

# The use of Australian bioregions as spatial units of analysis to explore relationships between climate and songbird diversity

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Biogeographers often investigate patterns of biodiversity at continental and global scales, using existing data georeferenced to a lattice of cells of latitude and longitude. Problems can arise with this approach when the available biological data are insufficient to adequately sample each cell and the cells are environmentally heterogeneous. An alternative, though less-often employed, approach is to use bioregions (defined as areas with distinctive biophysical environmental characteristics) as the basic sampling unit and to statistically control for unequal areas of regions. Here we applied this latter approach with the Interim Biogeographical Regionalisation of Australia (IBRA) to analyse continental patterns of songbird species richness in relation to mean annual precipitation, mean annual temperature, and mean wet season temperature, which are all predicted to substantially change given anthropogenic climate change. We used the Birds Australia database that has a large sample (>1,560,000) of distribution records covering Australia. For each of the 85 IBRAs, we determined the total number of songbird species and standardized these richness values accounting for the species-area effect by including the log of bioregion area as a covariate in the statistical models. Our analysis of standardized bioregion songbirds richness showed that the best supported model, based on information theory statistics included an interaction of mean annual temperature and precipitation (48.6% deviance explained). The fitted model showed declining richness with increasing temperature and declining precipitation, signalling that future climates may result in regional declines in songbird abundance. We suggest our simple empirical-statistical approach, using bioregions as the spatial unit, has promise for continental and global impact assessment of diversity changes and for conservation planning

Key words: biodiversity, bioregionalization, climate, conservation planning, songbirds, Passeriformes

## INTRODUCTION

DETECTION of biogeographic patterns is a critical step in formulating regional and global conservation plans. One challenge is to provide objective assessments of overall diversity for the different species and ecosystems within and between regions (beta and gamma diversity) (Whittaker 1972; Hunter 2002). Grid-based analyses of species richness have commonly been used to assess biodiversity hotspots, adequacy of conservation reserves, and to understand how geographical patterns of species richness may change in response to climate change (eg. Hnatiuk and Maslin 1988; Funk and Richardson 2002; Slatyer *et al.* 2007; Baselga and Araújo 2009; Ko *et al.* 2009, Powney *et al.* 2010). However, this approach has a number of problems related to the availability of data and the level of understanding of underlying biogeographic patterns. For example, Rahbek and Graves (2001) assessed avian richness in South America using grids of various scales. They found models based on large cells were geographically inaccurate, while models using small cells had lower explanatory power. As we outline below, an alternative to grid-based analyses are bioregions.

Bioregions define geographic areas that contain similar biophysical characteristics and are conventionally defined by boundaries in biomes (e.g., forest versus grassland), physiographical boundaries, or regions of distinctive regional biota. The mode of classificatory system and spatial scale of bioregions depends upon the purpose of the scheme (Mackey *et al.* 2008a). For example, Olson *et al.* (2001) defined the global ecoregions they developed for conservation planning as “relatively large units of land containing a distinct assemblage of natural communities and species, with boundaries that approximate the original extent of natural communities prior to major land-use change”. Likewise in Australia, Thackway and Cresswell (1995) demarked bioregions (Interim Biogeographical Regionalization of Australia; IBRA) to suit a diversity of planning purposes, including an evaluation of conservation status of species and ecosystems (e.g., Australian Government Department of Sustainability, Environment, Water, Population and Communities 2004; Land and Water Australia 2002).

Both the Olson *et al.* (2001) and Thackway and Cresswell (1995) schemes followed the

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established approach of defining bioregions — a naturally complex agglomeration of biophysical and ecological factors — largely on the basis of expert knowledge. Olson *et al.* (2001) argued that such a subjective approach will more accurately reflect the distribution of species and communities than geographical units based on gross biophysical features (such as rainfall, temperature, and vegetation structure), or spatial patterns in land surface characteristics revealed by remote-sensing analyses. These authors contend that the latter approaches do not adequately weight the effects of historical and evolutionary process that give rise to patterns of endemism and regional diversity such as biodiversity hotspots. Furthermore, expert knowledge approaches are often needed because of the lack of data. More quantitative and objective approaches require high quality data spatially distributed across the region or continent of study (Mackey *et al.* 2008a).

The IBRA bioregions provide spatial units of analysis that vary in area depending on underlying topography, substrate and primary productivity; variables known to influence biodiversity. McKenzie *et al.*'s (2007) analysis of contemporary and historical Australian mammal biogeography utilized the IBRA bioregions as the fundamental unit of data analysis. They argued that the IBRA sample units captured contrasting climates, histories, landforms and threatening processes. However, McKenzie *et al.* (2007) did not control for variation in the geographical size of each bioregion. This is a significant problem given it is well known, that it is important to take into account the species area effect. The theory of island biogeography shows that cumulative species counts tend to approach an asymptote as area increases (Arrhenius 1921; MacArthur and Wilson; 1969).

Here we use the IBRA bioregions to analyse continental patterns of songbird species richness in relation to climate variables while controlling for bioregion area. Songbirds are a power bio-indicator because species belong to contrasting ecological guilds (e.g., vertebrates and invertebrates predators and nectar, fruit or seed feeders) and have strong habitat and niche specificities (Ford and Paton 1985; MacNally 1994; Recher 2004) due to, in part, to a long evolutionary history in Australia (Barker *et al.* 2002; Ericson *et al.* 2002). Indeed, birds have been used as an indicator of environmental health for the Tasmanian State of Environment Report (Tasmanian Planning Commission 2009). There are continent-wide distributional records available for songbirds. Despite some inevitable geographic biases caused by inaccessibility and therefore less frequent record keeping (e.g., in the sparsely inhabited central deserts or wet-dry tropics) these bird data are the most

comprehensive for any Australian flora or faunal group. Critically, these data have been digitally compiled, facilitating analysis (Barrett *et al.* 2003).

Here we compare models of songbird richness relationship in relation to climate data using a grid and bioregional approach. We selected simple climate variables in our analysis (mean annual precipitation, mean annual temperature, and mean wet season temperature) as these variables are known to affect biological processes and primary productivity (Mackay *et al.* 2008b) and are all predicted to substantially change given anthropogenic climate change.

## METHODS

Sighting locations for 192 Australian songbird species (order Passeriformes) between 1996 and 2006 were derived from the Birds Australia Atlas (Birds Australia 2007). For each of the 85 IBRA bioregions (IBRA 6.1) the bird locations were summed with GIS (ArcMap 9.2) to calculate a species richness value for each bioregion and standardized to species density per 100,000 ha. For comparative purposes, richness was also calculated for a 0.5-degree grid across the continent. We plotted species accumulation curves by counting the number of new species with increasing area from the centroid of each bioregion (Supplementary material). Moran's I (Moran 1950) was calculated for both the grid richness and the standardized bioregion richness data.

Climate data for mean annual temperature (MAT), mean temperature of the wettest season (MWT) and mean annual precipitation (MAP), at 5 arc-minute resolution, were obtained from the WorldClim 1.4 data set (Hijmans *et al.* 1995; WorldClim 2009). Monthly gridded net primary productivity data was obtained from Van der Werf *et al.* (2006) analysis of MODIS satellite data, and was averaged for all months to produce an annual mean monthly NPP measure and the mean of these data were calculated for each of the 85 IBRA bioregions. A scatter plot of mean NPP was plotted against bioregion area, and the  $R^2$  was determined between NPP and MAP.

Generalized linear models (gamma distribution, log link) with information-theoretic multi-model inference based on Akaike's Information Criterion (AIC; Burnham and Anderson 2002) were used to identify the single and combined explanatory power of three climate variables (mean annual precipitation, mean annual temperature, and mean wet season) that best explain variation in songbird richness between IBRA bioregions. The natural log of bioregion area was included in the models

to account for the effect of bioregion area on the number of species (Arrhenius 1921). The strength of the interactions of variables in the top ranked model was also explored.

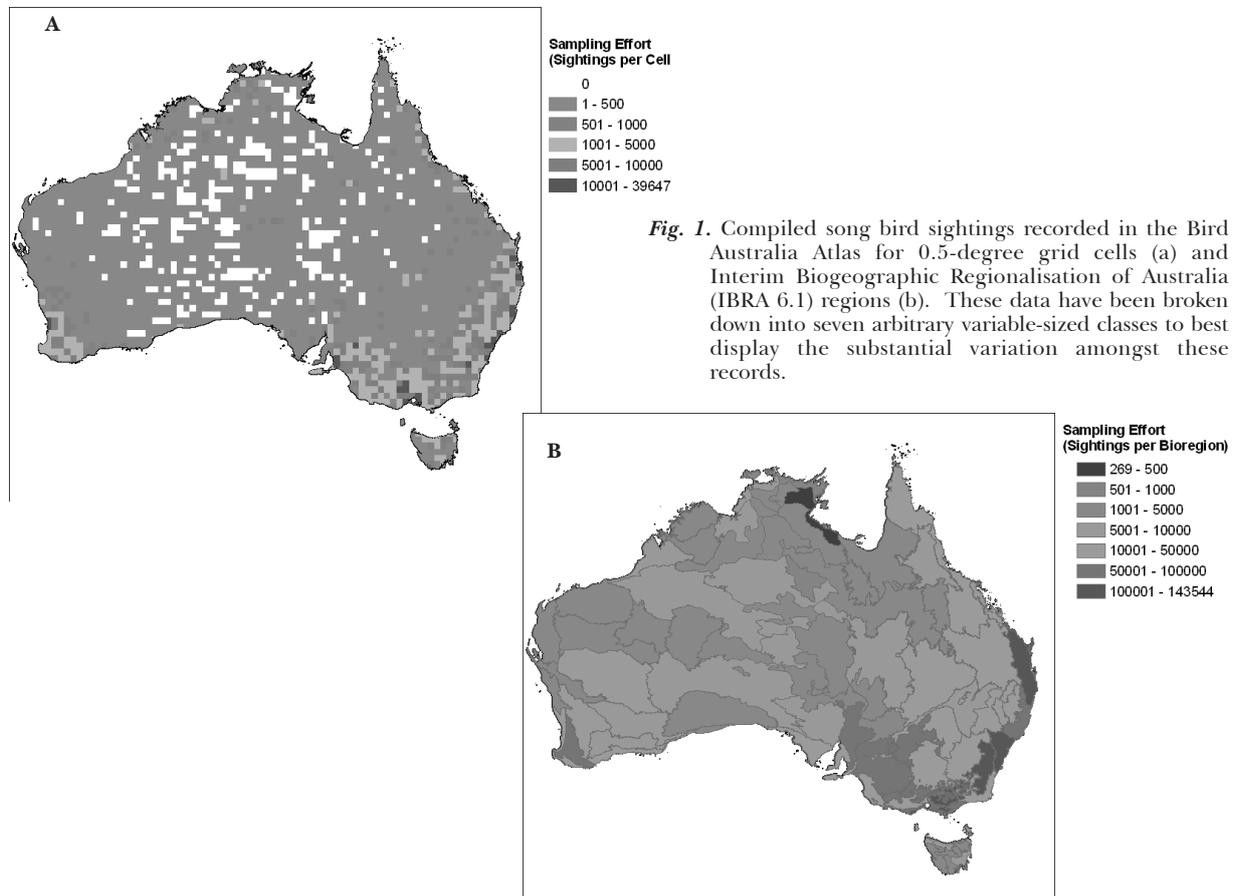
## RESULTS

### Sample bias

For reasons of differential survey intensity, sampling of bird species is uneven across Australia when these data are allocated to a lattice (Figure 1a), but this sampling bias is reduced when species presence is allocated to bioregions (Figure 1b). For example, even in the least-sampled bioregion of Central Arnhem Land there were 269 records representing 24 species. In comparison, 26% of the 0.5-degree grid cells in this region have no records present, and as a consequence, richness values for remote and arid regions are lower than the bioregion richness within which they fall. Conversely, the effect of varying sampling intensity as a function of proximity to settlements is apparent for bioregions in south-east and south-west Australia, and around regional outback towns such as Alice Springs and Mt. Isa relative to surrounding bioregions.

The IBRA regions provide better discrimination of richness across environmental gradients. For example, a species density of 3.77 per 100 000 ha is recorded in the mountainous Australian Alps regions, while the surrounding lower elevation South East Highlands has a species density of 0.9 per 100 000 ha (Figure 3a). In contrast, grid cells that overlap the boundary of these bioregions show little variation in richness.

No doubt more consistent sampling would improve estimates of songbird species richness in bioregions. Our species accumulation curve analyses showed that with increasing area there was a trend to consistently add new species, reflecting the capturing of new environments (Supplementary material). Few bioregions had "flat" species area curves indicating that the bioregional estimates of richness are not saturated and therefore provide a better measure of songbird richness compared to the high variability amongst grid cells within the same biophysical envelope. Although there is spatial significant ( $P < 0.01$ ) autocorrelation in both data sets, bird richness (standardized by area) bioregions have lower spatial autocorrelation than the richness of grids cells (Moran's I 0.66 vs. 0.94).



**Fig. 1.** Compiled song bird sightings recorded in the Bird Australia Atlas for 0.5-degree grid cells (a) and Interim Biogeographic Regionalisation of Australia (IBRA 6.1) regions (b). These data have been broken down into seven arbitrary variable-sized classes to best display the substantial variation amongst these records.

### Bioregion area and net primary productivity

There is a clear negative relationship between bioregion mean NPP and bioregion area (Figure 2), which is to be expected, because arid bioregions tend to be larger, reflecting their low NPP and general environmental uniformity, whereas bioregions with higher NPP are smaller, dividing steeper climatic gradients from the humid coast. NPP and mean annual precipitation are strongly related ( $r^2 = 64.9$ ) but the correlation with temperature is weaker ( $r^2 = 0.18$ ) because there is both high and low productivity environments in warm and hot areas.

### Gamma diversity and climate

The highest ranked model of songbird richness according to AIC weights was  $\log(\text{Area}) + \text{MAP} + \text{MAT}$  (Table 1), with 31.0% deviance explained (Table 1, Figure 4). Subsequently, we tested the interaction between MAT and MAP in addition to their individual additive components and this model was found to have a higher deviance explained to 48.6%, though based on AIC this model was less parsimonious (Table 1). Songbird richness was found to be highest in environments with higher rainfall and lower temperature, which also

correspond with areas of sustained, high levels of NPP because of the correlation between these climatic variables and (a) relatively higher and temporally stable rates of photosynthesis plus (b) relatively lower rates of respiration (Keith *et al.* 2008).

### Climate change sensitivity

The interaction between MAP and MAT and bird species richness is significant suggesting that that temperature increases have a greater impact on richness decline when coupled with lower precipitation. For example, a bioregion of mean log area, a temperature increase of 2°C, and a precipitation decrease of 100 mm would result in a predicted loss of around five species.

## DISCUSSION

Our analyses shows that over 49% of the variance in the richness of songbirds (standardized by area) in the Interim Biogeographical Regionalisation of Australia (IBRA) can be explained by the mean annual precipitation and mean annual temperature and their interaction. This connection between songbird richness and climate appears to be linked to net primary productivity, which covaries with these climate variables. Our results

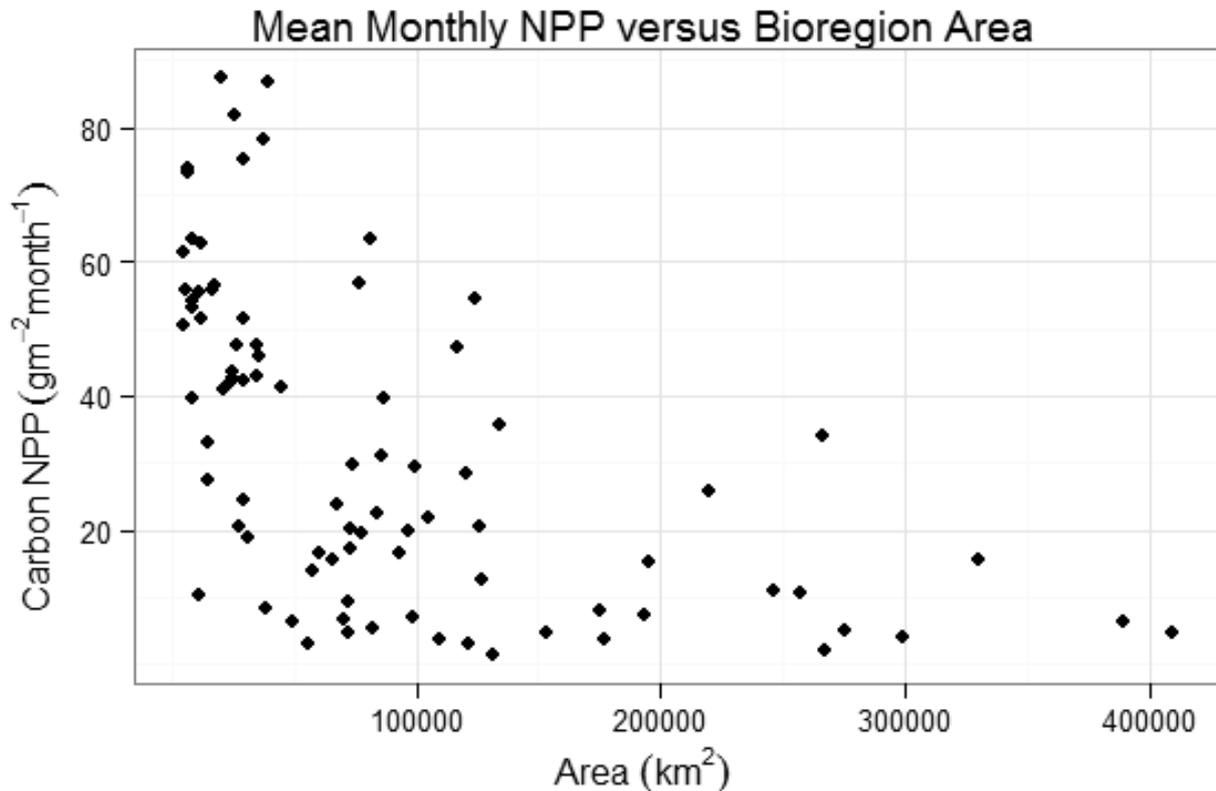
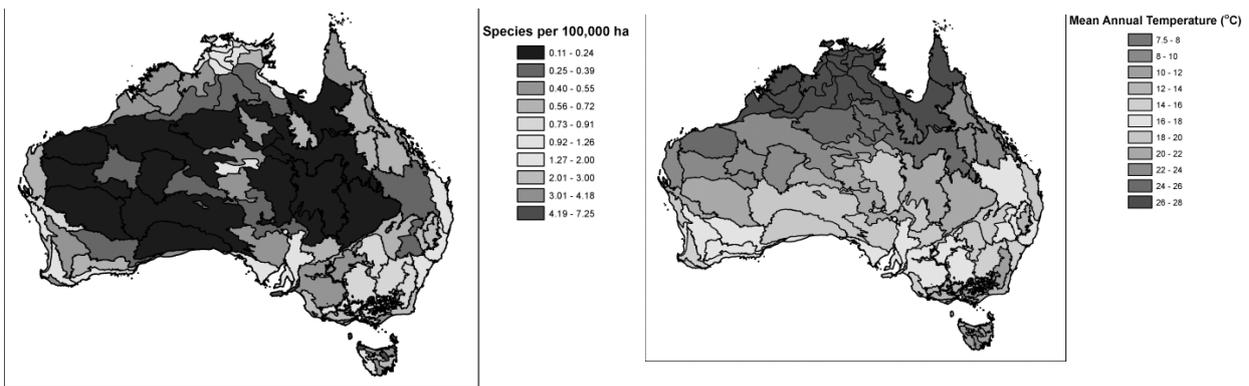


Fig. 2. The area of the 85 Interim Biogeographic Regionalization of Australia (IBRA) regions, plotted against satellite derived estimates of mean annual net primary productivity (NPP). The fit of the relationship is  $r^2 = 0.30$  and the equation is  $\text{NPP} = 44.6 - 0.00014 \times \text{Area}$ .

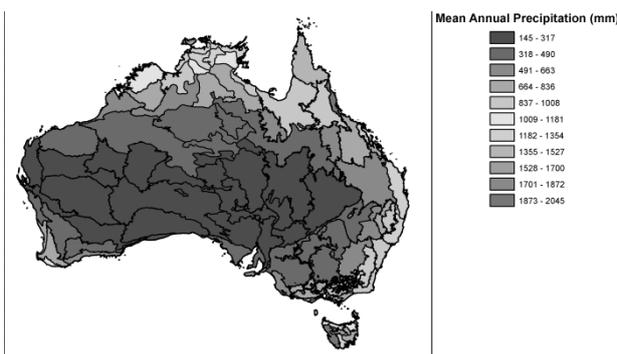
Table 1. Generalized linear modelling results of predicting songbird richness (standardized by area) for 85 Interim Biogeographic Regionalization of Australia (IBRA) bioregion using log10 of area of bioregion (AREA), and estimates of mean annual temperature (MAT), mean temperature of the wettest season (MWT) and mean annual precipitation (MAP), at 5 arc-minute resolution, were obtained from the WorldClim (2009). The GLM models are ranked by AIC weights, showing parameters (k), negative log-likelihood, corrected and delta-AIC, AIC weights, and percentage deviance explained. Following this analyses the interaction of the variables in the best model was also analysed (in bold).

	k	-LogLik	AICc	dAICc	wAIC	%DE
~Log(Area) + MAT * MAP	6	-326.07	664.14	-	-	48.6
~ Log(Area)+ MAT + MAP	5	-338.75	688.26	0	0.50	31.02
~ Log(Area)+ MAT	4	-340.74	689.98	1.72	0.21	27.76
~ Log(Area)+ MWT + MAP + MAT	6	-338.64	690.37	2.10	0.18	31.19
~ Log(Area)+ MWT + MAT	5	-340.46	691.69	3.43	0.09	28.23
~ Log(Area)+ MAP + MWT	5	-342.39	695.55	7.29	0.01	24.94
~ Log(Area)+ MWT	4	-343.89	696.29	8.03	0.01	22.28
~ Log(Area)	3	-347.97	702.24	13.98	0.00	14.59
~ Log(Area)+ MAP	4	-347.72	703.95	15.68	0.00	15.08
~ MWT + MAT	4	-350.93	710.37	22.11	0.00	8.54
~ MWT + MAP + MAT	5	-350.16	711.07	22.81	0.00	10.17
~ 1 (null or mean-field model)	2	-354.80	713.74	25.48	0.00	0.00
~ MAT	3	-353.73	713.75	25.49	0.00	2.44
~ MAT + MAP	4	-352.72	713.93	25.67	0.00	4.69
~ MAP	3	-353.87	714.04	25.78	0.00	2.12
~ MWT	3	-354.78	715.86	27.60	0.00	0.04
~ MAP + MWT	4	-353.82	716.15	27.89	0.00	2.22



(a) Richness per Area

(c) Bioregion Mean Annual Temperature



(b) Bioregion Mean Annual Precipitation

Fig. 3. Passerine bird richness per area for the 85 Interim Biogeographic Regionalization of Australia (IBRA) regions (a), mean annual precipitation (b) and Bioregion mean annual temperature (c). Climate data sourced from WorldClim (2009).

are consistent with many empirical studies regarding the relationships between primary productivity, vegetation complexity, habitat resources, and bird species richness (Recher *et al.* 1991), in particular the importance of water and energy as drivers (Hawkins *et al.* 2003).

Biogeographic data invariably have sampling biases, and we show bioregions are useful for statistical analysis of continental distributional data that have very uneven sampling intensities. Luck *et al.* (2010) attempted to remove sampling bias from the Australian bird distributional data by using a random sample of observations from each grid cells in the lattice, an approach which necessarily reduces estimates of species richness. Another problem with grid cells, but not bioregions, is that they have unequal land area when they span large latitudinal gradients or coastal lines. Luck *et al.* (2010) reported a low correlation between cell size and richness implying that area is not a key factor in driving

richness suggesting this sample bias inherent in grids was not an important issue. This conclusion is at odds with our species accumulation analyses, and may reflect that Luck *et al.* (2010) did not control for bioregion. For example, coastal grid cells with small proportion of land cover will have higher richness than grid cells from the arid zone with 100% land cover because of differences in primary productivity.

Bioregions such as IBRA are attractive for biogeographic analyses for several reasons. First, they are defined by a synthesis of expert biogeographic knowledge which can produce reliable results in the absence of the detailed spatially distributed or historic biological data required by quantitative approaches (Mackey *et al.* 2008a). Secondly, their variable spatial extent and shape can capture localized environmental heterogeneity better than a relatively coarse lattice-grid based sampling method. Indeed, we show that variable size of bioregions scales to net primary productivity. This consideration is important in Australia where biodiversity hot spots are relatively localized (e.g., the wet tropics of far north Queensland) compared to extensive landscapes over much of the Australia continent that support a more widely distributed biota. Thirdly, bioregions provide an efficient sampling unit for statistical analyses that can be treated as “random effect” in generalized linear mixed effects models (Burnham and Anderson 2002). Furthermore, phenomenological model outputs based on grids typically require some sort of post-hoc classification to portray geographic patterns of the predictions (e.g., Mackay *et al.* 2008b), yet in the case of bioregions the regionalization is hardwired into the analysis. Finally, these geographic constructs are widely used by government and other professionals as a pragmatic conservation planning tool (Australian Government Department of Sustainability, Environment, Water, Population and Communities, 2004; Land and Water Australia 2002; Mackay *et al.* 2008a). For example, an analysis of threatening processes in the IBRA bioregions has identified that biodiversity in the high productivity bioregions in southern Australia is already vulnerable because of European environmental impacts including habitat destruction, hydrological modifications, changed fire regimes and spread of introduced organisms (Land and Water Australia 2002). Our results provide further evidence in support of using IBRA regions as spatial units of analysis for studying biodiversity and impacting processes at a continental scale.

Our study also highlights the potential vulnerability of biodiversity to climate change.

This trend towards significant change in species richness-climatic domains under predicted future climate is in agreement with other studies that have used geographical-range based range modelling methods on individual species (Williams *et al.* 2003; Böhning-Gaese and Lemoinea 2004; Chambers *et al.* 2005). We suggest the use of bioregions as spatial units of analysis shows promise for large-scale impact assessment and conservation planning including consideration of climate change effects.

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#### SUPPLEMENTARY MATERIAL

Species-accumulation curves were calculated for each Interim Biogeographical Regionalization of Australia (IBRA) bioregion. The species accumulation curves were developed by finding the centroid of each bioregion and then counting cumulative species-presence records (Y axis) within circles of increasing diameter around the centroid (X axis). A spline curve was run through the points on the graphs to produce a smooth curve. The vertical line on the graph delimites the actual area of the bioregion (in km<sup>2</sup> also indicated in key), and the horizontal line represents the actual species richness. Where a horizontal, flat region of the curve coincides with the vertical line, the bioregion area contains a distinct species suite, and is therefore saturated with species. In cases where the vertical line intercepts a sloped part of the curve indicates the bioregion is not saturated with species. Few bioregions are to be saturated according to these criteria.

For each IBRA bioregion the mean and standard error climate data used in the analysis is listed in the key: mean annual temperature (MAT), mean temperature of the wettest season (WTempMean) and mean annual precipitation (MAP), at 5 arc-minute resolution (WorldClim (2009)). To access the supplementary material, go to <http://pcb.murdoch.edu.au/> and select “supplementary material” from the sidebar at the left.