therefore appears that the Temperature Calculator is of little predictive value in this particular system.

Table 3. Predicted species gains in specific buloke remnants as a function of probability bands derived from the Temperature Calculator. Numbers in columns refer to individual remnants. Correct predictions are in bold type.

Bird species	97–100%	90–97%	80–90%
Yellow-rumped thornbill *Acanthiza chrysorrhoa*	**1**	–	5,15
Red-capped robin *Petroica goodenovii*	**1**,24	–	5,**27**
Yellow thornbill *Acanthiza nana*	**1**,14	2,**13**	–
Australian magpie *Gymnorhina tibicen*	**26**	1,**9,24**	–
Willie wagtail *Rhipidura leucophrys*	6	1	**2**
White-plumed honeyeater *Lichenostomus penicillatus*	**6**	**13**	–
White-fronted honeyeater *Phylidonyris albifrons*	26	–	–
Hooded robin *Melanodryas cucullata*	**6**	**14**	**13**
Red-rumped parrot *Psephotus haematonotus*	–	**1,14**	**13**
Crested pigeon *Ocyphaps lophotes*	–	**26**	1,**13**
Chestnut-rumped thornbill *Acanthiza uropygialis*	**6**	**26**	–
Galah *Cacatua roseicapilla*	6	–	**1**,14
Mistletoebird *Dicaeum hirundinaceum*	–	**26**	–
Varied sittella *Daphoenositta chrysoptera*	–	26	–
Striated pardalote *Pardalotus striatus*	–	**6**	**14**
Dusky woodswallow *Artamus cyanopterus*	–	–	14
Rufous whistler *Pachycephala rufiventris*	–	–	**14**
Brown treecreeper *Climacteris picumnus*	–	6	–
Total predictions	12	16	14
Correct predictions	7	11	8
Percent correct	58	69	57

Table 4. Critical parameter details for the Bayesian analysis of success rates of local colonization predictions (see text). Data are presented as posterior probability distributions. "Posterior probability mass" (PPM) indicates how much of the posterior probability mass for a parameter exceeds 0 (positive differences) or is less than 0 (negative differences).

Parameter	Description	Mean ± SD	PPM (%)	95% credible interval
Model parameters				
α	Intercept	0.43 ± 0.57	–	– 0.69, 1.40
β_1	Linear coefficient	0.01 ± 0.10	59	– 0.22, 0.19
σ_ε	Band random effects	0.53 ± 1.01	–	0.03, 3.47
$\pi_{98.5}$	98.5% band probability	0.62 ± 0.12	–	0.35, 0.83
$\pi_{93.5}$	93.5% band probability	0.65 ± 0.10	–	0.45, 0.85
π_{85}	85% band probability	0.56 ± 0.13	–	0.28, 0.79
Band comparisons				
$\pi_{98.5}-\pi_{93.5}$	98.5% vs 93.5% bands	– 0.02 ± 0.13	51	– 0.32, 0.18
$\pi_{98.5}-\pi_{85}$	98.5% vs 85% bands	0.06 ± 0.19	66	0.43, 0.66
$\pi_{93.5}-\pi_{85}$	93.5% vs 85% bands	0.08 ± 0.14	70	0.39, 0.70

For the Temperature Calculator to be useful as a predictive tool in conservation management, the degree of nestedness in a fragmented system must increase through time (Wright and Reeves 1992). The bird assemblages of the buloke remnants met this requirement – they were more nested in the recent survey period (2001–02) than in the earlier (1994–95) survey period. However, an additional requirement for using the Temperature Calculator as a predictive tool is that the increase in nestedness must result from relatively conservative mechanisms. In other words, the majority of species presences in given sites must remain unchanged, although there may be some changes that result in the matrix 'settling' or 'relaxing' into a more highly nested configuration. Thus, change in species composition within a site and distributional change of any one species among sites is expected to be relatively minor, with most changes being a reduction in the number of unexpected presences and absences. This was not the case in our study system. The expectation that a system may become more nested over time due to the minimization of unexpected presences and absences implies that the order of sites in a maximally packed matrix should be similar at both times. However, the orders in which sites were arranged in our two maximally packed matrices were not correlated. Therefore, although some of the Temperature Calculator's predictions regarding unexpected presences and absences were supported, this cannot be interpreted as evidence that our system has undergone such a 'settling'. The greater degree of nestedness observed in the second survey period was thus not due solely to a reduction of unexpected species presences and absences.

The required increasing degree of nestedness is most likely to be observed in a system undergoing biotic relaxation following an event such as habitat fragmentation. The comparisons we undertook did not suggest that biotic relaxation was a dominant process in the system studied. Rather, the system of bird assemblages was, unexpectedly, highly dynamic. Although many of the species recorded (e.g. robins, thornbills) are generally considered to be unlikely to travel substantial distances over an inhospitable matrix (Reid 1999), the species composition of most sites differed considerably between the two survey periods. This is despite the fact that neither the sites themselves nor the matrix surrounding them changed appreciably between the two survey periods. Australia is prone to such fluctuations in bird populations due to its highly variable climate, which in turn influences resource availability (Collins and Briffa 1982, Collins and Newland 1986, Mac Nally 1995, 1996). A relatively large proportion of the avifauna is considered to be nomadic (Keast 1968). Exemplars of this strategy include two meliphagid honeyeaters recorded during one or both periods throughout the study area. The black honeyeater and white-fronted honeyeater *Phylidonyris albifrons* are poorly known species characteristic of more arid inland woodlands and shrublands, but both irrupted in the study area during 1994–95, and the latter species again was present during 2001–02. This species appeared to respond primarily to resource availability – mass flowering of mistletoe (Watson 1997). Bird species that in the past have been considered relatively sedentary also may exhibit more variability in local distributions than is often recognized (Mac Nally 1996). Thus, interpretation of distributional patterns among patches in this landscape may be affected by larger scale movement patterns and the temporal and spatial variability in resource availability. However, marked temporal variability is common among bird assemblages worldwide (Enemar et al. 1984, Hogstad 1993, Holmes and Sherry 2001). We think that workers should explore the utility of the nestedness matrix for making predictions for taxa that may have lower mobilities than birds, such as reptiles, small, non-volant mammals and certain invertebrates (probably excluding butterflies).

In addition to between-survey dynamism, the poor predictive power of the Temperature Calculator for this system may be related to time-since-fragmentation. The

Table 5. Predicted species losses from specific buloke remnants as a function of probability bands based on species occurrence frequencies during the first survey period. Numbers in columns refer to individual remnants. Correct predictions are in bold type.

Bird species	Probability classes				
	≤ 10%	10–20%	20–30%	30–40%	40–50%
Jacky winter *Microeca fascinans*	–	–	–	–	**1,2,6,9,17,20,22**,27
Grey fantail *Rhipidura fuliginosa*	–	–	–	–	1,6,**12,14**,16,**17**,21,**26**
Rufous whistler *Pachycephala rufiventris*	–	–	–	1,**2,6,11**,17,26,27	
Brown treecreeper *Climacteris picumnus*	–	–	–	5,15,23,24,25,26,27	
Singing honeyeater *Lichenostomus virescens*	–	–	–	1,6,12,13,14,20	–
Black honeyeater *Certhionyx niger*	–	–	–	**6,7,8,17,19**,**20**	
Spiny-cheeked honeyeater *Acanthagenys rufogularis*	–	–	2,5,12,13,14	–	–
Eastern rosella *Platycercus eximius*	–	–	5,**6**,8,11	–	–
Southern boobook *Ninox novaeseelandiae*	–	–	7,**13,12,26**	–	–
Brown falcon *Falco berigora*	–	**1**,9,**14**	–	–	–
Australian raven *Corvus coronoides*	–	**13,19,21**			
Blue bonnet *Northiel la haematogaster*	–	6,**14,19**	–	–	–
White-browed woodswallow *Artamus superciliosus*	–	**9**,15,**23**	–	–	–
Laughing kookaburra *Dacelo novaeguineae*	–	9,**15**,22	–	–	–
Grey shrike-thrush *Colluricincla harmonica*	–	1,**6,22**	–	–	–
Restless flycatcher *Myiagra inquieta*	–	**3**,26,**27**	–	–	–
Variegated fairy-wren *Malurus lamberti*	–	1,2,3	–	–	–
Black-faced cuckoo-shrike *Coracina novaehollandiae*	–	**3,25**	–	–	–
Noisy miner *Manorina melanocephala*	–	**13**,18	–	–	–
Nankeen kestrel *Falco cenchroides*	–	**13,14**	–	–	–
Welcome swallow *Hirundo neoxena*	–	**3**,25	–	–	–
Australian magpie-lark *Grallina cyanoleuca*	–	**24,25**	–	–	–
Purple-crowned lorikeet *Glossopsitta porphyrocephala*	–	**9**,15	–	–	–
Rufous song-lark *Cinclorhamphus mathewsi*	–	23,24	–	–	–
Southern whiteface *Aphelocephala leucopsis*	–	6,26	–	–	–
Brown-headed honeyeater *Melithreptus brevirostris*	–	**1,14**	–	–	–
Silvereye *Zosterops lateralis*	–	**10,22**	–	–	–
White-faced heron *Egretta novaehollandiae*	**21**	–	–	–	–
Black-shouldered kite *Elanus axillaris*	**13**	–	–	–	–
Barn owl *Tyto alba*	**16**	–	–	–	–
Long-billed corella *Cacatua tenuirostris*	**2**	–	–	–	–
Tree martin *Hirundo nigricans*	15	–	–	–	–
Black-faced woodswallow *Artamus cinereus*	**6**	–	–	–	–
Common bronzewing *Phaps chalcoptera*	**1**	–	–	–	–
Fan-tailed cuckoo *Cacomantis flabelliformis*	**10**	–	–	–	–
Black-eared cuckoo *Chrysococcyx osculans*	**5**	–	–	–	–
Horsfield's bronze-cuckoo *Chrysococcyx basalis*	**5**	–	–	–	–
White-winged triller *Lalage sueurii*	**6**	–	–	–	–
Golden whistler *Pachycephala pectoralis*	**1**	–	–	–	–
Gilbert's whistler *Pachycephala inornata*	**1**	–	–	–	–
White-browed babbler *Pomatostomus superciliosus*	**26**	–	–	–	–
Weebill *Smicrornis brevirostris*	1	–	–	–	–
Red wattlebird *Anthochaera carunculata*	**13**	–	–	–	–
White-eared honeyeater *Lichenostomus leucotis*	1	–			
Yellow-plumed honeyeater *Lichenostomus ornatus*	**5**	–	–	–	–
Fuscous honeyeater *Lichenostomus fuscus*	**1**	–	–	–	–
Total predictions	19	44	13	26	16
Correct predictions	16	27	4	9	11
Percent correct	84	61	31	35	69

buloke woodlands of western Victoria were fragmented ca 50–120 yr ago, which translates into > 40 generations for most bird species in the system. While this may seem ample time to expect changes in distribution patterns to be expressed, the generation times of birds may not be as relevant as the longevity and regeneration status of buloke trees. Indeed, the longevity of individual trees far exceeds the time since fragmentation, suggesting that the full effect of fragmentation has not yet been realized. While this need not lessen the relevance of research findings from recently modified landscapes, this mismatch of temporal scales may help explain the lack of predictive power in this study and in other studies taking similar approaches (Watson 2002). We suggest that

Table 6. Predicted species gains in specific buloke remnants as a function of probability bands based upon species occurrence frequencies in the first survey period. Numbers in columns refer to individual remnants. Correct predictions are in bold type.

Bird species	Probability classes		
	97–100%	90–97%	80–90%
Yellow-rumped thornbill *Acanthiza chrysorrhoa*	**1**,3,5,15,**20**,**22**,**23**,**25**	–	–
Yellow thornbill *Acanthiza nana*	–	**1**,2,3,5,**13**,14,15,**23**,25	
Red-capped robin *Petroica goodenovii*	–	–	**1**,3,5,**10**,15,18,**22**,**23**,24,**27**
Australian magpie *Gymnorhina tibicen*	–	–	1,3,5,**7**,**8**,**9**,**18**,23,**24**,**25**,**26**
Willie wagtail *Rhipidura leucophrys*	–	–	1,**2**,6,**7**,**8**,**10**,**15**,**16**,**17**,**23**,**25**
Total predictions	8	9	32
Correct predictions	5	3	21
Percent correct	62	33	66

repeat surveying of fragmented landscapes is one way of quantifying these long-term changes and we encourage other workers to adopt a similar approach. Alternatively, older landscapes such as forests fragmented by regional climate change thousands of years ago (Brown and Kodric-Brown 1977, Watson 2003) may be critical test arenas for the predictive approach.

We note that the standardized measures of nestedness for the buloke system, the Wright-Reeves C-values, are relatively low (<0.5) for terrestrial systems of habitat fragments (Wright and Reeves 1992), notwithstanding their statistical significance. This suggests that one ought not to dismiss summarily the potential usefulness of the packed matrix until its predictive capacity in more strongly nested fragmented systems is explored with follow-up survey data. However, our study indicates that in highly dynamic systems, the requirements for the Temperature Calculator to be a useful predictive tool are unlikely to be met. Unrecognized or undocumented dynamism may thwart efforts to use the Temperature Calculator predictively, particularly in assemblages of highly mobile animals, such as birds and bats, which are frequently used in nestedness analyses. We suggest that the Temperature Calculator may produce better predictive power for taxa that are less mobile than birds, such as reptiles and non-volant mammals. Further investigation of the predictive ability of the Temperature Calculator in systems more likely to be undergoing processes such as biotic relaxation is necessary before definitive conclusions on its usefulness can be drawn.

Acknowledgements – We are grateful to Lisa Morcom, formerly of the Stawell office of the Department of Natural Resources and Environment (DNRE), for sharing her extensive knowledge of the area, to Ian Voigt and Charles Hajek of the Catchment and Land Management team at the Horsham office, DNRE, for the use of a vehicle, to the Flora and Fauna Branch, DNRE, for providing financial assistance, and to the many landowners of the Wimmera for permission to access their land. MM and AL thank the Holsworth Wildlife Research Fund, the Stuart Leslie Bird Research Award, the Birds Australia VicGroup Award, and the School of Biological Sciences, Monash University for financial assistance. RM and DW acknowledge the support of the Australian Research Council. We thank E. Fleishman for providing comments on a preliminary draft of this paper. This is publication No. 30 from the Australian Centre for Biodiversity: Analysis, Policy and Management at Monash University.

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