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Symonds, Matthew R. E. and Johnson, Christopher N. 2008, Species richness and evenness in Australian birds, *American naturalist*, vol. 171, no. 4, pp. 480-490.

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Source: *The American Naturalist*, Vol. 171, No. 4 (April 2008), pp. 480-490
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/10.1086/528960
Accessed: 24/10/2011 00:08

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Species Richness and Evenness in Australian Birds

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Submitted May 2, 2007; Accepted October 4, 2007; Electronically published February 6, 2008

Online enhancement: appendix.

ABSTRACT: Species richness and evenness are the two major components of biodiversity, but the way in which they are interrelated is a subject of contention. We found a negative relationship between the two variables for bird communities at 92 woodland sites across Australia and sought an explanation. Actual evapotranspiration (AET) was by far the best predictor of species richness. When AET was controlled for, the relationship between richness and evenness became nonsignificant. Richness is greater at sites with higher AET because such sites support a greater number of individuals. However, such sites have a greater number of rare species, resulting in lower evenness. A complicating factor is that evenness is best predicted by degree of vegetation cover, with sparsely vegetated sites having significantly lower evenness. We conclude that there are two competing ecological processes, related to energy and water availability, that determine richness and evenness. The first drives total abundance (leading to high richness, low evenness), while the second drives productivity and niche availability (leading to high richness, high evenness). The relative strength of these two processes and the observed relationship between richness and evenness are likely to depend on the scale of the analysis and the species and range of habitats studied.

Keywords: abundance, community structure, energy availability, evapotranspiration, NDVI, species-energy theory.

Understanding the causes of variation in biodiversity is one of the fundamental aims of ecological research. Species richness is the simplest measure of species diversity, and patterns in species richness have been intensively studied. These patterns include the well-known latitudinal diversity gradient of increasing species richness from temperate to tropical regions (Willig et al. 2003). Likewise, the species-area relationship (the number of species present in a sample increases with sampling area) is almost an ecological law (Rosenzweig 1995).

Another measure of biodiversity is species evenness. The relative abundances of species in a community may be close to uniform. Alternatively, a community may be dominated by many individuals of one or a few species. In fact, the latter scenario tends to be the more commonly observed. The causes of such so-called hollow species-abundance curves is also a subject that has prompted a rich field of study (Bell 2001; Hubbell 2001)

How are species richness and species evenness interrelated? There is surprisingly little consensus on this point. One problem is that while quantifying species richness is fairly intuitive (at its simplest, one just counts the number of species present), measuring species evenness is more problematic. There are numerous methods by which species evenness or equitability can be estimated (see Smith and Wilson 1996; Kokko et al. 1999), each employing different assumptions. Consequently, the way in which richness and evenness relate to each other can depend crucially on how evenness is estimated.

Older models suggested that the two variables are straightforwardly and positively related (De Benedictis 1973; Hill 1973; May 1975), but this is probably because early evenness indices were directly mathematically linked to richness (De Benedictis 1973; see also Smith and Wilson 1996). If richness and evenness are meant to measure separate aspects of diversity, then clearly evenness should not automatically reflect richness in this way. However, a positive relationship has also been predicted more recently based on theoretical extrapolations from species-area models (He and Legendre 2002). From these models, one would expect to observe species-poor communities being dominated by one or two highly abundant species.

There is increasing evidence, however, that there may be no relationship, or even a negative relationship, between species richness and evenness. Studies from specific ecosystems have not found positive relationships (e.g., Weiher and Keddy 1999; Mulder et al. 2004; Ma 2005; Wilsey et

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Am. Nat. 2008. Vol. 171, pp. 480–490. © 2008 by The University of Chicago. 0003-0147/2008/17104-42583$15.00. All rights reserved.
DOI: 10.1086/528960

al. 2005), and a recent theoretical analysis claimed that in most cases we should expect a negative relationship (Gosselin 2006).

A meta-analysis compiling information from 48 studies (Stirling and Wilsey 2001) found that different assemblages are characterized by different richness/evenness relationships, with slopes tending to be positive for vertebrates and invertebrates but negative for plants and fungi. When results were combined in a path-analysis model, richness and evenness were consistently negatively related if one assumed that species richness directly influences species evenness. In an alternative model that assumed only indirect effects, the relationship was more equivocal, and the analysis suggested that such a relationship may be found only within certain higher taxonomic groups.

Many of the empirical studies of species richness/evenness relationships that have been conducted have been focused on small geographic extents and thus small assemblages of species. The mean species richness of the studies reviewed by Stirling and Wilsey (2001) was 31.9. There have been surprisingly few analyses at broader continental scales involving larger assemblages. One such study, on the diversity of New World bats at 32 locations across the Americas (Stevens and Willig 2002), found that tropical bat communities have high species richness but low species evenness, whereas subtropical communities have the opposite pattern. In contrast, Cotgreave and Harvey's (1994) analysis of 90 bird communities worldwide (based on published literature) found a significant positive association between species richness and evenness, but their measures of evenness were mathematically confounded by species richness (in the manner described by Smith and Wilson [1996]).

Australian birds provide an excellent assemblage with which to examine this relationship at a continental scale. The Australasian region has the largest number of endemic families of birds of any zoogeographic region except the Neotropics (Christidis and Boles 1994). More pertinently, there are excellent data on distribution and abundance of these birds from the Australian Bird Count (ABC) produced by Birds Australia (Clarke et al. 1999).

Apart from identifying the nature of the species richness/evenness gradient, we also need to understand the factors that may determine why any pattern exists. Species richness and species evenness are known to be associated with environmental factors. Species richness in birds is closely linked to patterns of actual evapotranspiration, a composite climatic variable reflecting levels of ambient energy and water availability (Wright 1983; Hawkins et al. 2003). Energy and water availability are themselves linked to primary productivity, and more direct measures of productivity have also been shown to link strongly with species richness (e.g., Hurlbert and Haskell 2003; Ding et al. 2006; Evans et al. 2006).

Species evenness, meanwhile, may be more closely linked to habitat complexity or heterogeneity. In their analysis of bats, Stevens and Willig (2002) argued that greater habitat heterogeneity might explain the relatively low species evenness (and high species richness) in the tropics. Those conditions should favor an increase in the number of rare species, presumably because there is a higher number of available niches. In contrast, Cotgreave and Harvey (1994) argued the exact opposite: that complex habitats, such as forests, have more even community structures because they have more niches available. Simple habitats, they argued, would have only one or two large niches, and this would be reflected in community structure. A similar argument was advanced by Drobner et al. (1998), although with the proviso that the pattern is scale dependent.

A key question, therefore, is whether the factors that affect species richness also influence species evenness and, if so, whether this explains associations between richness and evenness. In this study we aim to identify the nature of the relationship between the two variables in birds of woodland and forest habitats across Australia. We test whether this relationship has a biological explanation and whether the same or different environmental factors explain patterns of richness and evenness.

Methods

Species Richness and Abundance Data

We took data on incidence and abundance from the Australian Bird Count (ABC). The ABC is an enormous database of roughly 79,000 standard bird surveys carried out at 3,340 locations around Australia between January 1989 and August 1995. The census was compiled from surveys by skilled observers who visited sites of a defined size and recorded all birds present. Many sites were visited regularly over the nearly 7-year period of the ABC. This feature, along with the fact that the methodology used to carry out the surveys was consistent, indicates that reliable estimates of species richness and relative abundance can be generated for many sites.

We used data only on land birds because abundance of sea birds at coastal sites can be difficult to estimate accurately. We selected 92 survey sites for this analysis according to the following criteria. First, we chose sites that had been surveyed on more than 50 occasions, in order to maximize confidence in our estimates of richness and abundance. Second, because richness and abundance estimates are closely related to area sampled, all sites chosen were of identical area (3 ha). Third, all surveys were of equal duration (20 min). Finally, all sites were of similar

habitat type—specifically, woodland or forest—to reduce possible confounding effects of comparing across different habitats. The locations of the 92 sites are shown in the appendix in the online edition of the *American Naturalist.*

Species richness is here defined as the number of bird species estimated to be present at a site over the course of the survey period (1989–1995). Clearly, the likelihood of a species being recorded increases with frequency of survey. Therefore, any estimate of species richness needs to take sampling intensity into account. A wide range of methods is available for estimating species richness from biodiversity survey data, many of them based on species accumulation, or rarefaction, curves (for reviews, see Colwell and Coddington 1994; Gotelli and Colwell 2001; Chao 2005). We used "Jackknife1," a nonparametric first-order jackknife estimator (Burnham and Overton 1979; see also Colwell and Coddington 1994 for discussion), as implemented through the computer package EstimateS 7.5 (Colwell 2005). This measure was chosen because it gave the estimate of species richness with the narrowest range of 95% confidence intervals in the majority of cases.

The abundance of each species at a site was calculated as the total number of individuals of species i observed over all surveys at the site divided by the number of surveys in which species i was observed. The total abundance of individuals at the site was estimated as the sum of the individual species' abundances.

Species Evenness

From our point of view, it was vital that the measure of evenness we used did not automatically co-vary with richness. We used the evenness measure E_{var} developed by Smith and Wilson (1996). Simulation studies by Smith and Wilson (1996) and subsequent testing by Weiher and Keddy (1999) have shown that this measure is highly reliable and robust to a set of required and desirable features. Crucially, these studies have demonstrated that the measure varies independently of species richness. As its name implies, E_{var} measures the variance in the abundance among the species at a site; it is calculated by the formula

$$E_{\mathrm{var}} = 1 - \frac{2}{\pi}\arctan\left(\frac{\sum_{s=1}^{S}\left\{\ln(x_s) - \sum_{t=1}^{S}[\ln(x_t)/S]\right\}^2}{S}\right),$$

where x_s and x_t are the abundances of the sth and tth species, respectively, and S is the number of species in the sample. Note that these abundances are summed over S species, hence the need to divide through by S to ensure that the value is independent of species richness. The $1-2/\pi$ arctan transformation converts the evenness measure so that it falls between 0 and 1, where a value of 1 indicates that the species abundances are all equal (i.e., the variance in abundances is 0) and the value tends to 0 when they are highly unbalanced (i.e., the variance is infinitely large).

Vegetation Density

Although we have attempted to reduce variability due to habitat differences by using only sites in woodland and forest habitats, there is still considerable variation in the natures of these environments. A principal source of this variation is in the density of vegetation at each site. We quantified this variation in two ways. The first relates to the amount of vegetation cover at the site. Sites were categorized on the basis of whether tree cover was very dense ($\geq$70%), dense (30%–70%), sparse (10%–30%), or very sparse ($<$10%). The second method involved quantifying vegetation height. Sites were categorized based on whether the height of the main tree canopy was high ($\geq$30 m), intermediate (10–30 m), or low ($<$10 m).

Environmental Variables

We collated data on all but one of the environmental predictors used in a recent analysis of species richness in Australian birds by Hawkins et al. (2005). The variables are known from other studies to be associated with species richness gradients. The one missing variable here is land-cover diversity, which is a landscape-scale measure and not appropriate to a site-based analysis such as this.

The first variable, altitude (in mm), was taken from the site location information in the ABC. The second variable, the Normalized Difference Vegetation Index (NDVI) is a measure of the "greenness" of a site and is widely used as an indicator of net primary production (Kerr and Ostrovsky 2003). Annual average NDVI data were taken from raster data files produced by the Australian Bureau of Meteorology (http://www.bom.gov.au). Two measures of seasonality, temperature seasonality and rainfall seasonality, were extracted from the program Anuclim (http://cres.anu.edu.au/outputs/anuclim.php) at 0.05° resolution. These are measured as the coefficients of variation of weekly mean temperature (measured in K) and rainfall (m), respectively.

We included two measures of evapotranspiration: annual potential evapotranspiration (PET) and annual actual evapotranspiration (AET). PET reflects levels of ambient energy (its calculation being based on mean annual temperatures and day lengths), while AET reflects water availability in combination with ambient energy. Raster data in 0.5° grid cells were taken from the Global Resource Information Database (http://www.grid.unep.ch/data/download/gnv183.zip).

We used the program ArcView 3.2 (http://www.esri.com) to query these raster data files for estimates of NDVI, seasonality, and evapotranspiration at each of the 92 sites. The complete data set is presented in the appendix.

Statistical Analysis

Initial analysis of the relationship between species richness and evenness and environmental variables consisted of simple correlation tests. The effect of vegetation density on species richness and evenness was assessed by a two-factor ANOVA, with vegetation cover and vegetation height as categorical factors. A one-factor ANOVA was used to examine links between these vegetation parameters and environmental variables. Subsequently, all data on vegetation cover/height, evapotranspiration (AET and PET), altitude, NDVI, and seasonality were analyzed using general linear models with the Akaike information criteria (AIC), used to select models predicting variation in species richness, species evenness, and total abundance. We assessed all combinations of variables to this end. When comparing models with the AIC, it is important that all models are based on exactly the same data set (i.e., the sample size is constant). Because we had missing data for some of our variables for some sites, for this latter analysis we used a reduced data set of the 65 sites for which we had complete climatic information. We also employed model averaging (Burnham and Anderson 1998) to identify more accurately the relative importance of each variable in predicting species richness, species evenness, and total abundance. This involved taking the subset of the most likely models (cumulative Akaike weight ≤ 0.95), adjusting the Akaike weight for each model accordingly, and then calculating Akaike weights for each variable by summing the Akaike weights for each model in which the variable features. These scores range from 0 (the variable appears in none of the most likely models) to 1 (the variable appears in all of the most likely models)

Because data from sites that are close to each other may not be independent (the sites may have overlapping bird

Table 1: Pearson's correlation coefficients (r) of environmental variables, species richness, and species evenness

	Species evenness	Altitude	NDVI	AET	PET	Rainfall seasonality	Temperature seasonality
Species richness:							
r	□ .225	.043	.085	.499	.322	.036	.079
ν^*	95	72	99	12	64	55	55
P	.026	.720	.400	.071	.008	.791	.558
Species evenness:							
r		.075	.251	□ .129	□ .170	□ .097	□ .007
ν^*		103	82	138	52	68	79
P		.352	.021	.128	.220	.427	.954
Altitude:							
r			.089	.075	□ .144	□ .229	.416
ν^*			97	23	71	51	73
P			.383	.722	.227	.099	! .001
NDVI:							
r				.269	□ .050	□ .051	□ .126
ν^*				117	99	98	71
P				.003	.622	.608	.288
AET:							
r					.703	.207	□ .246
ν^*					17	18	14
P					.001	.385	.357
PET:							
r						.690	□ .218
ν^*						8	28
P						.027	.246
Rainfall seasonality:							
r							□ .452
ν^*							19
P							.038

Note: Reduced degrees of freedom (ν^*) are employed to control for effects of spatial autocorrelation. AET = annual actual evapotranspiration, NDVI = Normalized Difference Vegetation Index, PET = annual potential evapotranspiration.

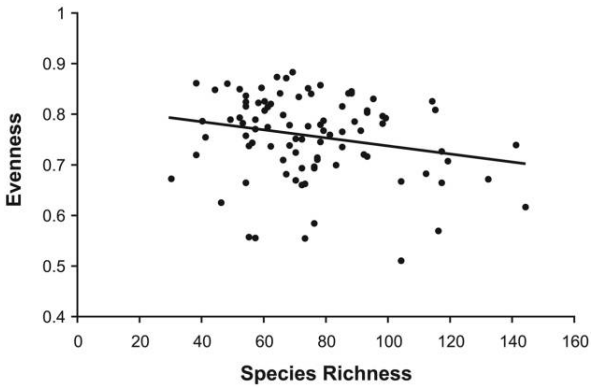

Figure 1: Relationship between estimated species richness and species evenness (E_{var}) of Australian birds across 92 woodland/forest sites.

populations), it is necessary to take into account the possible effects of spatial autocorrelation (Legendre 1993; Lennon 2000; Blackburn 2004). We followed the example of Hawkins et al. (2005) and assessed the significance using reduced degrees of freedom (ν^*), based on the geographically effective sample size (see Dutilleul 1993). The calculation of ν^* and consequent assessment of the probability values was carried out using the computer program Mod_t_test (Legendre 2000) and was based on Moran's *I* spatial autocorrelation coefficients calculated for each variable using 13 geographical distance classes. For multivariate analyses, we used the most conservative number of degrees of freedom, as ascertained through analysis of the bivariate correlations in Mod_t_test. Note that in some cases, as a result of spatial processes, ν^* may exceed ν (Dutilleul 1993).

Results

Our measure of species evenness, E_{var}, was significantly negatively correlated with species richness for birds across the 92 sites in our analysis (see table 1; fig. 1). In other words, there was a more even distribution of individuals of different species at relatively species-poor sites. Reduced species evenness at species-rich sites may result from there being more rare species at such sites or from one or two species being hyperabundant compared to the other species at the site. We tested the former possibility by counting the number of rare species (the number of species with minimum abundance; i.e., one individual). This value was weakly correlated with our measure of species evenness ($r = 0.190$, $\nu^* = 89$, $F = 3.341$, $P = .071$). However, when we took the abundance of the most abundant species for each site and correlated this with species evenness, we found a very strong relationship ($r = -0.810$, $\nu^* = 65$, $F = 124.337$, $P < .001$).

If some species are highly abundant (and dominate the bird community) at certain sites, then this could pose a problem for our interpretation of links between richness and evenness. Given this fact, under a null model, we might expect species-rich sites to have lower species evenness simply because they are more likely to have a hyperabundant species present than a species-poor site. Likewise, despite our best efforts and the results from previous simulation studies (Smith and Wilson 1996), it is possible that the measure of evenness E_{var} does exhibit some inverse dependence of species richness (since its calculation involves division by the number of species in the sample). To counter these possibilities, we tested our observed correlation coefficient ($r = -0.225$) against a null distribution of expected correlation coefficients generated from 1,000 random rearrangements of the species abundance data, with the number of species recorded at each site held constant. The mean of this null distribution was $r = -0.035$. Our correlation coefficient was significantly different from this value ($P = .037$).

The estimated species richness and total number of individuals at a site (total abundance) were strongly cor-

Table 2: Results of ANOVAs of species richness and species evenness with two aspects of vegetation density (amount of vegetation cover and vegetation height) as factors

Source of variation	r^2	Sum of squares	df	Mean square	F	P
Species richness	.151	7,417.945	11, 46	674.359	1.294	.258
Percent vegetation cover		1,044.351	3	348.117	.668	.576
Vegetation height		1,765.397	2	882.698	1.694	.195
Vegetation cover # vegetation height		5,883.539	6	980.590	1.882	.104
Error		41,689.131	46	521.114		
Species evenness	.172	.105	11, 80	.010	1.458	.164
Percent vegetation cover		.062	3	.021	3.273	.025
Vegetation height		.024	2	.012	1.854	.163
Vegetation cover # vegetation height		.020	6	.003	.513	.793
Error		.507	80	.006		

Note: Reduced degrees of freedom are used to control for effects of spatial autocorrelation.

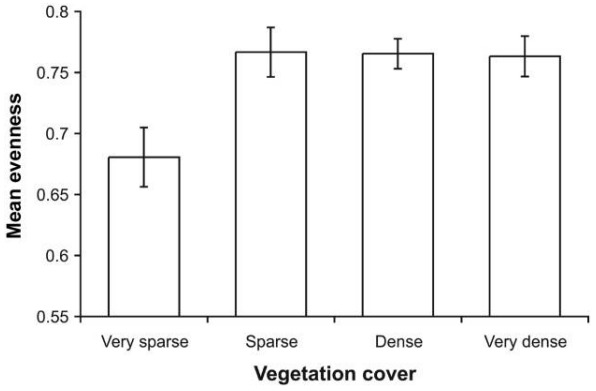

Figure 2: Mean evenness (E_{var}) of birds in relation to the degree of vegetation cover. Very sparse (! 10% tree cover; n p 10) sites have significantly reduced evenness.

related (r p 0.638, v* p 72, P ! .001). On the other hand, evenness and total abundance were strongly negatively related (r p □0.709, v* p 75, P ! .001).

Once the effects of spatial autocorrelation were taken into account, PET and, more weakly, AET appeared to be related positively to species richness. In the case of species evenness, the NDVI was the only significant correlate, with higher species evenness being observed at "greener" sites. There were predictable relationships between the environmental variables (e.g., AET and PET, measures of seasonality), and sites with higher AET also tended to exhibit higher productivity (i.e., NDVI).

The relationship between species richness and evenness remained significant when all other environmental variables, with the exception of AET, were controlled for (richness-evenness partial correlation coefficient p □0.250, P p .029 when all variables except AET were considered; partial correlation coefficient p □0.088, P p .507 when all variables including AET were considered). These results suggest that AET may account for the negative relationship between richness and evenness; AET was positively correlated with the former and negatively related to the latter (table 1), indicating that as energy and water availability increase, species richness increases, but species evenness declines.

The tropical sites in our analysis tended to be more species rich than temperate sites (correlation of species richness with latitude: r p □0.385, df p 91, P ! .001). Conversely, species evenness was, on average, lower in the tropics (correlation of evenness with latitude: r p 0.226, df p 91, P p .029). Because latitude is essentially a surrogate for the environmental variables in our analyses (Hawkins and Diniz-Filho 2004), we will not dwell on these results in the rest of this article.

There was no significant effect of either categorical measure of vegetation density on species richness (table 2). By contrast, species evenness showed a significant interaction with degree of vegetation cover (fig. 2). Relative abundances were more uneven at sites with very sparse tree cover (1 10%). However, there was no significant variation in evenness among sites with higher amounts of vegetation cover. Dense, tall vegetation was associated with high NDVI, and sites with higher AET and altitude also tended to have taller vegetation (table 3).

In our general linear model analyses, the level of unequivocal support for the most likely models predicting species richness, species evenness, and total abundance was extremely low (tables 4, 5). However, for species richness, AET was clearly the most important predictor, with an Akaike weight of 1, indicating that it featured in all 64 most likely models (table 6). AET was positively related to species richness and explained 24% of the variation in species richness in Australian birds in our analysis.

In the case of species evenness, determining the best model was particularly problematic, with even the most likely model having very low Akaike weight. Species richness appeared in the most likely model (table 4) and, with percent vegetation cover and vegetation height, explained 34.5% of the variation in species evenness (table 5). However, as a general rule, species richness was not one of the better predictor variables (table 6), with NDVI, AET, and both measures of vegetation density having more weight. Vegetation height's appearance as a significant predictor

Table 3: Summary of ANOVAs of environmental variables with measures of vegetation density

Variable	F	v*	P	Trend
Percent vegetation cover:				
Altitude	1.82	100	.148	…
NDVI	10.63	77	! .001	Positive
AET	.18	121	.912	…
PET	.11	85	.955	…
Rainfall seasonality	1.15	131	.332	…
Temperature seasonality	6.53	89	! .001	None[a]
Vegetation height:				
Altitude	4.23	79	.018	Positive
NDVI	3.34	109	.039	Positive
AET	6.90	16	.008	Positive
PET	1.62	120	.202	…
Rainfall seasonality	1.05	58	.356	…
Temperature seasonality	2.90	78	.061	None[a]

Note: Reduced degrees of freedom (v*) are employed to control for spatial autocorrelation. The general trend of the relationship is indicated where appropriate. AET p annual actual evapotranspiration, NDVI p Normalized Difference Vegetation Index, PET p annual potential evapotranspiration.

[a] Trends for temperature seasonality indicate highest levels of seasonality linked to intermediate levels of vegetation cover/height.

in the most likely model contrasted with the ANOVA, when only it and percent vegetation cover were considered (table 2). Examination of the residual values revealed that species evenness was significantly lower at sites where the canopy height was low (1 10 m), but there was no significant difference in mean evenness between sites with intermediate canopy and those with high canopy. AET, like species richness, was negatively correlated (table 1) with species evenness, again indicating that species distributions become more uneven but more species rich as water/energy availability increases. NDVI, in contrast, was positively associated with species evenness, a result that was consistent with the relationships of vegetation density to this variable.

The predictors of total abundance were very similar to those of species richness, with AET and NDVI exhibiting the strongest weightings (table 6) and featuring, with temperature seasonality, in the most likely model. Again, despite the generally positive association between AET and NDVI, the relationship of each variable to total abundance differed, with AET being positively related and NDVI negatively related (table 5, "total abundance").

Discussion

Species richness and evenness (measured as the variance in abundances of species at a site) were inversely related in our analysis of Australian birds. This relationship was significantly different from that predicted from a null model analysis, indicating that it had a functional basis. Pautasso and Gaston (2005), in an analysis of published bird surveys from around the world, also noted a negative relationship between richness and a different measure of evenness (Bulla 1994), but they did not expand on the finding. Our analysis allowed us to investigate the underlying causes of the inverse relationship in more detail.

Our partial correlation analysis suggests that actual evapotranspiration (AET), a combined measure balancing ambient energy and water availability, is a key environmental variable in explaining patterns of richness and abundance. AET was by far the strongest predictor of species richness, and indeed, it was the sole predictor in the most likely model explaining species richness in Australian birds (fig. 3). Our results strongly concur with those of Hawkins et al. (2005), who also found AET to be the underlying predictor of species richness in Australian birds. We consider this link to be particularly robust because Hawkins et al. (2005) used an entirely different methodology to estimate the spatial pattern of species richness in Australia, employing distribution maps of the presumed breeding ranges of the birds, rather than site-specific information.

The relationship between AET and species evenness was more equivocal. Although the two variables were negatively correlated, the relationship was weak. However, the

Table 4: Most likely models in descending order to explain variation in species richness, species evenness, and total abundance in Australian birds

Parameters	AIC_c	$DAIC_c$	Akaike weight	ER
Species richness:				
AET	399.977	0	.072	1
AET, NDVI	400.007	.03	.071	1.016
AET, NDVI, PET	400.601	.624	.053	1.366
AET, temperature seasonality	400.632	.655	.052	1.388
AET, NDVI, temperature seasonality	400.888	.911	.046	1.578
Species evenness:				
Percent vegetation cover, vegetation height, species richness	□ 320.589	0	.017	1
Percent vegetation cover, species richness	□ 320.449	.14	.016	1.073
Percent vegetation cover, vegetation height, AET, temperature seasonality	□ 320.280	.309	.015	1.167
Percent vegetation cover	□ 320.213	.376	.014	1.207
Percent vegetation cover, vegetation height, AET	□ 320.050	.539	.013	1.309
Total abundance:				
AET, NDVI, temperature seasonality	612.230	0	.100	1
AET, NDVI	612.353	.123	.094	1.063
AET, NDVI, PET, rainfall seasonality, temperature seasonality	613.258	1.028	.060	1.672
AET, NDVI, PET	613.294	1.064	.059	1.702
AET, NDVI, PET, temperature seasonality	613.294	1.064	.059	1.702

Note: AIC_c p Akaike's information criterion, corrected for multiple parameters and small sample size; AET p annual actual evapotranspiration; ER p evidence ratio (see Johnson and Omland 2004 for explanation of parameters); NDVI p Normalized Difference Vegetation Index; PET p annual potential evapotranspiration.

Table 5: Details of the most likely models predicting species richness, species evenness, and total abundance in Australian birds

Effect or source	r^2	Residual sum of squares	Coefficient	SE	Sum of squares	Mean square
Species richness	.240	28,748.31		21.362		
AET			.046	.010		
Constant			45.826	7.600		
Species evenness	.345	.331				
Percent vegetation cover					.069	.023
Vegetation height					.044	.022
Species richness			□ .001	.000	.025	.025
Intercept			.789	.072	2.562	2.562
Total abundance	.178	708,108.37		107.735		
AET			.170	.056		
NDVI			□ 3.131	1.289		
Temperature seasonality			.681	.479		
Constant			594.980	269.118		

Akaike weight for AET as a variable predicting evenness was moderately high (0.49), which made it an arguably better predictor of evenness than species richness (Akaike weight p 0.44). More importantly, the relationship between species richness and evenness was not independent of the effect of AET. The conclusion we draw from this is that AET influences the richness and evenness components of Australian bird diversity in different, antagonistic ways. But how might this work?

Species-energy theory predicts that increased available energy will result in increased numbers of individual organisms and, hence, more species (Wright 1983). One prediction from this is that sites with high energy, and therefore high species richness, will also have a greater number of rare species, if only through an increased sampling effect (see Evans et al. 2005). As the number of rare species at a site increases, however, the evenness of that community declines because of the increased mix of common and rare species.

We can demonstrate this relationship using a simple simulation (fig. 4). Consider a hypothetical regional species pool of 20 species, some rare, some common. Now consider a number of sites within the region that differ in the number of individuals they can support (i.e., they "sample" to different extents from the regional species pool). Not surprisingly, as the number of individuals at a site increases, so does the species richness (fig. 4*A*). However, because the appearance of rare species is more likely as species richness increases, evenness declines (fig. 4*B*). Consequently, richness and evenness are negatively related (fig. 4*C*). Our data support the idea that patterns of total abundance influence the negative correlation between richness and evenness. The relationship between richness and evenness, in fact, becomes significantly positive when total abundance is controlled for (partial correlation p 0.418, v^* p 72, P p .002).

Additional support for this species-energy explanation is provided by the fact that AET, as well as being a key predictor of species richness, was also the strongest predictor of total abundance. However, NDVI, an indicator of primary productivity, exhibited a negative relationship with total abundance, which seems counterintuitive in light of the fact that AET and NDVI are directly linked. Why might this be the case?

One possibility is that woodland environments that are greener do support greater numbers of individuals but that these individuals are not as easy to observe. Alternatively, we found that species evenness was positively associated with NDVI, which itself was strongly linked to the mea-

Table 6: Akaike weights for each variable in the most likely models predicting species richness, species evenness, and total abundance

Variable	Species richness	Species evenness	Total abundance
Percent vegetation cover	.025	.731	.043
Vegetation height	.161	.543	.112
Altitude	.289	.254	.268
NDVI	.525	.519	.885
AET	1.000	.488	.927
PET	.325	.314	.419
Rainfall seasonality	.305	.279	.339
Temperature seasonality	.384	.348	.542
Species richness	…	.440	…

Note: For species richness, 64 models were identified as most likely (i.e., accounting for a summed Akaike weight of 0.95). For species evenness, there were 334 most likely models, and for total abundance, there were 91. AET p annual actual evapotranspiration, NDVI p Normalized Difference Vegetation Index, PET p annual potential evapotranspiration.

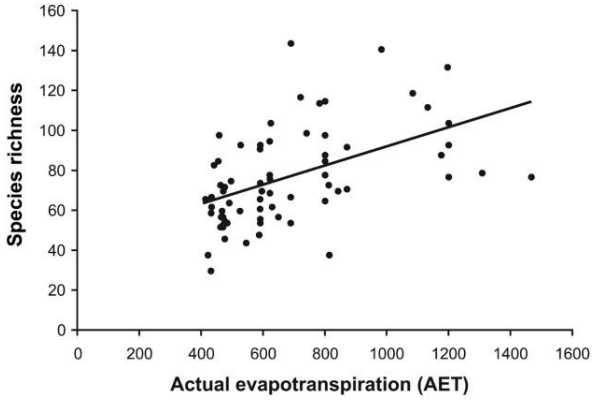

Figure 3: Relationship between estimated species richness of birds and a measure of energy/water balance (annual evapotranspiration) across 68 sites.

sures of vegetation density in our analysis. This is important because the other main result from our analysis was that vegetation cover and vegetation height were two key predictors of species evenness. Our analysis operated at a fine grain of resolution (albeit on a broad continental scale), with the area of the sites used being relatively small (3 ha). Therefore it is not possible to comment on habitat heterogeneity. However, it seems reasonable to suggest that vegetation cover and canopy height are at least related to niche availability, if only because they reflect the amount of three-dimensional structure available for perching and feeding. Although sites with intermediate to high levels of cover and taller vegetation did not exhibit any differences in evenness (possibly because such environments are more likely to vary in richness than in evenness; Tramer 1969), very sparse sites (vegetation cover ! 10%, canopy height ! 10 m) had significantly lower evenness. This finding would certainly be consistent with ideas linking greater habitat heterogeneity to greater availability of niches and, hence, the ability to support more specialist species more equitably (Rotenberry 1978; Stevens and Willig 2002; Hurlbert 2004; although our overall findings disagree with Hurlbert's, who found evenness and richness to be positively associated).

We therefore suggest that there are competing mechanisms at work that determine patterns of species richness and species evenness in Australian birds. On the one hand, higher energy/water availability at a site supports a greater number of individuals and higher species richness (including rare species) but with a consequent greater unevenness in the relative abundances of those species. On the other hand, higher energy/water availability also leads to higher productivity, greenness, and vegetation density, which in turn promote greater species evenness. The interactions of these variables in determining how evenness and richness are related are therefore complex and likely to vary under different circumstances. In our case, we would suggest that the former effect is stronger because there is a weaker relationship between NDVI and species richness than might be expected (our study compares sites

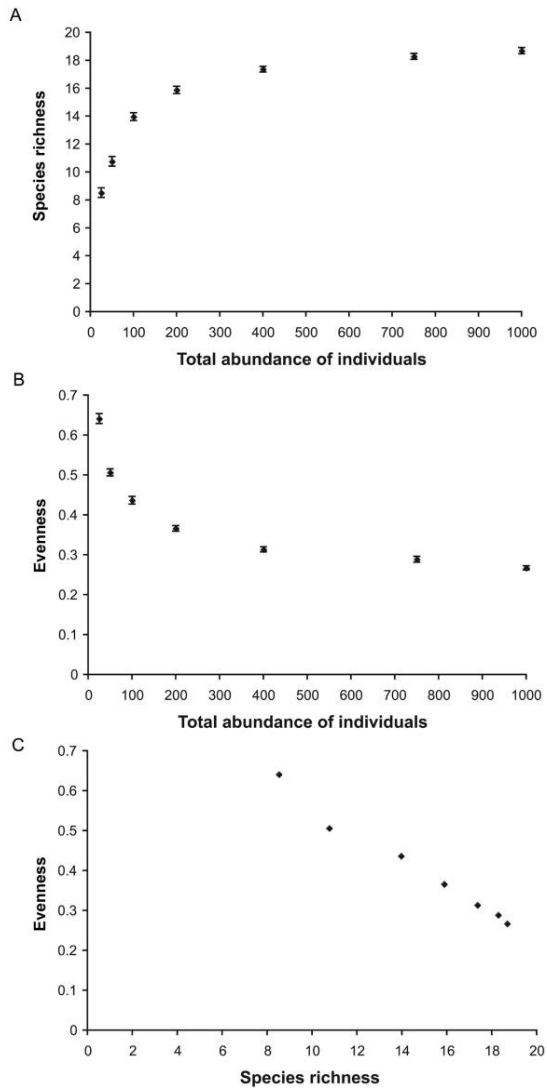

Figure 4: Results from theoretical simulations showing that (*A*) species richness increases with total abundance of individuals at a site, (*B*) species evenness (E_{var}) decreases with total abundance, and consequently, (*C*) species richness and species evenness are negatively related. The number of individuals of each species at a site was determined randomly based on their proportional abundances in the regional species pool (ranging from 40% of all individuals for the most dominant species to 0.1% for the rarest species). Each site was "sampled" 25 times to generate mean values of species richness and evenness.

over a limited range of habitats, so variation in NDVI is relatively small). Consequently, we observed a negative relationship between richness and evenness.

Our general argument is applicable to communities of organisms other than birds, although additional ecological processes such as migration and competition are also likely to play a role. Increased competition, particularly, can result in dominant species having greater proportional abundances, leading to decreased evenness (see, e.g., Wilsey and Stirling 2007). The biological nature of organisms involved is therefore important. Birds, by virtue of their ability to fly, have the capacity to easily move between favorable environments. These higher migration rates may therefore serve to inflate species richness at sites while reducing competition (since individuals can easily move elsewhere). We might not, therefore, expect the effect of competition on species evenness to be as strong in birds as it is in, say, plants.

The different factors (energy availability, productivity, and competition) influencing richness and evenness mean that there is unlikely to be a simple universal rule linking the two. The relationship may be negative, positive, or nonapparent, according to the scale of the analysis or the particular characteristics of the study organisms and environment. Further complications may ensue if patterns of species richness and species evenness do not co-vary with environment in linear ways (see, e.g., the humped-back model of species richness of Grime [1973], expanded to consider species evenness by Drobner et al. [1998]). A challenge for ecologists, therefore, is to better catalog the way in which species richness and evenness co-vary across a wider range of scales, species, and habitats.

Acknowledgments

We are indebted to M. Kearney for considerable time spent in assistance with ArcView software and for general discussion and comments; B. Brook and two anonymous reviewers for constructive criticism; A. Moussalli and N. Thompson for statistical advice; E. Van Lieshout for pointing out the need for a null model analysis; and S. Connolly and S. Williams for advice on species richness estimation. This research was funded by the Australian Research Council.

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