ECOGRAPHY

Research

Linking species richness and size diversity in birds and fishes

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The rapid development of mechanistic, trait-based models has resulted in increasingly reliable predictions of the functional diversity of individuals in populations and communities. However, a focus on individuals' traits differs from the prevailing focus on species in much of community ecology. We sought to identify correlative links between species richness and size diversity, focusing on size diversity as one component of functional diversity. These links could be used to extend individual, size-based models to predict patterns of species richness. We used the distribution of the sizes of individuals in a community – the individual–size distribution (ISD) – as a measure of size diversity, and constructed Bayesian regression models with species richness as the response variable and ISDs as the predictor variables. We used two methods to include ISDs in our analyses. First, we summarized the ISD with five common diversity indices and used these indices as predictor variables in our analyses. Second, we used functional data analysis to include the entire ISD (a continuous function) as a predictor variable in our analyses. Analyses of diversity indices identified consistent, positive associations between species richness and size diversity. Analyses of entire ISDs revealed that these associations were driven by numbers of small- and medium-sized individuals. In general, a combination of diversity indices predicted species richness as well as or better than continuous ISDs. However, models with ISDs as predictor variables were less sensitive to technical details of model fitting (e.g. discretization method) than those based on diversity indices, and the use of ISDs avoids the arbitrary selection of one or several diversity indices. Our use of functional data analysis allows any trait distribution to be included as a variable in statistical analyses, and has the potential to reveal new diversity patterns in ecology.

Keywords: biological diversity, function regression, size spectrum

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Introduction

Functional trait-based methods are increasingly used to address fundamental and practical questions in ecology (Cadotte et al. 2011, Violle et al. 2014). The use of trait-based methods has been supported by expanding trait databases (Fishtraits: Frimpong and Angermeier 2009, BIEN: Enquist et al. 2016) and substantial progress towards mechanistic models of populations and communities (Kooijman 2010, Scott et al. 2014, Falster et al. 2016, Guiet et al. 2016). Mechanistic, trait-based models have been used to explain many ecological and evolutionary processes, including community assembly, trophic and competitive dynamics, community responses to disturbance, and developmental and evolutionary processes (Laughlin et al. 2012, Blanchard et al. 2017, Falster et al. 2017).

Many mechanistic models, particularly for aquatic systems (Blanchard et al. 2017), emphasize the importance of individual sizes (e.g. length or body mass) (Scott et al. 2014). Size is a useful proxy for functional diversity because many morphological, physiological, and life-history traits are correlated with individuals' sizes (Peters 1983, White et al. 2007). Size-based models may have few (Brown et al. 2004) or many parameters (Maury and Poggiale 2013, Scott et al. 2014), and many of these models do not depend upon species' identities (Guiet et al. 2016). Disregarding species' identities leads to models that are easy to parameterize and that are computationally tractable, yet still capture key aspects of ecological dynamics (Scott et al. 2014, Guiet et al. 2016).

The distribution of individuals' sizes in a community – the individual–size distribution (ISD) or abundance–size spectrum – underpins many size-based models (White et al. 2007, Blanchard et al. 2017). ISDs are continuous functions, the value of which at a particular size reflects the density or abundance of that size in a community. ISDs are one of several related size distributions, all of which characterize the diversity of sizes in a community (White et al. 2007). Other size distributions focus on average sizes and abundances of species (species–size distributions; White et al. 2007) or on measures other than abundance, such as biomass or diversity indices calculated separately for size classes (Rice and Gislason 1996, Gislason and Rice 1998). Some recent empirical studies successfully predicted ISDs from environmental variables (dos Santos et al. 2017, Yen et al. 2017a, b, Zhao et al. 2017). Such studies are supported by efficient methods to measure individuals' sizes in the field without recording species' identities (Sheldon et al. 1972, Turnbull et al. 2014, Wheeland and Rose 2016).

A focus on individual sizes differs from a focus on species, which underlies much of biogeography, macroecology, and community ecology (McGill et al. 2006). Despite advances in mechanistic modeling of species richness (Gotelli et al. 2009), predictive models of species richness often rely on correlative analyses (Mittelbach et al. 2001, Hawkins et al. 2003, Stein et al. 2014). Given the practical importance of species richness in conservation management (Magurran and McGill 2011) and its role in macroecological theories (Harte 2011, Locey and White 2013), understanding the processes underpinning variation in species richness remains a core ecological goal (Gotelli et al. 2009).

Progress towards mechanistic trait- and size-based models (Blanchard et al. 2017, Falster et al. 2017) raises the possibility of modelling individual sizes or traits in communities without requiring knowledge of species' identities. Therefore, we asked whether increasingly sophisticated models of individual sizes and traits might explain observed patterns in species richness? Few studies have considered potential links between functional diversity and species richness (Petchey and Gaston 2002, Mayfield et al. 2010, Cadotte et al. 2011). Focusing on individual sizes, Cardillo (2002) noted positive associations between species richness and the number of small species in a community along a latitudinal gradient, and Brown and Nicoletto (1991) reported a similar pattern when comparing data from local to continental scales.

Three general associations between species richness and size diversity are possible. First, species richness might not be associated with size diversity (scenario A in Fig. 1). This might be the case in communities characterized by species that grow continuously (indeterminate growth), so that adults of each species span a potentially wide range of size classes (Werner and Gilliam 1984). Second, species richness might be associated directly with indices of size diversity (e.g. the range or Shannon entropy of sizes). This may arise in communities with species that grow to a fixed maximum adult body size (determinate growth), so that adults of each species belong to one or at most a few size classes (Sebens 1987). Third, species richness might be associated with size diversity, but the variation in size diversity might not be represented well by commonly used diversity indices (scenario B in Fig. 1). Information is lost when size diversity is condensed into a single-valued diversity index, which might obscure the associations between species richness and size diversity.

There are many measures to describe different components of functional diversity (Mason et al. 2005, Carmona et al. 2016). Although some measures require data on species' identities, many measures can be calculated from individual size or trait distributions (Carmona et al. 2016). Most of these measures characterize the full trait-frequency distribution by partitioning the distribution into independent components (e.g. richness, evenness, divergence; Mason et al. 2005) or by calculating the volume of functional space occupied by a given community (Carmona et al. 2016, Blonder et al. 2018). All of these approaches condense functional diversity into one or several numbers (e.g. a hypervolume or an index of functional richness or evenness).

The inclusion of one or several size-diversity indices in statistical analyses is straightforward (Fig. 2a). However, most indices have been developed to represent the same quantity: a trait-frequency distribution (e.g. the ISD) (Carmona et al. 2016). Ideally, the entire trait distribution should be used as a predictor (Fig. 2b). Functional data analysis meets this need, and allows continuous functions (e.g. ISDs) to be used as
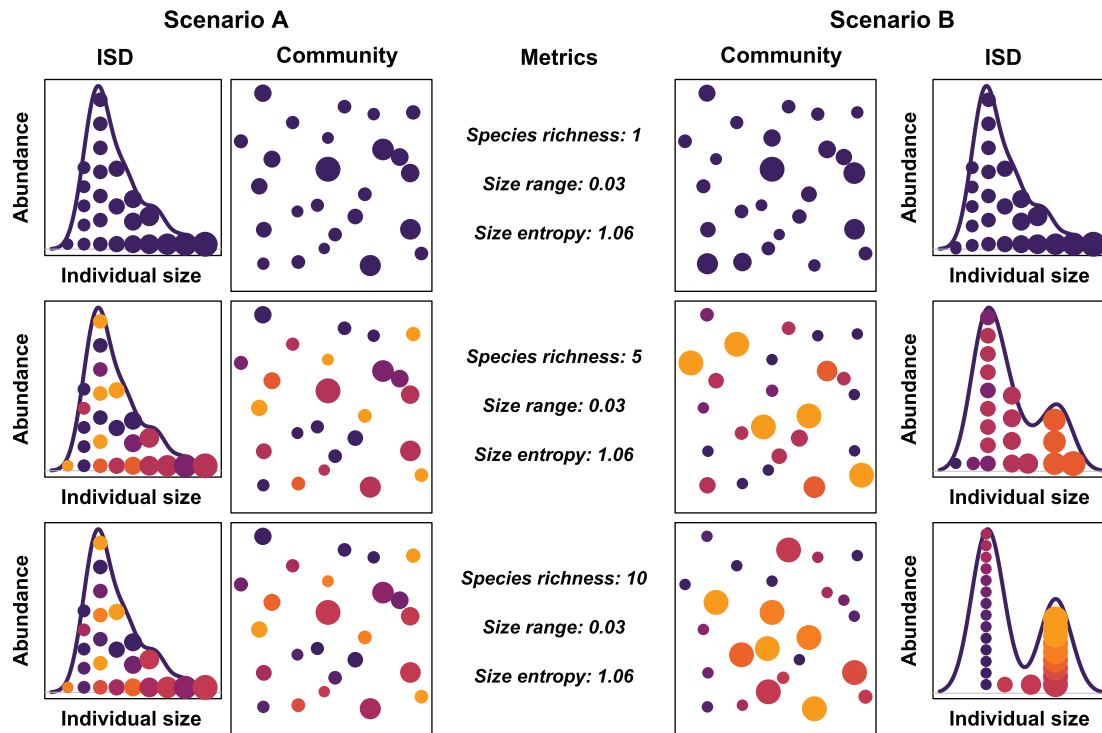
Figure 1. Hypothetical example of the links between species richness and size diversity. Size diversity is represented with two indices (the range of individual sizes and the Shannon entropy of individual sizes; centre panels) and with individual–size distributions (ISDs), which are continuous functions (far-left and far-right panels). In scenario A, there is no association between species richness and size diversity. The addition of new species to the communities does not alter the distribution of individual sizes (far-left panels). In scenario B, there is an association between species richness and ISDs. The addition of new species to the communities substantially alters the observed ISD by adding a second peak (far-right panels). The two size-diversity indices are not associated with species richness in either scenario.

response or predictor variables in statistical analyses (Ramsay and Silverman 2005, Yen et al. 2015a). By including trait distributions as predictor variables, functional data analysis can be used to detect complex associations between species richness and functional diversity. Functional data analysis might be used to identify relations between species richness and ISDs that are not apparent when ISDs are reduced to single-valued, size-diversity indices (e.g. size range, size entropy) (Fig. 1, 2d). We focus here on ISDs, which are one-dimensional distributions, but our method could equally be applied to distributions with multiple dimensions (Ramsay and Silverman 2005).

We sought to identify correlations between species richness and size diversity. We used field data from Australia and the United States on birds and fishes to compare taxonomic groups with disparate life histories. We used individual–size distributions (ISDs) as a measure of size diversity, and constructed Bayesian regression models with species richness as the response variable and size diversity as the predictor variable. In one set of analyses, we used single-valued, size-diversity indices as the predictor variables. In a second set, we used functional data analysis to include continuous, function-valued ISDs as predictor variables. Many different ISDs, generated by potentially distinct ecological processes, can yield the same value of a size-diversity index (Fig. 1).

Although a combination of indices is likely to capture differences in ISDs (Mason et al. 2005), we expected that the rich information content of ISDs might reveal associations that were not apparent in analyses of single-valued, size-diversity indices (e.g. scenario B in Fig. 1).

Methods

Data

We used four large data sets on birds and fishes from Australia and the United States (Table 1, Supplementary material Appendix 1). Lists of the species recorded, the number of records of each species, and means and standard deviations of species' body masses are in Supplementary material Appendix 2.

Bird data were collected from montane canyons in the Great Basin in the western United States (Fleishman et al. 2014, Fleishman 2015a, b, c, d) and from woodlands and forests in the box-ironbark region in southeastern Australia (Mac Nally et al. 2000, Radford et al. 2005, Bennett et al. 2014). Great Basin birds were surveyed annually from 2001 to 2014 at 472 points in 47 canyons in the central and western Great Basin (Supplementary material Appendix 1). Several
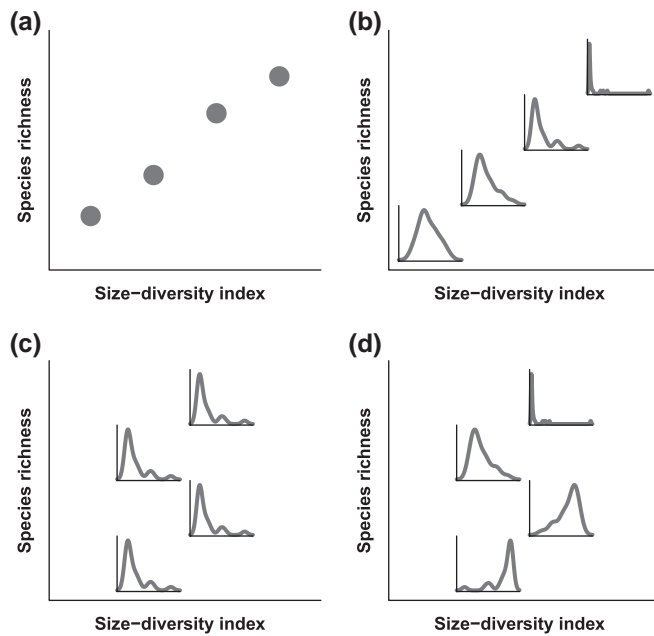
Figure 2. Conceptual outline of functional data analysis. Analyses of size-diversity indices condense entire individual–size distributions (ISDs) into a single number (blue circles in (a)). Variation in size-diversity indices might be apparent in ISDs, in which case ISDs or size-diversity indices will predict species richness well (a and b). Alternatively, there might be no association between species richness and size diversity (c). Associations between species richness and size diversity might be apparent when size diversity is represented with ISDs but not when size-diversity is condensed into a single-valued diversity index (d).

groups of birds are poorly sampled by point counts (e.g. raptors, waterfowl) (Supplementary material Appendix 2). We ran analyses with and without the species in these groups to determine whether their inclusion affected observed associations between species richness and ISDs.

Box-ironbark bird data were collected as part of two separate studies. In the first (fragment study), birds were surveyed along 2-ha transects at 139 sites from 1995–1997. Of these sites, 120 were resurveyed in 2010 and 2011 (Supplementary material Appendix 1). In the second (landscape study), birds were surveyed along 300 2-ha transects in 2006 and 2007 (Supplementary material Appendix 1). We analyzed

data from the fragment and landscape studies separately due to differences in the number of surveys in each period (Supplementary material Appendix 1).

We used fish data from 1438 sites in the National Water-Quality Assessment (NAWQA) program, which is conducted by the US Geological Survey (2001). These data included body sizes of fishes sampled in the United States from 1993 to 2012. Sites were stream or river reaches of lengths from 150–300 m (wadeable waters) or 500–1000 m (non-wadeable waters). The exact length of the sampled reaches was based on local geomorphology, such that the area sampled was comparable among reaches of different width and depth (US Geological Survey 2001).

Compiling individual–size distributions

We compiled individual–size distributions (ISDs) for birds and fishes by placing individuals into body-mass bins of equal width on a logarithmic scale. We used a logarithmic scale because ISDs typically are highly right-skewed, which means that if the data were binned on a natural scale, most would fall into the left-most bin. We compiled ISDs with 10, 20, 30 and 40 bins to assess whether our inferences were sensitive to bin widths. We present results for 20 bins and 40 bins below, and results for all bin widths in Supplementary material Appendix 3. The use of more than 40 bins was computationally prohibitive.

Body masses of individuals were measured during the fish surveys but not during the bird surveys. To estimate body masses of individual birds, we used species' body-mass means and standard deviations from a global database (Dunning 2007) to generate one random normal variate for each individual bird recorded. For Australian birds, we supplemented body-mass data from Dunning (2007) with data from Baker (1995) and Higgins (2006). If standard deviations were unknown, we used information on species body-mass ranges (standard deviation ≈ range/4; based on the range rule for standard deviations; Hozo et al. 2005). If the range was unknown, we set the standard deviation equal to the mean multiplied by 0.09, on the basis of a linear regression of the data in Dunning (2007) ([standard deviation of body mass] = 0.09 × [mean body mass], n = 3008, r^2 = 0.84). If data on body masses of males and females were available,

Table 1. Data sets used in our analyses. Details on data collection are in the Supplementary material Appendix 1.

Ecosystem and taxonomic group	Location	No. of data points	Random effects included in analyses	Years sampled	Reference
Great Basin birds	Mono County, California and Lander, Nye, Eureka, Mineral, Lyon, and Douglas Counties, Nevada, United States	322	year, mountain range, zoogeographic region	2001–2014	Fleishman et al. 2014, Fleishman 2015a, b, c, d
Box-ironbark birds – fragment study	southeastern Australia	518	season, survey period	1995–1997, 2010–2011	Mac Nally et al. 2000, Bennett et al. 2014
Box-ironbark birds – landscape study	southeastern Australia	600	site, season, landscape	2006–2007	Radford et al. 2005, Bennett et al. 2014
Fishes in the United States	United States (including Alaska and Hawaii)	1438	year	1993–2012	US Geological Survey 2001

we assigned the sex of each random variate with probabilities of 0.6 (male) and 0.4 (female). This sex ratio was based on global, empirical data for bird species (Donald 2007). Our method of estimating body masses of birds has been used in other studies of bird ISDs (Thibault et al. 2011) and has been suggested as a reliable way to recover individual trait diversity from species' average trait values (Carmona et al. 2016). This approach generates realistic size distributions and is robust to the assumption of normally distributed body masses within species (Yen et al. 2017a).

Calculating size-diversity indices

We calculated five indices of size diversity: the range of body masses; the relative richness of body masses, defined as the number of non-empty bins in the individual–size distribution (ISD); the Shannon entropy of body masses, calculated from compiled ISDs; the Pielou evenness of body masses, calculated from compiled ISDs; and the divergence of body masses. These indices often are used as measures of taxonomic and functional diversity (Mason et al. 2005, Schleuter et al. 2010), and are based on the same data as the ISDs. We calculated size-diversity indices from ISDs with 10, 20, 30, 40, 100, 500, 1000 and 5000 bins. The use of >1000 bins is common in kernel-based calculations of size-diversity indices (Carmona et al. 2016). We present results for 20 bins and 1000 bins, and include results for all bin widths in Supplementary material Appendix 3.

Statistical analysis – overview

We constructed regression models with species richness as the response variable and with size diversity as a predictor variable (Fig. 2). We used the individual–size distribution (ISD) as a measure of size diversity, and used two methods to include ISDs. First, we used five size-diversity indices as predictor variables (Fig. 2a). Second, we used functional data analysis to include the entire ISD as a predictor (Fig. 2b). The second method can distinguish between the true absence of an association between species richness and size diversity (Fig. 2c) and the inability of size-diversity indices to detect such an association (Fig. 2d). We fitted linear and quadratic versions of both models. We evaluated our models with cross validation to account for differences in the number of parameters between the two modelling methods. In the following sections, we provide statistical and computational details for the two analysis methods.

Statistical analysis – relating species richness to size-diversity indices

We related species richness to size-diversity indices with a linear regression model, response = intercept + slope × predictor, but we included random intercepts for clusters within the data (e.g. data collected in the same year or in the same region; Table 1). We fitted seven models with the five size-diversity indices included as predictors, either alone (five models), in combination (one model), or in combination with pairwise interactions (one model). The model structure was

$$y_i = \alpha + \Sigma_k \beta_k x_{i,k} + \Sigma_q \gamma_{q,G(i)} + \varepsilon_i$$

where y_i is the species richness of site i; α is the mean site-level species richness; β_k is the linear association between species richness and the kth size-diversity index, which takes value $x_{i,k}$ in site i; $\gamma_{q,G(i)}$ is a random intercept for level $G(i)$ of grouping variable q (e.g. year or region), where $G(i)$ is the group to which site i belongs; and ε_i is the residual for site i. Site refers to canyons aggregated over a given sampling year for the Great Basin bird data, transects aggregated over a given survey period and season for the box-ironbark bird data, and single surveys at each site for the fish data. We standardized species richness data and size-diversity indices to zero mean and unit standard deviation. We assumed that the ε_i (residual) terms were normally distributed, which was supported by inspection of model residuals.

We extended the linear regression model to test whether associations between species richness and size-diversity indices were quadratic, which would occur if size-diversity indices had a saturating or unimodal association with species richness (e.g. Fig. 1b). The quadratic model was

$$y_i = \alpha + \Sigma_k \beta_k x_{i,k} + \Sigma_k \delta_k x_{i,k}^2 + \Sigma_q \gamma_{q,G(i)} + \varepsilon_i$$

where δ_k is the quadratic association between species richness and the kth size-diversity index. All other variables are defined above. The addition of a quadratic term did not substantially alter model fit for any data set; results of quadratic models are in Supplementary material Appendix 3.

We used Bayesian parameter estimation and assigned vague normal prior distributions (zero mean and variance > 10) to α, β, and δ. We assigned inverse-gamma prior distributions with both parameters equal to 0.01 to the variance parameters for ε_i and $\gamma_{q,G(i)}$ (Supplementary material Appendix 4).

Statistical analysis – relating species richness to individual–size distributions

Scalar-response function regression is similar structurally to a linear regression model, except that the slope and predictor are functions rather than single values (Ramsay and Silverman 2005). Here, 'function' refers to a mathematical function and not to ecological functions or to functional diversity. The regression equation is *response = intercept + ∫ slope(m) × predictor(m) dm*, where *slope(m)* and *predictor(m)* are functions of the index variable *m* (body mass in this study) and *∫ f(m) dm* denotes integration of the function *f(m)* over all

values of m. In our analysis of individual–size distributions (ISDs) and species richness, the function *slope(m)* can be interpreted as a size-dependent, linear-regression coefficient, such that each point on the ISD has a different association with species richness (Fig. 3). We extended this model to include random intercepts for clusters within the data (Table 1). The model structure was

$$y_i = \alpha + \int \beta(m)z(m)\mathrm{d}m + \sum_q \gamma_{q,G(i)} + \varepsilon_i$$

where $\beta(m)$ is the size-dependent effect of the predictor function (the ISD) on the response variable (species richness), and $z(m)$ is the value of the predictor function (the ISD) for a given value of m. All other variables are defined above. We standardized species richness data to zero mean and unit standard deviation, and divided ISDs by their maximum value in all analyses.

We extended this model to include possible quadratic associations between species richness and ISDs, which would occur if the abundance of individuals within a given size class had a saturating or unimodal association with species richness. The quadratic model was

$$y_i = \alpha + \int \beta_1(m)z(m)\mathrm{d}m + \int \beta_2(m)z^2(m)\mathrm{d}m + \sum_q \gamma_{q,G(i)} + \varepsilon_i$$

where $\beta_1(m)$ is the linear effect of the ISD on species richness, $\beta_2(m)$ is the quadratic effect of the ISD on species richness, and $z^2(m)$ is the squared ISD. Other variables are as defined above. The fit of linear and quadratic models did not differ substantially; we report results for quadratic models in Appendix 3.

We used a B-spline basis to represent the continuous function $\beta(m)$ as a set of discrete coefficients. The fitted model was

$$y_i = \alpha + \sum_p \beta_p \left[\sum_j B_p(m_{i,j}) z_i(m_{i,j}) \right] + \sum_q \gamma_{q,G(i)} + \varepsilon_i$$

where β_p is the coefficient of the pth B-spline basis function, $B_p(m_{i,j})$ is the value of the pth B-spline basis function

(a)

(b)

(c) $S(m) = N(m) \times \beta(m)$

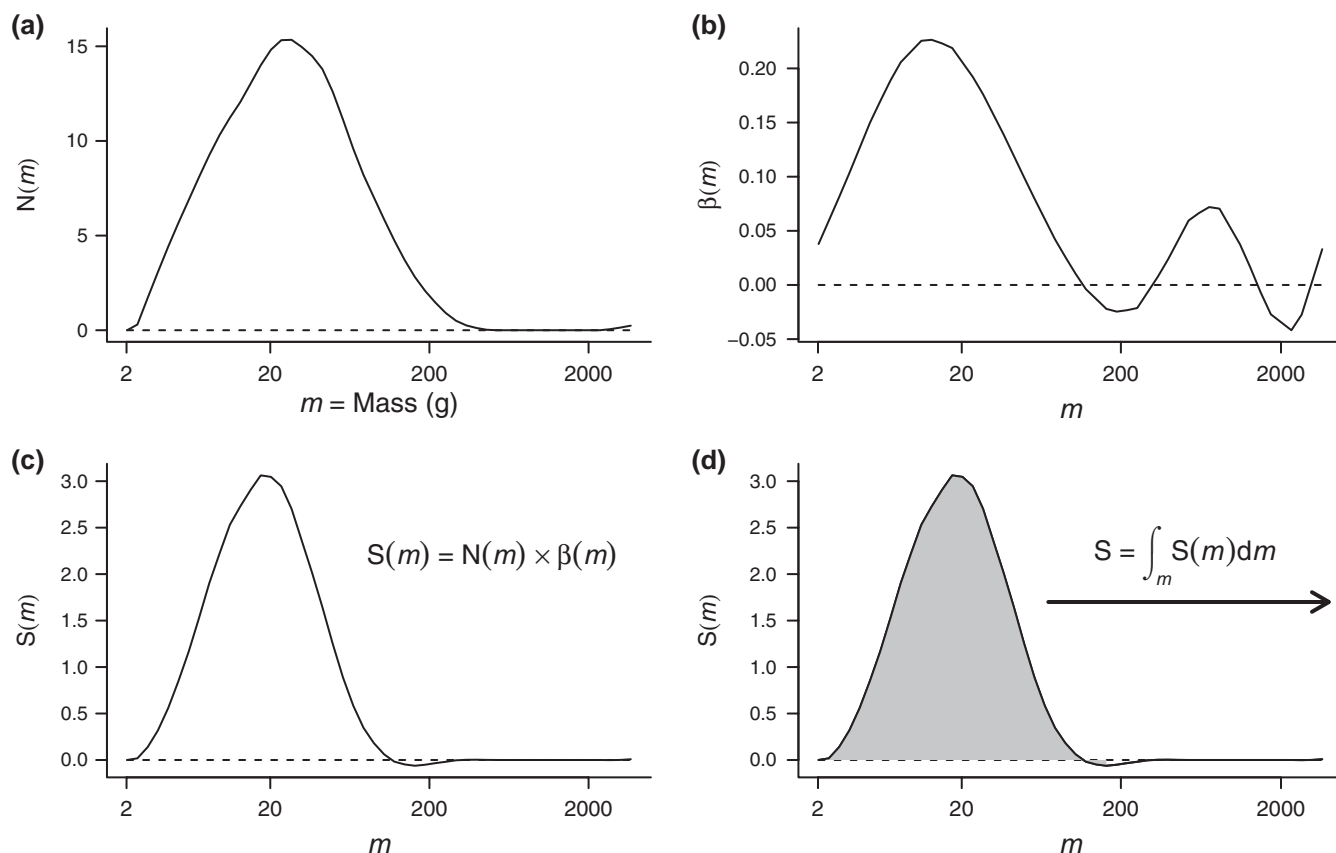**(d)** $S = \int_m S(m)\mathrm{d}m$

Figure 3. Interpretation of estimated coefficients from functional data analysis with species richness as the response variable and individual–size distributions (ISDs) as the predictor variable. The predictor variable is the entire, continuous ISD (a). The estimated coefficient is a continuous function spanning the full range of sizes in the ISD (b). The analysis calculates species richness in two steps. First, the estimated coefficient (b) is multiplied by the ISD (a), which yields an estimate of species richness as a function of individual sizes (c). Second, this size-dependent species richness is integrated over the entire range of sizes (d). The value of this integral (the area of the shaded region in d) is the model estimate of species richness.

evaluated at $m_{i,j}$, $m_{i,j}$ is the abscissa for the jth value of the predictor function in site i, and $z_i(m_{i,j})$ is the value of the predictor function at $m_{i,j}$. Other variables are defined above. We used Bayesian parameter estimation and assigned vague normal prior distributions (zero mean and variance > 10) to α and β_p. We assigned inverse-gamma prior distributions with both parameters set to 0.01 for the variance parameters for ε_i and $\gamma_{q,G(i)}$ (Supplementary material Appendix 4).

Computational details

We estimated parameters for all models with a Gibbs sampler (Gelfand 2000), which is a Markov chain Monte Carlo (MCMC) sampler that iteratively draws parameter estimates from their conditional densities. A full derivation of the conditional distributions and a description of the MCMC sampler are in Supplementary material Appendix 4.

We based parameter estimates on three chains of 40 000 MCMC iterations, which followed a 10 000 iteration burn-in period. We assessed convergence through inspection of parameter and likelihood chains. All models converged in fewer than 1000 iterations. We managed model outputs in R (<www.r-project.org>) and wrote the MCMC sampler in C++. The MCMC sampler is part of the 'function regression in ecology and evolution' (FREE) R package (Yen et al. 2015a), and data and code for our models are in Supplementary material Appendix 5 and 6.

Model comparisons and validation

We fitted eight models for each data set: a function regression model with the ISD as the predictor of species richness; and seven linear regression models with the five size-diversity indices included as predictors, either alone (five models), in combination (one model), or in combination with pairwise interactions (one model). We calculated both naïve (in-sample) and cross-validated (out-of-sample) model fit statistics (r^2 between observed data and fitted values) for all models. Cross-validated estimates of model fit were based on ten-fold cross validation. Low values of cross-validated model fit relative to naïve model fit indicate model overfitting, whereas high values of cross-validated model fit indicate a reliable model that is likely to be identifying a true association (Efron and Gong 1983).

Results

Relations between size-diversity indices and species richness

There were clear associations between species richness and size-diversity indices. Size-diversity indices with 20 bins explained 0.06–0.79 of the variation in species richness (naïve r^2-values) and predicted up to 0.30 of the variation in species richness (cross-validated r^2-values) (Table 2). Size-diversity indices with 1000 bins explained 0.11–0.83 of the variation in species richness and predicted up to 0.72 of the variation in species richness (Table 3). Size-diversity indices with 500, 1000 and 5000 bins explained and predicted similar amounts of the variation in species richness (Supplementary material Appendix 3).

With 20 bins, the richness of size classes predicted the greatest proportion of variation in species richness of box-ironbark birds (fragment study), and a combination of four indices with pairwise interactions predicted the greatest proportion of variation in species richness of birds in the other data sets (Table 2). The richness of size classes and combinations of indices with and without pairwise interactions predicted the greatest proportion of variation in species richness of fishes (Table 2, 3).

Size-diversity indices were associated positively with species richness in all data sets (all model coefficients > 0; Fig. 4). Size-class divergence had the strongest associations with species richness in all data sets, followed by the evenness and Shannon entropy of size classes (Fig. 4). However, coefficients for size-class divergence and evenness had wider credible intervals, hence more uncertain associations than

Table 2. Correlations (r^2) between observed species richness and species richness predicted by size-diversity indices or individual–size distributions compiled with 20 bins. Values are based on naïve model fit and the numbers in parentheses were derived from ten-fold cross validation. Values in boldface denote the best-performing predictor variable under cross validation. Values generated by quadratic models are in the Supplementary material Appendix 3. The combination of indices includes the range, richness, evenness, and divergence of body masses.

Predictor variable	Great Basin birds	Great Basin birds – no poorly sampled species	Box-ironbark birds – fragment study	Box-ironbark birds – landscape study	United States fishes
Size-diversity indices					
Range of body masses	0.42 (0.06)	0.41 (0.02)	0.12 (0.11)	0.78 (0.04)	0.24 (0.20)
Richness of body-mass classes	0.50 (0.17)	0.54 (0.25)	0.18 (0.15)	0.78 (0.18)	**0.28 (0.24)**
Shannon entropy of body masses	0.42 (0.06)	0.44 (0.12)	0.13 (0.09)	0.78 (0.07)	0.22 (0.18)
Evenness of body masses	0.37 (0.00)	0.39 (0.05)	0.09 (0.05)	0.79 (0.02)	0.16 (0.11)
Divergence of body masses	0.39 (0.00)	0.37 (0.00)	0.06 (0.00)	0.79 (0.00)	0.14 (0.09)
Combination of indices	0.52 (0.18)	0.55 (0.27)	0.18 (0.14)	0.79 (0.20)	**0.28 (0.24)**
Combination with pairwise interactions	0.54 (0.20)	0.56 (0.30)	0.18 (0.13)	0.78 (0.21)	**0.29 (0.24)**
Size-distribution measure					
Individual–size distributions	**0.68 (0.26)**	**0.69 (0.31)**	**0.36 (0.23)**	**0.84 (0.28)**	0.27 (0.20)

Table 3. Correlations (r^2) between observed species richness and species richness predicted by size-diversity indices compiled with 1000 bins or individual–size distributions compiled with 40 bins. Values are based on naïve model fit and the numbers in brackets were derived from ten-fold cross validation. Values in boldface denote the best-performing predictor variable under cross validation. Values generated by quadratic models are in the Supplementary material Appendix 3. The combination of indices includes the range, richness, evenness and divergence of body masses.

Predictor variable	Great Basin birds	Great Basin birds – no poorly sampled species	Box-ironbark birds – fragment study	Box-ironbark birds – landscape study	United States fishes
Size-diversity indices					
Range of body masses	0.42 (0.05)	0.42 (0.02)	0.14 (0.13)	0.78 (0.02)	0.25 (0.20)
Richness of body-mass classes	**0.75 (0.72)**	0.74 (0.70)	0.38 (0.28)	0.81 (0.36)	0.27 (0.21)
Shannon entropy of body masses	0.75 (0.71)	0.74 (0.70)	0.36 (0.26)	0.78 (0.30)	0.13 (0.07)
Evenness of body masses	0.75 (0.70)	0.74 (0.70)	0.36 (0.26)	0.78 (0.28)	0.11 (0.05)
Divergence of body masses	0.39 (0.00)	0.37 (0.00)	0.06 (0.00)	0.78 (0.00)	0.15 (0.09)
Combination of indices	0.76 (0.71)	**0.75 (0.71)**	0.39 (0.29)	0.82 (0.36)	**0.35 (0.29)**
Combination with pairwise interactions	**0.76 (0.72)**	**0.76 (0.71)**	**0.49 (0.37)**	**0.83 (0.40)**	**0.35 (0.29)**
Size-distribution measure					
Individual–size distributions	0.67 (0.26)	0.64 (0.28)	0.36 (0.23)	0.84 (0.35)	0.28 (0.21)

those for other indices (Fig. 4). Estimated coefficients for most size-diversity indices were greatest for fishes, and were lowest for birds in the box-ironbark landscape study (Fig. 4). Increasing the number of bins to calculate size-diversity indices altered the absolute magnitude of estimated coefficients but did not affect the direction of associations or their relative magnitudes (Supplementary material Appendix 3). For Great Basin birds, the removal of species poorly sampled by point counts increased the magnitude of the fitted association between species richness and the range of size classes, but
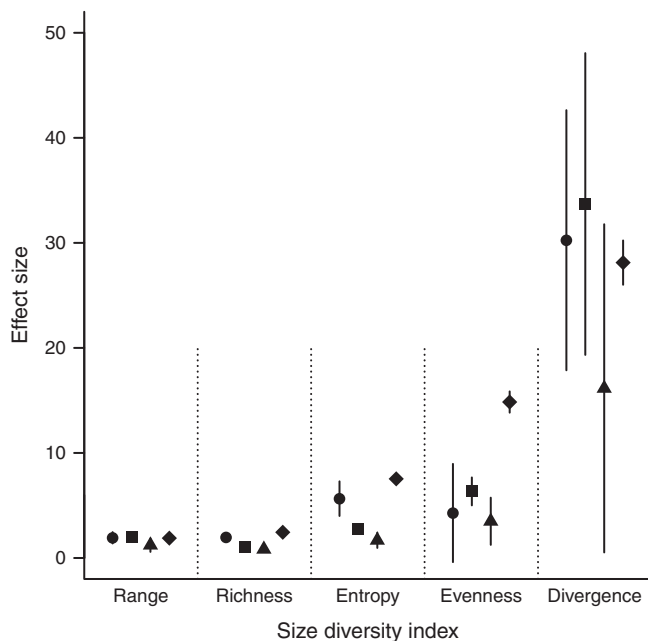

Figure 4. Estimated coefficients from a linear regression with species richness as the response variable and one of five size-diversity indices as the predictor variable for Great Basin birds (circles), box-ironbark birds – fragment study (squares), box-ironbark birds – landscape study (triangles), and fishes in the United States (diamonds). Points are mean fitted effects and lines indicate one standard deviation of the mean fitted effect.

did not substantially alter associations for other size-diversity indices (Supplementary material Appendix 3).

Relations between individual–size distributions and species richness

With 20 bins, individual–size distributions (ISDs) explained 0.27–0.84 of the variation in species richness of birds and fishes (naïve r^2-values; Table 2). ISDs predicted 0.20–0.31 of the variation in species richness (cross-validated r^2-values; Table 2). The proportion of variation explained and predicted was similar when ISDs were compiled with 40 bins (Table 2, 3).

Fitted associations between species richness and ISDs can be interpreted as size-specific associations between species richness and abundance (Fig. 3). The association was unimodal for Great Basin birds, with a peak between 10 g and 50 g (Fig. 5a). There was little evidence of an association between species richness and the number of individuals > 200 g (Fig. 5a). The addition of 15 10-g individuals was associated an increase of one in species richness, but additions of individuals > 200 g were not associated with changes in species richness based on the magnitude of the associations in Fig. 5a. The omission of species poorly sampled by point counts reduced the size range of the sampled community, but the fitted relation remained consistent, with a positive association between species richness and the abundance of individuals with body masses <100 g (Supplementary material Appendix 3).

The fitted association between species richness and ISDs was unimodal for birds in the box-ironbark fragment study, with a peak between 50 g and 200 g (Fig. 5b). This association was positive for all birds < 5000 g, but there was little evidence of an association between species richness and the number of individuals > 5000 g (Fig. 5c). The magnitude of this association was similar to that observed in Great Basin birds (Fig. 5a–b).

The association between species richness and ISDs was positive and unimodal for birds in the box-ironbark landscape study, with a peak at 200 g (Fig. 5c). This association indicates
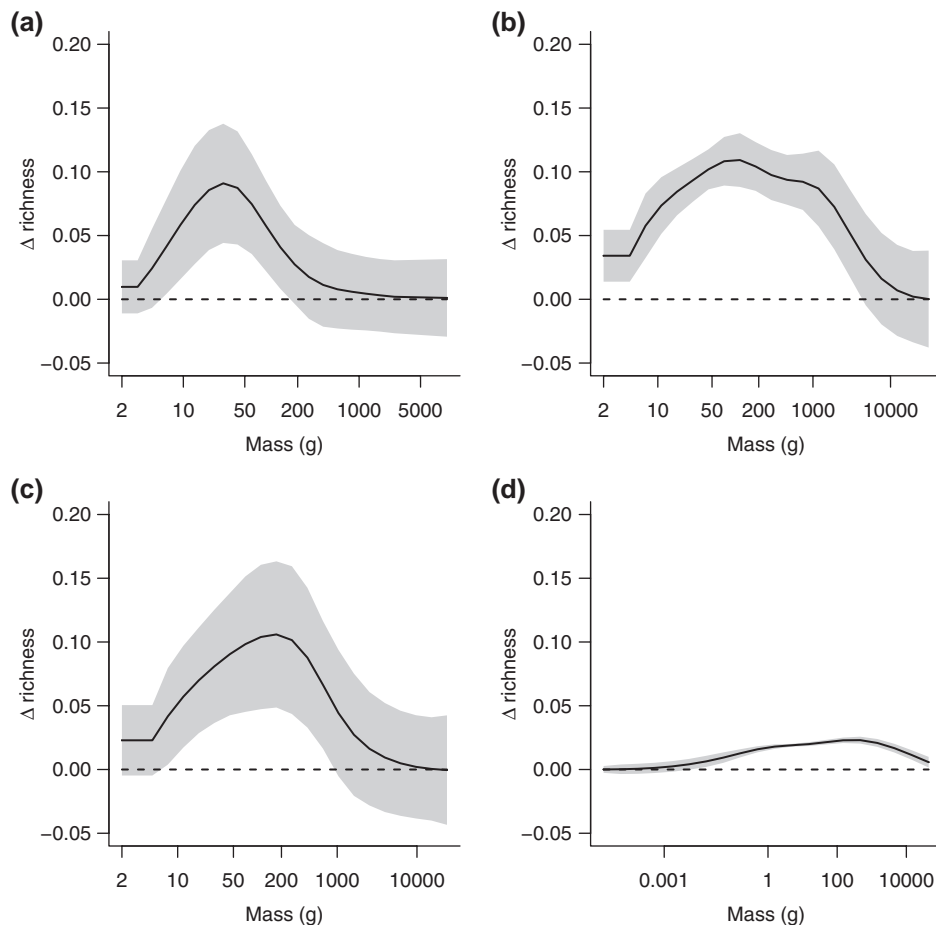
Figure 5. Estimated coefficients from functional data analysis with species richness as the response variable and individual–size distributions (ISDs) as the predictor variable for Great Basin birds (a), box-ironbark birds – fragment study (b), box-ironbark birds – landscape study (c), and fishes in the United States (d). Estimated coefficients display the expected change in species richness (Δ richness) as an individual of a given size is added to a community. Grey shading indicates one standard deviation of the mean fitted effect.

that species richness is positively associated with abundances of birds < 1000 g. However, near-zero regression values for individuals >1000 g suggest that the abundance of these larger birds is not closely associated with species richness (Fig. 5c).

The fitted effect of fish ISDs on species richness was positive for fishes > 0.01 g and did not differ substantially from zero for smaller individuals (Fig. 5d). This association indicates a consistent, positive association between species richness and abundances of fishes > 0.01 g (Fig. 5d). In all data sets, associations between species richness and ISDs were relatively insensitive to changes in the number of bins used to calculate ISDs. Increasing the number of bins produced smoother curves but did not alter their shapes (Supplementary material Appendix 3).

Comparison between size-diversity indices and individual–size distributions

When based on 20 bins, individual–size distributions (ISDs) predicted 3–53% more variation in bird species richness than did size-diversity indices (Table 2). Size-diversity indices predicted 20% more variation in species richness of fishes

than did ISDs (0.24 and 0.20, respectively; Table 2). With 40 bins, size-diversity indices explained 4–68% more variation in species richness of Great Basin birds, box-ironbark birds (fragment study), and fishes than did ISDs (Supplementary material Appendix 3). ISDs predicted 17% more variation in species richness of box-ironbark birds (landscape study) than did size-diversity indices (0.35 and 0.30, respectively; Table 3). With 1000 bins, size-diversity indices predicted 14–177% more variation in species richness than did ISDs compiled with 40 bins (Table 3).

The omission of species poorly sampled by point counts for Great Basin birds more than doubled cross-validated r^2-values for size-diversity indices and increased the cross-validated r^2-value for ISDs by 0.05 (Table 2). The inclusion of quadratic terms in the regression model had little effect on naïve and cross-validated r^2-values for ISDs and size-diversity indices (Supplementary material Appendix 3).

Discussion

There were clear links between species richness and size diversity in birds and fishes, which suggest that mechanistic,

size-based models might be extended to predict variation in species richness. Associations between size diversity and species richness generally were strongest when we included multiple size-diversity indices with pairwise interactions as predictor variables. However, the proportion of variation in species richness explained by models with continuous individual–size distributions (ISDs) as predictor variables was similar to that explained by models based on size-diversity indices for several data sets, and the ISD-based models were largely insensitive to details of model fitting, such as the number of bins used to discretize ISDs. Although size-diversity indices identified complex associations between size diversity and species richness, functional data analysis provided other inferences, such as the size classes that underpin observed associations. Analyses of continuous ISDs showed that small- and medium-sized individuals drive observed associations between species richness and size diversity. We believe that broader use of functional data analysis would enrich ecological inferences from analyses of taxonomic or functional diversity indices.

There are two practical benefits of functional data analysis. First, outcomes from functional data analysis appeared to be relatively insensitive to differences in the calculation of ISDs, such as the number and width of bins. By contrast, the number of bins used to compile ISDs was strongly associated with the predictive accuracy of size-diversity indices (Supplementary material Appendix 3). In many cases, this association was unimodal, so using a very large number of bins did not guarantee high predictive accuracy (Supplementary material Appendix 3). Second, models based on ISDs had similar accuracy regardless of whether poorly sampled species were included, whereas model predictions based on size-diversity indices improved when poorly sampled species were excluded. Analyses using entire ISDs may be less sensitive to changes in the range of observed sizes or the presence of specific size classes than comparable analyses based on size-diversity indices.

There were positive associations between species richness and size-diversity indices for all indices and data sets, so that, for the data sets considered here, increases in size diversity were associated with increases in species richness. This is consistent with the results of our analysis of species richness and ISDs in which species richness was positively associated with the number of individuals in most size classes in all data sets (Fig. 5). Increases in the abundances of individuals in multiple size classes typically would be associated with increases in size-diversity indices because increases in the number of individuals in these size classes would result in a more-even ISD spanning more size classes. Close associations between species richness and size-diversity indices do not provide detailed insight into which size classes are driving the observed associations. Increases in size-class richness could result from the addition of individuals into any absent size class, but our analysis of ISDs showed that positive associations between species richness and size diversity were determined by small and medium-sized individuals (< 100 g for

Great Basin birds, < 1000 g for box-ironbark birds) (Fig. 5a–c). The abundances of individuals in larger size classes were not associated with a change in species richness of birds (Fig. 5a–c). We found a similar, but weaker, pattern for fishes, with the strength of the associations between species richness and ISDs decreasing for large size classes (>5000 g; Fig. 5d).

Our aim was to identify correlative links between species richness and size diversity. Although it is possible that size diversity is causally linked to species richness, species richness and size diversity may be linked indirectly through the ecological processes that determine community structure and dynamics, including competition and niche partitioning, trophic interactions and ecological drift. The primary contribution of the current study is the quantification of links between size diversity and species richness, which suggests that mechanistic, size-based models (Scott et al. 2014) might be used to predict patterns in species richness. Size-based models often do not include species' identities but can incorporate many ecological processes. Our study provides a link between the outputs of these models (typically ISDs) and species richness, which has always been and continues to be a critical quantity in much of community ecology, macroecology and biogeography (Gotelli et al. 2009).

Although we did not set out to identify a causal link between species richness and size diversity, our work provides insight into the processes that determine species richness. One might expect that both ISDs and size-diversity indices are associated with size-dependent niche partitioning, where the addition of a species is likely to fill an empty size class or extend the range of observed size classes. The links between species richness and size-class richness suggests that size-dependent niche partitioning occurs in the systems that we considered. Weaker associations between species richness and abundances in larger size classes (e.g. > 100 g for Great Basin birds, > 1000 g for box-ironbark birds) might reflect the intensity of interactions between species in these size classes and other species in the community. Weak associations between species richness and larger-bodied species might be expected in the box-ironbark region given that many of these species are wide-ranging resource-trackers (Mac Nally and McGoldrick 1997), which would be expected to have limited, temporally and spatially variable interactions with woodland bird communities (Mac Nally 1995).

Right-skewed associations between species richness and ISDs of birds in the Great Basin and the box-ironbark landscape study indicate that the number of species was positively correlated with the proportion of small individuals (Fig. 5a, c). These studies covered a range of land-cover types (e.g. woodlands, riparian zones, non-native grasses). Therefore, concurrent changes in species richness and ISDs might be due to changes in species composition or to body sizes among land-cover types (e.g. shifts to fewer, larger species in less-vegetated sites; Fischer et al. 2008). The fitted association between species richness and ISDs of birds in the box-ironbark fragment study was less skewed (Fig. 5b), probably reflecting that the number of individuals, but not

the proportion of small individuals, increased as species richness increased. Sampling in the box-ironbark fragment study was restricted primarily to the interior of native woodland fragments, most of which were > 40 ha. Therefore, associations between species richness and size diversity may not have been associated strongly with differences in land-cover type. Concurrent changes in species richness and abundance might be due to changes in ecological function, with the number of species and individuals increasing as productivity increased (the more-individuals hypothesis; Srivastava and Lawton 1998). A relatively constant, positive association between species richness and ISDs of fishes from 1–1000 g (Fig. 5d) might reflect differences in ecological function, with a greater number of species and individuals in more-productive sites.

That the proportion of small individuals in species-rich bird communities was greater than the proportion of large individuals is consistent with evidence that the proportion of small species is greater than that of large species (Hutchinson and MacArthur 1959), and with observations that there are proportionally more small species in species-rich communities than in species-poor communities (Meiri and Dayan 2003). We can relate ISDs to community metabolic rate (i.e. the rate at which a community processes energy and materials) by applying allometric scaling relations [$metabolic\ rate \propto (body\ size)^{0.75}$] and summing over all individuals in a community (Yen et al. 2015b). Coupled with our observation that the number of small individuals increased as species richness increased, these allometric scaling relations suggest that increases in species richness may be associated with increases in community metabolism, which is consistent with hypothesized positive links between species richness and ecosystem function (Loreau et al. 2001, Hooper et al. 2005). Shifts in the proportion of small and large individuals were less apparent among fishes than among birds, which suggests that macroecological patterns recorded in terrestrial bird and mammal communities may not occur in freshwater fish communities (see also Le Feuvre et al. 2015).

Our analysis assumes that data on individual sizes are available but that species' identities are unknown. Data on individual sizes often are collected in aquatic systems and in terrestrial plant assemblages. Although such data typically are collected alongside data on species' identities, we believe our approach is useful in two situations. First, some mechanistic models of individual traits and many mechanistic models of individual sizes do not model individual species (Blanchard et al. 2017). It would be useful to predict species richness from the outputs of these increasingly sophisticated models. Second, there are efficient techniques to measure individual sizes without identifying species, particularly in aquatic systems (Sheldon et al. 1972, Turnbull et al. 2014, Wheeland and Rose 2016). Relating the data sets from these techniques to species richness would yield rapid estimates of species richness without the often substantial additional effort of identifying species.

Estimating species richness from the outputs of mechanistic, size-based models would generate predictions of species richness associated with any of the many ecological processes considered in recent size-based models (Blanchard et al. 2017). Our results also suggest that functional data analysis can be used to interpret associations in more detail than is possible with single-valued diversity indices. Our approach is applicable to any variable that can be represented as a distribution or function (e.g. land-cover diversity, trait diversity). We expect that broad application of this approach will identify previously undetected links among these different components of biological diversity.

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