

UC Merced

Frontiers of Biogeography

Title

The macroecology of community energy use in terrestrial vertebrates

Permalink

<https://escholarship.org/uc/item/8fw8t2bc>

Journal

Frontiers of Biogeography, 14(3)

Authors

Carter, Benjamin E.
Alroy, John

Publication Date

2022

DOI

10.21425/F5FBG56553

Supplemental Material

<https://escholarship.org/uc/item/8fw8t2bc#supplemental>

Copyright Information

Copyright 2022 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed



The macroecology of community energy use in terrestrial vertebrates

Benjamin E. Carter^{1*}  and John Alroy¹ 

¹School of Natural Sciences, Macquarie University, Sydney, NSW 2109, Australia.

*Correspondence: Benjamin E. Carter, benjamin.carter1@hdr.mq.edu.au

Abstract

Energy is a fundamental macroecological property as it governs all ecological processes and interactions. Understanding variation in community energy use and its correlations is crucial to knowing how communities function across the globe. As an organism's metabolic rate equates to its rate of energy flow, individual rates can predict community-level functioning. Here, daily rates of community energy flow are calculated for 118 bat, 109 bird, and 196 non-volant small mammal inventories from around the world. These were scaled up from individual metabolic rates that were obtained for the 416 bat, 1880 bird, and 562 small mammal species present in the samples. While controlling for spatial autocorrelation, rates were contrasted and compared to various ecological, environmental, geographic, and anthropogenic variables, using a method of sequential regression that renders the variables orthogonal to each other, thus addressing the issue of collinearity. In all groups, there is a strong positive correlation between community energy use and community mass, with biomass being the primary determinant of community energy flow. More surprisingly, there are strong biogeographic differences within and between groups. Bat communities have consistently higher rates of energy flow in the Neotropics, while small mammal communities have higher rates relative to mass in Holarctic realms. Investigations of individual-level patterns reveal that these differences are a direct result of contrasting patterns of abundance, average individual mass, and metabolic rates. These results indicate that community energy use is strongly linked to differences in ecology and evolutionary history within and among groups.

Highlights

- Global variation in vertebrate community energy use is quantified for the first time.
- There are strong biogeographic differences in energy use in all groups.
- Contrasting patterns in ecology and metabolism produce the observed differences.
- Individual metabolic rates directly impact energetics at higher organisational levels.

Keywords: bats, biogeography, birds, community ecology, energy use, macroecology, metabolic rate, small mammals

Introduction

Large-scale spatial patterns are fundamental in ecology. Understanding the causes of variation in the abundance, diversity, and distribution of species across the globe is crucial for predicting the effects of global change and anthropogenic impacts (Kerr et al. 2007). The core drivers of such macroecological and biogeographical patterns usually fall into one of two main categories: ecological effects, which relate to differences in climate and other environmental

factors, and historical effects, which primarily involve differences in evolutionary history. While several studies have reported that a combination of ecological and historical factors likely drive species-level patterns (Fraser and Currie 1996, Crisci et al. 2006, Schuldt and Assmann 2009), here we investigate how these factors influence community-level energetics. By doing so, we show that strong historical and ecological biogeographic patterns affect the spatial structure and function of ecological communities.

Energy is a fundamental property of nature that governs all ecological processes and interactions (Odum 1968, Hannon 1973). On the individual level, an organism's metabolic rate equates to its rate of energy use. The most common and widely studied rate measure is basal metabolic rate (BMR), the rate of energy consumption of an adult organism while at rest in a thermo-neutral environment and post-absorptive state (McNab 1997, Hulbert and Else 2000). BMR is well-known for its strong relationship with body mass, typically scaling as an allometric power function in multicellular organisms (West et al. 1997, White and Seymour 2003, 2005, White et al. 2006, McNab 2008). Although there is often considerable variation in the value of the scaling exponent within and among major groups (Glazier 2005, White et al. 2009), larger organisms nevertheless have higher metabolic rates, with rates lower relative to body size in large organisms due to the hypoallometric relationship.

While metabolic rate is an important measure of energy use on the individual level, it also has relevance to higher levels of organisation. Metabolic rate ultimately dictates the flow of energy at all levels from individuals to populations, communities, and entire ecosystems (Enquist et al. 2003, Brown et al. 2004, Allen et al. 2005, Schramski et al. 2015). Consequently, individual metabolic rates can be scaled up to measure the energy usage of populations and communities (Marquet et al. 2005). As the sum of individual rates of a community represents its rate of energy flow, variation in individual metabolism is a key driver of community metabolism. Previous research scaling community metabolism up from individual metabolic rates has shown that it can predict whole community functioning (Barneche et al. 2014, Ghedini et al. 2018). Understanding how energy use varies on the community level, the underlying causes of this variation, and how rates of energy flow correlate with and are impacted by various factors such as biomass, abundance, and other ecological and environmental attributes, is crucial to knowing how communities function across the globe.

Despite being an active area of research, most studies quantifying energy use at higher levels are usually either limited to a specific community from one location (e.g. Russo et al. 2003, Hayward et al. 2009, Williams et al. 2010, Sewall et al. 2013), are based on communities grown experimentally (e.g. Ghedini et al. 2018, 2020), or are concerned with communities on a continental scale (e.g. Ernest 2005, Fristoe 2015). Furthermore, while global analyses have been conducted assessing spatial variation in density and energy use of populations of different groups (Currie and Fritz 1993, Silva et al. 1997, Santini et al. 2018), no study has yet quantified spatial variation in community energy use across the globe using real-world abundance data.

Here, daily rates of community energy flow are calculated for 423 ecological samples from around the world. They represent three highly important terrestrial endothermic groups: bats, birds, and non-volant small mammals. The rate of energy flow for each community

is scaled up from individual BMR and compared to various climate, environmental, geographic, and anthropogenic variables. Rates of energy flow are also compared to community mass, with additional metrics examined to explore how variation in community energy use relates to differences in abundance, individual mass, and metabolism.

It is hypothesised that community energy use will vary in relation to these attributes in a way that depends on variation in individual-level patterns of BMRs, together with the specific ecological patterns seen in the three groups. While body size is the primary determinate of BMR, and community mass is predicted to be strongly correlated with community energy use as a result, there is large residual variation in individual metabolism, with rates strongly influenced by ecological factors (McNab 2015). One of the most important correlates is environmental temperature, which is usually negatively associated with BMR in these groups (Lovegrove 2003, White et al. 2007, Jetz et al. 2008, Naya et al. 2013, Luna et al. 2017). Temperature should therefore impact rates of community energy flow along with other environmental variables that covary with temperature. In addition, rates also likely vary geographically, due to reasons other than temperature, given the contrasting patterns seen with BMR in different biogeographic realms among the three groups: birds and small mammals have higher BMRs in Holarctic zones (Lovegrove 2000, Londoño et al. 2015), while bats have higher BMRs in tropical realms (Speakman and Thomas 2003). Lastly, community energy use is expected to be impacted by anthropogenic factors due to the strongly detrimental effects human activities have on species diversity and composition, and on ecosystem functioning and well-being (Maurer 1996, Jetz et al. 2007, Revilla et al. 2015, Newbold et al. 2015, Alroy 2017).

Regardless of the differences in individual metabolic variation and its possible effects on community energy use, community metabolism is likely to be strongly impacted by differences in biomass and abundance. Quantifying how biomass and abundance affect community energy use is important for understanding higher-level scaling relationships, how these differ to those on the individual level (Ghedini et al. 2018), and how relative differences in biomass and abundance impact rates of energy flow. It is expected that group-specific patterns in biomass and abundance across the globe will drive patterns of community energy use, along with variation in metabolism.

Materials and Methods

Samples

Ecological inventories were downloaded between 27 and 29 January 2020 from the Ecological Register (<http://ecoregister.org>, see Alroy, 2015, 2017, 2019). Samples for bats, birds, and non-volant small mammals – which include rodents, lagomorphs, lipotyphlan insectivores, marsupials, and other groups – were downloaded separately. For bats and birds, only samples collected using mist netting were included.

For small mammals, all sampling methods were included with the exception of camera trapping. Samples from small oceanic islands were excluded. Duplicate samples, meaning those from the same published paper that had the same habitat type, altered habitat, and disturbance category, as well as identical area coordinates (0.1 by 0.1 degrees across), were also excluded: only the largest sample (in terms of total abundance) of each set of duplicate samples was downloaded. Of the 713 samples downloaded in total, only the 423 with abundance data recorded in count-per-day units were used in the subsequent analyses. This brought the totals down to 118 bat, 109 bird, and 196 small mammal samples (Appendix S1).

Bat and bird communities are primarily restricted to understory species due to the fact that mist nets are usually placed close to the ground. Canopy species and non-passerine birds are less represented, although not missing entirely. Likewise, non-volant small mammal communities are mainly restricted to ground-dwelling species because traps are normally placed on the ground, but do also include some facultatively arboreal species.

The species pool of each sample is drawn from one location and habitat type, with the abundances reflecting the number of captures per day, per trap, for each site. This is analogous to standard line transects. The difference is simple. For line transects, an observer walks out a literal transect with a particular radius over a fixed period of time. For the data utilised here, the animals themselves walk into the radius of the traps over a fixed period of time. As such, each trap corresponds to a separate virtual transect, and so the number of trap days effectively standardises by area. The fact that the sample points are scattered throughout a site of a specific habitat type is actually advantageous because this averages out small-scale variation in population density. For these reasons, and as each sample is representative of a single, local community, the samples are fully comparable with each other.

BMR and body mass

BMR values were obtained through an intensive search of the primary scientific literature and the Dryad Data Repository (<https://datadryad.org/>). Of the 416 species of bats, 1880 species of birds, and 562 species of small mammals that were present in the samples, BMR data were obtained for 70, 384, and 184, respectively (Appendix S2). The BMRs of the remaining species were predicted based on mass using three separate regression models (one per group) constructed using R v.4.1.2 (R Core Team 2021). Ordinary least squares (OLS) regression was used as it is preferred when predicting BMR from body mass (White 2011). All BMR measurements were recorded in units of millilitres of oxygen consumption per hour ($\text{ml O}_2 \text{ h}^{-1}$); for studies in which BMR was recorded in other units (e.g., watts), BMR values were converted first into kJ hr^{-1} and then into $\text{ml O}_2 \text{ h}^{-1}$ using the conversion factor $1 \text{ kJ hr}^{-1} = 47.8 \text{ ml O}_2 \text{ h}^{-1}$ (Fristoe et al. 2015, Supporting

Information). Once BMR measurements were obtained, they were converted from $\text{ml O}_2 \text{ h}^{-1}$ into kJ day^{-1} .

A large majority of species had body mass measurements already recorded in the Ecological Register, which were obtained from primary sources. Remaining values were obtained from either the same papers as the BMR measurements; online databases and encyclopedias such as the *Handbook of the Birds of the World Alive* (Del Hoyo et al. 2018) for birds and the *Encyclopedia of Life* (<https://eol.org>, Parr et al. 2014) for mammals; and the primary literature. If no reliable mass measurement could be obtained for a particular species, its mass was calculated by taking the geometric mean of the masses of all the other species of its genus that were present in the Ecological Register. Masses were calculated for one bat, 21 bird, and five small mammal species in this way (Appendix S2).

In addition, there were 80 indeterminate species records across the three groups, denoted with a 'sp.' or 'spp.' following the genus name (Appendix S2). These species also had their mass values calculated by taking the geometric mean for congeners present in the Ecological Register, and their BMRs were predicted using the respective regression models for each group.

Community energy flows

Once BMR and mass values were obtained for all species in all samples, the total rate of community energy flow (EF_{com}) for each ecological sample was calculated using the equation

$$EF_{com} = \sum_{i=1}^n (N_i * M_i) \left[\text{kJ trap}^{-1} \text{ day}^{-2} \right] \quad (1)$$

where n is the number of species in the sample, N_i is the abundance of species i , measured by count per trap per day, and M_i is the metabolic rate of a species, measured in kilojoules per day (kJ day^{-1}). In other words, the rate of community energy flow for an ecological sample was calculated as the product of the abundance and metabolic rate of each species in the sample summed across all species in the sample (Fig. 1). The total community mass (measured in grams per trap per day; $\text{g trap}^{-1} \text{ day}^{-1}$) was calculated in the same way and was analysed alongside total energy flow.

In addition to the total rate of energy flow and total mass, several other metrics were also calculated (Fig. 1). To determine the strength of energy flow relative to a community's mass, the per-gram (or mass-specific) rate of community energy flow ($\text{kJ g}^{-1} \text{ trap}^{-1} \text{ day}^{-1}$) was calculated by taking the ratio between total community energy flow and total community mass. As the per-gram rate of community energy flow is analogous to the individual mass-specific metabolic rate, which is greater in smaller organisms due to the allometric scaling of BMR, two more metrics were also examined in order to distinguish between the effects of abundance and body size on rates of energy flow. These were an abundance-weighted average individual rate of energy flow ($\text{kJ trap}^{-1} \text{ day}^{-1}$) and an abundance-weighted average individual

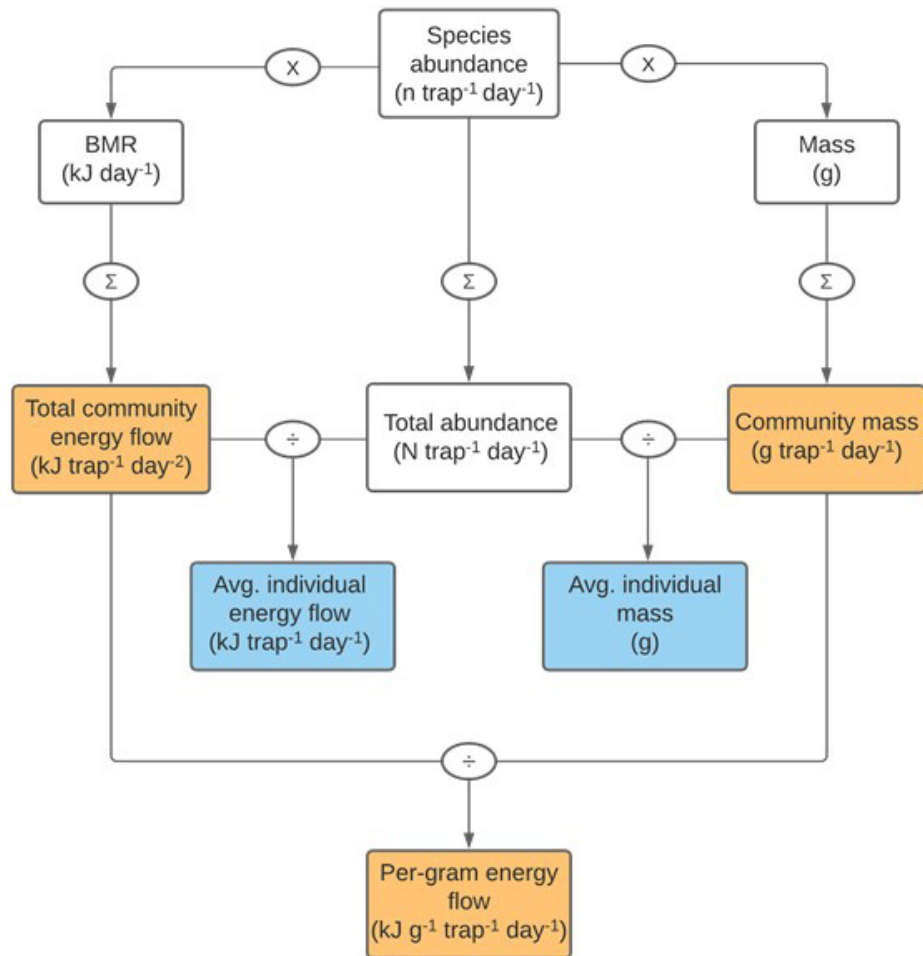


Figure 1. A flow diagram showing the different metrics analysed and how they were calculated. The five dependent variables are colour-coded: the orange boxes represent the three community metrics, while the blue boxes indicate the individual-level metrics that were also examined. The species abundance (n) data correspond to individual species records for each site downloaded from the Ecological Register. These were then summed (Σ) across all species in each sample to obtain the primary community metrics, including total abundance (N), from which the others are derived. The units for each metric are in parentheses.

mass (g). These were both calculated by dividing the total community energy flow or total community mass by the total abundance (total count per trap per day) of the community. They represent the typical rate of energy flow or mass of an average individual in that community. The subsequent analyses were thus performed on a total of five dependent variables: total community energy flow, total community mass, per-gram rate of community energy flow, average individual energy flow, and average individual mass (Fig. 1).

Climate, anthropogenic, and geographic variables

Climate variable data, including mean annual temperature (MAT), mean annual precipitation (MAP), temperature annual range (TAR), and precipitation seasonality (PS) were obtained from the WorldClim database (<https://www.worldclim.org>, Fick and Hijmans 2017), if such data could not be drawn directly from the primary literature. MAT and MAP are

recorded in the Ecological Register, and pertain to the individual sample locations whenever possible. If not, climate values for the closest possible locations are often recorded. Other environmental variables, such as soil nitrogen content, actual evapotranspiration (AET), and net primary productivity (NPP), were respectively obtained from the ORNL Distributed Active Archive Center (<https://daac.ornl.gov>, Global Soil Data Task Group 2000), TerraClimate (Abatzoglou et al. 2018), and SEDAC (Imhoff et al. 2004, Imhoff and Bounoua 2006). Anthropogenic factors including human population density, per capita GDP based on purchasing power parity (PPP), and various land use data were also downloaded from SEDAC (Nordhaus 2006, Nordhaus and Chen 2016, Ellis and Ramankutty 2008a, 2008b). The land use data were simplified into five categories: urban, village, cropland, rangeland, and forest areas. Each sample's value was the proportion of 25 evenly spaced points within each surrounding $1 \times 1^\circ$ cell that

fell within the relevant category. Lastly, five binary geographic variables were created, representing each of the six main biogeographic realms, with the Indomalayan and Australasian realms combined (dubbed “Indo-Australasia”) due to the paucity of samples in Australasia for most groups. This resulted in a combined total of 19 predictor variables.

Statistical analysis

All analyses were conducted using R v.4.1.2 (R Core Team 2021). Due to the large number of predictor variables and the issue of collinearity, which can often bias analyses with many confounding factors (Dormann et al. 2013), the data were analysed using Graham’s (2003) “sequential regression” method, which we term predictor residuals regression (PRR) to avoid confusion with several other methods called “sequential regression”. The PRR analyses were conducted using functions from package ‘*spdep*’ (Bivand 2022).

Unlike more traditional methods such as model selection and regular multiple regression, PRR determines which underlying latent variables are the strongest predictors of Y, even when the predictor variables are collinear. By identifying the best predictor of Y, regressing each subsequent predictor against the best predictor, replacing each relevant X variable with its residuals, and then regressing Y against the best predictor plus the residuals of the other predictors, PRR effectively carries out a geometric rotation of the variable coordinates. This is analogous to a principal components analysis (PCA), although unlike PCA, PRR retains the identity of the original variables. As the residual predictors are orthogonal to one another, the collinearity between the variables is completely removed (Dormann et al. 2013).

PRR was favoured for these reasons. Furthermore, due to its ordination-style rotation, the fitted and r-squared values produced by PRR are identical to those produced by regular multiple regression. PRR is therefore equally interpretable. Graham (2003) and Dormann et al. (2013) did not provide an objective criterion for ordering the independent variables during the sequential calculation. We solved this problem by using a fast algorithm to find the orderings that maximise the sum of the absolute values of the slopes produced by the multiple regression, which guarantees that the contributions of the variables are as distinct as possible (J. Alroy unpublished). This procedure is analogous to the varimax rotation criterion used in factor analysis (Kaiser 1958).

Another common issue that needs to be controlled for in analyses involving spatial data is spatial autocorrelation (Lichstein et al. 2002). To account for any potential spatial pattern in the data, the nearest neighbour (nn) great circle distances for each sample were calculated and added to the analyses as an extra predictor variable. Samples located less than 1° away from each other were excluded from the nn calculations as these have effectively the same environmental characteristics, so including them would make it hard to discern spatial and environmental effects. Calculating

nn distances is effectively the same as the procedures used by other methods that control for autocorrelation, such as spatial autoregression (Bivand and Piras 2015), which also depends on identifying nearest neighbours. Identification of nns was required for computational reasons: spatial autoregression is not easily combined with PRR calculations, which are intensive.

The five dependent variables were each compared to the now 20 predictors for each group, with each Y variable being regressed first on the best predictor, followed by the residuals of all the other predictors. The significance level was set at $\alpha = 0.001$, and *p*-values between 0.001 and 0.01 were considered marginal. Each dependent variable was log-transformed, and the MAP data were square-root transformed because this normalised the data better than log-transforming. To test the effectiveness of the nn predictors, Moran’s *I* tests were conducted on both the raw data and the residuals that resulted when nns were included for each of the 15 total comparisons. Regardless of whether there was any spatial autocorrelation in the underlying data, the tests on the nn residuals all returned non-significant results, indicating the nn calculations adequately controlled for spatial autocorrelation.

Finally, total community energy flow and community mass were regressed on each other to show how community- and individual-level relationships between mass and energy use compare. Total rates of energy flow were also compared to average community mass to further explore these relationships. Here, standardised major axis (SMA) regressions with the package ‘*smatr*’ (Warton et al. 2012) were used. SMA regression was preferred to OLS regression as SMA is more suitable when characterising structural relationships between two closely-related variables, especially when both variables have measurement error (Warton et al. 2006, 2012) and when prediction is not an issue. To test for any potential circularity in the data, these regressions were conducted a second time with communities consisting of only species with properly measured BMR values.

Results

Community energy flow and mass

As expected, community mass was a highly significant predictor of total community energy flow across all three groups (Table 1, Fig. 2), akin to how individual body mass is the best predictor of BMR. However, unlike the allometric scaling relationship between body mass and BMR, the community scaling relationships are far more isometric (i.e., with slopes closer to one) except for small mammal communities, which retain an allometric scaling relationship (Table 1, Fig. 2). This pattern is also presented by the regressions against average community mass (Table 1, Fig. 2), and the results were replicated when using only species with measured BMR values. These strong correlations explain the overall connection observed between community energy flow and the predictor variables (see discussion).

Table 1. R^2 , slope, and p -values for the regressions between body mass and BMR on the individual level (top) and those between mass and energy flow on the community level (bottom) for each group. OLS and SMA statistics are given for the species-level analyses. The two sets of community regressions contrast the rate of total energy flow with (1) total and (2) average community mass and are both calculated using SMA. BMRs of individual species lacking data were predicted using the OLS coefficients.

Individual regressions	Bats (OLS)	Birds (OLS)	Small mammals (OLS)	Bats (SMA)	Birds (SMA)	Small mammals (SMA)
n	70	384	184	70	384	184
R^2	0.7624	0.8059	0.7988	0.7624	0.8059	0.7988
Slope	0.7693	0.5928	0.6069	0.8811	0.6603	0.6790
p -value	< 2e-16	< 2e-16	< 2e-16	< 2.22e-16	< 2.22e-16	< 2.22e-16
Community regressions	Bats (Total)	Birds (Total)	Small mammals (Total)	Bats (Average)	Birds (Average)	Small mammals (Average)
n	118	109	196	118	109	196
R^2	0.9873	0.9530	0.8610	0.7762	0.6685	0.7888
Slope	0.9822	0.9626	0.8738	0.9113	0.9760	0.8176
p -value	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16	< 2.2e-16

Residual regressions

Total energy flow and mass

For bats, the results of the total energy flow and total mass regressions were identical. The Indo-Australasia and Nearctic variables both negatively correlate, with bat communities in these realms having lower total rates of energy flow and mass than those in other regions (Table 2, Figs. 3-4). The rangelands variable also negatively correlates in both (Table 2). For birds, positive correlations were seen with the Palearctic and Urban variables for total energy flow and mass, respectively (Table 2). For small mammals, the Indo-Australasia and NPP variables were both positive correlates in the community mass regression, while AET was a positive correlate in the total energy flow regression (Table 2).

Per-gram rate of energy flow

The per-gram rate of energy flow (total energy flow divided by total mass) regressions yielded further group-specific results. For bats, there was a strong negative correlation with the Afrotropics variable: Afrotropical bat communities have extremely low per-gram rates of energy flow (Table 2, Fig. 5). This was contrasted with the positive correlation seen with the Palearctic variable (Table 2). Birds and small mammals both exhibited negative correlations with the Indo-Australasia variable. In addition, birds showed a negative correlation with the Urban variable, with further strong negative correlations seen with MAT and NPP in small mammals (Table 2).

Abundance-weighted individual energy flow and mass

For the average abundance-weighted individual rate of energy flow variable (total energy flow divided

by total community abundance), there were mostly positive correlations seen in each group. These include strong correlates with the Afrotropics and Neotropics variables for bats, as well as with the Urban and AET variables for birds and small mammals, respectively (Table 2). The Neotropics variable was also significant in the bird regression, being the only negative correlate (Table 2).

For the average abundance-weighted individual mass variable (total mass divided by total community abundance), all correlations were positive. The Neotropics result for individual energy flow was repeated for bats, as was the Urban result for birds (Table 2). Otherwise, the correlations differed. Both MAT and the Indo-Australasia variable were correlates for birds, while MAT and NPP were correlates for small mammals (Table 2).

Discussion

In this discussion we will address the following aspects of community energy use: (1) its relationship with community mass, the most important predictor of rates of energy flow, (2) the strong group-specific relationships seen with per-gram rates of energy flow, and (3) the abundance-weighted mass and energy use patterns seen on the individual level for each group, specifically discussing how these determine the patterns seen on the community level.

Total energy flow and mass

In all groups, there is a strong positive relationship between community mass and total community energy flow (Table 1, Fig. 2). Rates of community energy flow are, first and foremost, clearly dependent on the overall mass of a community, with a greater community biomass resulting in a higher rate of

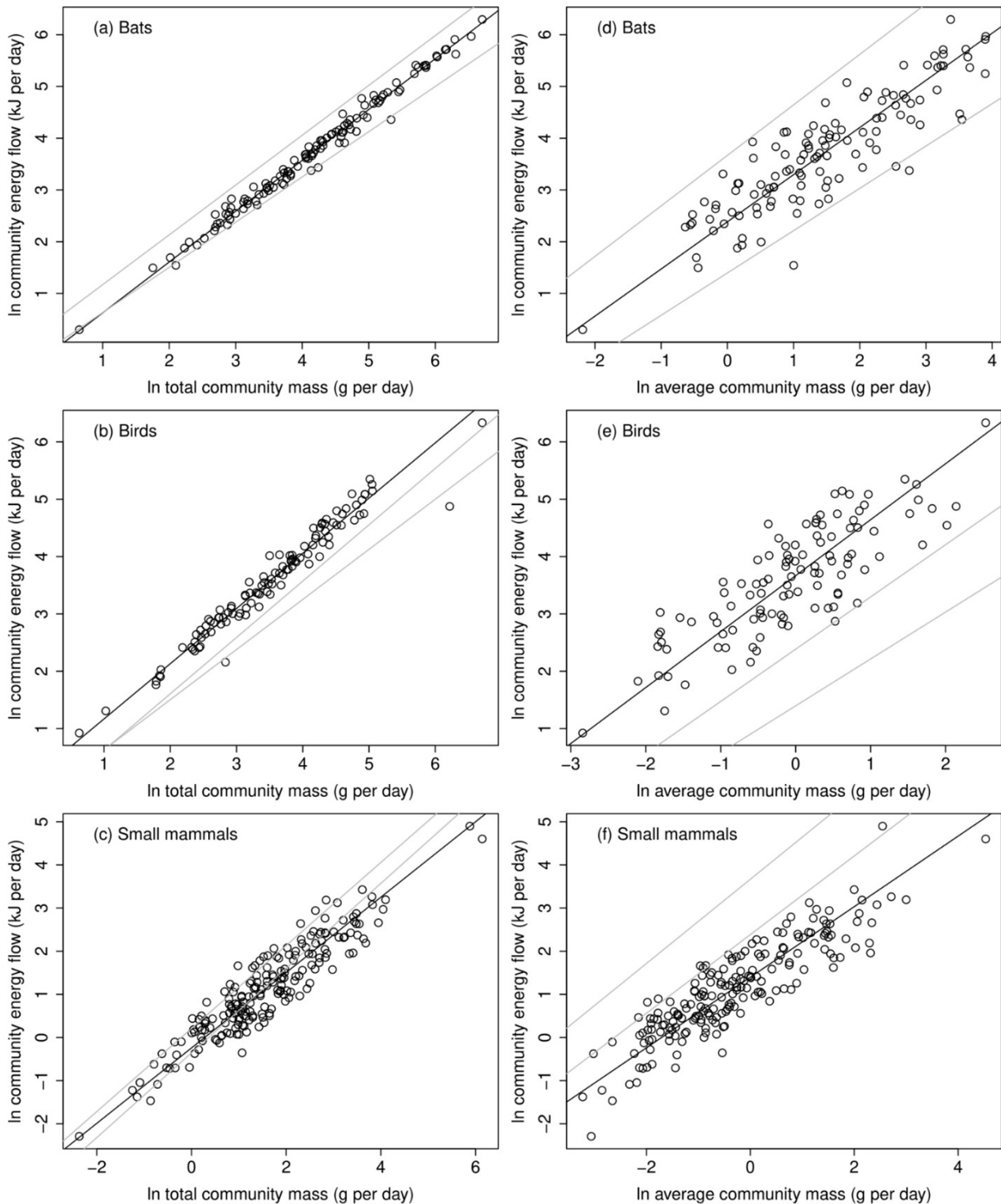


Figure 2. Linear models regressing log total community energy flow against both log total (a to c) and log average (d to f) community mass for the three groups. In each panel, the black line shows the relationship for the focal group and the grey lines show those for the other two groups. Thus, the same three lines appear in each panel in each column. The regression slopes and R^2 values are reported in Table 1. $n = 118$ for bats, 109 for birds, and 196 for small mammals.

energy flow (Fig. 2). This relationship held when community energy flow was compared to average community size (Table 1), with larger populations in

communities also yielding higher rates of energy flow (results not illustrated). This suggests that different sized communities do not have relatively equal

Table 2. The statistically significant independent variables yielded by the predictor residuals regressions for all response variables and all three groups. NN = nearest neighbour values; when listed, this indicates there is a significant spatial autocorrelation pattern. SM = small mammals. Non-significant variables are not included. n = 113 for bats, 104 for birds, and 184 for small mammals, when omitting samples with incomplete data.

Dependent variable (units)	Group	Predictor	R ²	Slope	p	
Total energy flow (kJ day ⁻²)	Bats	Indo-Aust.	0.1200	-0.2968	0.0012	
		Nearctic	0.1200	-0.2541	0.0051	
		Rangelands	0.1200	-0.2514	0.0056	
	Birds	NN	0.0941	-0.3078	0.0015	
		Palaearctic	0.0941	0.3233	0.0009	
	SM	AET	0.0541	0.2076	0.0044	
Total mass (kg day ⁻¹)	Bats	Indo-Aust.	0.1263	-0.2694	0.0030	
		Nearctic	0.1263	-0.2654	0.0034	
		Rangelands	0.1263	-0.2795	0.0021	
	Birds	NN	0.0638	-0.2794	0.0044	
		Urban	0.0638	0.2633	0.0071	
	SM	Indo-Aust.	0.1674	0.3066	<0.0001	
		NPP	0.1674	0.2378	0.0005	
	Per-gram energy flow (kJ g ⁻¹ day ⁻¹)	Bats	Afrotropics	0.4099	-0.5197	<0.0001
			Palaearctic	0.4099	0.4186	<0.0001
Birds		Indo-Aust.	0.2569	-0.5039	<0.0001	
		Urban	0.2569	-0.2982	0.0007	
SM		NN	0.4571	0.5806	<0.0001	
		Indo-Aust.	0.4571	-0.1572	0.0044	
		MAT	0.4571	-0.3145	<0.0001	
Individual energy flow (kJ day ⁻¹)		Bats	NPP	0.4571	-0.2183	<0.0001
			NN	0.5714	0.5735	<0.0001
	Afrotropics		0.5714	0.3796	<0.0001	
	Birds	Neotropics	0.5714	0.3128	<0.0001	
		PS	0.5714	0.1960	0.0021	
		Neotropics	0.1579	-0.2437	0.0085	
SM	Urban	0.1579	0.4346	<0.0001		
Individual mass (kg)	Bats	AET	0.2228	0.4609	<0.0001	
		NN	0.5279	0.5367	<0.0001	
		Neotropics	0.5279	0.4725	<0.0001	
	Birds	Indo-Aust.	0.1850	0.2433	0.0076	
		MAT	0.1850	0.2955	0.0013	
		Urban	0.1850	0.4063	<0.0001	
	SM	NN	0.3420	0.4385	<0.0001	
		MAT	0.3420	0.3658	<0.0001	
		NPP	0.3420	0.2455	<0.0001	

rates of energy flow, as would be expected based on the energy equivalence rule for individual species (Isaac et al. 2013). While energy equivalence has been shown for entire feeding guilds (Sewall et al. 2013), as well as for communities grown under experimental conditions (Ghedini et al. 2020), studies of population energy use in natural communities that do not

support energy equivalence (e.g. Russo et al. 2003, Hayward et al. 2009) suggest this is likely also the case for communities here, despite them corresponding to taxonomically defined assemblages. While presences of other, unstudied taxa may alter the observed pattern, these would have to systematically cancel out the signal to support energy equivalence. Since larger

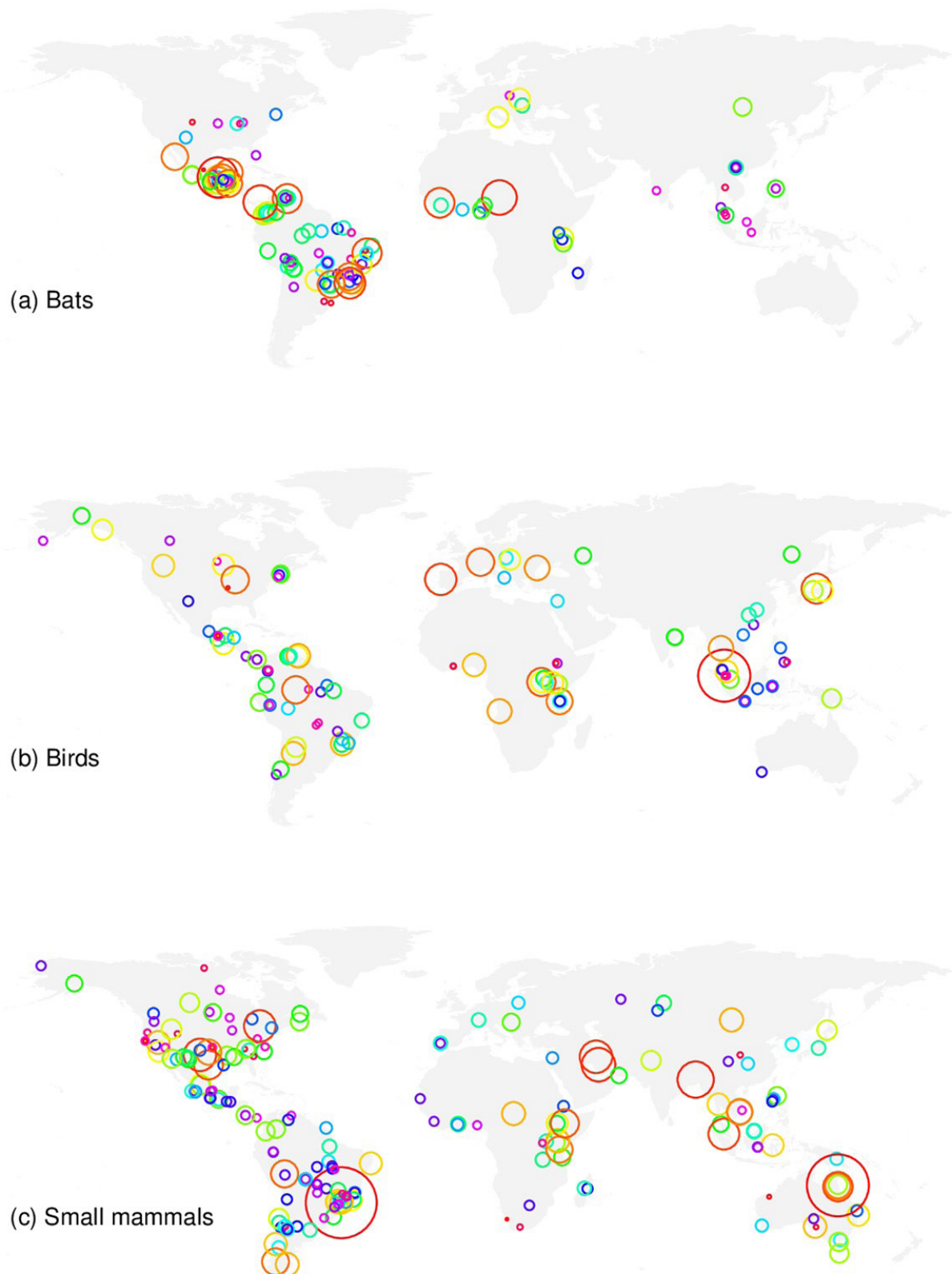


Figure 3. The relative strength of total community energy flows for (a) bats ($n = 118$), (b) birds ($n = 109$), and (c) small mammals ($n = 196$). The colour and size of the circles represent the strength of energy flow, with small blue circles indicating low values and large red circles indicating high ones. The circle colour and sizes are based on logged and scaled data.

species have higher metabolic rates (McNab 2008, 2009) and populations of larger organisms use far more

energy than those of smaller ones (Isaac et al. 2011), communities with greater relative abundances of larger

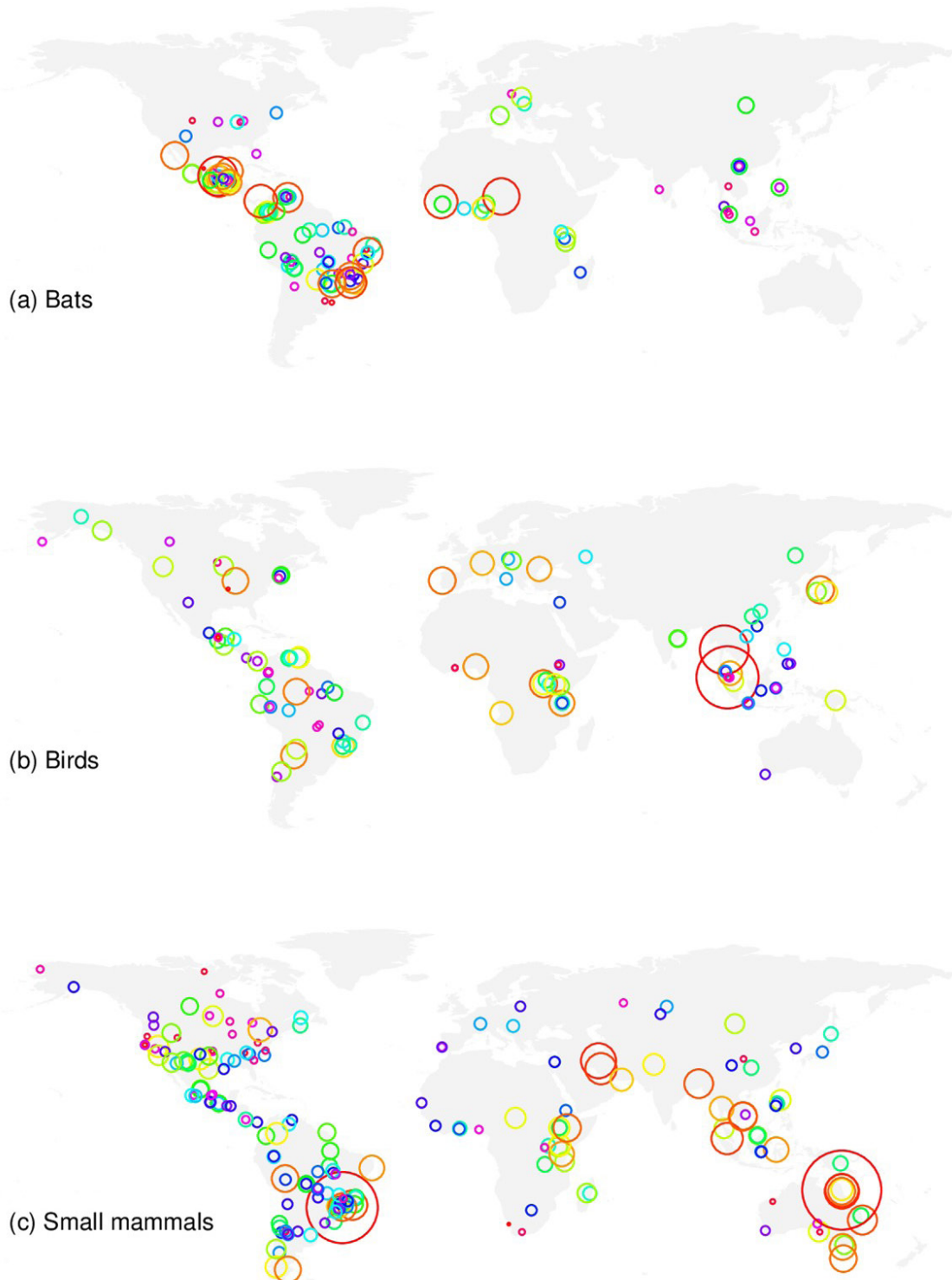


Figure 4. The relative size of community masses for (a) bats ($n = 118$), (b) birds ($n = 109$), and (c) small mammals ($n = 196$). Colour and size of the circles are scaled as in Fig. 3. Community masses correspond well with total rates of community energy flow (Fig. 3).

organisms will have increased rates of energy flow compared to those with higher relative abundances of smaller organisms.

Bats are a good example. Total energy flow and mass negatively correlate with both the Indo-Australasia

and Nearctic variables, which together suggests that bat communities in certain tropical realms are highly distinct, such as in the Neotropics (Table 2, Figs. 3-4). This is due to the extraordinarily high species richness and phylogenetic diversity of Neotropical bats (Stevens

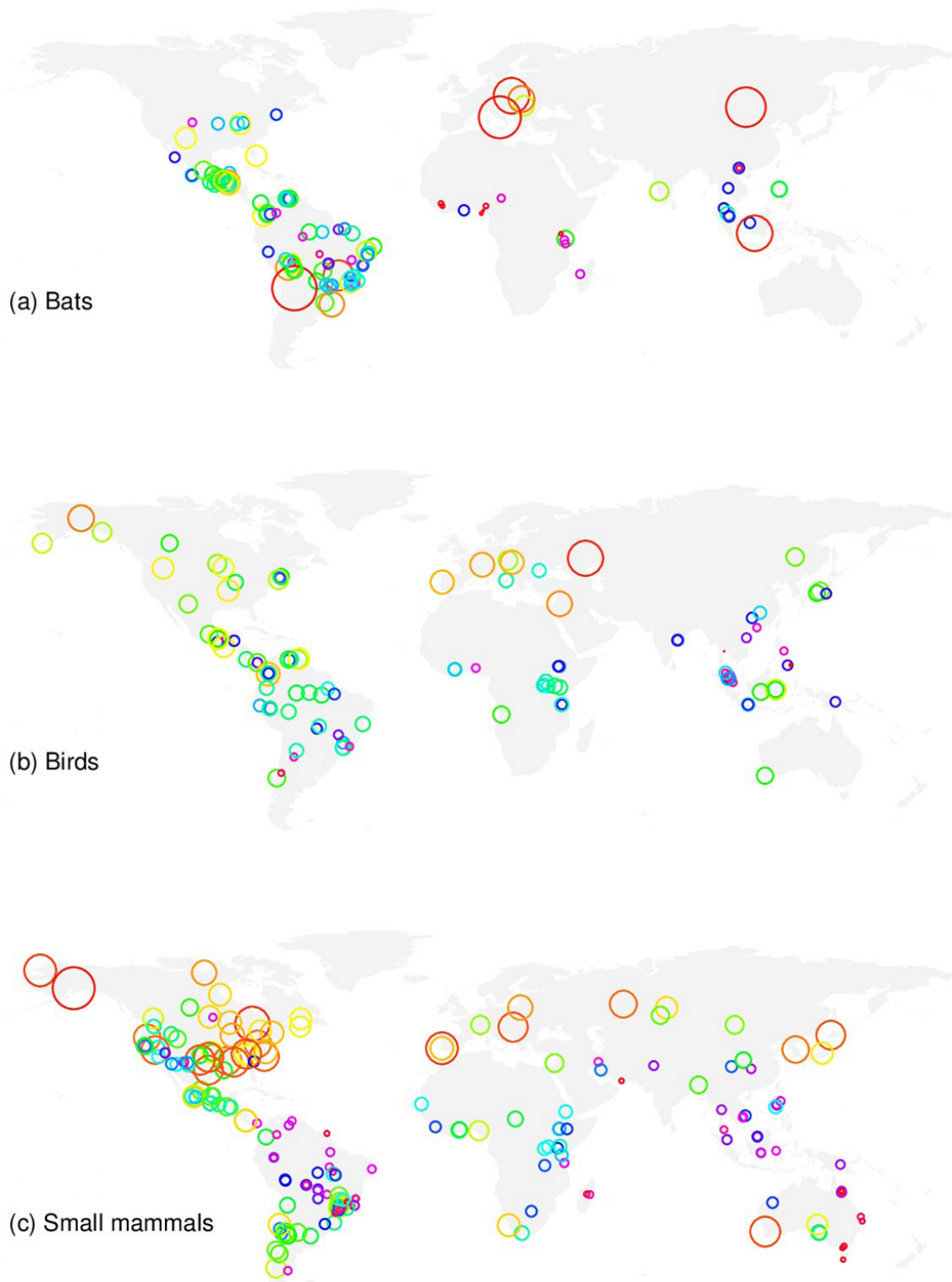


Figure 5. The relative strength of per-gram rates of community energy flow for (a) bats ($n = 118$), (b) birds ($n = 109$), and (c) small mammals ($n = 196$). Colour and size of the circles are scaled as in Fig. 3.

and Willig 2002, López-Aguirre et al. 2018, 2019) and the increased abundance, density, co-occurrence, and diversity of groups such as the phyllostomids, which include large-bodied nectarivore and frugivore

species (Willig and Selcer 1989, Villalobos and Arita 2010, Rojas et al. 2012, Alroy 2019). The high diversity and overall abundance of Neotropical bats is a direct consequence of a rapid evolutionary radiation that

produced a great diversity of dietary habits and foraging strategies (Rojas et al. 2012, Rossoni et al. 2017). The consequently high biomass and rates of energy flow of bat communities in this region is a prime example of how communities with greater abundances of larger organisms have higher rates of energy flow.

While biomass is clearly the primary determinate of community energy flow, akin to how individual body mass is the best predictor of BMR (White and Seymour 2005, McNab 2008), there are interesting differences in the scaling relationships between the individual and community levels. Specifically, the scaling relationship on the community level is considerably more isometric (Table 1). This is to be expected considering community energy flow is more a function of total abundance rather than individual scaling relationships. For instance, if two communities were composed of exactly the same single species with the same average BMR and body mass values, but one had exactly double the number of individuals, then its mass and total energy flow would also be doubled regardless of the allometric species-to-species scaling relationship between body mass and BMR.

In other words, differences in abundance explain the isometric scaling of mass and energy flow on the community level, despite these scaling allometrically on the individual level (Ghedini et al. 2018). Notably, small mammals exhibit a considerably lower community scaling exponent than the other two groups (Table 1). This is likely due to the low alpha diversity and high spatial turnover of small mammal communities: the same species are not found in each place and there are too few species in any one of them to obscure scaling relationships, so species-level allometry is more visible. The relationships between community abundance, mass, and energy use also explain the fact that total energy flow for birds and small mammals correlates with hardly anything, as these all vary rather homogeneously across the globe in both cases. The bats seem to be the exception, having clearly increased rates of energy flow and mass in certain realms (e.g., the Neotropics) than in others (e.g., Indo-Australasia) (Figs. 3-4). While the Indo-Australasia variable was a positive predictor of community mass for small mammals, likely due to the greater prevalence of larger-bodied rats and marsupials in these regions, a similar result was not seen in the corresponding total energy flow regression (Table 2).

Per-gram rates of energy flow

While the total energy flux of communities is mostly homogenous around the world (Fig. 3), per-gram (or mass-specific) rates are more varied, showing interesting group-specific differences. Indo-Australasia was a negative correlate of per-gram rates for both birds and small mammals, with MAT and NPP also being negative predictors for small mammals (Table 2). Bats, meanwhile, have similarly lower rates in the Afrotropics, and higher ones in the Palearctic (Table 2, Fig. 5). As per-gram rates are greater when total rates of energy flow are higher relative to the community's

mass, these patterns are likely due to the contrasting patterns of BMR seen in these groups.

For both birds and small mammals, BMR is considerably lower at lower latitudes where mean annual temperatures are greatest (Lovegrove 2003, White et al. 2007, Naya et al. 2013, Londoño et al. 2015). Conversely, at higher latitudes, these organisms have higher BMRs, a likely consequence of the greater energy requirements of living in colder climates (Naya et al. 2013, Swanson et al. 2017). Thus, Holarctic realms present higher per-gram rates than do tropical realms, as seen most evidently in non-volant small mammals (Fig. 5). The strong pattern here also likely results from the increased biomass seen in tropical regions (Table 2, Fig. 4), further decreasing the rate of energy flow relative to mass in tropical small mammal communities, resulting in their consistently low per-gram rates (Fig. 5). In addition, while this per-gram energy flow gradient is not as strong in birds (further discussed below), the strong negative result seen with Indo-Australasia is likely due to these same mechanisms: increased biomass in tropical realms coupled with low BMRs of tropical species (Table 2, Figs 4-5).

For bats, the per-gram rate regressions showed a similar pattern, with rates being lower in the tropical Afrotropics and higher in the temperate Palearctic (Table 2). However, despite this, there is no clear and straightforward latitudinal gradient, as seen in other groups. This is particularly evident in Figure 5a: Afrotropical bat communities have far lower per-gram rates than in other tropical realms, especially the Neotropics, while Nearctic rates are lower than those of the Palearctic. This also matches the patterns seen with BMR in this group. The lack of a clear latitudinal gradient in bat BMRs is likely due to their particular life habits, such as roosting behaviours and highly energetic foraging flights, which may alleviate the demand for the greater thermogenic capacities associated with higher BMRs at higher latitudes (see Speakman and Thomas 2003). Conversely, the higher per-gram rates seen in the Neotropics are to be expected as BMRs for this group are mainly associated with diet and phylogeny, being particularly high in frugivorous and nectarivorous species (Cruz-Neto et al. 2001). As these guilds are particularly abundant in the Neotropics (Rojas et al. 2012, Alroy 2019), bat communities in the Neotropics have higher rates of energy flow relative to their mass, and thus, have higher per-gram rates (Fig. 5).

Abundance-weighted energy flow and mass

The results for average abundance-weighted individual energy flow and average abundance-weighted individual mass further highlight the strong biogeographic differences in rates of community energy flow within and between groups, and reveal how these are impacted by differences in abundance, average individual size, and metabolism.

Bats

Bats have higher total and per-gram rates of community energy flow in the Neotropics (Figs. 3, 5).

This is evidenced by the fact that total energy flow is lower in Indo-Australasia, while per-gram rates are lower in the Afrotropics (Table 2).

Bat communities in the Afrotropics have far lower per-gram rates of energy flow, whilst their rates of total energy flow are more similar to those in the Neotropics (Figs. 3, 5). This difference is likely because Afrotropical bat communities have low total abundances and more large-bodied individuals. The Afrotropics are known to have far lower rates of species co-occurrence and abundance than other tropical realms (Herkt et al. 2016, Peixoto et al. 2018), while the greater relative abundance of large-bodied individuals is due to the prevalence of large, almost entirely frugivorous pteropodids (Dumont and O'Neal 2004). The exceptionally high BMRs of the frugivorous pteropodids likely compensate for the greatly reduced abundances of Afrotropical bat communities, resulting in similar rates of total energy flow to those seen in the Neotropics (Fig. 3). Meanwhile, the low per-gram rates are due to the lower total abundances in the Afrotropics, resulting in lower rates of community energy flow relative to mass when compared to the Neotropics (Fig. 5).

The highly positive correlations seen with the Neotropics and Afrotropics in the individual mass and energy flow regressions supports this interpretation: the Afrotropics result was not replicated in the individual mass regression (Table 2). The Afrotropical pattern therefore reveals how individual metabolism is a key contributing factor to rates of community energy flow despite the primary effects of abundance. The Neotropics results are not surprising given the high abundances of the large-bodied, high-BMR phyllostomids in this realm (discussed above). Although both the average abundance-weighted rate of energy flow and average abundance-weighted mass of individuals is higher in this region, Neotropical bats still have higher BMRs than expected based on their size, resulting in the higher per-gram rates seen on the community level (Fig. 5). Conversely, Nearctic and Palearctic communities have clearly reduced average rates of individual energy flow and mass due to a greater prevalence of the small insectivorous vespertilionids (Stevens 2004; Figs. S1-S2), in turn resulting in lower total rates of energy flow (Fig. 3). The overall greater per-gram rates seen in the Palearctic (Fig. 5) is likely due to the generally greater abundances of Palearctic bat communities compared to those of the Nearctic.

Small mammals

While non-volant small mammals present fewer geographic differences, the individual mass regression returned strong positive correlations with MAT and NPP, while the individual energy flow regression presented a similarly strong positive correlation AET (Table 2). The average abundance-weighted mass, and consequently energy flow, of individual small mammals (primarily rodents) is larger in regions with increased MAT and other variables associated with tropical environments (Rodríguez et al. 2008, Maestri et al.

2016). This contrasts with the low per-gram rates of small mammal communities seen in tropical regions, which tend to increase with latitude (Fig. 5). This suggests small mammals in more temperate regions have higher metabolisms than expected despite their smaller size due to the colder climate. This difference between average individual mass and metabolism is particularly evident in the Nearctic realm (see Supplemental Figs. S1 and S2). The higher mass-independent metabolisms of small mammals in colder, high-latitude environments (Naya et al. 2013), together with their decreased size and reduced community biomass, further results in temperate communities having greater rates of energy flow relative to their mass, producing their correspondingly high per-gram rates (Fig. 5).

Birds

For birds, a primary result for both individual regressions were strong positive correlations with the proportion of urban area (Table 2). The similarly positive result for total community mass is likely due to the attendant increase in abundance-weighted individual masses of birds in urban areas. The contrasting negative correlation seen with community per-gram rates is in turn a probable result of the increase in avian biomass in urban habitats (Chace and Walsh 2006, Ortega-Álvarez and MacGregor-Fors 2009). As urban habitats favour certain bird species over others (Kark et al. 2007), the increased abundances of common species with greater average individual masses and rates of energy flow produce the higher community masses and, consequently, reduce per-gram rates of energy flow.

Similarly, the negative correlation with the Indo-Australasia variable for per-gram rates is contrasted with a positive result for abundance-weighted individual mass (Table 2). This, together with the negative Neotropics and positive MAT results in the individual energy flow and mass regressions, respectively, further suggests that the low per-gram rates of bird communities in tropical realms (Table 2, Fig. 5) are due to a combination of the lower BMRs (White et al. 2007, Londoño et al. 2015) and the greater abundance-weighted masses of birds in warmer habitats.

However, while per-gram rates of bird communities are lower in the tropics, the pattern is clearly not as strong as that seen in small mammals (Fig. 5). The overall more homogenous pattern of community energy use seen in birds is likely primarily due to long-distance migration and the consequently large seasonal fluctuations in local avian diversity and abundance across the globe. Variation in bird community composition due to migration – which is greatest in more northerly latitudes (Somveille et al. 2013), possibly explaining the positive Palearctic result for total energy flow (Table 2) – likely reduces the usual differences in mass and energy use seen between tropical and temperate regions (Fristoe 2015), explaining why the latitudinal pattern for birds is not as strong as in non-migratory groups.

In addition, migratory birds are commonly caught in mist netting, even in localities that may not have a resident population of such species at any time of the year (Komenda-Zehnder et al. 2010). However, despite abundances of bird communities fluctuating throughout the year, which leads to genuine changes in mass and energy use that homogenise these patterns across the globe, and considering migratory birds are typically well-represented in mist net samples, the still highly significant results of the bird regressions suggest that the patterns described above are accurate, and would likely be just as strong as in other groups if not for the impacts of migration.

Conclusions

Rates of community energy flow vary across the globe in fascinating ways. While total rates are fairly uniform and are primarily influenced by community mass, there are strong group-specific patterns in the strength of energy flow relative to community mass. These patterns vary both within and between groups, and result from clear differences in individual metabolic rate, size, and abundance, further illustrating that organismal patterns affect higher levels of organisation. The strong biogeographic results indicate that these are closely linked to specific differences in the ecology and evolutionary history of lineages in different regions. Bats are the best example: for them, historical effects are clearly more important than ecological effects in determining variation in energy use on the community level. For birds and small mammals, ecological effects, specifically differences between tropical and temperate environments, are more likely to produce the observed patterns, suggesting a combination of historical and ecological factors drive rates of energy flow in vertebrate communities across the globe.

As the energy flow rates calculated here are scaled up from BMR, they only represent what community rates would be if all individuals were constantly at basal metabolic levels. However, scaling community energy use up from different rate measures such as field metabolic rate (FMR) – an organism's rate during regular activity – should not have any necessary implications. Like BMR, FMR also allometrically scales with body mass, with exponent values similar to those reported with BMR (Nagy et al. 1999; Nagy 2005; Hudson et al. 2013). The similarity in the scaling relationships of both these measures (Koteja 1991) indicates that, while rates of community energy flow scaled up from BMR are far lower than if scaled up from FMR, the relationships between these and the variables tested should not differ considerably. Nevertheless, comparing rates of community energy flow using other rate measures and among other ecological groups would be beneficial in order to better determine how community energy use varies spatially, the underlining causes of this variation, and how it relates to other factors such as biomass and population density.

Finally, the ecological effects on energy use shown here suggest that community energetics will be greatly altered as a result of the current warming

climate. For instance, per-gram rates of small mammal communities are likely to decrease in Holarctic realms if warming results in a significant reduction in metabolic rates. Further quantifying how energy use varies within and among real-world communities with different compositions, abundance levels, and population densities, may thus enable a greater understanding of how community energy use will be impacted by future ecological changes.

Acknowledgments

This study was funded by a Macquarie University Research Excellence Scholarship (MQRES-MRES; number 20201634 to BC). The authors declare there to be no conflicts of interest with this work. This is publication number 8 of the Ecological Register.

Author Contributions

JA and BC designed the study. BC downloaded the sample data, collated and calculated the metabolic rate data, calculated rates of community energy flow, and performed the analyses with assistance from JA. JA collected the sample data, downloaded and collated the data for the climate, environmental, and anthropogenic variables, and further developed the regression method. BC wrote the manuscript, while JA edited the manuscript.

Data Availability

The data and R code supporting the results are available online as part of the Frontiers of Biogeography supplementary documentation (Appendix S3).

Supplemental Material

The following materials are available as part of the online article at <https://escholarship.org/uc/fb>

Figure S1. The relative strength of the average abundance-weighted rate of individual energy flows for bats, birds, and small mammals.

Figure S2. The relative size of average abundance-weighted individual masses for bats, birds, and small mammals.

Appendix S1. Complete lists of all 118 bat, 109 bird, and 196 small mammal samples downloaded from the Ecological Register and used in the analysis.

Appendix S2. Mass and basal metabolic rate (BMR) measures for all 416 bat, 1880 bird, and 562 small mammal species present in the samples.

Appendix S3. R code for conducting the analyses, including the predictor residuals regression method.

References

- Abatzoglou, J.T., Dobrowski, S.Z., Parks, S.A. & Hegewisch, K.C. (2018) TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958-2015.

- Scientific Data, 5, 170191. <https://doi.org/10.1038/sdata.2017.191>
- Allen, A.P., Gillooly, J.F. & Brown, J.H. (2005) Linking the global carbon cycle to individual metabolism. *Functional Ecology*, 19, 202-213. <https://doi.org/10.1111/j.1365-2435.2005.00952.x>
- Alroy, J. (2015) The shape of terrestrial abundance distributions. *Science Advances*, 1, 1500082. <https://doi.org/10.1126/sciadv.1500082>
- Alroy, J. (2017) Effects of habitat disturbance on tropical forest biodiversity. *Proceedings of the National Academy of Sciences USA*, 114, 6056-6061. <https://doi.org/10.1073/pnas.1611855114>
- Alroy, J. (2019) Latitudinal gradients in the ecology of New World bats. *Global Ecology and Biogeography*, 28, 784-792. <https://doi.org/10.1111/geb.12892>
- Barneche, D.R., Kulbicki, M., Floeter, S.R., Friedlander, A.M., Maina, J. & Allen, A.P. (2014) Scaling metabolism from individuals to reef-fish communities at broad spatial scales. *Ecology Letters*, 17, 1067-1076. <https://doi.org/10.1111/ele.12309>
- Bivand, R. (2022) R packages for analyzing spatial data: a comparative case study with areal data. *Geographical Analysis*. <https://doi.org/10.1111/gean.12319>
- Bivand, R. & Piras, G. (2015) Comparing implementations of estimation methods for spatial econometrics. *Journal of Statistical Software*, 63, 1-36. <https://doi.org/10.18637/jss.v063.i18>
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, 85, 1771-1789. <https://doi.org/10.1890/03-9000>
- Chace, J.F. & Walsh, J.J. (2006) Urban effects on native avifauna: a review. *Landscape and Urban Planning*, 74, 46-69. <https://doi.org/10.1016/j.landurbplan.2004.08.007>
- Crisci, J.V., Sala, O.E., Katinas, L. & Posadas, P. (2006) Bridging historical and ecological approaches in biogeography. *Australian Systematic Botany*, 19, 1-10. <https://doi.org/10.1071/SB05006>
- Cruz-Neto, A.P., Garland Jr., T. & Abe, A.S. (2001) Diet, phylogeny, and basal metabolic rate in phyllostomid bats. *Zoology*, 104, 49-58. <https://doi.org/10.1078/0944-2006-00006>
- Currie, D.J. & Fritz, J.T. (1993) Global patterns of animal abundance and species energy use. *Oikos*, 67, 56-68. <https://doi.org/10.2307/3545095>
- Del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (2018) *Handbook of the birds of the world alive*. Lynx Edicions, Barcelona.
- Dormann, C.F., Elith, J., Bacher, S., et al. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27-46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Dumont, E.R. & O'Neal, R. (2004) Food hardness and feeding behavior in Old World fruit bats (Pteropodidae). *Journal of Mammalogy*, 85, 8-14. <https://doi.org/10.1644/bos-107>
- Ellis, E.C. & Ramankutty, N. (2008) Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment*, 6, 439-447. <https://doi.org/10.1890/070062>
- Ellis, E.C., & Ramankutty, N. (2008b) *Anthropogenic biomes of the world, version 1*. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). <https://doi.org/10.7927/H4H12ZXD>
- Enquist, B.J., Economo, E.P., Huxman, T.E., Allen, A.P., Ignace, D.D. & Gillooly, J.F. (2003) Scaling metabolism from organisms to ecosystems. *Nature*, 423, 639-642. <https://doi.org/10.1038/nature01671>
- Ernest, S.K.M. (2005) Body size, energy use, and community structure of small mammals. *Ecology*, 86, 1407-1413. <https://doi.org/10.1890/03-3179>
- Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302-4315. <https://doi.org/10.1002/joc.5086>
- Fraser, R.H. & Currie, D.J. (1996) The species richness-energy hypothesis in a system where historical factors are thought to prevail: coral reefs. *American Naturalist*, 148, 138-159. <https://doi.org/10.1086/285915>
- Fristoe, T.S. (2015) Energy use by migrants and residents in North American breeding bird communities. *Global Ecology and Biogeography*, 24, 406-415. <https://doi.org/10.1111/geb.12262>
- Fristoe, T.S., Burger, J.R., Balk, M.A., Khaliq, I., Hof, C. & Brown, J.H. (2015) Metabolic heat production and thermal conductance

- are mass-independent adaptations to thermal environment in birds and mammals. *Proceedings of the National Academy of Sciences USA*, 112, 15934-15939. <https://doi.org/10.1073/pnas.1521662112>
- Ghedini, G., Malerba, M.E. & Marshall, D.J. (2020) How to estimate community energy flux? A comparison of approaches reveals that size-abundance trade-offs alter the scaling of community energy flux. *Proceedings of the Royal Society B*, 287, 20200995. <https://doi.org/10.1098/rspb.2020.0995>
- Ghedini, G., White, C.R. & Marshall, D.J. (2018) Metabolic scaling across succession: do individual rates predict community-level energy use? *Functional Ecology*, 32, 1447-1456. <https://doi.org/10.1111/1365-2435.13103>
- Glazier, D.S. (2005) Beyond the '3/4-power law': Variation in the intra- and interspecific scaling of metabolic rate in animals. *Biological Reviews of the Cambridge Philosophical Society*, 80, 611-662. <https://doi.org/10.1017/S1464793105006834>
- Global Soil Data Task Group (2000) Global gridded surfaces of selected soil characteristics (IGBP-DIS). ORNL DAAC, Oak Ridge, Tennessee, USA.
- Graham, M.H. (2003) Confronting multicollinearity in ecological multiple regression. *Ecology*, 84, 2809-2815. <https://doi.org/10.1890/02-3114>
- Hannon, B. (1973) The structure of ecosystems. *Journal of Theoretical Biology*, 41, 535-546. [https://doi.org/10.1016/0022-5193\(73\)90060-X](https://doi.org/10.1016/0022-5193(73)90060-X)
- Hayward, A., Khalid, M. & Kolasa, J. (2009) Population energy use scales positively with body size in natural aquatic microcosms. *Global Ecology and Biogeography*, 18, 553-562. <https://doi.org/10.1111/j.1466-8238.2009.00459.x>
- Herkt, K.M.B., Barnikel, G., Skidmore, A.K. & Fahr, J. (2016) A high-resolution model of bat diversity and endemism for continental Africa. *Ecological Modelling*, 320, 9-28. <https://doi.org/10.1016/j.ecolmodel.2015.09.009>
- Hudson, L.N., Isaac, N.J.B. & Reuman, D.C. (2013) The relationship between body mass and field metabolic rate among individual birds and mammals. *Journal of Animal Ecology*, 82, 1009-1020. <https://doi.org/10.1111/1365-2656.12086>
- Hulbert, A.J. & Else, P.L. (2000) Mechanisms underlying the cost of living in animals. *Annual Review of Physiology*, 62, 207-235. <https://doi.org/10.1146/annurev.physiol.62.1.207>
- Imhoff, M.L. & Bounoua, L. (2006) Exploring global patterns of net primary production carbon supply and demand using satellite observations and statistical data. *Journal of Geophysical Research Atmospheres*, 111, D22S12. <https://doi.org/10.1029/2006JD007377>
- Imhoff, M.L., Bounoua, L., Ricketts, T., Loucks, C., Harriss, R. & Lawrence, W.T. (2004) HANPP collection: global patterns in net primary productivity (NPP). Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). <https://doi.org/10.7927/H40Z715X>
- Isaac, N.J.B., Storch, D. & Carbone, C. (2011) Taxonomic variation in size-density relationships challenges the notion of energy equivalence. *Biology Letters*, 7, 615-618. <https://doi.org/10.1098/rsbl.2011.0128>
- Isaac, N.J.B., Storch, D. & Carbone, C. (2013) The paradox of energy equivalence. *Global Ecology and Biogeography*, 22, 1-5. <https://doi.org/10.1111/j.1466-8238.2012.00782.x>
- Jetz, W., Freckleton, R.P. & McKechnie, A.E. (2008) Environment, migratory tendency, phylogeny and basal metabolic rate in birds. *PLoS ONE*, 3, e3261. <https://doi.org/10.1371/journal.pone.0003261>
- Jetz, W., Wilcove, D.S. & Dobson, A.P. (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, 5, 1211-1219. <https://doi.org/10.1371/journal.pbio.0050157>
- Kaiser, H.F. (1958) The varimax criterion for analytic rotation in factor analysis. *Psychometrika*, 23, 187-200. <https://doi.org/10.1007/BF02289233>
- Kark, S., Iwaniuk, A., Schalimtzek, A. & Banker, E. (2007) Living in the city: can anyone become an 'urban exploiter'? *Journal of Biogeography*, 34, 638-651. <https://doi.org/10.1111/j.1365-2699.2006.01638.x>
- Kerr, J.T., Kharouba, H.M. & Currie, D.J. (2007) The macroecological contribution to global change solutions. *Science*, 316, 1581-1584. <https://doi.org/10.1126/science.1133267>
- Komenda-Zehnder, S., Jenni, L. & Liechti, F. (2010) Do bird captures reflect migration

- intensity? – Trapping numbers on an alpine pass compared with radar counts. *Journal of Avian Biology*, 41, 434-444. <https://doi.org/10.1111/j.1600-048X.2010.04891.x>
- Koteja, P. (1991) On the relation between basal and field metabolic rates in birds and mammals. *Functional Ecology*, 5, 56-64. <https://doi.org/10.2307/2389555>
- Lichstein, J.W., Simons, T.R., Shriver, S.A. & Franzreb, K.E. (2002) Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs*, 72, 445-463. [https://doi.org/10.1890/0012-9615\(2002\)072\[0445:SAAMI\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2002)072[0445:SAAMI]2.0.CO;2)
- Londoño, G.A., Chappell, M.A., Castañeda, M.R., Jankowski, J.E. & Robinson, S.K. (2015) Basal metabolism in tropical birds: latitude, altitude, and the 'pace of life'. *Functional Ecology*, 29, 338-346. <https://doi.org/10.1111/1365-2435.12348>
- López-Aguirre, C., Hand, S.J., Laffan, S.W. & Archer, M. (2018) Phylogenetic diversity, types of endemism and the evolutionary history of New World bats. *Ecography*, 41, 1955-1966. <https://doi.org/10.1111/ecog.03260>
- López-Aguirre, C., Hand, S.J., Laffan, S.W. & Archer, M. (2019) Zoogeographical regions and geospatial patterns of phylogenetic diversity and endemism of New World bats. *Ecography*, 42, 1188-1199. <https://doi.org/10.1111/ecog.04194>
- Lovegrove, B.G. (2000) The zoogeography of mammalian basal metabolic rate. *American Naturalist*, 156, 201-219. <https://doi.org/10.1086/303383>
- Lovegrove, B.G. (2003) The influence of climate on the basal metabolic rate of small mammals: A slow-fast metabolic continuum. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, 173, 87-112. <https://doi.org/10.1007/s00360-002-0309-5>
- Luna, F., Naya, H. & Naya, D.E. (2017) Understanding evolutionary variation in basal metabolic rate: an analysis in subterranean rodents. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology*, 206, 87-94. <https://doi.org/10.1016/j.cbpa.2017.02.002>
- Maestri, R., Luza, A.L., de Barros, L.D., Hartz, S.M., Ferrari, A., de Freitas, T.R.O. & Duarte, L.D.S. (2016) Geographical variation of body size in sigmodontine rodents depends on both environment and phylogenetic composition of communities. *Journal of Biogeography*, 43, 1192-1202. <https://doi.org/10.1111/jbi.12718>
- Marquet, P.A., Quiñones, R.A., Abades, S., Labra, F., Tognelli, M., Arim, M. & Rivadeneira, M. (2005) Scaling and power-laws in ecological systems. *Journal of Experimental Biology*, 208, 1749-1769. <https://doi.org/10.1242/jeb.01588>
- Maurer, B.A. (1996) Relating human population growth to the loss of biodiversity. *Biodiversity Letters*, 3, 1-5. <https://doi.org/10.2307/2999702>
- McNab, B.K. (1997) On the utility of uniformity in the definition of basal rate of metabolism. *Physiological Zoology*, 70, 718-720. <https://doi.org/10.1086/515881>
- McNab, B.K. (2008) An analysis of the factors that influence the level and scaling of mammalian BMR. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 151, 5-28. <https://doi.org/10.1016/j.cbpa.2008.05.008>
- McNab, B.K. (2009) Ecological factors affect the level and scaling of avian BMR. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 152, 22-45. <https://doi.org/10.1016/j.cbpa.2008.08.021>
- McNab, B.K. (2015) Behavioral and ecological factors account for variation in the mass-independent energy expenditures of endotherms. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, 185, 1-13. <https://doi.org/10.1007/s00360-014-0850-z>
- Nagy, K.A. (2005) Field metabolic rate and body size. *Journal of Experimental Biology*, 208, 1621-1625. <https://doi.org/10.1242/jeb.01553>
- Nagy, K.A., Girard, I.A. & Brown, T.K. (1999) Energetics of free-ranging mammals, reptiles, and birds. *Annual Review of Nutrition*, 19, 247-277. <https://doi.org/10.1146/annurev.nutr.19.1.247>
- Naya, D.E., Spangenberg, L., Naya, H. & Bozinovic, F. (2013) How does evolutionary variation in basal metabolic rates arise? A statistical assessment and a mechanistic model. *Evolution*, 67, 1463-1476. <https://doi.org/10.1111/evo.12042>

- Newbold, T., Hudson, L.N., Hill, S.L.L., et al. (2015) Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45-50. <https://doi.org/10.1038/nature14324>
- Nordhaus, W.D. (2006) Geography and macroeconomics: New data and new findings. *Proceedings of the National Academy of Sciences USA*, 103, 3510-3517. <https://doi.org/10.1073/pnas.0509842103>
- Nordhaus, W.D., & Chen, X. (2016) Global gridded geographically based economic data (G-Econ), version 4. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). <http://doi.org/10.7927/H42V2D1C>
- Odum, E.P. (1968) Energy flow in ecosystems: a historical review. *Integrative and Comparative Biology*, 8, 11-18. <https://doi.org/10.1093/icb/8.1.11>
- Ortega-Álvarez, R. & MacGregor-Fors, I. (2009) Living in the big city: effects of urban land-use on bird community structure, diversity, and composition. *Landscape and Urban Planning*, 90, 189-195. <https://doi.org/10.1016/j.landurbplan.2008.11.003>
- Parr, C.S., Wilson, N., Leary, P., et al. (2014) The encyclopedia of life v2: providing global access to knowledge about life on earth. *Biodiversity Data Journal*, 2, e1079. <https://doi.org/10.3897/BDJ.2.e1079>
- Peixoto, F.P., Braga, P.H.P. & Mendes, P. (2018) A synthesis of ecological and evolutionary determinants of bat diversity across spatial scales. *BMC Ecology*, 18, 18. <https://doi.org/10.1186/s12898-018-0174-z>
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Revilla, T.A., Encinas-Viso, F. & Loreau, M. (2015) Robustness of mutualistic networks under phenological change and habitat destruction. *Oikos*, 124, 22-32. <https://doi.org/10.1111/oik.01532>
- Rodríguez, M.Á., Olalla-Tárraga, M.Á. & Hawkins, B.A. (2008) Bergmann's rule and the geography of mammal body size in the Western Hemisphere. *Global Ecology and Biogeography*, 17, 274-283. <https://doi.org/10.1111/j.1466-8238.2007.00363.x>
- Rojas, D., Vale, Á., Ferrero, V. & Navarro, L. (2012) The role of frugivory in the diversification of bats in the Neotropics. *Journal of Biogeography*, 39, 1948-1960. <https://doi.org/10.1111/j.1365-2699.2012.02709.x>
- Rossoni, D.M., Assis, A.P.A., Giannini, N.P. & Marroig, G. (2017) Intense natural selection preceded the invasion of new adaptive zones during the radiation of New World leaf-nosed bats. *Scientific Reports*, 7, 11076. <https://doi.org/10.1038/s41598-017-08989-6>
- Russo, S.E., Robinson, S.K. & Terborgh, J. (2003) Size-abundance relationships in an Amazonian bird community: implications for the energetic equivalence rule. *American Naturalist*, 161, 267-283. <https://doi.org/10.1086/345938>
- Santini, L., Isaac, N.J.B., Maiorano, L., Ficetola, G.F., Huijbregts, M.A.J., Carbone, C. & Thuiller, W. (2018) Global drivers of population density in terrestrial vertebrates. *Global Ecology and Biogeography*, 27, 968-979. <https://doi.org/10.1111/geb.12758>
- Schramski, J.R., Dell, A.I., Grady, J.M., Sibly, R.M. & Brown, J.H. (2015) Metabolic theory predicts whole-ecosystem properties. *Proceedings of the National Academy of Sciences USA*, 112, 2617-2622. <https://doi.org/10.1073/pnas.1423502112>
- Schuldt, A. & Assmann, T. (2009) Environmental and historical effects on richness and endemism patterns of carabid beetles in the western Palaearctic. *Ecography*, 32, 705-714. <https://doi.org/10.1111/j.1600-0587.2009.05763.x>
- Sewall, B.J., Freestone, A.L., Hawes, J.E. & Andriamanarina, E. (2013) Size-energy relationships in ecological communities. *PLoS ONE*, 8, e68657. <https://doi.org/10.1371/journal.pone.0068657>
- Silva, M., Brown, J.H. & Downing, J.A. (1997) Differences in population density and energy use between birds and mammals: a macroecological perspective. *Journal of Animal Ecology*, 66, 327-340. <https://doi.org/10.2307/5979>
- Somveille, M., Manica, A., Butchart, S.H.M. & Rodrigues, A.S.L. (2013) Mapping global diversity patterns for migratory birds. *PLoS ONE*, 8, e70907. <https://doi.org/10.1371/journal.pone.0070907>
- Speakman, J.R. & Thomas, D.W. (2003) Physiological ecology and energetics of bats. In: *Bat ecology* (ed. by T.H. Kunz and M.B. Fenton), pp. 430-490. University of Chicago Press, Chicago, IL.

- Stevens, R.D. (2004) Untangling latitudinal richness gradients at higher taxonomic levels: familial perspectives on the diversity of New World bat communities. *Journal of Biogeography*, 31, 665-674. <https://doi.org/10.1111/j.1365-2699.2003.01042.x>
- Stevens, R.D. & Willig, M.R. (2002) Geographical ecology at the community level: perspectives on the diversity of New World bats. *Ecology*, 83, 545-560. [https://doi.org/10.1890/0012-9658\(2002\)083\[0545:Geatcl\]2.0.Co;2](https://doi.org/10.1890/0012-9658(2002)083[0545:Geatcl]2.0.Co;2)
- Swanson, D.L., McKechnie, A.E. & Vézina, F. (2017) How low can you go? An adaptive energetic framework for interpreting basal metabolic rate variation in endotherms. *Journal of Comparative Physiology B*, 187, 1039-1056. <https://doi.org/10.1007/s00360-017-1096-3>
- Villalobos, F. & Arita, H.T. (2010) The diversity field of New World leaf-nosed bats (Phyllostomidae). *Global Ecology and Biogeography*, 19, 200-211. <https://doi.org/10.1111/j.1466-8238.2009.00503.x>
- Warton, D.I., Duursma, R.A., Falster, D.S. & Taskinen, S. (2012) smatr 3 – an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution*, 3, 257-259. <https://doi.org/10.1111/j.2041-210X.2011.00153.x>
- Warton, D.I., Wright, I.J., Falster, D.S. & Westoby, M. (2006) Bivariate line-fitting methods for allometry. *Biological Reviews of the Cambridge Philosophical Society*, 81, 259-291. <https://doi.org/10.1017/S1464793106007007>
- West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science*, 276, 122-126. <https://doi.org/10.1126/science.276.5309.122>
- White, C.R. (2011) Allometric estimation of metabolic rates in animals. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology*, 158, 346-357. <https://doi.org/10.1016/j.cbpa.2010.10.004>
- White, C.R., Blackburn, T.M., Martin, G.R. & Butler, P.J. (2007) Basal metabolic rate of birds is associated with habitat temperature and precipitation, not primary productivity. *Proceedings of the Royal Society B*, 274, 287-293. <https://doi.org/10.1098/rspb.2006.3727>
- White, C.R., Blackburn, T.M. & Seymour, R.S. (2009) Phylogenetically informed analysis of the allometry of mammalian basal metabolic rate supports neither geometric nor quarter-power scaling. *Evolution*, 63, 2658-2667. <https://doi.org/10.1111/j.1558-5646.2009.00747.x>
- White, C.R., Phillips, N.F. & Seymour, R.S. (2006) The scaling and temperature dependence of vertebrate metabolism. *Biology Letters*, 2, 125-127. <https://doi.org/10.1098/rsbl.2005.0378>
- White, C.R. & Seymour, R.S. (2003) Mammalian basal metabolic rate is proportional to body mass $2/3$. *Proceedings of the National Academy of Sciences USA*, 100, 4046-4049. <https://doi.org/10.1073/pnas.0436428100>
- White, C.R. & Seymour, R.S. (2005) Allometric scaling of mammalian metabolism. *Journal of Experimental Biology*, 208, 1611-1619. <https://doi.org/10.1242/jeb.01501>
- Williams, S.E., Shoo, L.P., Henriod, R. & Pearson, R.G. (2010) Elevational gradients in species abundance, assemblage structure and energy use of rainforest birds in the Australian wet tropics bioregion. *Austral Ecology*, 35, 650-664. <https://doi.org/10.1111/j.1442-9993.2009.02073.x>
- Willig, M.R. & Selcer, K.W. (1989) Bat species density gradients in the New World: a statistical assessment. *Journal of Biogeography*, 16, 189-195. <https://doi.org/10.2307/2845093>

Submitted: 26 February 2022

First decision: 4 May 2022

Accepted: 27 May 2022

Edited by Jan Beck and Robert J. Whittaker