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RESEARCH PAPER

What drives the positive correlation between human population density and bird species richness in Australia?

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ABSTRACT

Aim To test six hypotheses that could explain or mediate the positive correlation between human population density (HPD) and bird species richness while controlling for biased sampling effort. These hypotheses were labelled as follows: productivity (net primary productivity, NPP); inherent heterogeneity (diversity of vegetation types); anthropogenic heterogeneity (diversity of land uses); conservation policy (proportion of conservation land); increased productivity (human-induced productivity increases); and the reduced-slope hypothesis (which predicts that humans have a negative impact on species numbers across the full range of variation in HPD).

Location Australia.

Methods All data were collected at a spatial resolution of 1° across mainland Australia. Bird species richness was from 2007 atlas data and random subsampling was used to account for biased sampling effort. HPD was from the 2006 census. All other data were from government produced geographic information system layers. The most important biotic or abiotic factors influencing patterns in both species richness and HPD were assessed using simultaneous autoregressive models and an information theoretic approach.

Results NPP appeared to be one of the main factors driving spatial congruence between bird species richness and HPD. Inherent habitat heterogeneity was weakly related to richness and HPD, although an interaction between heterogeneity and NPP indicated that the former may be an important determinant of species richness in low-productivity regions. There was little evidence that anthropogenic landscape heterogeneity or human-induced changes in productivity influenced the relationship between species richness and HPD, but conservation policy appeared to act as an important mediating factor and species richness was positively related to the proportion of conservation land only in regions of high HPD.

Main conclusions The spatial congruence between bird species richness and HPD occurs because both respond positively to productivity and, in certain circumstances, habitat heterogeneity. Our results suggest that conservation policy could mediate this relationship, but further research is required to determine the importance of conservation reserves in supporting species in regions densely populated by humans.

Keywords

Australia, birds, human population density, landscape heterogeneity, land-use policy, potential energy, primary productivity, sampling effort, spatial covariance, species richness.

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INTRODUCTION

Over the past decade, a growing number of studies have demonstrated a positive correlation between human population density (HPD) and species richness for a variety of taxonomic groups (e.g. Balmford *et al.*, 2001; Araújo, 2003; Gaston & Evans, 2004; Luck *et al.*, 2004; Fjeldså & Burgess, 2008). Luck (2007a) conducted a meta-analysis on 25 of these studies and found a strong, positive population effect size (which represents correlation coefficients combined across studies) of 0.57 between HPD and richness. However, there was substantial heterogeneity across studies driven by factors such as taxonomic group and variation in the spatial extent and grain size (i.e. the size of the sampling unit) used by researchers (also see Pautasso, 2007). The strongest relationships occurred between HPD and bird species richness (population effect size 0.59) and at larger grain sizes (> 0.5°) across broad spatial extents (e.g. continental).

The spatial congruence between people and species richness raises substantial challenges for meeting conservation objectives in densely population regions (Fjeldså & Rahbek, 1998; Luck *et al.*, 2004; Araújo & Rahbek, 2007). Yet conservation near human settlements is vital for at least two reasons. First, there is growing recognition of the importance of human–nature interactions and exposure to a diverse natural world for psychological well-being, developing empathy for the environment and promoting conservation among the broader community (Mayer & Frantz, 2004; Dunn *et al.*, 2006; Fuller *et al.*, 2007). Second, species diversity can be crucial for the delivery of ecosystem services, many of which are generated and used locally (Díaz *et al.*, 2006).

Given the above, the human population–species richness correlation has substantial management implications in addition to being an intriguing biogeographic pattern. It is therefore crucial to attempt to identify the key drivers of this relationship. These drivers fall into two major categories: (1) underlying biotic or abiotic conditions that influence patterns in both species richness and human populations; and (2) human modification of the landscape increasing species richness near human settlements. In the first category, researchers have found that contemporary potential energy (Evans & Gaston, 2005; Schlick-Steiner *et al.*, 2008), net primary productivity (Luck, 2007b) or habitat heterogeneity (Steck & Pautasso, 2008) positively covary with species richness and HPD. Others have speculated that historical climatic stability has led to the spatial congruence between people and species richness (Fjeldså & Rahbek, 1998), although this hypothesis is difficult to test. In the second category, Hugo & van Rensburg (2008) compared four hypotheses, primarily related to human land-use policy (see below), as potential drivers or mediators of the bird species–people correlation in South Africa.

Yet, to our knowledge, no study has conducted a comprehensive comparison of various explanatory hypotheses from the two categories listed above or controlled for biased sampling effort prior to testing these hypotheses. The latter is crucial because biased sampling effort could yield positive HPD–species richness correlations if sampling effort is greatest in areas of high population density (Luck *et al.*, 2004). While Evans *et al.* (2007) found that variation in sampling effort did not explain the HPD–bird species correlation in Britain, and Pautasso & McKinney (2007) demonstrated the same for plant species in the United States, these studies did not go on to examine the relationships among HPD, species richness and various explanatory variables after controlling for sampling effort (indeed, this was not the aim of their respective studies).

Here, we examine six hypotheses that could explain the co-occurrence of people and species richness, or mediate this relationship, while accounting for biased sampling effort and spatial autocorrelation. The first hypothesis is energy/productivity (which we refer to as 'productivity' hereafter), which represents the strong interrelationships between available energy and primary productivity owing to mutual underlying factors such as solar radiation and water availability. This is a strong driver of patterns in species richness (Rahbek & Graves, 2001; Willig *et al.*, 2003) and could also explain variation in HPD. While human distribution patterns may be influenced by a range of factors such as distance to coast, elevation, soil fertility, cultural background and transport networks (e.g. Cohen & Small, 1998; Small & Nicholls, 2003; Vitousek *et al.*, 2004; Huston, 2005), our emphasis here is on broad-scale drivers that potentially explain both species richness *and* human distribution patterns.

The second hypothesis is habitat heterogeneity, which we measure across broad extents as the horizontal diversity of native habitat types and refer to as inherent heterogeneity. Our expectation from the first two hypotheses is that species richness and HPD will both be positively related to productivity and inherent heterogeneity, and that productivity and inherent heterogeneity will be included in highly ranked predictive models of species richness even when HPD is included as a predictor. Moreover, previous studies (e.g. Kerr & Packer, 1997) have demonstrated that the relationship between habitat heterogeneity and species richness can vary in regions of high or low energy/productivity. Therefore, we include an interaction term (productivity : inherent heterogeneity) in our models (see Methods).

The third hypothesis is anthropogenic landscape heterogeneity (Fairbanks, 2004). This hypothesis predicts that human activities increase species richness near human settlements by creating more heterogeneous landscapes and this leads to the species richness–HPD correlation. Therefore, we expect species richness and anthropogenic heterogeneity to be positively related, and the latter to be included in highly ranked predictive models of species richness even when HPD is included as a predictor. The fourth hypothesis is increased productivity (Hugo & van Rensburg, 2008), and this predicts that species richness is higher in regions of high HPD because human activities have increased productivity over time and relative to regions of lower HPD. Therefore, positive changes in productivity should be more prevalent in areas of high HPD.

The fifth hypothesis is conservation policy (Gaston, 2005), and this suggests that the level of conservation action is an important determinant of spatial variation in species richness irrespective of

HPD. Hence, HPD and species richness are correlated because both positively covary with conservation activities (this does not appear to be true in Australia; see Luck, 2007b) or that the strength of conservation action mediates the relationship between people and richness. To test for the latter, we include an HPD : conservation interaction term in our models and examine the relationship between species richness and the proportion of conservation land across varying values of HPD, and between species richness and HPD across varying values of conservation land. Our expectation is that the relationship between species richness and proportion of conservation land will be strongly positive in regions of high HPD and weaker (or negative) in regions of low HPD, and that the relationship between HPD and species richness will be strongly positive in regions with a high proportion of conservation land, and weaker (or negative) in regions with a low proportion of conservation land.

The sixth and final hypothesis is the 'reduced slope' hypothesis (*sensu* Hugo & van Rensburg, 2008, following Gaston, 2005), which predicts that humans have a negative impact on species richness across the full range of variation in HPD, even though relative richness may still be higher in regions of high HPD. If humans are having a negative impact on richness, we expect that the slope of a regression between richness and some other predictor (e.g. net primary productivity) will be shallower for a model that also includes HPD as a predictor versus one that does not. The aim of our analysis is twofold: (1) to determine the best combination of biotic and abiotic factors that explain spatial variation in both HPD and species richness, and (2) to examine the role of human activities in driving or moderating spatial patterns in richness.

METHODS

Study area, species richness and human population data

This study was conducted across mainland Australia (excluding Tasmania) with a sampling grain of 1° grid cells. We included coastal cells with less than 100% land cover since many Australians live near the coast, but explored the effects of grid cell area in the data analysis. Variation in study extent or grain size can affect conclusions about people–species relationships (Pautasso, 2007) and different drivers are likely to operate at different scales. Here, we aimed to explore drivers at the grain size where the HPD–species richness correlation is strongest (i.e. $> 0.5°$; Luck, 2007a). Moreover, we included the most comprehensively surveyed taxonomic group (birds), which consistently records strong positive correlations with HPD across many different contexts (see Luck, 2007a), and for which data on sampling effort were available. Data on bird species richness and sampling effort in each 1° grid cell were obtained from the Australian Bird Atlas (Barrett *et al.*, 2003). The database is continually updated with new records and we sourced data from the 2007 version. We excluded vagrant and marine species and explored relationships with native species only and native plus non-native species (total species).

Sampling effort in the Australian Bird Atlas is biased towards areas of higher HPD (Luck *et al.*, 2004). We controlled for this by including only 10 surveys per grid cell (a randomly selected subsample) for cells that were surveyed at least 10 times using standardized 2-ha, 20-min searches. This resulted in a total sample size (number of grid cells) of 611 with 532 species in the dataset. Standardized species richness (i.e. the sum of species from the 10 surveys) was positively correlated with HPD (Spearman rank correlation on untransformed data, $r_s = 0.46$, $n = 611$ unless otherwise stated), suggesting that variation in sampling effort is not the main driver of the HPD–species richness relationship. Sampling bias may also arise through factors such as observers being more familiar with survey areas closer to population centres, leading to greater knowledge of where to find the most species (Evans *et al.*, 2007). However, data were unavailable to allow us to control for such biases.

HPD was obtained from the 2006 Australian census (see Table S1 in Supporting Information). Population data at the census district level were converted to number of people per 1° grid cell (expressed as population density km^{-2}) using a modified version of a weighted distance–decay redistribution function to fit a smoothed surface to the data with the following equation (Martin & Tate, 1997):

$$W_{ij} = \left[(d-s)^2/(d+s)^2\right]^{\alpha}.$$

Here, d is the local average inter-centroid distance between census districts, s is the distance between cell i and centroid j, and $\alpha = 1$. (Modifying α adjusts the slope of the distance–decay function; a value of 1 results in a straight distance–decay line. See Appendix S1 for further details.)

Predictor variables and hypotheses

We initially included the following response and predictor variables in our analyses, presented as measures per grid cell (data handling, transformations and sources are detailed in Table S1): (1) response variables were native species richness, total species richness (including non-natives) and HPD; (2) predictor variables were mean annual areal actual evapotranspiration (AET), net primary productivity (NPP), the diversity of native vegetation types (inherent heterogeneity), the diversity of anthropogenic land uses (anthropogenic heterogeneity), the proportion of land area in each grid cell classified as conservation or minimal use, and HPD. We assessed multi-collinearity and pairwise relationships among transformed variables by first examining Pearson correlations and then calculating variance inflation factors through linear regressions, regressing a given independent variable against all others (Neter *et al.*, 1996).

Native species richness and total species richness were very strongly correlated ($r = 0.99$) and yielded the same results in subsequent modelling, largely because introduced species are a very small component of the total dataset (14 of 532 species). Therefore, only results with native species richness are presented. Although 1° grid cells are approximately 100 km by 100 km, their area can vary slightly with latitude, and coastal

Table 1 Pair-wise spatial correlations between all continuous variables. HPD $n = 514$, all others $n = 611$.

	SR	HPD	NPP	AET	IH	AH
HPD	0.38*					
NPP	0.38*	0.39*				
AET	0.28*	–0.04	0.76**			
IH	0.20	–0.05	0.02	–0.16		
AH	0.30	0.66**	0.52**	0.09	0.02	
CL	–0.36*	–0.12	–0.14	–0.13	–0.22	0.11

SR, species richness; HPD, human population density; NPP, net primary productivity; AET, actual evapotranspiration; IH, inherent heterogeneity; AH, anthropogenic heterogeneity; CL, the proportion of conservation land in each grid cell. $^{*}P < 0.05$, $^{**}P < 0.01$.

cells often contain less land area than inland cells. In our study, cell area ranged from 300 km^2 to 12,000 km^2, although 86% of cells fell within the bounds of 9000 km^2 and 12,000 km^2. While area is often positively correlated with species richness, in our study grid cell area was negatively correlated with both richness ($r_s = -0.13$) and HPD ($r_s = -0.49$). This is an artefact of most Australians living near the coast and coastal grid cells containing less land area and also more species (particularly in eastern Australia) relative to many inland grid cells. Moreover, results from regression models of species richness versus predictor variables were essentially the same with or without controlling for area.

The energy/productivity [productivity] hypothesis was represented by NPP. AET and NPP were strongly positively correlated (spatial correlation, $r = 0.76$, $F = 43.2_{31.6}$, $P < 0.01$) most likely because they capture similar dynamics (i.e. the interrelationships among solar radiation, water availability and plant growth). However, NPP had a stronger relationship with both HPD and species richness (see Table 1) and was therefore retained as the sole measure representing the productivity hypothesis.

The inherent heterogeneity hypothesis was represented by the Shannon diversity index of native vegetation types, while the anthropogenic heterogeneity hypothesis was represented by the Shannon diversity index of anthropogenic land uses (see Table S1). To test if the relationship between habitat heterogeneity and species richness varies in regions with different levels of productivity (see Introduction), we included an inherent heterogeneity–NPP interaction term in our regression models. To assist in interpreting this interaction, we split the NPP data into quartiles and correlated inherent heterogeneity with species richness in each quartile, and also split the heterogeneity data into quartiles and correlated NPP with species richness in each quartile (see Fig. S1). While categorizing the data in this way is arbitrary, it provides more information for interpretation than the interaction term alone.

The increased productivity hypothesis was tested using data on current NPP and estimates of NPP prior to European settlement of Australia ('historical' NPP; see Table S1). For each grid cell, we subtracted historical NPP from current NPP and then correlated the proportional change in NPP [i.e. (current NPP – historical NPP)/historical NPP] with HPD across cells. In the historical estimates, NPP is given a nominal value of zero in arid and semi-arid regions and we removed zero values prior to calculations. This did not affect our conclusions because we recorded a negative relationship between HPD and change in NPP (see Results). If grid cells with zero values for historical NPP had been included in the analysis, these would have recorded a positive change in NPP when compared with current estimates, because current estimates of NPP in arid and semi-arid grid cells are greater than zero. Arid and semi-arid regions are characterized by very low HPD – hence including the zero-value grid cells would have only strengthened the negative relationship. We considered it more conservative to exclude these cells knowing that it is highly unlikely that historical NPP would have been zero.

To test the conservation policy hypothesis, we determined the percentage cover of land uses classified as nature conservation, managed resource protection and other minimal use in each grid cell (see Table S1). As minimal use areas can contribute to species conservation, but may not be included in the conservation reserve system, we preferred a broad definition of conservation land use.

We included the proportional cover of conservation land use as a continuous variable in the regression models. We also included the interaction term HPD : conservation land use to test if conservation policy mediates the relationship between HPD and species richness. To assist in interpreting this interaction, we split the HPD data into quartiles and correlated proportional cover of conservation land use with species richness in each quartile, and also split the conservation land use data into quartiles and correlated HPD with species richness in each quartile (see Fig. S2). If conservation policy mediates the relationship between HPD and species richness, we expect the form and strength of this relationship to vary among regions with different levels of conservation land use (see Introduction).

We tested the reduced slope hypothesis by calculating the slope of the relationship between species richness and NPP (the variable with the strongest positive relationship with richness) in models that included and excluded HPD. We compared the overlap of both 95% and 84% confidence intervals (CIs) of slope estimates because 95% CIs are widely used in the literature, and the overlap of 84% CIs corresponds to testing at an alpha level of 0.05 (see Payton *et al.*, 2003) and this approach has been used in related studies (e.g. Evans *et al.*, 2006b; Hugo & van Rensburg, 2008). If HPD is having a negative impact on species richness across the full range of variation in density, then the slope of the model including HPD should be shallower than the one excluding it, significantly so if confidence intervals do not overlap.

Data analysis

All modelling was undertaken using S-PLUS 7.0® and the Spatial Analysis in Macroecology (SAM) version 3.0 software (Rangel *et al.*, 2006). Spatial correlations were calculated between each continuous variable using the method of Dutilleul (1993) in the software program SAM.

We analysed relationships between HPD and species richness (response variables) and the predictor variables using spatial models that accounted for spatial autocorrelation and were based on ordinary least squares regression. The spatial structure in the data was explored using Moran's *I* coefficient and related spatial correlograms. This indicated the presence of spatial autocorrelation in response and predictor variables. Therefore, we employed simultaneous autoregressive models that assume that the autoregressive process is found in the error term. Such models have been shown to perform well in a variety of spatial pattern scenarios (Kissling & Carl, 2008). We report r^2 values for these models, which incorporate the effects of both the predictor variables and space (Rangel *et al.*, 2006).

With species richness as the response variable, we fitted models based on all possible combinations of the predictor variables NPP, inherent heterogeneity, anthropogenic heterogeneity and conservation land use including and excluding HPD (we did not include 'increased productivity' in this analysis because this was represented by a different [smaller] set of grid cells). We also fitted the following two interaction terms: (1) NPP : inherent heterogeneity, and (2) HPD : conservation land use (see explanation above). With HPD as the response variable, we fitted models based on all possible combinations of the predictor variables NPP and inherent heterogeneity, including the interaction term. We do not believe that anthropogenic heterogeneity or conservation land use should be considered as predictors of HPD at the broad scale considered here; indeed, HPD as a predictor of the former is more appropriate.

Models were ranked using an information theoretic approach (ITA) based on Akaike's information criterion (AIC; Burnham & Anderson, 2002). We compared the difference in the criterion values of the best ranked model with model i (Δ_i) only for those models where the response data were the same (i.e. included the same grid cells). The best ranked model (with the smallest AIC value; $\text{AIC}_{\min}$) always has a Δ_i value of 0. For subsequent models, $\Delta_i = \text{AIC}_i - \text{AIC}_{\min}$, where AIC_i is the AIC value of the model being compared with the best ranked model. Models where Δ_i is < 2 are usually considered to have substantial empirical support; values between 2 and 4 suggest some support, while values > 4 indicate little support in the suite of models being considered (Burnham & Anderson, 2002, 70). Akaike weights (w_i) were also calculated for each model and these represent the relative likelihood of the model and can be interpreted as the probability that any given model is the best model given the data at hand. We present the results from the 99% confidence set of models (i.e. where w_i summed across models equals 0.99) in the text and the results from all models in Table S2.

We also calculated the summed Akaike weights for each predictor and interaction term (i.e. summing w_i across the models that the predictor/interaction term occurred in) as a measure of the relative importance of each variable, and model-averaged estimates of effects (model coefficients). In general, Akaike weights for each predictor should only be summed across models if each variable occurs in the same number of models. This is not the case when interaction terms are included in models (they occur in fewer models than each individual predictor). Therefore, the Akaike weights for interaction terms can be reduced relative to the other variables because they occur in fewer models. This issue had only a minor effect on our results since the summed Akaike weight for HPD : conservation land use was 1 (the maximum Akaike weight value that can be obtained) and 80% of the models ($n = 10$) including the interaction term NPP : inherent heterogeneity had an Akaike weight < 0.001; hence, additional models including this interaction would be likely to have small Akaike weights and add little to its total summed Akaike weight. In line with this, model-averaged coefficients were calculated only for those models in which the variable or interaction term occurred.

We looked for simple nonlinear relationships by including quadratic terms in each model, but these failed to improve model fit. The data for HPD were heavily skewed and the distribution was not improved with standard transformations. Therefore, we removed zero values (reducing the sample size to 514 after excluding 97 grid cells) and employed a Box–Cox power law transformation (Box & Cox, 1964) using the following equation:

$$y = (x^{\lambda} - 1)/\lambda.$$

Here, x is the variable to be transformed and λ is constrained between 0 and 1. A value of 0.1 for λ yielded a distribution for HPD that approximated normality.

RESULTS

NPP and inherent heterogeneity

NPP was strongly positively correlated with both species richness and HPD (Table 1, Fig. 1). It was also included in all spatial models of species richness in the 99% confidence set of models where $\Delta_i \leq 4$, along with HPD, conservation land use, and the HPD : conservation land use interaction (Table 2). Moreover, the summed Akaike weight for NPP was 1 (Table 3), suggesting it is an important predictor of species richness and is possibly an underlying driver of the spatial correlation between HPD and richness.

Inherent heterogeneity had a weaker positive relationship with species richness, and was essentially uncorrelated with HPD (Table 1, Fig. 1). Moreover, the summed Akaike weight for

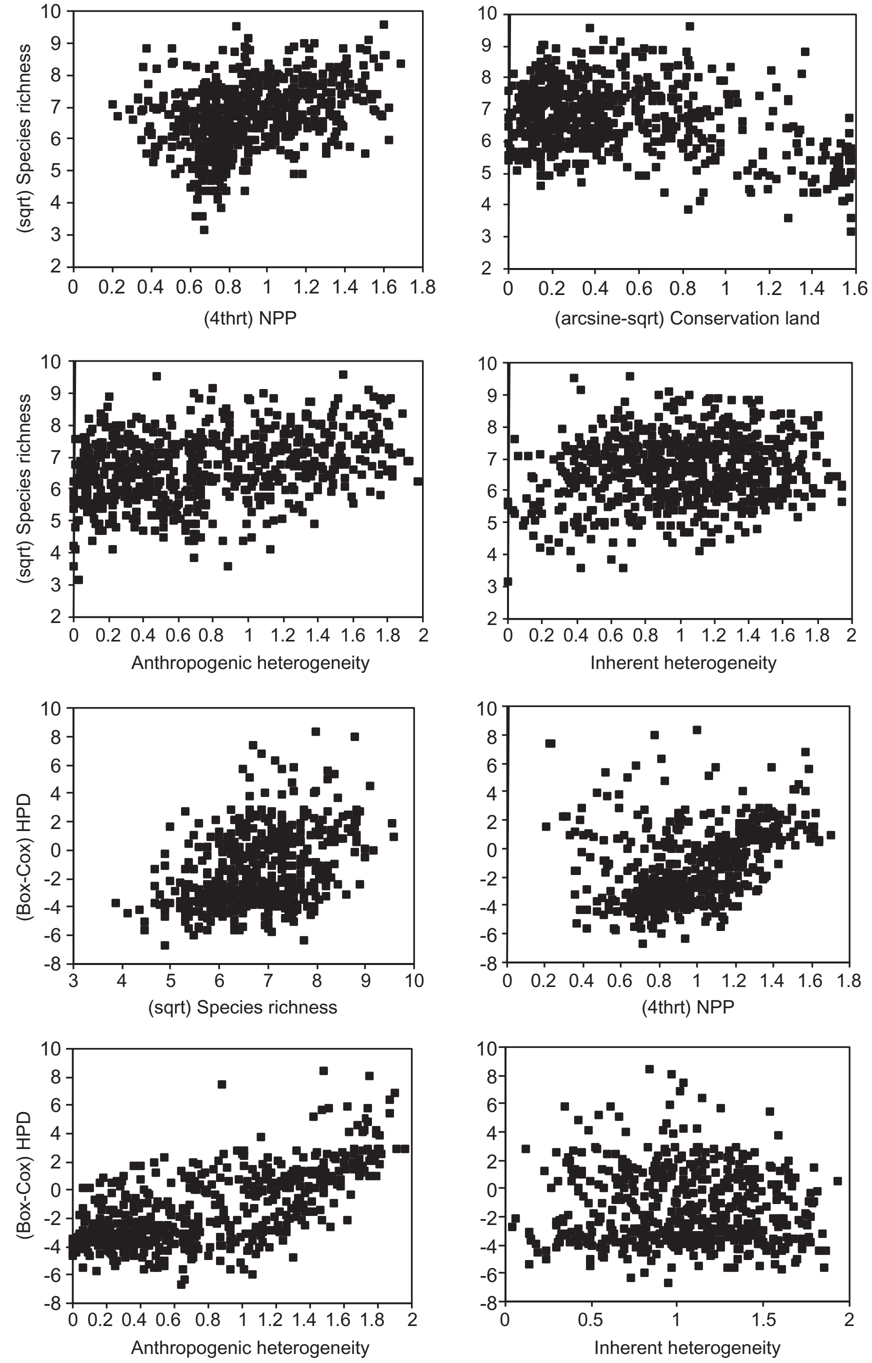

Figure 1 Relationships between species richness ($n = 611$) and human population density (HPD; $n = 514$) and each of the predictor variables. NPP = net primary productivity, conservation land = the proportion of conservation land in each grid cell, sqrt = square root transformation, 4thrt = fourth-root transformation, arcsine-sqrt = arcsine square-root transformation, Box-Cox = Box–Cox power law transformation (see text and Table S1 for further details).

this variable was relatively small (0.43; Table 3). However, the variable was prominent in highly ranked multivariate models, suggesting its effects are mediated in the presence of other factors. Indeed, the model coefficients for inherent heterogeneity in models of species richness were always larger when the NPP : inherent heterogeneity interaction was included in the model (this was also true for NPP in many cases; Tables 2 & S2), although the NPP : inherent heterogeneity interaction term was not an important predictor of species richness with a summed Akaike weight of just 0.14 (Table 3).

This NPP : inherent heterogeneity interaction term had a negative coefficient. Examination of the correlations between NPP and species richness for different quartiles of inherent heterogeneity showed that NPP and species richness were most

Table 2 Spatial models of species richness ($n = 611$) and human population density (HPD; $n = 514$).

Model	r^2	AIC	Δ_i	w_i
Response variable: species richness				
HPD (0.04; 0.02) + NPP (0.66; 0.15) + conservation (–0.11; 0.14) + HPD : conservation (0.09; 0.02)	0.31	1605.56	0	0.37
HPD (0.03; 0.02) + NPP (0.53; 0.15) + conservation (–0.21; 0.15) + anthropogenic heterogeneity (0.22; 0.09) + HPD : conservation (0.08; 0.02)	0.31	1606.80	1.24	0.20
HPD (0.04; 0.02) + NPP (0.67; 0.15) + conservation (–0.15; 0.14) + inherent heterogeneity (0.21; 0.09) + HPD : conservation (0.07; 0.02)	0.31	1606.93	1.37	0.19
HPD (0.03; 0.02) + NPP (0.55; 0.15) + conservation (–0.25; 0.15) + inherent heterogeneity (0.21; 0.09) + anthropogenic heterogeneity (0.22; 0.09) + HPD : conservation (0.07; 0.02)	0.31	1608.27	2.71	0.09
HPD (0.04; 0.02) + NPP (1.07; 0.36) + conservation (–0.14; 0.14) + inherent heterogeneity (0.55; 0.29) + HPD : conservation (0.07: 0.02) + NPP : inherent heterogeneity (–0.38; 0.31)	0.31	1608.28	2.72	0.09
*HPD (0.03; 0.02) + NPP (0.91; 0.37) + conservation (–0.23; 0.15) + inherent heterogeneity (0.52; 0.29) + anthropogenic heterogeneity (0.21; 0.09) + HPD : conservation (0.07; 0.02) + NPP : inherent heterogeneity (–0.34; 0.31)	0.31	1609.70	4.14	0.05
Response variable: HPD				
*Inherent heterogeneity (0.93; 0.88) + NPP (3.67; 1.04) + NPP : inherent heterogeneity (–1.32; 0.91)	0.13	2398.39	0	0.42
Inherent heterogeneity (–0.29; 0.25) + NPP (2.27; 0.40)	0.13	2398.60	0.21	0.38
NPP (2.31; 0.39)	0.12	2399.96	1.57	0.19
Inherent heterogeneity (–0.43; 0.26)	0.05	2442.01	43.62	< 0.001

Model coefficients and standard errors are shown in brackets. Also shown are r^2 (incorporating the effects of the predictors and space), Akaike's information criterion (AIC), the difference in criterion values (Δ_i) and Akaike weights (w_i). NPP = net primary productivity, conservation = the proportion of conservation land in each grid cell. The full (saturated) model is indicated by *.
Only the top models are shown (99% confidence set; $\Delta_i \leq 4$); see Table S2 for all models.

Table 3 Summed Akaike weights (w_i) for each predictor variable and interaction term, and model-averaged coefficients and standard errors (SE).

	Summed w_i	Averaged coefficient	SE
Response variable: species richness			
NPP	1	0.68	0.20
HPD	1	0.04	0.02
Conservation	1	–0.16	0.14
HPD : conservation	1	0.08	0.02
Inherent heterogeneity	0.43	0.32	0.18
Anthropogenic heterogeneity	0.34	0.22	0.09
NPP : inherent heterogeneity	0.14	–0.37	0.31
Response variable: HPD			
NPP	0.99	2.87	1.14
Inherent heterogeneity	0.80	0.35	0.95
NPP : inherent heterogeneity	0.42	–1.32	0.91

NPP, net primary productivity; HPD, human population density; conservation, the proportion of conservation land in each grid cell.

strongly correlated in regions of low heterogeneity ($r_s = 0.54$, $P < 0.001$), with the correlation weakening as heterogeneity increased (although always remaining significantly positive; see Fig. S1a). Moreover, the correlation between inherent heterogeneity and species richness was significantly positive for the lowest quartile of values for NPP ($r_s = 0.38$, $P < 0.001$), and substantially weaker and non-significant as productivity increased (see Fig. S1b).

Anthropogenic heterogeneity and increased productivity

Anthropogenic heterogeneity had a weak positive spatial correlation with species richness and a significant positive correlation with HPD (probably reflecting the relationship between human population growth and land conversion and diversification of land use; Table 1, Fig. 1). It was also significantly positively correlated with NPP. While anthropogenic heterogeneity was included in three of the top six models predicting species richness (Table 2), its summed Akaike weight was relatively small (0.34; Table 3). Therefore it does not appear to be an important predictor of species richness and its relationship with richness probably reflects interactions with HPD and NPP.

There was no evidence to suggest that the HPD–species richness correlation is a result of increased landscape productivity near human settlements. The correlation between HPD and proportional change in NPP from pre-European to the present day was negative ($r_s = -0.56$, $n = 339$) indicating that, on average, productivity has increased more in areas of low HPD.

Conservation land and reduced slope hypothesis

The proportion of conservation land in each grid cell was negatively correlated with both species richness and HPD, although the relationship was significant only for species richness (Table 1, Fig. 1). This variable was included in all of the 99% confidence set of models (Table 2) and had a summed Akaike weight of 1 (Table 3). However, its coefficient was always reduced (i.e. less negative) in models including the interaction between HPD and conservation (Table S2). This interaction term was also included in all of the top six models and had a summed Akaike weight of 1 (Tables 2 & 3). This suggests that the proportion of land managed for conservation could moderate the relationship between species richness and HPD, in line with predictions from the conservation policy hypothesis (see above). The form of this moderation is clear when examining correlations between species richness and conservation land across quartiles of HPD. At the lowest values of HPD, species richness and the proportion of conservation land are significantly negatively correlated ($r_s = -0.51$, $P < 0.001$), only becoming significantly positively correlated at the highest values of HPD ($r_s = 0.21$, $P = 0.01$; see Fig. S2a). Further, the correlation between HPD and species richness is weakest (although still positive and significant) across the lowest quartile of conservation land values, becoming consistently stronger as the proportion of conservation land increases (see Fig. S2b).

There was also some support for the reduced slope hypothesis. The slope of the relationship between species richness and NPP was reduced when HPD was included in the regression model (i.e. 1.12 HPD excluded vs. 0.59 HPD included), and while the 95% CIs overlapped (0.83–1.41 and 0.30–0.88, respectively) the 84% CIs did not (0.91–1.34 and 0.38–0.81), suggesting that the difference was significant at $\alpha = 0.05$.

Model outcomes and HPD

The highest ranked spatial model for species richness included HPD, NPP, conservation land and the HPD : conservation interaction [$r^2 = 0.31$ (incorporating the effects of the predictor variables and space); $w_i = 0.37$; Table 2]. However, three models had substantial support ($\Delta_i < 2$) and six models were included in the 99% confidence set of models ($\Delta_i \leq 4$). Importantly, HPD was included in all of these models and appeared to be an important predictor of species richness with a summed Akaike weight of 1 (Table 3). This suggests that while we may have identified some of the key drivers of the correlation between HPD and richness, other factors influence this relationship (see Discussion). The highest ranked model predicting variation in HPD included inherent heterogeneity, NPP and the interaction between these variables ($r^2 = 0.13$; $w_i = 0.42$), although, again, three models had substantial support, with the strongest univariate relationship occurring with NPP (Table 2), which also had the largest summed Akaike weight (Table 3).

DISCUSSION

Net primary productivity appears to be one of the main factors driving the spatial congruence between HPD and the species richness of birds in Australia. Birds and people are responding to a productivity gradient with values that generally increase from central Australia towards the coast, particularly eastwards. Therefore, the broader energy/productivity hypothesis is supported. There was only weak support for the inherent heterogeneity hypothesis, although its effects on species richness and HPD were mediated by an interaction with NPP (see below). There is little to no evidence to suggest that human activities in the form of anthropogenic landscape heterogeneity or increased net primary productivity contribute independently to greater species richness near human settlements, contrary to previous results (Fairbanks, 2004; Hugo & van Rensburg, 2008). However, conservation policy appears to moderate the relationship between birds and people, and conservation areas may be particularly important in protecting species in regions of high HPD (see below).

There is also some evidence to suggest that human activities have a negative impact on species richness across the full range of variation in human density (the reduced slope hypothesis). However, this pattern should be interpreted with caution because the slope of the relationship between species richness and NPP may be reduced when HPD is included as a predictor, owing to collinearity between HPD and NPP. Evans & Gaston (2005) provided an extensive discussion of this issue, although they concluded that in their study the reduced slope between species richness and energy when taking HPD into account was not likely to be completely explained by the collinearity between HPD and energy because the tolerance value for HPD was 0.4 (generally, collinearity is only a concern when tolerance values are <0.1), and the slope of the relationship between species richness and energy was not significantly different when HPD was replaced by another predictor (mean altitude) that was similarly correlated with energy availability. We repeated the analysis of Evans & Gaston (2005) using our data (see Appendix S1). This analysis showed that the reduced slope of the relationship between species richness and NPP was unlikely to be fully explained by the collinearity between HPD and NPP, although we stress that this pattern requires further investigation.

The relationship between bird species richness and NPP (and richness and AET) was relatively weak compared with previous studies. For example, Hawkins *et al.* (2005) reported a positive correlation of 0.78 between both native bird species richness and AET, and species richness and the normalized difference vegetation index (a surrogate for NPP) across Australia at a grain size comparable to ours. The weaker relationships reported in our study may be a factor of controlling for sampling effort, which helps to account for the inter-relationships among environmental variables, HPD, sampling effort and species richness. For example, Luck (2007b) reported a rank correlation of 0.70 between bird species richness and NPP across Australia without controlling for sampling effort. This calls into question the strength of reported relationships between species richness and broad-scale environmental factors when variation in sampling effort is not considered. However, comparisons among studies should be made cautiously, owing to, for example, differences in data sources, scale and approach.

Previous studies have demonstrated how energy/productivity covaries with species richness and HPD (e.g. Chown *et al.*, 2003; Evans & Gaston, 2005; Schlick-Steiner *et al.*, 2008). The positive relationship between richness and energy is a well-recognized biogeographic pattern, although relationships vary across scales and taxonomic groups (Mittelbach *et al.*, 2001; Whittaker & Heegaard, 2003). Although human settlement patterns are undoubtedly influenced by a complex array of socio-economic and cultural factors (Huston, 2005), it appears that primary productivity, and its likely effects on patterns of early settlement, is an important determinant of current population distribution (see Luck, 2007b, for further discussion of the factors influencing human distribution in Australia).

Key components of productivity (and AET) include solar radiation and rainfall/water availability – the latter being particularly important in relatively dry regions such as Australia (Hawkins *et al*., 2003). Climate change will see long-term variations in these factors influencing the energy/productivity characteristics of landscapes. Spatio-temporal shifts in the distribution of productivity have implications for future spatial congruence between HPD and species richness, and this is an important topic for upcoming research. Rainfall is predicted to decline by between 2 and 5%, and temperature to increase by between 1 and 1.5 °C, across much of southern Australia, which harbours the majority of the country's population (climate changes based on mid-range predictions and medium greenhouse gas emissions; CSIRO, 2007). These changes are likely to be even greater in inland Australia with the potential result that species unable to adapt *in situ* will, if possible, demonstrate shifts in geographic ranges towards the coast. Assuming humans do not also show major shifts in distribution (rapid shifts are unlikely given current investment in infrastructure) this will potentially increase the spatial congruence between people and species richness.

This possibility further underscores the vital importance of conservation reserves and other low-impact land use in protecting species near human settlements. Our study suggests a mediating effect of conservation policy on the species richness–HPD relationship. Species richness and HPD were negatively correlated with the proportion of conservation land in each grid cell. This relationship was significant only for richness, but previous work by Luck (2007b) has demonstrated a significant negative relationship between HPD and the size of conservation reserves. These results are consistent with previous studies in Australia showing that conservation reserves are mostly confined to the least productive regions that are largely unsuitable for human use (e.g. Pressey, 1994). They are also broadly in agreement with studies from South Africa and Britain showing that, while species richness and the amount of protected land are positively related, the relationship is quite weak (Evans *et al*., 2006a; Jackson *et al*., 2009).

In our study, the interaction term HPD : conservation land was included in all of the top six ranked models (99% confidence set) and had a summed Akaike weight of 1 (the largest that can be obtained). Further exploration of this interaction demonstrated that, despite a negative relationship overall, the correlation between species richness and the proportion of conservation land was in fact significantly positive in regions of high HPD (the top quartile of values). Moreover, the correlation between HPD and species richness was weakest, albeit still significantly positive, in regions with the lowest proportion of conservation land. This suggests that conservation reserves near human settlements are important for protecting species as human populations grow. However, the positive relationship between HPD and richness in regions with low conservation land cover indicates that off-reserve conservation must be an important component of any comprehensive protection strategy. Moreover, some doubt remains about the absolute importance of the HPD : conservation interaction in moderating the HPD–species richness relationship, as it only explained a small proportion of additional variance (*c*. 1–2%) in regression models that included the term versus comparable models that did not. Nevertheless, in total, our results suggest the interrelationship between human population density, species richness and species conservation is a crucially important issue deserving much greater attention.

Over broad scales, habitat heterogeneity is generally positively related to species richness (studies reviewed in Tews *et al*., 2004). The overall relationship between inherent heterogeneity and bird richness in our study was weak, but increased substantially in importance in low- compared with high-productivity regions. This contrasts with previous studies (e.g. Kerr & Packer, 1997), although comparisons among studies should be made cautiously owing to different measures of heterogeneity and the use of different grain sizes and taxonomic groups. In Australia, it is reasonable to hypothesize that inherent habitat heterogeneity might be more important in regions of low productivity in dictating patterns of animal species richness. Assuming that NPP positively correlates with resource abundance, highly productive regions would contain abundant resources even when broad-scale habitat heterogeneity was low, and variation in productivity would be a more important determinant of the capacity of landscapes to support a given number of species. Conversely, in low-productivity regions, diversity of vegetation types (closely tied to the availability of water) becomes more critical in supplying a range of resources that can be exploited by a greater number of species. Such a relationship has important implications for conservation policy across regions of varying productivity, and this hypothesis requires further assessment.

Although we have identified some of the potential drivers of the spatial correlation between HPD and species richness, HPD was an important predictor (summed Akaike weight of 1) of richness in models that included other variables. Therefore, other factors not considered here may be contributing to the spatial congruence between people and bird richness. These could include species introductions (e.g. McKinney, 2002; although we largely controlled for this by focusing on native species only) and the provision of resources through human activities (e.g. bird feeding stations; Fuller *et al*., 2008).

A number of studies show that relationships among species, humans and environmental variables differ across scales and for different species groupings (e.g. threatened species, endemic species and common species; Luck, 2007a). While it is important to acknowledge this, it is also critical to examine key drivers at particular scales, and our primary purpose here was to focus on the relationship between *total* species richness and HPD. Analyses using large sampling grains (e.g. 1°) across broad extents are important for informing regional management strategies, recognizing that the impacts of human settlements extend well beyond the settlement boundary. Moreover, they highlight the need to meld conservation and development in a given region to ensure local human populations have easy access to the variety of goods and services provided by local ecosystems.

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SUPPORTING INFORMATION

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

Figure S1 Correlations between net primary productivity (NPP) and bird species richness for each quartile of inherent heterogeneity, and between inherent heterogeneity and bird species richness for each quartile of NPP.

Figure S2 Correlations between the proportion of conservation land in each grid cell and bird species richness for each quartile of human population density (HPD), and between HPD and bird species richness for each quartile of conservation land.

Table S1 Each response and predictor variable, data handling procedures, transformations and sources of information.

Table S2 All spatial models of species richness and human population density.

Appendix S1 Population interpolation methods and reduced slope hypothesis.

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