



Untangling ecological complexity on different scales of space and time

David Storch^{a,b,*}, Kevin J. Gaston^c

^aCenter for Theoretical Study, Charles University, Jilská 1, 110 00-CZ Praha 1, Czech Republic

^bSanta Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA

^cBiodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

KEYWORDS

Macroecology;
Biodiversity;
Species distribution;
Body size;
Geographic range;
Abundance;
Species richness;
Species–area;
Species–energy;
Local and regional

Summary

Ecological systems are complex and essentially unpredictable, because of the multitude of interactions among their constituents. However, there are general statistical patterns emerging on particular spatial and temporal scales, which indicate the existence of some universal principles behind many ecological phenomena, and which can even be used for the prediction of phenomena occurring on finer scales of resolution. These generalities comprise regular frequency distributions of particular macroscopic variables within higher taxa (body size, abundance, range size), relationships between such variables, and general patterns in species richness. All the patterns are closely related to each other and although there are only a few major explanatory principles, there are plenty of alternative explanations. Reconciliation of different approaches cannot be obtained without careful formulation of testable hypotheses and rigorous quantitative empirical research. Two especially promising ways of untangling ecological complexity comprise: (1) analysis of invariances, i.e. universal quantitative relationships observed within many different systems, and (2) detailed analysis of the anatomy of macroecological phenomena, i.e. explorations of how emergent multispecies patterns are related to regular patterns concerning individual species.

© 2004 Elsevier GmbH. All rights reserved.

Zusammenfassung

Ökologische Systeme sind komplex und im Wesentlichen aufgrund der Vielzahl von Interaktionen zwischen ihren Bestandteilen nicht vorhersagbar. Dennoch gibt es allgemeine statistische Muster, die in bestimmten räumlichen und zeitlichen Skalen auftreten. Dies weist auf die Existenz von einigen universellen Prinzipien hinter diesen ökologischen Phänomenen hin, die sogar für die Vorhersage von Phänomenen genutzt

*Corresponding author. Center for Theoretical Study, Charles University, Jilská 1, 110 00-CZ Praha 1, Czech Republic. Tel.: +420-221416937; fax: +420-222220653.

E-mail address: storch@cts.cuni.cz (D. Storch).

werden können, die auf kleineren Skalen auftreten. Diese Allgemeingültigkeiten bestehen aus Häufigkeitsverteilungen von bestimmten makroskopischen Variablen innerhalb höherer Taxa (Körpergröße, Abundanz, Arealgröße), den Beziehungen zwischen diesen Variablen und allgemeinen Mustern des Artenreichtums. Alle Muster stehen in enger Beziehung zueinander und obwohl es nur wenige bedeutende Erklärungsprinzipien gibt, existieren viele alternative Erklärungen. Die Abstimmung zwischen verschiedenen Ansätzen kann ohne eine sorgfältige Formulierung von testbaren Hypothesen und rigorose quantitative empirische Forschung nicht erreicht werden. Zwei besonders vielversprechende Wege ökologische Komplexität zu entwirren beinhalten (1) die Analyse von Invarianten, d.h. universellen quantitativen Beziehungen, die innerhalb verschiedener Systeme beobachtet werden, und (2) detaillierte Analysen der Anatomie von makroökologischen Phänomenen, d.h. Untersuchungen darüber, in welcher Beziehung die auftauchenden Muster von Multi-Arten-Systemen zu regulären Mustern individueller Arten stehen.

© 2004 Elsevier GmbH. All rights reserved.

Introduction

Ecological communities and ecosystems are good examples of complex systems (Levin, 1999). They comprise large numbers of interacting entities, on many scales of observation, and their dynamics are often nonlinear (causes are not proportional to consequences). This leads to unpredictability and even apparent randomness. Charles Darwin was perhaps the first to recognise this feature of natural communities in his famous consideration of processes contributing to the composition of plant species covering an entangled bank: "What a struggle between the several kinds of trees must here have gone on during long centuries, each annually scattering its seeds by the thousands; what war between insect and insect – between insects, snails, and other animals with birds and beasts of prey – all striving to increase, and all feeding on each other or on the trees or their seeds and seedlings, or on the other plants which first clothed the ground and thus checked the growth of the trees!" (Darwin, 1859). Often, as is almost certainly the case here, it is not possible accurately to predict or assess trajectories of community development and population dynamics leading to the features of a particular community. This is not solely because of the multitude of factors that affect the life histories of individuals and populations, but also because of the inherent properties of the dynamics themselves – even simple processes can lead to complex patterns (May, 1976; Bascompte & Solé, 1995).

This does not mean that everything in community ecology is unpredictable or chaotic. Although it may not be possible to predict the fates of all of the individual plants inhabiting Darwin's entangled bank and perhaps neither the exact population sizes nor the precise community composition, it

would still be possible to predict some community properties. For instance, it is almost certain that most of the plant species will be relatively rare there, and only a few will be common (Gaston, 1994). The same pattern will hold for animal inhabitants of the entangled bank, large animals probably being rarer than the small ones, both in terms of the number of individuals and the number of species. In addition, although the abundances of individual plant and animal species will change and will depend on many circumstances, it is probable that the species that are more widely distributed in the region within which the entangled bank lies will also be more common on the bank (Brown, 1984; Gaston & Blackburn, 2000).

These properties can be predicted on the basis of some general statistical regularities concerning the abundance and distribution of species. Some other features can be predicted on the basis of the geographic location of the respective community. Thus, although exact species richness depends on many factors, including the productivity of the environment and the competitive abilities of all the species (Tokeshi, 1999), an entangled bank in the tropics will surely contain many more species than will a similar bank in the temperate zone, simply because species richness decreases from the tropics toward the poles (e.g. Dobzhansky, 1950; Stevens, 1989), and because local species richness depends on the species richness of whole regions (e.g. Cornell & Lawton, 1992; Caley & Schluter, 1997). Species richness will depend also on the size of landmass within which the community resides (Rosenzweig, 1995): on islands the richness will be lower than on continents, and on larger continental landmasses it will be highest. There are also some geographical trends in species characteristics that will determine other features of any local community. For example, toward higher latitudes the

degree of polyploidy tends to be higher in plants (Rosenzweig, 1995), and body size and the number of eggs individuals lay tends to increase in many animal taxa (Bergmann, 1847; Lack, 1954; Fleming & Gross, 1990). Many features of any local assemblage can therefore be predicted from knowledge of major geographical statistical trends in the properties of biota. Local assemblages are not closed systems, and although their openness can thwart predictions based on knowledge of the dynamics and behaviour of individual components, it might at the same time lead to deeper understanding using knowledge of the patterns and processes on larger spatial and temporal scales.

In short, ecological complexity is a matter of point of view. What seems to be complex from one perspective may be relatively simple from another. Macroecology is founded on the recognition that some simple statistical regularities emerge when considering large sets of species or locations, despite, and sometimes even because of, the complexity of local dynamics. These regularities are interesting not only for their own sake, but also because they are very helpful for understanding more local patterns in nature. This top-down approach might seem very different from the traditional one employed by exact science, in which understanding of a system results from decomposing it into parts that are simpler and more tractable to study. However, this view may be false (Maurer, 1999). Success in a field such as physics, the archetypal 'exact' science, is not due to reductionism (i.e. the ability to measure precisely the interactions between all individual fundamental units), but results in large part from careful formulation of theories concerning the statistical regularities apparent on any particular scale of observation: understanding of macroscopic physical objects is not attainable by measuring all of the interactions between all individual molecules, but instead from knowledge of the statistical patterns and features that emerge from them. Just as temperature, for example, summarises the interactions between lots of constituent particles, macroecological patterns summarise the multitude of effects of many different, individual organisms.

The above said, the existence of simple large-scale statistical patterns is not a panacea. Even if they are helpful in predicting the properties of local assemblages, why these patterns exist often is not well understood. Since the large-scale patterns are emergent, they are not simply explicable in terms of knowledge of small-scale processes. Relative certainty and simplicity of large-scale

patterns is balanced by uncertainty and complexity of their explanations. The greatest achievement of macroecology is the recognition of the influence of the large-scale constraints on small-scale patterns and processes, whereas its greatest challenge is to understand how these large-scale regularities actually emerge, and moreover, how they are connected to each other.

Major macroecological patterns and their interconnections

The principal statistical regularities that occur on large scales comprise patterns in the frequency distributions of different species characteristics, the relationships between these characteristics, and patterns in species richness. Although these regularities largely have been studied independently, they represent quite complex wholes, with many interconnections. Within assemblages of higher taxa (e.g. angiosperms, beetles, birds or mammals), some of the major patterns are as follows:

Patterns in frequency distributions of species characteristics

- (i). Species–abundance distribution—populations of most species are small, and those of only a few are large (Preston, 1948; Gaston, 1994). This pattern holds for most species assemblages, both at the small scale and at that of whole regions (e.g. continents). The frequency distribution of abundances is strongly right-skewed, and becomes approximately normal when plotting abundance classes on a logarithmic scale (when it constitutes a lognormal distribution), or over large regions becomes slightly left-skewed on a logarithmic scale (Fig. 1A, B).
- (ii). Species–range size distribution – in a related vein, most species in an assemblage are also rare in terms of their extent of occurrence or area of occupancy (Gaston, 1994). The pattern differs, however, with spatial scale: when comparing the entire geographic range sizes of species (a 'comprehensive' analysis; Gaston & Blackburn, 1996a), the distribution is approximately normal under logarithmic transformation although commonly with some left-skew (Gaston, 1996, 1998), but within areas too small to embrace the entire geographic ranges of most of the species (a 'partial' analysis; Gaston & Blackburn, 1996a) the distribution is often more or less

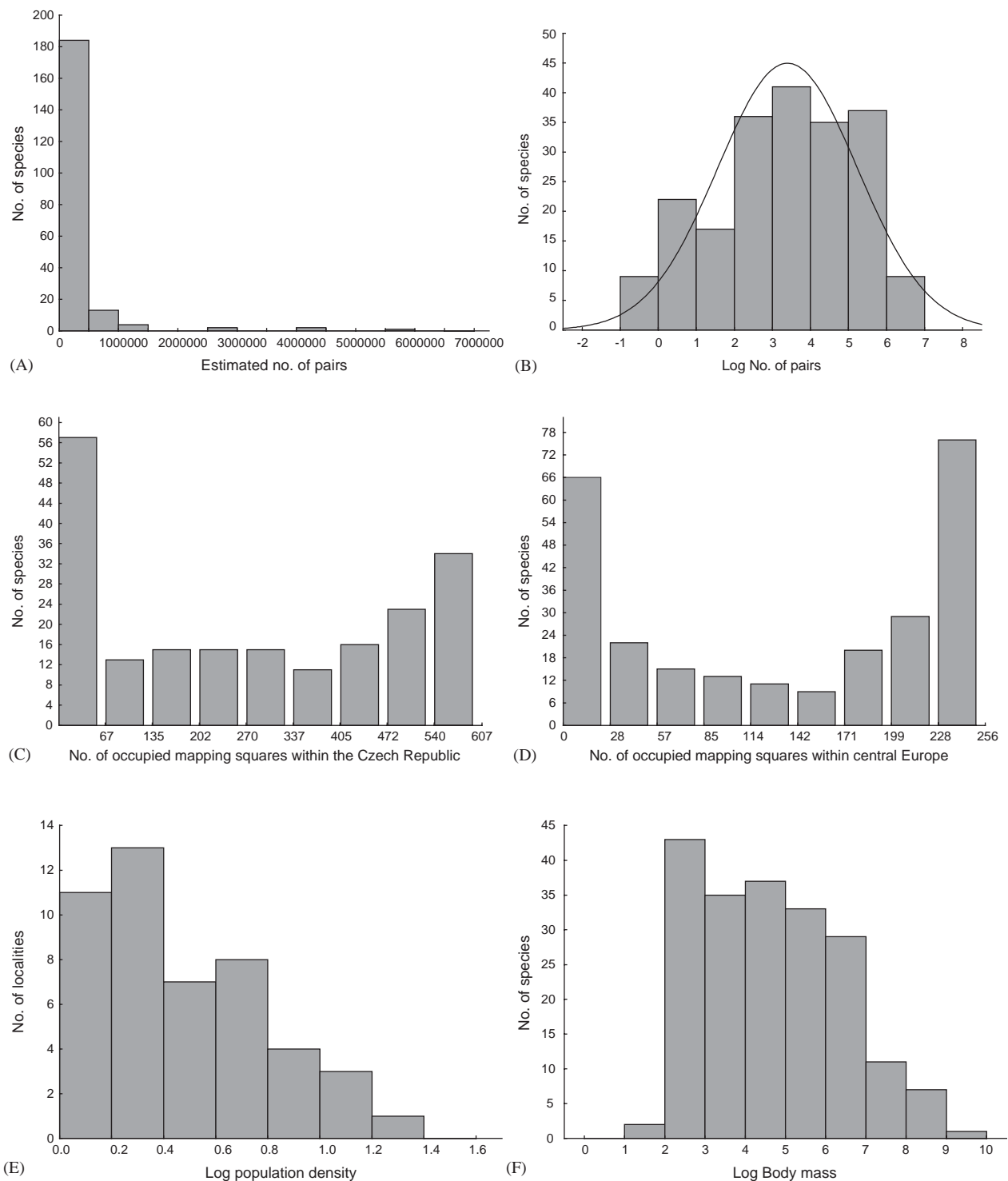


Fig. 1. Patterns in the frequency distributions of species characteristics for central European birds: abundances of birds in the Czech Republic using (A) arithmetic; (B) logarithmic scale abundance classes (Data from Hudec, Chytil, Štastný, & Bejček, 1995); number of occupied sites within (C) the Czech Republic and (D) central Europe (After Storch & Šizling, 2002); (E) local densities of a species (*Sylvia communis*) within different bird communities censused in the area of the Czech Republic (Data from Storch & Kotecký, 1999); and (F) body masses of birds of the Czech Republic.

bimodal (Fig. 1C,D) with many species occupying much of the area (Hanski, 1982; Storch & Šizling, 2002).

(iii). Spatial variation in abundance – abundance of a species is highly unequally distributed within its range (Fig. 1E). All species,

including the most common, occur at relatively low abundances in most of the sites that they occupy, and reach high densities in only a small proportion (Gaston, 1994, 2003; Brown, Mehlman, & Stevens, 1995). The spatial distribution of individuals is mostly aggregated (Taylor, Woiwood, & Perry, 1978) and species abundances are more similar at sites that are closer to each other: they tend to show positive patterns of spatial autocorrelation that decline as distances increase.

- (iv). Species–body size distribution—most species are small-bodied, and only a few are large-bodied (Van Valen, 1973, Blackburn & Gaston, 1994). If body sizes are logarithmically transformed, the species–body size distribution is right-skewed (Blackburn & Gaston, 1994), which means that although the very small species are also comparatively rare, the number of species generally progressively decreases with their body size (Fig. 1F).

Patterns in relationships between species' characteristics

- (i). Abundance–range size relationship—species that are locally abundant tend also to be widely distributed (Fig. 2A); there is a positive correlation between local density and number of occupied sites or geographic range size (Hanski, 1982; Gaston et al., 2000). In consequence, the inequality of species in terms of their commonness and rarity is even higher than predicted on the basis of abundance alone (Brown, 1995).
- (ii). Abundance–body size relationship—smaller species generally reach higher abundances. However, although comparison across a wide range of animals on the Earth gives a negative correlation between body size and abundance, for individual higher taxa at the scale of continents or countries (Fig. 2B), the relationships become quite weak (Cotgreave, 1993). Maximum population abundance seems to be more limited in bigger animals, but, on the other hand, also in the smallest ones (Brown & Maurer, 1987). For lower taxa (e.g. families or tribes in the case of birds), the pattern may even be reversed, bigger animals sometimes reaching higher abundances (Cotgreave, 1994).
- (iii). Range size–latitude relationship (Rapoport's rule) — there has been much debate as to how general is a trend for the geographic range sizes of species to decline towards lower latitudes (Rapoport, 1982; Stevens, 1989; Gaston, Blackburn, & Spicer, 1998; Cardillo, 2002). The strongest evidence is from the northern hemisphere (Fig. 2C), particularly between mid- to high latitudes, but it is not clear whether range sizes are generally smaller in the tropics (Gaston et al., 1998; Gaston, 2003).
- (iv). Body size–latitude relationship (Bergmann's rule) — within higher taxa, the mean body sizes of species toward higher latitudes tend to be larger than those of species toward lower latitudes (Fig. 2D), particularly for vertebrates (Bergmann, 1847; Blackburn, Gaston, & Loder, 1999). This pattern does not, however, translate into a simple trend in maximum body size; many of the largest species occur in tropical regions.

Patterns in species richness

- (i). Species–area relationship—species richness tends to increase with the area censused (Arrhenius, 1921; Rosenzweig, 1995), and the relationship is mostly approximately linear on a log–log scale (Fig. 3A). The slope is higher for isolated areas than for areas nested within one continuous mainland: in islands, a reduction in area to one-tenth results in a loss of approximately half of species in a typical case. The highest slope of the relationship is attained by comparison among different continents or other biotic provinces.
- (ii). Local–regional species richness relationship — local species richness tends to be positively correlated with the size of the regional species pool. The number of species at a locality increases more or less linearly with the number of species within the whole region (Cornell & Lawton, 1992; Caley & Schluter, 1997), although curvilinear relationships can be sometimes observed as well.
- (iii). Species–energy relationship — areas with higher amounts of available energy, i.e. higher productivity, generally host more species (Currie, 1991; Whittaker, Willis, & Field, 2001), but the pattern seems to be scale-dependent and not absolutely consistent. At a relatively local scale, there is a marked tendency for a hump-shaped relationship, the most productive areas having fewer species than little bit less productive ones (Rosenzweig, 1995), whereas on regional to global scales there is mostly a linear increase in species richness with available energy (Fig. 3B; Gaston, 2000), although some

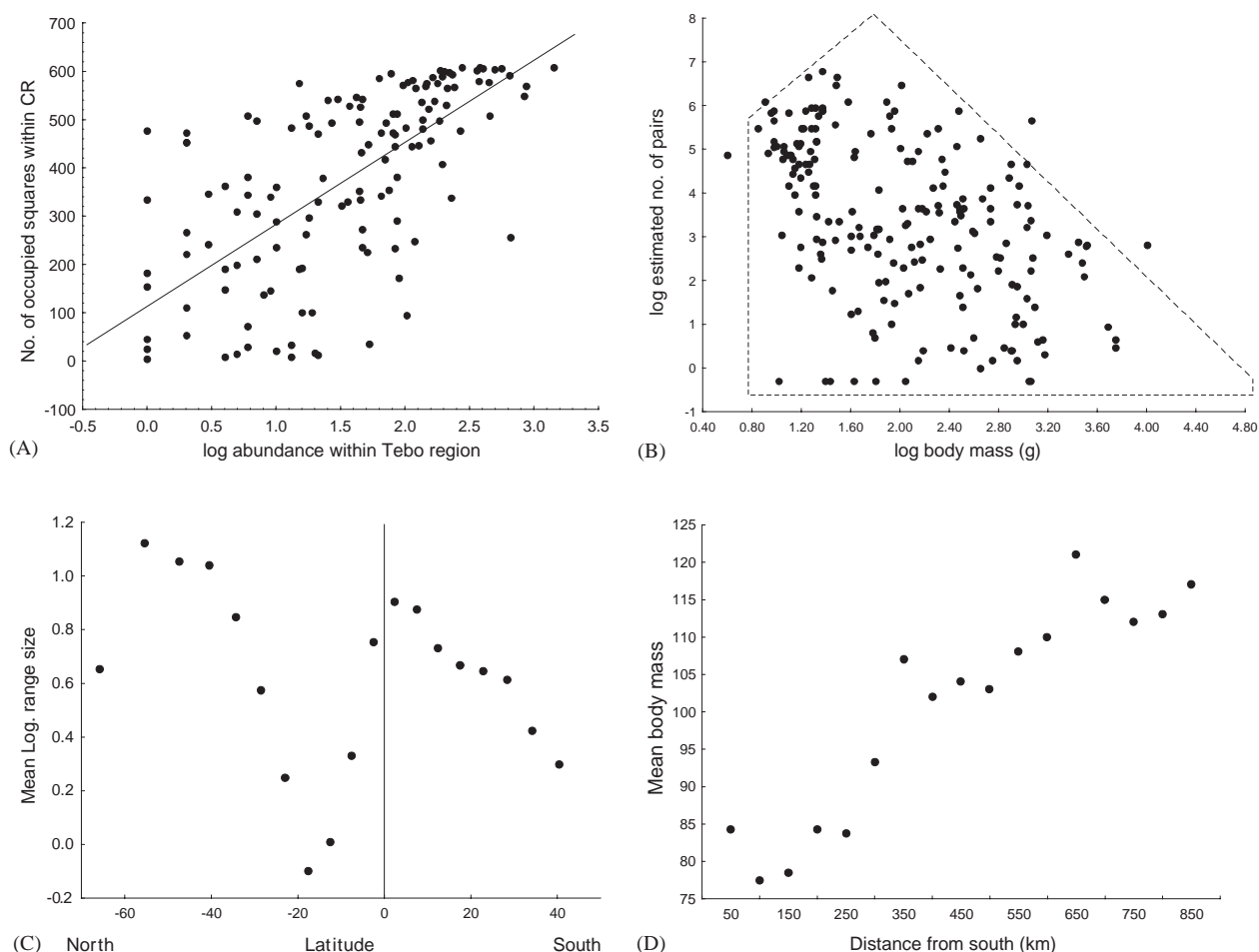


Fig. 2. Examples of relationships between species' macroecological characteristics: (A) relationship between local abundance and range size (measured as number of occupied mapping squares) for the birds of the Czech Republic (Data from Storch et al., unpublished, and Štastný et al., 1996). (B) Relationship between body size and total abundance for the birds of the Czech Republic; the polygon that restricts possible combinations of body weights and abundances has been drawn up on the basis of whole-continent censuses (Data from Hudec et al., 1995). (C) Relationship between geometric mean body mass and latitude for the birds of Britain (After Gaston & Blackburn, 2000). (D) Relationship between range size and latitude for birds in the New World (After Gaston & Blackburn, 2000).

evidence for the hump-shaped pattern also exists on these scales (Balmford et al., 2001).

- (iv). Latitudinal gradient in species richness — species richness decreases from the tropics to the poles in the vast majority of taxa and most habitat types (e.g. Dobzhansky, 1950; MacArthur, 1969; Stevens, 1989; Turner, this volume). The gradient is often quite steep (Fig. 3C), tropical assemblages being several times more speciose than temperate ones, and has been a strikingly persistent feature of biodiversity throughout much of its history (Gaston, 2000).

Inter-relationships

These 12 regularities do not constitute a comprehensive list of all macroecological patterns. Others

include a positive interspecific relationship between body size and geographic range size (Brown & Maurer, 1987), increasing clutch sizes (Lack, 1954; Fleming & Gross, 1990) and animal population density (Currie & Fritz, 1993) with latitude, and the relationship between species richness and altitude (Rahbek, 1995), temperature (Lennon, Greenwood, & Turner, 2000; Allen, Brown, & Gillooly, 2002) or environmental stability (Fjeldsa, Lambin, & Mertens, 1999). However, relationships even between the patterns listed above are quite complex. Some seem simply to be a by-product of the others. For instance, the linear relationship between regional and local species richness should be viewed as a direct consequence of the species–area relationship, since the constant slope of the species–area relationship on a log–log scale means that the species number within a particular fraction

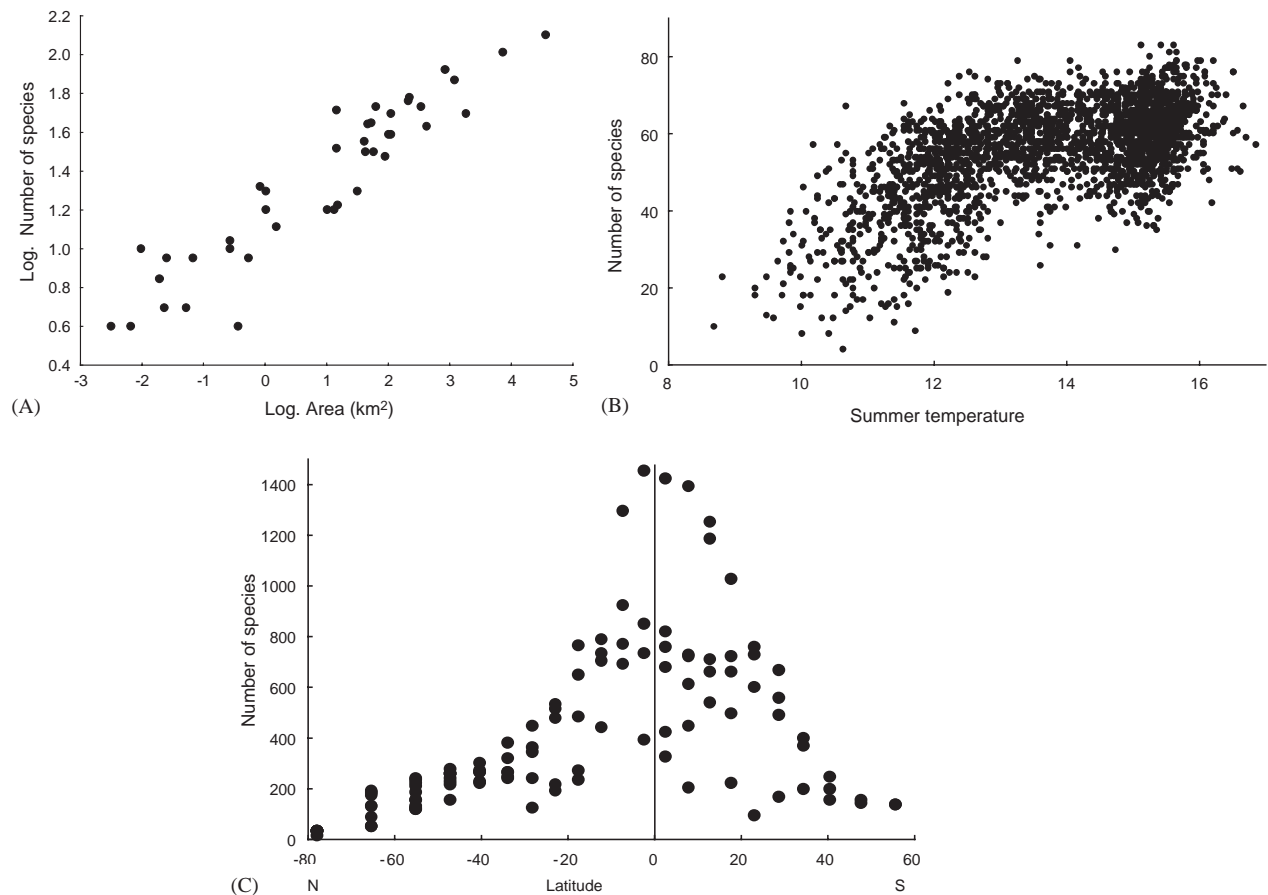


Fig. 3. Examples of patterns in species richness: (A) Species–area relationship for birds on the Bismarck islands (From data in [Mayr & Diamond, 2001](#)), (B) species–energy relationship for mean monthly summer temperature (°C) and richness of breeding birds in Britain (grid cells of 10 km × 10 km) (After [Lennon et al., 2000](#)), and (C) latitudinal gradient in species richness of birds across the New World (grid cells of ~611,000 km²) (After [Gaston & Blackburn, 2000](#)).

of an area will always represent some constant proportion of overall species richness ([Rosenzweig & Ziv, 1999](#); [Bartha & Ittész, 2001](#)).

Some other macroecological patterns may be partly, but perhaps not fully, explained by the others. For example, the species abundance distribution within local assemblages has been attributed to the abundance distribution of a species within its range, considering that most species have low abundances in most locations, and thus within one such location most species will be rare ([Hengeveld, Kooijman, & Taillie, 1979](#); [Brown, 1995](#); [Gaston, 2003](#)). However, this is of course not sufficient to explain whole-continental or global abundance distributions, which are also well characterised by a prevalence of rare species (e.g. [Gaston & Blackburn, 1996b](#)).

The relationships between some macroecological patterns are not simply unidirectional and causal, although it is obvious that they are connected. Thus, it is clear that the species–area relationship

must somehow be related to all the patterns of commonness and rarity, because the slope of the relationship is driven by the fact that some species occur only in part of the whole area ([Šizling & Storch, 2004](#)); if all species were distributed everywhere, their number in one location would be equal to the richness of the whole area and no species–area relationship would occur. Some patterns are connected in a rather complicated way; especially, when a set of variables is compared from different points of view, as is the case for the interrelations between latitude, body size, abundance and range size, where each pairwise correlation is actually only one projection of their multidimensional relationship. In wildfowl, for instance, both body size and abundance correlate with latitude, and as a consequence the expected negative relationship between body size and abundance does not occur ([Gaston & Blackburn, 1996b](#)). Likewise, the global body size distribution of taxa could, for instance, be affected by the fact

that most species live in the tropics (latitudinal gradient in species richness) and tropical species are generally smaller (Bergmann's rule).

In summary, although the general macroecological patterns are quite simple, the relationships between them are complex and not straightforward.

Major explanatory principles in macroecology

The general causes of these macroecological patterns are not clear. Indeed, several often very different explanations exist for each of them (for review see [Gaston & Blackburn, 2000](#), [Blackburn & Gaston, 2003](#)). However, most are based on only a few basic principles governing major features of life on Earth.

Energetic limitation

The first principle is that of energetic limitation: because maintenance and growth of biomass requires energy, populations of species within an area are somehow limited by the energy available to them, which can be allocated to either many small-bodied or few large-bodied individuals. Thus, large animals are generally expected to be less abundant (abundance–body size relationship), assuming that different species have similar energy requirements ([Blackburn & Gaston, 2001](#)). Energetic constraints on population size govern directly or indirectly many macroecological patterns, especially in combination with the following principle.

Extinction probability

The second main principle is based on the observation that population extinction probability is directly related to population size (in terms of both abundance and range size) because smaller populations are more vulnerable to even small disturbances or environmental fluctuations ([Pimm, Jones, & Diamond, 1988](#)). Combined with the first principle this gives one of several explanations of the species–body size distribution: large-bodied species will be much less numerous because they have less abundant populations which are more vulnerable to extinction ([Johst & Brandl, 1997](#)). The negative relationship between population size and extinction probability, however, has far wider consequences. It is the key to understanding relatively impoverished biota on islands (limited area does not support large populations) as well as

the positive relationship between the area of a biotic province and species richness – smaller areas contain smaller populations, which should lead to a higher mean rate of extinctions ([Rosenzweig, 1995](#)). A similar line of argument concerns the species–energy relationship, since productivity can promote larger populations (because of the first principle, i.e. energetic constraints on populations) and thus decreases extinction probability ([Wright, Currie, & Maurer, 1993](#)). Both large area and high productivity are regarded as contributing to the latitudinal pattern of species richness, since the tropics are the largest and most productive climatic zone.

Climatic variability

The geographical trends in distribution of organisms (and their features) can be affected not only by energy availability that is related to climatic factors like temperature and rainfall (see [Whittaker et al., 2001](#)), but also by climatic variability. Larger climatic oscillations in higher latitudes are supposed to lead to adaptations promoting higher environmental tolerance of species which could be attained by larger body sizes (Bergmann's rule; [Lindstedt & Boyce, 1985](#)) and which might lead in consequence to wider geographic distribution (Rapoport's rule) in these latitudes ([Stevens, 1989](#)). Also, other latitudinal patterns, like larger clutch sizes in birds ([Lack, 1954](#)) or higher proportion of polyploid species in plants ([Rosenzweig, 1995](#)) can be regarded as adaptations to less stable conditions. Lower climatic oscillations in the tropics can contribute to their species richness, due either to higher specialisation ([Stevens, 1989](#)) or lower extinction probability ([Dynesius & Jansson, 2000](#)).

Positive feedback in population dynamics

Several major macroecological patterns concern the huge inequality among species: most species are rare, and moreover, locally rare species have a tendency also to be globally rare ([Brown, 1984](#)). Plenty of models consider the rare-common difference, and most of them share one general property of population dynamics, the positive feedback due to the multiplicative nature of biological reproduction. This feedback ensures that large populations can become even larger, whereas small populations mostly remain small or go extinct. Small population size and/or range size thus represent a dynamic trap that is not easy to evade. Some models assume unidirectional causality between abundance and

range size, leading from higher population densities to spreading and colonising most suitable areas (Holt, Lawton, Gaston, & Blackburn, 1997), whereas other assume positive feedback between these variables (Hanski, 1982). However, the self-reinforcement of population dynamics is explicitly or implicitly presents in most models and thus represents the fourth major explanatory principle.

Interspecific niche differences and habitat heterogeneity

Last but not least, the fifth major principle in macroecology concerns different habitat requirements of species combined with spatial variability in environmental parameters. The niche differences among species have been regarded as responsible for the abundance–range size relationship (Brown, 1984) and environmental heterogeneity is partially responsible for the species–area relationship within continuous areas (Storch, Šizling, & Gaston, 2003), since larger areas contain more habitat types suitable for more species. Within-species spatial variability in abundance has been attributed to spatial environmental variability as well (Brown et al., 1995).

Apart from these five key principles, there have been attempts to explain major patterns in distribution, abundance and species richness by one unifying theory based on as few assumptions as possible (Bell, 2001; Hubbell, 2001; Maurer & McGill, this issue). These “neutral” theories assume only a limited total number of individuals within an assemblage, absolute ecological equivalency among species and limited dispersal. Populations fluctuate randomly and colonise adjacent areas. These models predict the shape of species–abundance distributions, as well as some other distributional patterns (species–area relationship, spatial variability of abundance), but their assumptions – although regarded as minimal – are actually unrealistically restrictive for many taxa (Enquist, Sanderson, & Weiser, 2002). However, similar approaches promise that there might be some general and very simple principles behind many of the patterns that perhaps somehow subsume most of those mentioned above.

Conclusions and perspectives

Macroecological patterns give keys to understanding many ecological phenomena even at smaller scales. This does not mean, however, that the large-scale processes unidirectionally affect the

small-scale ones – many of them actually emerge from the local processes, and on the large scales are but more apparent and regular. Note that although, for example, the local–regional species richness relationship has been interpreted as evidence that local processes (like interspecific competition or habitat selection) are relatively unimportant in comparison with the role of the regional species pool, it has been shown that the reverse might be true (Herben, 2000; Lepš, 2001): even if only local population dynamics plays a role, the relationship between local and regional diversity would be linear. Macroecology cannot replace more traditional small-scale population ecology, but it can offer new approaches and conceptual tools.

Perhaps the major contribution of macroecology is that it is no longer necessary to keep the principal features of the biota of a particular region as an independent variable that somehow constrains local patterns and processes, but that is itself not accessible by scientific inquiry. Now we can also ask about the reasons for these large-scale properties of nature. Of course, the answers will be appropriate to the scales of the patterns, and thus will deal mainly with topics like speciation and extinction dynamics, and general trends in species adaptations or species dispersal on large spatial and temporal scales, i.e. the processes traditionally covered by disciplines like biogeography and evolutionary biology rather than classical ecology. The major achievement of macroecology lies in the interconnection of these disciplines with other fields of ecological research.

Although how local processes are connected to large-scale patterns has been learned, and though the main principles behind most of these patterns have been suggested, we are still far from complete understanding. Whereas qualitative patterns seem to be comprehensible – albeit from many different points of view – the exact quantitative relationships remain obscure. It is easy to understand why the number of species increases with area, but it is much more difficult to explain why the species–area relationship is mostly linear on a log–log scale, and why it has a particular slope under particular geographic conditions (Rosenzweig, 1995; He & Legendre, 1996). The quantitative properties of macroecological patterns, however, can provide a clue to a deeper understanding of principles and mechanisms behind them. The relationships between body size, metabolic rate and population density, for instance, are often approximately linear in a logarithmic space, with the slope or regression lines being close to a multiplier of 0.25 (i.e. -0.75 , 1.25 , etc., see Brown

et al., 2002). This has led to the development of a "metabolic theory of ecology" (Brown, Gillooly, Allen, Savage, & West, 2004), with its ambition to explain interspecific differences in life-history characteristics, individual and population growth (West, Brown, & Enquist, 2001; Savage, Gillooly, Brown, West, & Charnov, 2004), and even global patterns in species richness (Allen, Brown, & Gillooly, 2002) on the basis of fundamental principles of physics, chemistry and biology (West, Brown, & Enquist, 1997, 1999). Although this theory is still far from proven or definite, the approach based on rigorous consideration of universal quantitative relationships is promising.

The other promising way to gain an improved understanding of macroecological patterns is through their "anatomy", i.e. through revealing the way in which multispecies statistical patterns are connected to the regularities at the species level. The power-law species–area relationship has been shown, for example, to be attributable to self-similarity of spatial distribution of individual species (Šizling & Storch, 2004), and the species–energy relationship is inevitably related to the distribution of species ranges along productivity gradients (Bonn, Storch & Gaston, 2004). How the distribution of individual species is affected by the macroscopic variables so that the macroecological phenomena emerge, is surprisingly poorly known. Although most explanations of the species–energy relationship, for example, rely on the assumption that the amount of resources available for each individual species increases with productivity, the evidence is scarce and often contradictory (Allen et al., 2002; Storch, 2003; Bonn, Storch & Gaston, 2004), sometimes indicating that species rather more finely divide their resources than simply increase their resource base in more productive areas. The way in which species divide resources and energy at large scales have been treated as the core topics of macroecology (Brown & Maurer, 1989). Resolving such questions will require combining the metabolic (i.e. individual-based) approach to ecological systems with the analysis of the relationships between species-level patterns and emergent macroecological phenomena.

Acknowledgements

This work was supported by a Royal Society/NATO postdoctoral fellowship to D.S. and Grant Agency of the Academy of Sciences of the Czech Republic (KJB6197401). T.M. Blackburn, S.F. Jackson and A. Nagy kindly commented on the manuscript.

References

- Allen, A. P., Brown, J. H., & Gillooly, J. F. (2002). Global biodiversity, biochemical kinetics and the energetic-equivalence rule. *Science*, 297, 1545–1548.
- Arrhenius, O. (1921). Species and area. *Journal of Ecology*, 9, 95–99.
- Balmford, A., Moore, J. L., Brooks, T., Burgess, N., Hansen, L. A., Williams, P., & Rahbek, C. (2001). Conservation conflicts across Africa. *Science*, 291, 2616–2619.
- Bartha, S., & Ittész, P. (2001). Local richness-species pool ratio: a consequence of the species–area relationship. *Folia Geobotanica*, 36, 9–23.
- Bascompte, J., & Solé, R. V. (1995). Rethinking complexity: modelling spatiotemporal dynamics in ecology. *Trends in Ecology and Evolution*, 10, 361–366.
- Bell, G. (2001). Neutral macroecology. *Science*, 293, 2413–2418.
- Bergmann, C. (1847). Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, 3, 595–708.
- Blackburn, T. M., & Gaston, K. J. (1994). Animal body size distribution: patterns, mechanisms and implications. *Trends in Ecology and Evolution*, 9, 471–474.
- Blackburn, T. M., & Gaston, K. J. (2001). Linking patterns in macroecology. *Journal of Animal Ecology*, 70, 338–352.
- Blackburn, T. M., & Gaston, K. J. (Eds.) (2003). *Macroecology: concepts and consequences: 43rd symposium of the British Ecological Society*. Cambridge: Cambridge University Press.
- Blackburn, T. M., Gaston, K. J., & Loder, N. (1999). Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions*, 5, 165–174.
- Bonn, A., Storch, D., & Gaston, K. J. (2004). Structure of the species–energy relationship. *Proceedings of the Royal Society of London B*, 271, 1685–1691.
- Brown, J. H. (1984). On the relationship between abundance and distribution of species. *The American Naturalist*, 124, 255–279.
- Brown, J. H. (1995). *Macroecology*. Chicago: University of Chicago Press.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, in press.
- Brown, J. H., Gupta, V. K., Li, B.-L., Milne, B. T., Restrepo, C., & West, G. B. (2002). The fractal nature of nature: power laws, ecological complexity and biodiversity. *Philosophical Transactions of the Royal Society of London B*, 357, 619–626.
- Brown, J. H., & Maurer, B. A. (1987). Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the American avifauna. *The American Naturalist*, 130, 1–17.
- Brown, J. H., & Maurer, B. A. (1989). Macroecology: the division of food and space among species on continents. *Science*, 243, 1145–1150.

- Brown, J. H., Mehlman, D. W., & Stevens, G. C. (1995). Spatial variation in abundance. *Ecology*, 76, 2028–2043.
- Caley, M. J., & Schluter, D. (1997). The relationship between local and regional diversity. *Ecology*, 78, 70–80.
- Cardillo, M. (2002). The life-history basis of latitudinal diversity gradients: how do species traits vary from poles to the equator? *Journal of Animal Ecology*, 71, 79–87.
- Cornell, H. V., & Lawton, J. H. (1992). Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*, 61, 1–12.
- Cotgreave, P. (1993). The relationship between body size and population abundance in animals. *Trends in Ecology and Evolution*, 8, 244–248.
- Cotgreave, P. (1994). The relationship between body size and abundance in a bird community: the effects of phylogeny and competition. *Proceedings of the Royal Society London B*, 256, 147–149.
- Currie, D. J. (1991). Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist*, 137, 27–49.
- Currie, D. J., & Fritz, J. T. (1993). Global patterns of animal abundance and species energy use. *Oikos*, 67, 56–68.
- Darwin, C. R. (1859). *On the origin of species by means of natural selection or the preservation of the favoured races in the struggle for life*. London: John Murray.
- Dobzhansky, T. (1950). Evolution in the tropics. *American Scientist*, 38, 209–221.
- Dynesius, M., & Jansson, R. (2000). Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences USA*, 97, 9115–9120.
- Enquist, B. J., Sanderson, J., & Weiser, M. D. (2002). Modelling macroscopic patterns in ecology. *Science*, 295, 1835–1837.
- Fjeldsa, J., Lambin, E., & Mertens, B. (1999). Correlation between endemism and local bioclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. *Ecography*, 22, 63–78.
- Fleming, I. A., & Gross, M. R. (1990). Latitudinal clines: a trade-off between egg number and size in Pacific Salmon. *Ecology*, 71, 1–11.
- Gaston, K. J. (1994). *Rarity*. London: Chapman & Hall.
- Gaston, K. J. (1996). Species-range-size distribution: patterns, mechanisms and implications. *Trends in Ecology and Evolution*, 11, 197–201.
- Gaston, K. J. (1998). Species-range-size distribution: products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society London B*, 353, 219–230.
- Gaston, K. J. (2000). Global patterns in biodiversity. *Nature*, 405, 220–227.
- Gaston, K. J. (2003). *The structure and dynamics of geographic ranges*. Oxford: Oxford University Press.
- Gaston, K. J., & Blackburn, T. M. (1996a). Range size–body size relationships: evidence of scale dependence. *Oikos*, 75, 479–485.
- Gaston, K. J., & Blackburn, T. M. (1996b). Global scale macroecology: interactions between population size, geographic range size and body size in the Anseriformes. *Journal of Animal Ecology*, 65, 701–714.
- Gaston, K. J., & Blackburn, T. M. (2000). *Pattern and process in macroecology*. Oxford: Blackwell Science.
- Gaston, K. J., Blackburn, T. M., Greenwood, J. J. D., Gregory, R. D., Quinn, R. M., & Lawton, J. H. (2000). Abundance–occupancy relationships. *Journal of Applied Ecology*, 37(Suppl. 1), 39–59.
- Gaston, K. J., Blackburn, T. M., & Spicer, J. I. (1998). Rapoport's rule: time for an epitaph? *Trends in Ecology and Evolution*, 13, 70–74.
- Hanski, I. (1982). Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos*, 38, 210–221.
- He, F. L., & Legendre, P. (1996). On species-area relations. *The American Naturalist*, 148, 719–737.
- Hengeveld, R., Kooijman, S. A. L. M., & Taillie, C. (1979). A spatial model explaining species–abundance curves. In J. K. Ord, G. P. Patil, & C. Taillie (Eds.), *Statistical distribution in ecological work* (pp. 333–347). Fairland, Maryland: International Co-operative Publishing House.
- Herben, T. (2000). Correlation between richness per unit area and the species pool cannot be used to demonstrate the species pool effect. *Journal of Vegetation Science*, 11, 123–126.
- Holt, R. D., Lawton, J. H., Gaston, K. J., & Blackburn, T. M. (1997). On the relationship between range size and local abundance: back to basics. *Oikos*, 78, 183–190.
- Hubbell, S. P. (2001). *A unified theory of biodiversity and biogeography*. Princeton: Princeton University Press.
- Hudec, K., Chytil, J., Št'astný, K., & Bejček, V. (1995). Birds of the Czech Republic. *Sylvia*, 31, 97–149.
- Johst, K., & Brandl, R. (1997). Body size and extinction risk in a stochastic environment. *Oikos*, 78, 612–617.
- Lack, D. (1954). *The natural regulation of animal numbers*. Oxford: Clarendon Press.
- Lennon, J. J., Greenwood, J. J. D., & Turner, J. R. G. (2000). Bird diversity and environmental gradients in Britain: a test of the species-energy hypothesis. *Journal of Animal Ecology*, 69, 581–598.
- Lepš, J. (2001). Species-pool hypothesis: limits to its testing. *Folia Geobotanica*, 36, 45–52.
- Levin, S. A. (1999). *Fragile dominion: complexity and the commons*. Reading: Perseus books.
- Lindstedt, S. L., & Boyce, M. S. (1985). Seasonality, fasting endurance, and body size in mammals. *The American Naturalist*, 125, 873–878.
- MacArthur, R. H. (1969). Patterns of communities in the tropics. *Biological Journal of the Linnean Society*, 1, 19–30.
- Maurer, B. A. (1999). *Untangling ecological complexity? The macroscopic perspective*. Chicago: University of Chicago Press.

- May, R. M. (1976). Simple mathematical models with very complicated dynamics. *Nature*, 261, 459–467.
- Mayr, E., & Diamond, J. (2001). *The birds of Northern Melanesia: speciation ecology, and biogeography*. New York: Oxford University Press.
- Pimm, S. L., Jones, H. L., & Diamond, J. (1988). On the risk of extinction. *American Naturalist*, 132, 757–785.
- Preston, F. W. (1948). The commonness, and rarity, of species. *Ecology*, 29, 254–283.
- Rahbek, C. (1995). The elevational gradient of species richness: a uniform pattern? *Ecography*, 18, 200–205.
- Rapoport, E. H. (1982). *Areography: geographical strategies in species*. Oxford: Pergamon.
- Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge: Cambridge University Press.
- Rosenzweig, M. L., & Ziv, Y. (1999). The echo pattern of species diversity: pattern and processes. *Ecography*, 22, 614–628.
- 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*, in press.
- Šizling, A. L., & Storch, D. (2004). Power-law species-area relationships and self-similar species distributions within finite areas. *Ecology Letters*, 7, 60–68.
- Stevens, G. C. (1989). The latitudinal gradient in geographical range size: how so many species co-exist in tropics. *American Naturalist*, 140, 893–911.
- Štastný, K., Bejček, V., & Hudec, K. (1996). Atlas hnízdního rozšíření ptáků v České republice 1985–1989. H & H, Jinočany (in Czech).
- Storch, D. (2003). Comment on 'Global biodiversity, biochemical kinetics, and the energetic-equivalence rule'. *Science*, 299, 346b.
- Storch, D., & Kotecký, V. (1999). Structure of bird communities in the Czech Republic: the effect of area, census technique and habitat type. *Folia Zoologica*, 48, 265–277.
- Storch, D., & Šizling, A. L. (2002). Patterns in commonness and rarity in central European birds: reliability of the core-satellite hypothesis within a large scale. *Ecography*, 25, 405–416.
- Storch, D., Šizling, A. L., & Gaston, K. J. (2003). Geometry of the species–area relationship in central European birds: testing the mechanism. *Journal of Animal Ecology*, 72, 509–519.
- Taylor, L. R., Woiwod, I. P., & Perry, J. N. (1978). The density dependence of spatial behaviour and the rarity of randomness. *Journal of Animal Ecology*, 47, 383–406.
- Tokeshi, M. (1999). *Species coexistence: ecological and evolutionary perspectives*. Oxford: Blackwell Science.
- Van Valen, L. (1973). Body size and numbers of plants and animals. *Evolution*, 29, 87–94.
- 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.
- West, G. B., Brown, J. H., & Enquist, B. J. (1999). The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science*, 284, 1677–1679.
- West, G. B., Brown, J. H., & Enquist, B. J. (2001). A general model for ontogenetic growth. *Nature*, 413, 628–631.
- Whittaker, R. J., Willis, K. J., & Field, R. (2001). Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, 28, 453–470.
- Wright, D. H., Currie, D. J., & Maurer, B. A. (1993). Energy supply and patterns of species richness on local and regional scales. In R. E. Ricklefs, & D. Schuller (Eds.), *Species diversity in ecological communities* (pp. 66–74). Chicago: University of Chicago Press.