



The paradox of energy equivalence

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ABSTRACT

Energy equivalence, the notion that population energy flux is independent of body mass, has become a key concept in ecology. We argue that energy equivalence is not an ecological ‘rule’, as claimed, but a flawed concept beset by circular reasoning. In fact, the independence of mass and energy flux is a null hypothesis. We show that our mechanistic understanding of size–density relationships (SDRs) follows directly from this null model and the assumption that energy limits abundance. Paradoxically, without this assumption energy equivalence has no meaning and we lack a mechanistic understanding for SDRs. We derive an expression for the strength (r^2) of SDRs under the null model, which provides a framework within which to compare published SDRs. This confirms that tight correlations between mass and abundance are a trivial consequence of the span of body masses considered. Our model implies that energy flux varies by five to six orders of magnitude among similarly sized mammals and to a far greater extent in birds. We conclude that the energetic paradigm can be strengthened by considering alternative, non-energetic, hypotheses.

Keywords

Abundance, Damuth’s rule, ecology, energetics, invariance, macroecology, metabolic scaling, null models, size–density relationship.

INTRODUCTION

The relationship between body size and abundance is a key focus of research in ecology (White *et al.*, 2007). Damuth reported a size–density relationship (SDR) following a power law with a scaling exponent close to $-3/4$ (equation 1a), first among mammals (Damuth, 1981) and later across a wide range of vertebrate taxa (Damuth, 1987). He realized that this value was the inverse of Kleiber’s metabolic scaling exponent $3/4$ (equation 1b), which implies that the population energy flux per unit area, estimated as the product of metabolic rate and abundance, will be independent of body mass (equation 1c). In the scaling jargon, energy flux is said to be ‘invariant’ with respect to mass, M . Nee *et al.* (1991) reported the same pattern among British birds, and coined the phrase ‘energetic equivalence rule’ for situations where the allometric scaling exponents for whole-organism metabolic rate, I , and population density, N , sum to zero. This was formalized as part of the metabolic theory of ecology (Brown *et al.*, 2004) in the context of the availability (supply rate) of resources, R :

$$N \propto M^{-b} \quad (1a)$$

$$I \propto M^b \quad (1b)$$

$$R \propto IN \propto M^0. \quad (1c)$$

This set of relationships constitutes the general concept of energy equivalence (EE), which has become a cornerstone of macroecology and forms the basis of theories about population dynamics (Savage *et al.*, 2004) and biodiversity patterns (Allen *et al.*, 2002). EE is underpinned by the assertion that abundance is directly dependent on energy available to the population: an increase in energy input leads to an increase in abundance, mediated by the energy requirements of each individual (Brown *et al.*, 2004; Ernest *et al.*, 2008, 2009). We refer to this paradigm as the ‘energetic view of abundance’ (see also Taper & Marquet, 1996; Morlon *et al.*, 2009).

Some authors considered the independence of body mass and energy flux to be a fundamental rule. For example, it has been stated that EE ‘reflects mechanistic connections . . . and the partitioning of available energy among species in a community’ (Allen *et al.*, 2002), and ‘suggests that some combination of physiological and ecological processes results in energetic trade-offs, such that resources are divided equally across species’ (White *et al.*, 2007). However, there is no strong theoretical basis

for EE across species (Damuth, 1981; Brown, 1995; Brown *et al.*, 2004; Carbone *et al.*, 2007; White *et al.*, 2007), although there have been several attempts to fill this gap. Charnov *et al.* (2001) suggested that EE in mammals is a consequence of life-history trade-offs (between fecundity and longevity) and population dynamics (including density-dependent juvenile survival). Damuth (2007) developed a simulation model that produced EE through competitive interactions between pairs of species. Harte *et al.* (2008) have argued that EE may be a consequence of the maximum entropy principle, i.e. that it results from the most probable statistical distributions of body sizes, species and individuals in space within particular constraints given by total number of individuals, total number of species and total energy available within given area.

EE has been challenged on both empirical and conceptual grounds. Marquet *et al.* (1995) described problems with both the assumptions of EE and the statistical approaches to testing EE. A growing number of studies have reported patterns inconsistent with EE at a variety of spatial scales (Blackburn & Gaston, 1997; Russo *et al.*, 2003; Hayward *et al.*, 2009; Morlon *et al.*, 2009; Isaac *et al.*, 2011b), although Carbone *et al.* (2007) showed that geometric considerations could lead to a range of SDR exponents even when mass and energy flux are uncorrelated. Others have proposed non-energetic explanations for the SDR (Blackburn *et al.*, 1993; Cotgreave, 1993).

Here we argue that EE is not a useful concept in ecology. We highlight logical flaws in the concept of EE itself, and of the evidence used to test it. We discuss what insights might be possible from the SDR, and suggest new directions for research in this field.

THE PARADOX

We contend that the concept of EE is at best misunderstood and at worst fundamentally flawed. Equation 1c does not imply that all species use equal amounts of energy, merely that energy flux is independent of mass. The absence of a correlation between mass and energy should not be surprising: it is, after all, a null hypothesis which does not require any specific mechanism. Accepting EE as the null has two important implications: (1) that neither resource partitioning nor inter-specific competition need to be invoked; (2) that authors claiming to find support for EE have fallen into that most basic statistical trap, namely of accepting the null hypothesis rather than failing to reject it.

Such shortcomings of logic might be explained by the fact that energy flux is never measured, but is inferred as the sum of individual metabolic rates (equation 1c). The ‘evidence’ (or lack thereof) for EE is usually based on a simple comparison of the SDR exponent with some nominal value of the metabolic scaling exponent (usually 3/4). This too is flawed: the coincidence of scaling exponents (equations 1a and 1b) does not constitute evidence either for EE or for the wider energetic paradigm, unless alternative hypotheses can be rejected. However, without the energetic view of abundance we lack a mechanistic understanding for SDRs: by assuming that abundance is driven by energy availability, the coincidence of scaling

exponents becomes a trivial consequence of the fact that population energy flux is unbiased with respect to body size. From this it follows, paradoxically, that energy equivalence is a trivial and uninformative pattern under the energetic view of abundance, but is a meaningless concept if we take the opposing (non-energetic) view.

TIGHT-FITTING SIZE-DENSITY RELATIONSHIPS ARE NOT SURPRISING

Inferences about energy partitioning are usually based on the tightness (or lack thereof) of the SDR. The tightness of SDRs is strongly related to the range of body sizes considered (Tilman *et al.*, 2004; Hayward *et al.*, 2010): we extend this observation to emphasize that EE is trivial, and that it has no real predictive power.

We derived an analytical expression (see Appendix S1 in Supporting Information) for the predictive power of body mass in SDRs under the strict version of the energetic paradigm and the null expectation of no correlation between species body mass, M , and energy flux, R . In our model, M and R are independent random variables, but species abundance, N , is wholly determined by $R/M^{3/4}$. We refer to this as the ‘energetic null model’. Our model reveals that tight relationships occur when the variance in mass is high relative to the variance in energy flux (or resource availability). Indeed, high r^2 is inevitable with a large enough span in body mass (more than 10 orders of magnitude; Fig. 1), regardless of the distribution of energy flux (cf. Hayward *et al.*, 2010).

Our energetic null model provides a framework within which to compare the fit of published SDRs whilst controlling for the span in body mass. Not surprisingly, the best-fitting SDRs (relative to the mass range) are found among studies that controlled for key factors influencing underlying variation in organism abundance, such as access to resources. For example, Carbone & Gittleman (2002) showed that prey biomass is a key determinant of abundance among mammalian carnivores: controlling for prey availability provides a dramatic improvement in the predictive power of body mass. Likewise, a study based on carrying capacity in single-species stands of plants (i.e. without inter-specific competition) showed a similarly tight-fitting SDR (Enquist *et al.*, 1998).

Damuth’s classic mammalian SDR (Damuth, 1981, 1987) has $r^2 = 0.65$ across nearly six orders of magnitude in body mass: random subsets with smaller mass ranges have correspondingly weaker fits (Fig. 2). These patterns are consistent with the energetic null model in which $\log_{10}(\text{energy flux})$ is a random normal deviate with a standard deviation in the range 1.25–1.65, corresponding to 95% confidence intervals of 80,000- and 3,000,000-fold variation in energy flux for each size class. This magnitude of variation seems at odds with the notion of EE as an ecological ‘rule’ with predictive power, even after accounting for error variance in estimating the abundance of wild mammal populations, many of which are probably below carrying capacity. The much weaker fit among bird SDRs implies still higher levels of variation (seven to eight orders of magnitude variation in energy

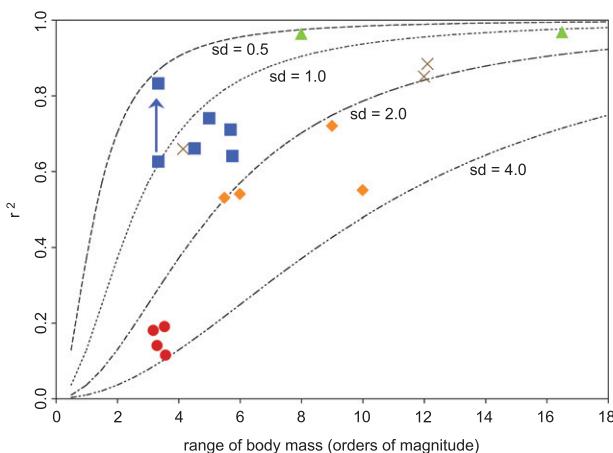


Figure 1 Explanatory power of body mass in size–density relationships (SDRs; expressed as r^2) plotted against the number of orders of magnitude in mass range. Lines are derived from our expression (see Appendix S1) for the energetic null model with differing amounts of variation (expressed as standard deviations) in $\log_{10}(\text{energy flux})$ among species. The points are SDRs reported in the literature for birds (circles), mammals (squares), invertebrates (diamonds), animals (crosses) and plants and phytoplankton (triangles) (data from Damuth, 1981, 1987; Peters, 1983; Marquet *et al.*, 1990; Cotgreave & Harvey, 1992; Ebensman *et al.*, 1995; Enquist *et al.*, 1998; Belgrano *et al.*, 2002; Carbone & Gittleman, 2002). The arrow links two points for mammalian carnivores (Carbone & Gittleman, 2002): the lower point is raw abundance data, the upper is corrected for prey abundance.

flux). Overall, given the implied range of variation in energy flux, it seems reasonable to reject the notion that these patterns emerge from ‘resource partitioning’ or ‘energetic trade-offs’ (Allen *et al.*, 2002).

THE WAY AHEAD

The problems associated with EE should not be interpreted as an attack on the energetic view of abundance, which has contributed much to our understanding of large-scale patterns in community structure (Brown *et al.*, 2004; Ernest *et al.*, 2008, 2009; McGill, 2008), and which we find to be plausible in the broadest sense. Rather we urge researchers to discard the notion of energy equivalence as an ecological ‘rule’ and to focus instead on the mechanisms underpinning abundance–energy relationships, and to consider alternative (i.e. non-energetic) determinants of species abundance.

To some degree, this is already happening, using data on abundances within communities. New applications of species abundance distributions, using currencies of energy and biomass, have provided novel insights into the partitioning of resources among species (Connolly *et al.*, 2005; Reuman *et al.*, 2008; Morlon *et al.*, 2009; Henderson & Magurran, 2010). A related example is the concept of zero-sum dynamics, in which the energy flux of communities remains stable whilst the abundance (and body size) of individual species fluctuates in a way

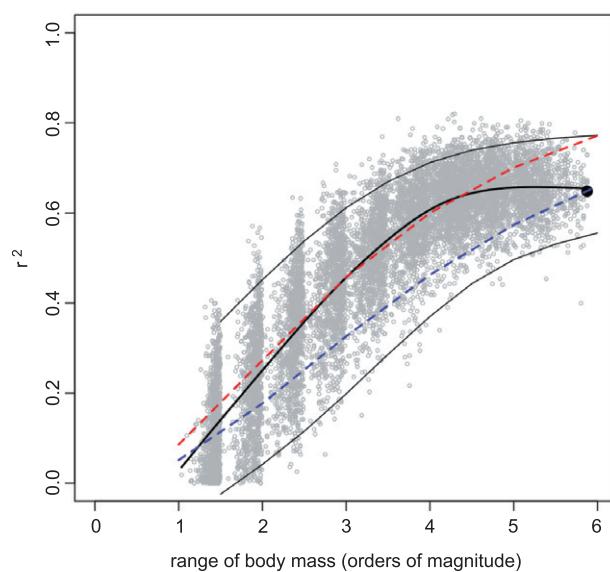


Figure 2 Explanatory power of the mammalian size–density relationship (expressed as r^2) is strongly related to the range of body masses considered. Grey points are 10,000 random subsets of 50 species, each with a constrained range of body mass: narrow black lines indicate the mean and 95% confidence intervals. The black circle is the unconstrained dataset of 467 species. Data are taken from Damuth (1987). The upper and lower dashed lines are the expected r^2 derived from our analytical expression of the null model, with standard deviations in $\log(\text{energy flux})$ of 1.25 and 1.65, respectively (see Appendix S1 for further details).

that reflects individual metabolic requirements (Ernest *et al.*, 2008, 2009). Another prediction of the energetic paradigm is that abundance should increase with available energy: evidence supporting this prediction has been reported for a range of taxa (McNaughton *et al.*, 1989; Meehan *et al.*, 2004; Meehan, 2006; Barton & Zalewski, 2007; Pettorelli *et al.*, 2009; Kaspari & Weiser, 2012), but counter-examples also exist (Currie & Fritz, 1993; Isaac *et al.*, 2011a).

Studies taking the energetic view of abundance should be more explicit about their assumptions. A good example is how individual energy requirements are estimated: most studies use basal metabolic rates, rather than field rates (which scale more steeply; Nagy, 2005). Many studies approximate metabolic rates as $M^{3/4}$ (Ernest *et al.*, 2008, 2009): this is reasonable for a large range in mass, but for small (less than one order of magnitude) ranges the predictive power of Kleiber’s ‘law’ is much reduced (Isaac & Carbone, 2010). In addition, correlations between mass and energy flux should be accompanied by an estimate of the power to reject the null model (with specific reference to the span of body masses under consideration).

We have alluded to the fact that the energetic view of abundance is not universally accepted. Blackburn *et al.* (1993) presented an explanation for the SDR based on the distribution of species body sizes and the fact that rare species tend to go unrecorded. An alternative ‘non-energetic’ view is that abundance could be conceived as a random variable between hard bounda-

ries (Marquet *et al.*, 1995). Cotgreave (1993) has pointed out that body size imposes a physical limit on population density, and that space-filling would generate a scaling in the upper boundary of $-2/3$ (contrast this with the $-3/4$ upper boundary that would be expected from energy monopolization: Blackburn & Gaston, 2001). We could equally envisage a lower boundary of ecological abundance based on the fact that individuals must be able to meet each other to reproduce. Minimum density can be defined as the density at which population growth rate becomes negative due to Allee effects (Courchamp *et al.*, 1999). We expect that minimum density would be related to daily distance traversed, which itself scales with body size (Carbone *et al.*, 2005). Estimating extreme population densities is problematic, and probably prevents this idea from being seriously tested (but see Silva & Downing, 1994). However, similar non-energetic models might derive testable predictions. We believe that macroecology will be advanced by considering both energetic and non-energetic hypotheses in concert, and comparing the predictions of these divergent perspectives.

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REFERENCES

- Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, **297**, 1545–1548.
- Barton, K.A. & Zalewski, A. (2007) Winter severity limits red fox populations in Eurasia. *Global Ecology and Biogeography*, **16**, 281–289.
- Belgrano, A., Allen, A.P., Enquist, B.J. & Gillooly, J.F. (2002) Allometric scaling of maximum population density: a common rule for marine phytoplankton and terrestrial plants. *Ecology Letters*, **5**, 611–613.
- Blackburn, T.M. & Gaston, K.J. (1997) A critical assessment of the form of the interspecific relationship between abundance and body size in animals. *Journal of Animal Ecology*, **66**, 233–249.
- Blackburn, T.M. & Gaston, K.J. (2001) Linking patterns in macroecology. *Journal of Animal Ecology*, **70**, 338–352.
- Blackburn, T.M., Lawton, J.H. & Pimm, S.L. (1993) Nonmetabolic explanations for the relationship between body-size and animal abundance. *Journal of Animal Ecology*, **62**, 694–702.
- Brown, J.H. (1995) *Macroecology*. Chicago University Press, Chicago, IL.
- 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.
- Carbone, C. & Gittleman, J.L. (2002) A common rule for the scaling of carnivore density. *Science*, **295**, 2273–2276.
- Carbone, C., Cowlishaw, G., Isaac, N.J.B. & Rowcliffe, J.M. (2005) How far do animals go? Determinants of day range in mammals. *The American Naturalist*, **165**, 290–297.
- Carbone, C., Cowlishaw, G., Rowcliffe, J.M. & Isaac, N.J.B. (2007) The scaling of abundance in consumers and their resources: implications for the energy equivalence rule. *The American Naturalist*, **170**, 479–484.
- Charnov, E.L., Haskell, J. & Ernest, S.K.M. (2001) Density-dependent invariance, dimensionless life histories and the energy-equivalence rule. *Evolutionary Ecology Research*, **3**, 117–127.
- Connolly, S.R., Hughes, T.P., Bellwood, D.R. & Karlson, R.H. (2005) Community structure of corals and reef fishes at multiple scales. *Science*, **309**, 1363–1365.
- Cotgreave, P. (1993) The relationship between body-size and population abundance in animals. *Trends in Ecology and Evolution*, **8**, 244–248.
- Cotgreave, P. & Harvey, P.H. (1992) Relationships between body size, abundance and phylogeny in bird communities. *Functional Ecology*, **6**, 248–256.
- Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999) Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution*, **14**, 405–410.
- Currie, D.J. & Fritz, J.T. (1993) Global patterns of animal abundance and species energy use. *Oikos*, **67**, 56–68.
- Damuth, J. (1981) Population density and body size in mammals. *Nature*, **290**, 699–700.
- Damuth, J. (1987) Interspecific allometry of population-density in mammals and other animals – the independence of body-mass and population energy-use. *Biological Journal of the Linnean Society*, **31**, 193–246.
- Damuth, J. (2007) A macroevolutionary explanation for energy equivalence in the scaling of body size and population density. *The American Naturalist*, **169**, 621–631.
- Ebenman, B., Hedenstrom, A., Wennergren, U., Ekstam, B., Landin, J. & Tyrberg, T. (1995) The relationship between population density and body size: the role of extinction and mobility. *Oikos*, **73**, 225–230.
- Enquist, B.J., Brown, J.H. & West, G.B. (1998) Allometric scaling of plant energetics and population density. *Nature*, **395**, 163–165.
- Ernest, S.K.M., Brown, J.H., Thibault, K.M., White, E.P. & Goheen, J.R. (2008) Zero sum, the niche, and metacommunities: long-term dynamics of community assembly. *The American Naturalist*, **172**, E257–E269.
- Ernest, S.K.M., White, E.P. & Brown, J.H. (2009) Changes in a tropical forest support metabolic zero-sum dynamics. *Ecology Letters*, **12**, 507–515.
- Harte, J., Zillio, T., Conlisk, E. & Smith, A.B. (2008) Maximum entropy and the state-variable approach to macroecology. *Ecology*, **89**, 2700–2711.
- 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.
- Hayward, A., Kolasa, J. & Stone, J.R. (2010) The scale-dependence of population density body mass allometry:

- statistical artefact or biological mechanism? *Ecological Complexity*, **7**, 115–124.
- Henderson, P.A. & Magurran, A.E. (2010) Linking species abundance distributions in numerical abundance and biomass through simple assumptions about community structure. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1561–1570.
- Isaac, N.J.B. & Carbone, C. (2010) Why are metabolic scaling exponents so controversial? Quantifying variance and testing hypotheses. *Ecology Letters*, **13**, 728–735.
- Isaac, N.J.B., Girardello, M., Brereton, T.M. & Roy, D.B. (2011a) Butterfly abundance in a warming climate: patterns in space and time are not congruent. *Journal of Insect Conservation*, **15**, 233–240.
- Isaac, N.J.B., Storch, D. & Carbone, C. (2011b) Taxonomic variation in the size–density relationship challenges the notion of energy equivalence. *Biology Letters*, **7**, 615–618.
- Kaspari, M. & Weiser, M.D. (2012) Energy, taxonomic aggregation, and the geography of ant abundance. *Ecography*, **35**, 65–72.
- McGill, B.J. (2008) Exploring predictions of abundance from body mass using hierarchical comparative approaches. *The American Naturalist*, **172**, 88–101.
- McNaughton, S.J., Oesterheld, M., Frank, D.A. & Williams, K.J. (1989) Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, **341**, 142–144.
- Marquet, P.A., Navarrete, S.A. & Castilla, J.C. (1990) Scaling population-density to body size in rocky intertidal communities. *Science*, **250**, 1125–1127.
- Marquet, P.A., Navarrete, S.A. & Castilla, J.C. (1995) Body-size, population-density, and the energetic equivalence rule. *Journal of Animal Ecology*, **64**, 325–332.
- Meehan, T.D. (2006) Energy use and animal abundance in litter and soil communities. *Ecology*, **87**, 1650–1658.
- Meehan, T.D., Jetz, W. & Brown, J.H. (2004) Energetic determinants of abundance in winter landbird communities. *Ecology Letters*, **7**, 532–537.
- Morlon, H., White, E.P., Etienne, R.S., Green, J.L., Ostling, A., Alonso, D., Enquist, B.J., He, F.L., Hurlbert, A., Magurran, A.E., Maurer, B.A., McGill, B.J., Olff, H., Storch, D. & Zillio, T. (2009) Taking species abundance distributions beyond individuals. *Ecology Letters*, **12**, 488–501.
- Nagy, K.A. (2005) Field metabolic rate and body size. *Journal of Experimental Biology*, **208**, 1621–1625.
- Nee, S., Read, A.F., Greenwood, J.J.D. & Harvey, P.H. (1991) The relationship between abundance and body size in British birds. *Nature*, **351**, 312–313.
- Peters, R.H. (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge.
- Pettorelli, N., Bro-Jorgensen, J., Durant, S.M., Blackburn, T. & Carbone, C. (2009) Energy availability and density estimates in African ungulates. *The American Naturalist*, **173**, 698–704.
- Reuman, D.C., Mulder, C., Raffaelli, D. & Cohen, J.E. (2008) Three allometric relations of population density to body mass: theoretical integration and empirical tests in 149 food webs. *Ecology Letters*, **11**, 1216–1228.
- Russo, S.E., Robinson, S.K. & Terborgh, J. (2003) Size–abundance relationships in an Amazonian bird community: implications for the energetic equivalence rule. *The American Naturalist*, **161**, 267–283.
- Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B. & Charnov, E.L. (2004) Effects of body size and temperature on population growth. *The American Naturalist*, **163**, 429–441.
- Silva, M. & Downing, J.A. (1994) Allometric scaling of minimal mammal densities. *Conservation Biology*, **8**, 732–743.
- Taper, M.L. & Marquet, P.A. (1996) How do species really divide resources? *The American Naturalist*, **147**, 1072–1086.
- Tilman, D., Hillerislambers, J., Harpole, S., Dybzinski, R., Farajone, J., Clark, C. & Lehman, C. (2004) Does metabolic theory apply to community ecology? It's a matter of scale. *Ecology*, **85**, 1797–1799.
- White, E.P., Ernest, S.K.M., Kerkhoff, A.J. & Enquist, B.J. (2007) Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution*, **22**, 323–330.

SUPPORTING INFORMATION

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

Appendix S1 Analytical derivation for the expected explanatory power of the size–density relationship under the energetic null model.

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BIOSKETCHES

Nick Isaac conducts research on species distribution and abundance over large scales, using data on insects, mammals and birds. Of particular interest is the relative contribution of traits and environmental factors in shaping biodiversity, and how these patterns change with scale.

David Storch is interested in macroecology, evolutionary ecology and ecological theory, with particular emphasis on patterns of species distribution and diversity.

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