Journal of Biogeography (*J. Biogeogr.*) (2008) **35**, 483–500

SPECIAL ISSUE

Ecogeographical rules: elements of a synthesis

Kevin J. Gaston[1]*, Steven L. Chown[2] and Karl L. Evans[1]

[1]*Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK,* [2]*Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa*

*Correspondence: K. J. Gaston, Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK.
E-mail: k.j.gaston@sheffield.ac.uk

ABSTRACT

The development of a more synthetic approach to understanding spatial patterns in biogeography, particularly of the way in which these patterns interact, constitutes a major challenge for the field. Here we propose some key elements of such a synthesis for what can broadly be termed 'ecogeographical rules', that is spatial patterns in biological traits. These include understanding: (1) the different kinds of patterns (intraspecific, interspecific and assemblage), and the distinctions between them; (2) the unifying role that geographical ranges play in linking the patterns together; (3) that this unification can be obscured by the methodological assumptions made in documenting some patterns (e.g. assuming that intraspecific variation does not significantly influence interspecific and assemblage patterns in traits); (4) the implications of other methodological issues for the nature of observed patterns (e.g. how ranges are located on positional or environmental axes for interspecific patterns); (5) the need for further development of models linking different types of traits; (6) the nature of the generality of documented patterns at all levels, and particularly the difference between the frequency with which patterns are documented in the literature and the variety of extant species; and (7) the constraints that the form of intraspecific patterns place on interspecific and assemblage patterns, and that interspecific patterns place on assemblage patterns.

Keywords

Areography, ecogeographical rules, environmental gradients, geographical range, latitudinal gradients, macroecology, macrophysiology, spatial gradients.

INTRODUCTION

Three general sets of spatial patterns in biological traits have long dominated much thinking in biogeography. The first are spatial patterns in the traits exhibited within individual species, reflecting their covariation with either positional (e.g. latitude, longitude, altitude, depth) or environmental (e.g. temperature, precipitation, salinity, productivity) variables. Commonly it is assumed that environmental variation can explain positional variation. These patterns include systematic trends in morphology (principally body size; e.g. Ray, 1960; Chown & Gaston, 1999; Jonas & Geber, 1999; Ashton *et al.*, 2000; Ashton, 2002; Ashton & Feldman, 2003; Blanckenhorn & Demont, 2004; Litzgus *et al.*, 2004; Meiri *et al.*, 2004a; Blanckenhorn *et al.*, 2006; Yom-Tov & Geffen, 2006), physiology (e.g. Spicer & Gaston, 1999; Hoffmann *et al.*, 2001; Klok & Chown, 2003; Lardies & Bozinovic, 2006), life history (e.g. Fleming & Gross, 1990; Jonas & Geber, 1999; Jenkins & Hockey, 2001; Cooper *et al.*, 2005; Halsall *et al.*, 2005; Heibo *et al.*, 2005; Lardies & Bozinovic, 2006), population dynamics (e.g. Brown, 1984; Philippart *et al.*, 1998; Brewer & Gaston, 2002, 2003; Post, 2005; Crozier & Zabel, 2006) and genetic variation (e.g. Green *et al.*, 1996; Weeks *et al.*, 2002; Hutchison, 2003; Collinge *et al.*, 2006). Where particular trends are common and exceptions appear to be sufficiently scarce, some such patterns have come to be regarded as classical examples of ecogeographical rules. They include the neo-Bergmannian rule (*sensu* James, 1970) or James's rule (*sensu* Blackburn *et al.*, 1999a; namely, an increase in the size of a species towards higher latitudes or lower temperatures – this is frequently referred to as Bergmann's rule, although as originally defined this pattern was not intraspecific), Foster's or the island rule

doi:10.1111/j.1365-2699.2007.01772.x

(smaller species become larger and larger species smaller on islands compared with mainland areas; Foster, 1964; Adler & Levins, 1994; Wu *et al.*, 2006), Gloger's rule (populations of endothermic animal species in warm and humid areas are more heavily pigmented than in cool dry areas – pigments are typically black in warm humid environments, red and yellow in dry areas, and generally reduced in cool areas; Gloger, 1883; Lincoln *et al.*, 1982), Jordan's rule (fish species develop more vertebrae in a cold environment than in a warm one; Jordan, 1891; Lincoln *et al.*, 1982) and one of Rensch's rules (populations of mammal species have larger litters and bird species larger clutches of eggs in cold climates than in warmer climates; Rensch, 1938; Lincoln *et al.*, 1982). Views vary as to whether one should regard all relatively simple spatial patterns of this kind as constituting ecogeographical rules. Mayr (1956) reserved the term for geographical gradients in intraspecific morphological variation, regarding the terms 'climatic rules' and 'ecological rules' as being more all-encompassing. Others have employed much broader definitions (e.g. Lomolino *et al.*, 2006a,b).

The second group of spatial patterns are those in interspecific variation. These reflect differences in the traits of species occurring in different parts of the world. The best documented examples typically concern variation of traits with latitude, altitude or depth, although as with intraspecific patterns along positional gradients these are almost invariably explained in terms of environmental variation. In some cases the traits are expressed at the level of the individual organism, mirroring those examined intraspecifically, with the values typically being derived as means or medians across multiple individuals (e.g. body size, metabolic rate, clutch size, thermal tolerance; Kulesza, 1990; Hawkins & Lawton, 1995; Addo-Bediako *et al.*, 2000; Böhning-Gaese *et al.*, 2000; Blackburn & Ruggiero, 2001; Gibert & Huey, 2001; Cardillo, 2002a; Clegg & Owens, 2002; Cruz *et al.*, 2005; Symonds *et al.*, 2006). In other cases the traits are expressed at the level of the species (e.g. geographical range size, population density, global population size; Letcher & Harvey, 1994; Gaston & Blackburn, 1996; Cardillo, 2002a; Reed, 2003; Cruz *et al.*, 2005; Symonds *et al.*, 2006). Again, some interspecific trends have been recognized as classic ecogeographical patterns, including Allen's rule (amongst closely related endothermic vertebrates, forms in warmer environments have longer appendages; Allen, 1878; Lincoln *et al.*, 1982) and Bergmann's rule (amongst closely related species body size increases with ambient temperature; Bergmann, 1847).

The final group of spatial patterns are those in assemblage variation. These are patterns in the structure of the assemblages occurring in different places. The simplest are perhaps spatial patterns in species richness (e.g. Currie, 1991; Rahbek, 1995; Gaston, 2000; Hawkins *et al.*, 2003; Hillebrand, 2004a; Orme *et al.*, 2005). Others comprise spatial patterns in additional aspects of assemblage size and composition, such as in total abundance, total biomass or total energy use (e.g. Enquist & Niklas, 2001; Hurlbert, 2004; Pautasso & Gaston, 2005; Evans *et al.*, 2006a), or in the numbers or proportions of different functional or behavioural groups (e.g. Newton & Dale, 1996; Stevens *et al.*, 2003; Heino, 2005; Micheli & Halpern, 2005). Yet others concern spatial trends in the mean state of the traits exhibited by those species co-occurring in an area, such as their body size (e.g. Cushman *et al.*, 1993; Hawkins, 1995; Hawkins & Lawton, 1995; Blackburn & Gaston, 1996a; Knouft, 2002; Chown & Klok, 2003; Blackburn & Hawkins, 2004; Kaspari, 2005; Olalla-Tárraga *et al.*, 2006; Rodríguez *et al.*, 2006), clutch size (e.g. Yom-Tov, 1994; Yom-Tov *et al.*, 1994) or geographical range size (e.g. Stevens, 1989; Letcher & Harvey, 1994; Hawkins & Diniz-Filho, 2006; Orme *et al.*, 2006). Finally, a few studies have examined spatial variation between assemblages in the nature of frequency distributions of traits (e.g. body size, geographical range size; Cardillo, 2002b; Knouft, 2004; Graves & Rahbek, 2005). Spatial patterns that are manifested through assemblage variation and that have been regarded by some as ecogeographical rules include Rapoport's rule [an increase in range size with latitude was termed 'Rapoport's rule' by Stevens (1989), following Rapoport (1982), although it was originally identified much earlier by Lutz (1921)] and Thorson's rule (a switch with increasing latitude in the dominant mode of development of marine invertebrates from pelagic to direct; Thorson, 1950).

In practice, the distinctions between these different kinds of patterns are often not made explicit. For example, 'Bergmann's rule' has variously been tested using intraspecific (e.g. Ashton *et al.*, 2000; Ashton, 2002; Ashton & Feldman, 2003; Blanckenhorn & Demont, 2004; Meiri *et al.*, 2004a; Blanckenhorn *et al.*, 2006), interspecific (Freckleton *et al.*, 2003; Katti & Price, 2003; Cruz *et al.*, 2005) and assemblage patterns (Roy & Martien, 2001; Blackburn & Hawkins, 2004; Kaspari, 2005; Olalla-Tárraga *et al.*, 2006; Rodríguez *et al.*, 2006). The 'island rule' has been tested with intraspecific (e.g. Lomolino, 1985; Meiri *et al.*, 2004b) and interspecific data (Meiri *et al.*, 2005), and apparently with combinations thereof (Foster, 1964; Clegg & Owens, 2002). Rapoport's rule has been examined using interspecific patterns (Blackburn & Gaston, 1996b; Orme *et al.*, 2006) and assemblage patterns (Stevens, 1989; Rohde *et al.*, 1993). The methodological distinction between intraspecific and other patterns is well understood, although studies sometimes state that comparisons were made with a population's nearest relative, which does not necessarily distinguish intraspecific from interspecific methodologies. Moreover, interspecific and assemblage patterns have both been referred to as interspecific patterns (e.g. Roy & Martien, 2001; Cruz *et al.*, 2005; Olalla-Tárraga *et al.*, 2006; Rodríguez *et al.*, 2006). The distinction between the two is frequently overlooked, the contents of the abstracts of many relevant papers do not enable one to identify the approach used and the implications of this distinction for the generalities that these different methods uncover have not been well explored.

The three kinds of spatial patterns – intraspecific, interspecific and assemblage – must interact. Intraspecific patterns are essentially descriptors of the structure of the geographical ranges of species (Gaston, 2003). Interspecific patterns reflect differences in the location of the geographical ranges of species exhibiting differences in a particular trait or, put another way, are derived from the location and the structure of geographical ranges. Finally, assemblage patterns again reflect differences in the locations of the geographical ranges of individual species and the traits that they exhibit, but also the number of ranges (the range overlaps) in an area. Indeed, one might perhaps argue both that the geographical range plays a unifying role in linking spatial patterns together and that a sensible approach to understanding interspecific and assemblage variation would, where feasible, be to deconstruct these patterns into their more basic intraspecific components. In this paper we selectively review the nature of intraspecific, interspecific and assemblage spatial patterns, their connections and their mechanisms, and highlight several significant, outstanding issues.

GEOGRAPHICAL RANGE STRUCTURE AND $R \times C$ MATRICES

Intraspecific, interspecific and assemblage patterns, and their inter-relationships, can usefully be thought of in terms of simple species × sites ($r \times c$) matrices, in which species are given in rows (r) and sites (or areas) in columns (c). Indeed, such matrices may be key to a synthetic view of these patterns. Traditionally, the entries in such a matrix would either be the presence/absence of each species in each site, or the population density of each species in each site (e.g. Simberloff & Connor, 1979; Bell, 2003). However, the approach can be generalized to any trait of interest. In considering spatial patterns, the sites can usefully be thought of as sequenced in terms of the gradient of interest (positional or environmental) (e.g. Lomolino, 1996), although in practice we are often interested in the relative position of sites along a continuum of that gradient.

Considering a single species first, the variation of a trait along the gradient (a row of an $r \times c$ matrix) is essentially a pattern in the structure of the geographical range of that species. Traditionally such structure tends to be thought of in terms of the presence/absence or local abundance of the species, but can be conceived of much more generally to embrace traits as divergent as colour, body size, clutch size and genetic diversity. Intraspecific patterns are about how ranges are structured, and the mechanisms underpinning those patterns are what structure ranges.

Interspecific spatial patterns are based on row sums, means or, more seldom, variances from a species × sites matrix, usually just for those sites at which the species is present. These are plotted against some overall characteristic of the sites that are occupied by each species, usually their positional midpoint or some average environmental condition.

Assemblage spatial patterns are based on the column sums, means or variances of the species × sites matrix, and the relationships between these variables and other properties of the sites. Based on species presences and absences across sites these give patterns in species richness; based on summed species abundances or biomasses across sites these give patterns in assemblage size; and based on mean traits such as species body size, clutch size or abundance, or the frequency distributions of such traits, they give patterns in assemblage structure.

Arguably, four principal outstanding issues pertain to documenting and understanding spatial patterns at intraspecific, interspecific and assemblage levels, namely: (1) the nature of patterns in traits, (2) the generality of patterns, (3) the interactions between patterns in different traits, and (4) models and mechanisms for patterns. We begin with intraspecific patterns.

INTRASPECIFIC PATTERNS

The nature of the patterns

Two rather divergent broad theoretical frameworks for the form of intraspecific patterns have developed. These can be termed, respectively, the gradient model and the peak model. In the gradient model, species traits are seen as changing monotonically along positional gradients (e.g. latitude, longitude, altitude, depth) across the geographical range, usually as a consequence of species responses to gradients in particular environmental axes. A wide variety of traits has been explored in this context (see Introduction). In the peak model, species traits are seen as changing systematically from the core to the periphery of the geographical range, such that a roughly central peak arises, usually as a consequence of trade-offs in the responses of species to multiple environmental axes (Hengeveld & Haeck, 1982; Brown, 1984; Lawton, 1993). The primary traits that have been explored in this context are occupancy, abundance, temporal variability in abundance, local extinction and genetic variation (e.g. Brown, 1984; Curnutt *et al.*, 1996; Green *et al.*, 1996; Doherty *et al.*, 2003; Vucetich & Waite, 2003; Murphy *et al.*, 2006; for reviews see Sagarin & Gaines, 2002; Gaston, 2003; Sagarin *et al.*, 2006).

Although they are easily recognized in the abstract, empirical fit to the gradient and peak models can be more difficult to ascertain. First, if data are not obtained from across the full geographical range of a species then sampling of gradients may be insufficient, and simple trends may be observed where more complex functions better describe the full pattern (Sagarin & Gaines, 2002; Gaston, 2003). Second, the fits of data to peak models can be difficult to ascertain visually, and to test analytically, and a number of indirect analytical approaches that have been employed (e.g. autocorrelograms) have not proved to be sufficiently definitive (Ives & Klopfer, 1997; Gaston, 2003). Third, the extent to which data fit either model may vary with the size of the areas over which traits such as abundance are measured, with perhaps a general tendency for data collected at larger spatial grains to smooth out local variations in density and thus result in better model fits (Blackburn *et al.*, 1999b). Fourth, the extent to which data fit either model may be influenced by whether trait values at different sites are treated as distinct data points, or whether values for sites sharing a similar position (e.g. latitudinal band) or environment (e.g. temperature range) are averaged, with the latter tending to favour the detection of simple patterns. Fifth, the different populations of a species used in testing for intraspecific patterns are phylogenetically non-independent and thus, just as for interspecific comparisons (see below), phylogenetic comparative techniques should be employed. This is seldom done at the intraspecific level (but see Angilletta *et al.*, 2004), and the implications for the patterns that have been documented remain unknown.

These comments notwithstanding, in general it is becoming clear that there is far better evidence for the fit of data to gradient models than to peak ones, and the long-held supposition that a peak model typifies key aspects of the spatial structure of geographical ranges is not well supported (Sagarin & Gaines, 2002; Gaston, 2003; Sagarin *et al.*, 2006); a similar conclusion may not hold for all traits along environmental axes (Gaston, 2003). Such a conclusion could be taken to imply that the structure of geographical ranges is commonly rather simple. However, this is undoubtedly not the case, with strong suspicions that the literature is heavily biased towards cases in which such simple structures have been documented. Certainly, there is a growing number of good examples in which apparently key variables in the structuring of geographical ranges exhibit no such simple patterns (see Sagarin *et al.*, 2006).

Generality

Even accepting the conclusions of empirical analyses at face value, considerable contention surrounds how widely intraspecific spatial patterns in given traits generalize across species (i.e. how similar are the patterns along different rows of an $r \times c$ matrix). There has, for example, been much discussion of the relative frequency of increases in body size with latitude and/or temperature, decreases with latitude and/or temperature, and an absence of any simple pattern (e.g. McNab, 1971; Chown & Gaston, 1999; Ashton *et al.*, 2000; Ashton, 2002; Meiri & Dayan, 2003; Blanckenhorn & Demont, 2004; Meiri *et al.*, 2004a). Likewise, how often the local abundances of species show central peaks and peripheral declines across geographical ranges has been much debated (Hengeveld & Haeck, 1982; Brown, 1984; Brown *et al.*, 1996; Sagarin & Gaines, 2002; Gaston, 2003).

In part, different conclusions result from different views as to what constitutes a generality. At one extreme, Mayr (1956) recognized a rule as being constituted if a pattern was displayed by more than 50% of the species studied. At the other extreme, one might regard evidence of any exception as sufficient to prevent an otherwise general pattern from being regarded as a rule. Most commentators seem to regard each of these positions as too severe, but what criteria they would find reasonable as a basis for a rule or a simple generalization remains unclear (Blackburn *et al.*, 1999a; Lawton, 1999).

In part, different conclusions also result from different views on the point at which the published set of empirical analyses is considered adequate to determine the generality of a particular intraspecific pattern. Invariably, the number of species that have been studied remains extremely small, and geographically and taxonomically highly biased (see below). Thus, grounds exist for arguing that the current data are inadequate to reach any conclusions about the generality of patterns. It is unclear, given the number and variety of extant species, at what point this would cease to be the case. To complicate matters further, on the basis of existing evidence the degree of generality may vary markedly depending on the focal taxonomic group. For example, the proportion of vertebrate species that follow a neo-Bergmannian rule (*sensu* James, 1970) varies from less than a third of those studied in lizards, snakes and fish to more than three-quarters in turtles and birds (Millien *et al.*, 2006). Such differences may be useful in understanding the mechanisms that give rise to patterns.

In fact, many intraspecific patterns seem unlikely to be truly general because the majority of species have relatively small geographical ranges. For example, at least a quarter of the world's bird species have ranges that are smaller than the area of Great Britain (Orme *et al.*, 2006). They are therefore often distributed across relatively narrow ranges of spatial variation in environmental conditions, and are unlikely to experience selection that would result in marked intraspecific patterns (Gaston, 2003; Philimore *et al.*, 2007); narrowly distributed species on steep environmental gradients would be an obvious exception. Moreover, gene flow or limited genetic variance might limit the potential for variation in local adaptation across the ranges of narrowly distributed species (Blows & Hoffmann, 2005; Chown & Terblanche, 2007). Indeed, the choice of focal species with which to investigate spatial patterns tends to be biased towards those with substantially larger ranges. This is certainly the case for avian species for which Bergmann's rule and latitudinal patterns in clutch size have and have not been studied (Fig. 1), which could perhaps result from a bias towards such studies being conducted in northern temperate regions, where range sizes tend to be larger (Orme *et al.*, 2006). However, it seems likely also to result from a conscious focus on those species that are expected to exhibit such patterns.

Interactions

With rather few exceptions, the interactions between different intraspecific spatial patterns remain poorly understood. This is despite the fact that, if exhibited by the same species, they would concern the same individuals occurring in the same places. One reason that the interactions have largely been ignored is that patterns in different kinds of traits tend to be most readily (and therefore are in practice) determined for different kinds of species. As a broad generalization, morphological variables have principally been studied for insects and vertebrates, physiological variables for insects, amphibians and reptiles, life-history variables for freshwater fish and birds, population dynamic variables for insects and birds, and genetic variables principally for plants (phylogeographical studies embrace a wide diversity of taxa, but primarily concern the relatedness of individuals across geographical ranges rather than broader issues of the genetic structure of ranges). Even

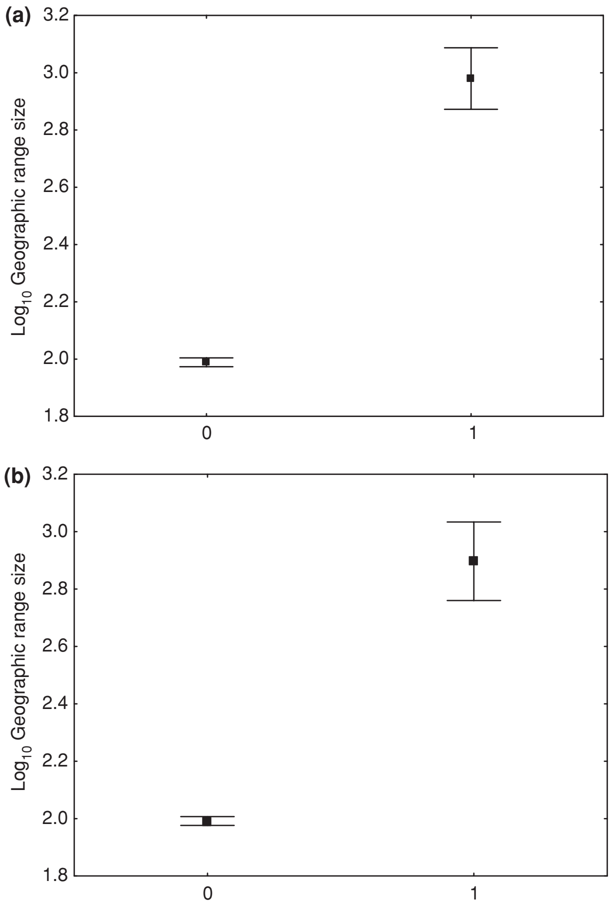

Figure 1 Mean (±95% confidence interval) $\log_{10}$ breeding geographical range sizes of non-marine bird species for which studies have (1) and have not (0) reported the results of empirical analyses for (a) Bergmann's rule and (b) relationships between clutch size and latitude, regardless of the outcomes of those analyses. Species are categorized based on the studies of Bergmann's rule listed by Meiri & Dayan (2003), and an unpublished collation of studies of latitudinal patterns of clutch size by the authors. Geographical range sizes are from the data base of Orme *et al.* (2006).

where the same taxon is a focus of attention for different kinds of variables, the same species are seldom considered. For example, of the six traits typically investigated in studies of insect environmental physiology (metabolic rate, development rate, water loss, upper and lower thermal tolerances and thermoregulation), all six have been investigated in fewer than five species (Chown *et al.*, 2002). Spatial patterns in traits of multiple types have thus been examined for rather few species (but see Klok *et al.*, 2003; Angilletta *et al.*, 2004; Heibo *et al.*, 2005; Rinde & Sjotun, 2005; Lardies & Bozinovic, 2006).

The foremost vertebrate exception is doubtless the house sparrow, *Passer domesticus*. Being widespread, often relatively abundant and occurring in close proximity to humans, the species was the subject of natural history and basic ecological studies in the late 1800s and early 1900s (e.g. Bumpus, 1899). Building on this work, and fresh data collection, studies in the 1970s in particular established several spatial patterns in its traits (e.g. Pinowski & Kendeigh, 1977). In part this was motivated by concerns over the house sparrow's status as a pest species. In part it was also spurred by the opportunities that the rapid and dramatic spread of the species in North America presented for contrasting patterns in the native and introduced parts of its geographical range. Subsequently, extensive work has been conducted using the house sparrow as a model organism for examining many physiological, behavioural and ecological issues. For this species, spatial patterns have been investigated in morphological traits (Johnston & Selander, 1964, 1973; Johnston, 1969; Baker, 1980; Fleischer & Johnston, 1982; Murphy, 1985), physiological traits, mainly metabolic rate and immune function (Threadgold, 1960; Blem, 1974; Kendeigh, 1976; Martin *et al.*, 2004, 2005), life-history traits (Dyer *et al.*, 1977; Murphy, 1978; Anderson, 1994; Baker, 1995) and genetic traits (Johnston & Klitz, 1977; Parkin & Cole, 1985; Bjordal *et al.*, 1986). Even so, whilst major reviews have sought to bring much of this material together (Summers-Smith, 1988; Anderson, 2006), and similar environmental variables have been proposed to explain the trends in many traits, the connections between the different patterns have been little explored.

Amongst terrestrial invertebrates, the model organism *Drosophila melanogaster* is one of the most widely investigated (Singh & Long, 1992; Hoffmann *et al.*, 2003). The ease with which it can be collected and reared, as well as a comprehensive and growing body of data on its biology and evolution, including a recently sequenced genome, arguably made and continue to make the species tractable (Powell, 1997; Adams *et al.*, 2000). Like the house sparrow, its colonization of a wide variety of regions has undoubtedly also spurred many studies. Spatial variation in a wide variety of traits has been investigated, resulting in a substantial literature. Investigations of morphological variation include body size and wing size clines (David & Bocquet, 1975; James *et al.*, 1997; Van't Land *et al.*, 2000), physiological traits include thermal biology, water balance and ethanol tolerance (Cohan & Graf, 1985; Hoffmann *et al.*, 2001, 2002, 2003; Bubliy *et al.*, 2002), life-history traits include development rate, male sterility, incidence of diapause, fertility and longevity (James & Partridge, 1995; Mitrovski & Hoffmann, 2001; Rohmer *et al.*, 2004; Schmidt *et al.*, 2005; Sgrò *et al.*, 2006) and a variety of genetic traits has been studied (van Delden & Kamping, 1997; Van't Land *et al.*, 2000; Verrelli & Eanes, 2001; Frydenberg *et al.*, 2003; Umina *et al.*, 2005). Recent work has begun to explore the relationships between clinal variation in molecular markers, morphological traits and biochemical and physiological variation (Gockel *et al.*, 2002; de Jong & Bochdanovits, 2003; Sezgin *et al.*, 2004; Rako *et al.*, 2006). Perhaps unsurprisingly, clinal variation in population dynamics has been less well scrutinized.

Even in these two well-studied species the interactions occurring between spatial patterns in different traits that will arise from constraints and trade-offs in trait development have rarely been explicitly studied.

Models

The combination of a heavy focus on the possible generality of individual intraspecific patterns and a paucity of studies of how different patterns for the same species might interact has resulted in the development of rather distinct literatures exploring the mechanisms underlying different kinds of intraspecific patterns. This is despite some evident commonalities in the postulated mechanisms, and the fact that different patterns concern the same individual organisms. For example, geographical clines in body size have variously been postulated to result from the following broadly classified mechanisms: (1) the thermodynamics of heat conservation (Bergmann, 1847) and dissipation (Brown & Lee, 1969); (2) factors (such as primary productivity, starvation resistance, seasonality, competition and their interactions) that are ultimately concerned with interactions between the size dependences of production rate and mortality rate (Rosenzweig, 1968; Roff, 1980; Lindstedt & Boyce, 1985; Kozłowski *et al.*, 2004); (3) amongst ectotherms, a physiological by-product of the effects of temperature on cell division and replication or on growth and differentiation leading to positive correlations between cell size and animal size (Partridge *et al.*, 1994; van der Have & de Jong, 1996; Starostová *et al.*, 2005; Walters & Hassall, 2006); and (4) covariation between body mass and other traits that have selective advantages at high latitudes (Cushman *et al.*, 1993). Likewise, latitudinal trends in clutch size have been argued to result from: (1) thermodynamic factors related to the cost of heating eggs and maintaining the incubation temperature (Sanz, 1999; Reid *et al.*, 2000); (2) the effects of temperature on egg viability (Stoleson & Beissinger, 1999; Cooper *et al.*, 2005); (3) factors (such as food availability, day length and seasonality; Lack, 1947; Martin, 1987; Ashmole, 1963) that are ultimately concerned with the interactions between resource availability, reproductive effort and mortality; and (4) nest predation rates (Skutch, 1949).

Variation in progeny size in arthropods has been attributed to a similar variety of mechanisms (Fox & Czesak, 2000). The plethora of putative mechanisms that have been suggested to drive these intraspecific patterns is not unusual in geographical-scale studies, and highlights the difficulties associated with providing conclusive evidence for any one mechanism (Gaston & Blackburn, 1999). However, few studies have attempted to disentangle these mechanisms by examining their predictions either within strong inference, hypothesis testing (Huey *et al.*, 1999) or information theoretic model selection (e.g. Johnson & Omland, 2004) frameworks. In general, it is highly likely that a particular pattern will arise through a number of processes whose relative contributions may vary both spatially and taxonomically.

No generic models exist as yet that link intraspecific patterns in the different kinds of species traits that have been investigated. Rather attention has principally been paid to how each trait responds to environmental variation and why, with variation in one or more of the other sets of traits often assumed to be of significance. It seems likely, however, that considerable progress might be made in understanding the determinants of these patterns by focusing attention on how these different sets of traits themselves interact across space (positional or environmental), especially given that investigations of subsets of the possible interactions have resulted in such progress (e.g. Brown *et al.*, 2004; Kozłowski *et al.*, 2004). Taking the four broad types of traits (morphology, physiology, life history and population dynamics), models have been developed for aspects of each of the six pair-wise combinations of trait type: morphology and physiology (van der Have & de Jong, 1996; West *et al.*, 2001; Kozłowski *et al.*, 2003; Makarieva *et al.*, 2005), morphology and life history (Abrams *et al.*, 1996; Economo *et al.*, 2005; Walters & Hassall, 2006), morphology and population dynamics (Abrams, 1994; van Kooten *et al.*, 2004), physiology and life history (Sibly & Calow, 1986; Gilchrist, 1995; Ricklefs & Wikelski, 2002; Voituron *et al.*, 2002; Savage *et al.*, 2004; Frazier *et al.*, 2006; Lardies & Bozinovic, 2006), physiology and population dynamics (Lynch & Gabriel, 1987; Kingsolver, 1989; Dunham, 1993; Ives & Gilchrist, 1993; Murdoch, 1993; Crozier & Dwyer, 2006) and life history and population dynamics (Roff, 2002; Koons *et al.*, 2006; Stahl & Oli, 2006). For each combination much more model development is required, especially in a spatial context. Such spatially explicit modelling is likely to be complex given that it should ultimately take interactions between migration, environmental variance, phenotypic plasticity and cross-environment genetic correlations into account (Chown & Terblanche, 2007), especially if the goal is to understand geographical range structure.

INTERSPECIFIC PATTERNS

The nature of the patterns

Interspecific patterns typically concern single values of traits for each of a number of species, usually belonging to a single taxon or clade. In most cases these traits are expressed at the level of the individual organism, and a mean or median value across a sample of individuals for each species is used. These values can thus be thought of as representing some measure of central tendency of a pattern of intraspecific variation in the trait of interest (a row of an $r \times c$ matrix). If, on average, all species exhibited similar spatial patterns of variation in a trait across their geographical ranges, then interspecific patterns would essentially capture the scaling of this variation with changes in environmental conditions.

The implicit assumption tends to be made that this intraspecific variation is much smaller than the observed interspecific variation, and that the former can therefore reasonably be ignored. However, plainly, circumstances exist under which this is not so, and the interplay between intraspecific and interspecific patterns may be vitally important in understanding mechanisms. Intraspecific and interspecific spatial variation in a trait are expected to be more similar when: (1) species are closely related, and thus more likely to respond to environmental conditions in similar ways; and (2) one or more species have very large geographical ranges and thus include different individuals that experience a range of environmental conditions similar to that experienced by the entire suite of species. In this regard it is noteworthy that, following earlier comments about the influence of geographical range size on the expression of intraspecific patterns, interspecific patterns are sometimes only apparent, or are stronger, amongst the more widely distributed species (e.g. Ruggiero & Lawton, 1998; Blackburn & Ruggiero, 2001).

In testing, and explaining, interspecific spatial patterns much more attention needs to be paid to the manner in which species-specific trait data are collated. Typically such data are averaged across a very small number of individuals. For example, in the most comprehensive collation of data on avian species body mass, the values for each species are averaged over a mean of 70 individuals and a median of just 10 (Olson *et al.*, unpublished data). These individuals may not be representative of the species as a whole, particularly if they originate from a limited portion of the species' range. The downstream consequences of such a lack of representativeness have been explored in other contexts (e.g. McKechnie & Wolf, 2004; Farrell-Gray & Gotelli, 2005).

Attention also needs to be paid to the variable used to characterize the positions of the geographical ranges of species in geographical or environmental space (Blackburn & Hawkins, 2004). Typically this is the midpoint of the geographical range (latitudinally or gravitationally) or the conditions at that midpoint (e.g. Ruggiero & Lawton, 1998; Cardillo, 1999; Blackburn & Ruggiero, 2001; Orme *et al.*, 2006). However, it seems doubtful that this serves to characterize much about the distribution of a species, and progressively less so as the geographical range of the species becomes larger (and the likelihood of intraspecific patterns being expressed potentially increases). More sophisticated methods would seem desirable.

Generality

The availability of data with which to test for interspecific spatial patterns exhibits marked taxonomic biases. For example, and again concerning avian species, even at the family level data on such a fundamental trait as body size is not available for 9% of the world's avian families, with this value increasing to 18% of families for an estimate of annual fecundity (Bennett & Owens, 2002). The magnitude of such gaps in our knowledge of trait values increases markedly if one considers the species level; for example, body-size data are only available for 77% of the world's bird species (Olson *et al.*, unpublished data). Trait data are more likely to be missing for tropical species and those with small ranges, and this raises concerns regarding the extent to which interspecific patterns can be said to generalize. More positively, estimates of the geographical range sizes for nearly all of the extant species in some vertebrate classes have recently been made (Ceballos *et al.*, 2005; Grenyer *et al.*, 2006; Orme *et al.*, 2006).

Arguably as a consequence of these constraints, empirical studies of spatial patterns in trait variation at the interspecific level are much scarcer than those of intraspecific and assemblage variation. As a result of these issues it seems premature to assess the likely generality of almost any of the interspecific patterns that have been documented. The most marked exception is examination of latitudinal trends in range size. Whilst several patterns have been described, at best the relationship between latitude and range size appears to be weak (e.g. Orme *et al.*, 2006; see below for a discussion of assemblage level patterns in range size). A number of interspecific studies have also demonstrated positive relationships between clutch size and latitude, but even here the many hundreds of species studied comprise a relatively small proportion of the total (Lack, 1948; Kulesza, 1990; Böhning-Gaese *et al.*, 2000; Cardillo, 2002a). Similarly, even though several studies have investigated intraspecific patterns in body size, far fewer have investigated such patterns at the interspecific level (but see Hawkins & Lawton, 1995; Cardillo, 2002a). Therefore, even for the most thoroughly investigated traits, the generation of an additional and taxonomically diverse range of case studies, followed by a formal meta-analysis, is required before firm conclusions can be reached regarding generalities.

Interactions

Given the relative paucity of empirical examples of interspecific spatial patterns, little is known about the interactions between these patterns (but see Cartron *et al.*, 2000). However, this could readily be resolved if, in increasing the numbers of such examples, care was taken to focus particularly on case studies for which combinations of morphological, physiological, life-history and/or population dynamics variables could be measured on the same spatial or environmental gradients.

Models

The more similar the intraspecific and interspecific spatial patterns in traits in which intraspecific variation exists, and the more obviously interspecific patterns simply extend the intraspecific, the more likely it is that common mechanisms underlie the two. The mechanisms discussed as potentially underpinning latitudinal gradients in body size, for example, tend to be broadly the same at intraspecific and interspecific levels (e.g. Jones *et al.*, 2005; Makarieva *et al.*, 2005; Herfindal *et al.*, 2006; Rodríguez *et al.*, 2006). However, differences exist. Whilst variation in dispersal ability related to body size has been proposed as one possible mechanism driving interspecific patterns (Newton & Dale, 1996; Blackburn & Hawkins, 2004), this would seem unlikely to apply at an intraspecific level. Likewise, whilst studies of both intraspecific and interspecific latitudinal patterns in clutch size have focused on the roles of food availability, seasonality and predation risk (e.g. Koenig, 1984; Martin *et al.*, 2000; Evans *et al.*, 2005a), investigations focusing on the impacts of clutch cooling and heating (see above) have to date only been applied intraspecifically

(Stoleson & Beissinger, 1999; Reid *et al.*, 2000; Cooper *et al.*, 2005, 2006). However, for body size, clutch size and other traits, studies are largely wanting that document both intraspecific and interspecific spatial patterns for the same sets of species, and thus enable the two levels of variation to be contrasted (although the species-level heritability of intraspecific patterns has been explored; e.g. de Queiroz & Ashton, 2004). Understanding of spatial patterns in interspecific variation in traits that are expressed at the level of the individual obviously necessitates a phylogenetic framework, and consideration of the statistical non-independence of species as data points (Harvey & Pagel, 1991). These traits are likely to be more similar amongst closely related than distantly related species. Given that the same will be true of more closely related populations of a given species, a phylogenetic framework would be the most logical format within which simultaneously to examine intraspecific and interspecific spatial patterns in a trait.

In other interspecific patterns, the traits are expressed at the level of the species. A key issue here has also proven to be the degree of phylogenetic constraint on these traits. Because of the level at which they are expressed, such phylogenetic constraints arise from species selection. Attention has particularly focused on the heritability of geographical range sizes. Here, studies have variously reported statistical significance or non-significance in the correlations between the range sizes of ancestor–descendant species pairs or sister species pairs, in the proportions of variance in species range sizes explained at higher taxonomic levels or in phylogenetic autocorrelations in range sizes (e.g. Jablonski, 1987; Gaston, 1998; Webb & Gaston, 2003, 2005; Martinez-Meyer *et al.*, 2004; Pfenninger, 2004; Hunt *et al.*, 2005). The evidence would seem to favour a lack of significant heritability, but interpretations have varied and recent reviews have reached divergent conclusions (e.g. Gaston, 2003; Webb & Gaston, 2003, 2005; Hunt *et al.*, 2005). Regardless of this, when statistically significant patterns are found they seem not to be sufficiently marked to have biological significance (Webb & Gaston, 2005). This is important because it suggests that if the expression of intraspecific patterns in traits is, in part at least, a function of geographical range size (see above), then these patterns may nonetheless occur across a diversity of taxonomic groups.

ASSEMBLAGE PATTERNS

The nature of pattern

In some cases, most notably that of geographical range size, the difference between interspecific and assemblage spatial patterns has been framed in methodological terms. Thus, tests for a gradient of increasing geographical range size with increasing latitude, altitude or depth have employed one of three methods: analysing variation in the mean geographical range sizes of species in an area (e.g. Stevens, 1989; Arita *et al.*, 2005), in the mean range sizes of those species whose geographical midpoint falls in an area (midpoint method; e.g. Rohde *et al.*, 1993; Reed, 2003) or treating each species as a separate data point (e.g. Blackburn & Gaston, 1996b; Orme *et al.*, 2006). The first two plainly document assemblage patterns, whilst the last one documents an interspecific pattern. Nonetheless, they are all related and the expression of one pattern must constrain the possibilities for the others, in that all are founded on the same species × sites ($r \times c$) matrix. However, the first method documents the average expression of a trait in an area, the second the average expression of that trait in an area for a subset of species and the third the average expression of a trait by a species. None of the approaches is any more correct than the others as they address different issues, although arguments have been made for the superior merits of interspecific and assemblage pattern analyses (e.g. Cardillo, 2002a; Blackburn & Hawkins, 2004).

This said, in establishing assemblage spatial patterns many of the same issues apply as for interspecific patterns. For example, as with interspecific patterns, frequently when using mean traits to establish assemblage patterns the state of the trait is treated as being constant throughout the geographical range of a species, effectively assuming that intraspecific patterns do not exist.

Generality

The generality of assemblage patterns based on species richness has attracted the most extensive and intensive scrutiny of spatial patterns at intraspecific, interspecific or assemblage levels. Qualitative, semi-quantitative and/or formal meta-analyses exist for most of the key patterns in richness including the increase in species richness at low latitudes (Hillebrand, 2004a,b), altitudinal patterns (Hodkinson, 2005; Rahbek, 2005), mid-domain effects (Zapata *et al.*, 2003; Colwell *et al.*, 2005), the species–area relationship (Drakare *et al.*, 2006) and species–energy relationships (Waide *et al.*, 1999). Nonetheless, disputes persist as to the typical form taken by some such patterns and the circumstances under which other forms occur. One of the most prominent examples is the debate regarding whether species–energy relationships are typically hump-shaped or linear, and the effects of spatial scale on the predominance of the different forms (Waide *et al.*, 1999; Mittelbach *et al.*, 2001, 2003; Whittaker & Heegaard, 2003; Gillman & Wright, 2006).

Empirical studies of spatial patterns in other aspects of assemblage size and composition, such as in total abundance, total biomass or total energy use, or the numbers or proportions of different functional or behavioural groups, have accumulated much more slowly. However, it is clear that the existence of some such patterns is predicted from particular mechanisms that have been suggested to explain spatial patterns in species richness, which has motivated much more work in this area (e.g. Kaspari *et al.*, 2003; Hurlbert, 2004; Evans *et al.*, 2005b, 2006b; Pautasso & Gaston, 2005).

As with intraspecific patterns, there is still contention over the generality in several assemblage patterns based on the mean state of the traits exhibited by those species co-occurring in an area (e.g. body size: Cousins, 1989; Blackburn & Gaston, 1996a; Blackburn *et al.*, 1999a; Blackburn & Hawkins, 2004; Rodríguez *et al.*, 2006; geographical range size: Stevens, 1989; Gaston *et al.*, 1998; Orme *et al.*, 2006). One important issue has repeatedly arisen here, has been suggested to be important in understanding the patterns of species richness (Darlington, 1957; Marquet *et al.*, 2004) and applies equally to spatial patterns in other aspects of assemblage size and composition. This is the extent to which particular patterns are shaped by spatial or environmental changes in the contribution of different clades to an assemblage, and the extent to which the component clades themselves exhibit the patterns (Hawkins & Lawton, 1995). In other words, the extent to which assemblage patterns generalize to the component clades. In some instances one or more of the component clades themselves do not seem to demonstrate the overall pattern, or do so much less strongly (Astorga *et al.*, 2003; Real *et al.*, 2003; Hawkins *et al.*, 2006), whilst in other cases all clades behave in a similar fashion. This variation between clades in the demonstration of ecogeographical rules can be useful in assessing the underlying processes generating the occurrence, or lack, of such patterns.

Interactions

The potential interactions between different spatial assemblage patterns have been integral to many attempts to try to understand the mechanistic basis of these patterns. For example, there has been much discussion of the covariation between spatial patterns in assemblage biomass, total numbers of individuals, species richness, mean body size and geographical range size, with causal connections having been proposed between many pairs of these patterns (e.g. Brown, 1995; Gaston & Blackburn, 2000; Blackburn & Gaston, 2003). In many cases, these links have a foundation in theory (Blackburn & Gaston, 2001). However, not infrequently the expected covariation between two characteristics of assemblages in space is argued from knowledge of the spatial patterns that the two display. Unfortunately, unless these latter patterns are particularly marked, such arguments prove to be rather weak. The likely correlation, for example, between variables x and z is only predictable from the correlations between x and y and between y and z if these last two are strong; Cartron *et al.* (2000) provide a more detailed discussion of the mathematical constraints on patterns of covariation.

Models

Whilst interspecific patterns usually have a marked phylogenetic non-independence of data points, assemblage patterns as most commonly expressed usually have a marked spatial non-independence (Gaston & Blackburn, 2000). This spatial non-independence comes from two sources. First, areas closer together are likely to experience more similar environmental conditions. Second, areas closer together are likely to share more species. This latter issue highlights the more general question of which species contribute most to assemblage patterns. Intuitively, it was long held that species richness patterns, for example, were largely determined by the more narrowly distributed species. However, recent analyses have shown the converse to be the case, with the more widespread species accounting for the bulk of patterns of species richness (Jetz & Rahbek, 2002; Lennon *et al.*, 2004) and being more strongly associated with patterns of spatial variation in environmental conditions (Evans *et al.*, 2005c; Rahbek *et al.*, 2006). Similar results have also been found for patterns of spatial turnover in species composition (Gaston *et al.*, 2007). This greater contribution of widespread species thus matches the situation regarding the relative strength of intraspecific patterns, which are likely to be stronger for widespread species as these experience greater environmental variation and local adaptation (see above). The extent to which the more widespread species shape other assemblage patterns remains unknown, but it would seem quite likely that this is the case. For assemblage patterns based on the summed abundances or biomasses of species in an area, this would follow from the general positive interspecific abundance–range size relationship (Gaston *et al.*, 2000; Gaston, 2003). For patterns based on the average expression of a trait in an area, it may follow from the disproportionate contribution of trait values to different areas (recognizing that the more widespread species typically do not occupy all or even most areas).

CONCLUSIONS

Despite a vast literature concerning geographical patterns in biological traits, a synthetic understanding of these patterns remains elusive. Significant steps towards such a synthesis include understanding: (1) the different kinds of patterns (intraspecific, interspecific and assemblage) and the distinctions between them; (2) the unifying role that geographical ranges play in linking the patterns together; (3) that this unification can be obscured by the methodological assumptions made in documenting some patterns (e.g. assuming that intraspecific variation does not significantly influence interspecific and assemblage patterns in traits); (4) the need for further development of models linking different types of traits; (5) the implications of other methodological issues for the nature of observed patterns (e.g. how ranges are located on positional or environmental axes for interspecific patterns); (6) the nature of the generality of documented patterns at all levels, and particularly the difference between the frequency with which patterns are documented in the literature and the variety of extant species; and (7) the constraints that the form of intraspecific patterns place on interspecific and assemblage patterns, and that interspecific patterns place on assemblage patterns.

ACKNOWLEDGEMENTS

We are grateful to I.P.F. Owens and the avian hotspots consortium for kindly providing access to range size data, to

A. Mackenzie for support, P. Bennett and P. Johnson for assistance, and L. Cantu-Salazar, R.G. Davies and two anonymous referees for discussion and comments. K.J.G. holds a Royal Society-Wolfson Research Merit Award. K.L.E. is funded by the Natural Environment Research Council.

REFERENCES

Abrams, P.A. (1994) Evolutionarily stable growth-rates in size-structured populations under size-related competition. *Theoretical Population Biology*, **46,** 78–95.

Abrams, P.A., Leimar, O., Nylin, S. & Wiklund, C. (1996) The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *The American Naturalist*, **147,** 381–395.

Adams, M.D., Celniker, S.E., Holt, R.A. *et al.* (2000) The genome sequence of *Drosophila melanogaster*. *Science*, **287,** 2185–2195.

Addo-Bediako, A., Chown, S.L. & Gaston, K.J. (2000) Thermal tolerance, climatic variability and latitude. *Proceedings of the Royal Society B: Biological Sciences*, **267,** 739–745.

Adler, G.H. & Levins, R. (1994) The island syndrome in rodent populations. *Quarterly Review of Biology*, **69,** 473–490.

Allen, J.A. (1878) The influence of physical conditions in the genesis of species. *Radical Review*, **1,** 108–140.

Anderson, T.R. (1994) Breeding biology of house sparrows in northern lower Michigan. *Wilson Bulletin*, **106,** 537–548.

Anderson, T.R. (2006) *Biology of the ubiquitous house sparrow: from genes to populations*. Oxford University Press, Oxford.

Angilletta, M.J., Niewiarowski, P.H., Dunham, A.E., Leaché, A.D. & Porter, W.P. (2004) Bergmann's clines in ectotherms: illustrating a life-history perspective with sceloporine lizards. *The American Naturalist*, **164,** E168–E183.

Arita, H.T., Rodríguez, P. & Vázquez-Domínguez, E. (2005) Continental and regional ranges of North American mammals: Rapoport's rule in real and null worlds. *Journal of Biogeography*, **32,** 961–971.

Ashmole, N.P. (1963) The regulation of numbers of tropical oceanic birds. *Ibis*, **103b,** 458–473.

Ashton, K.G. (2002) Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Global Ecology and Biogeography*, **11,** 505–523.

Ashton, K.G. & Feldman, C.R. (2003) Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution*, **57,** 1151–1163.

Ashton, K.G., Tracy, M.C. & de Queiroz, A. (2000) Is Bergmann's rule valid for mammals? *The American Naturalist*, **156,** 390–415.

Astorga, A., Fernandez, M., Boschi, E. & Lagos, N. (2003) Two oceans, two taxa, and one mode of development: latitudinal diversity patterns of South American crabs and test for possible causal processes. *Ecology Letters*, **6,** 420–427.

Baker, A.J. (1980) Morphometric differentiation in New Zealand populations of the house sparrow (*Passer domesticus*). *Evolution*, **34,** 638–653.

Baker, M. (1995) Environmental component of latitudinal clutch-size variation in house sparrows (*Passer domesticus*). *The Auk*, **112,** 249–252.

Bell, G. (2003) The interpretation of biological surveys. *Proceedings of the Royal Society B: Biological Sciences*, **270,** 2531–2542.

Bennett, P.M. & Owens, I.P.F. (2002) *Evolutionary ecology of birds – life histories, mating systems and extinction*. Oxford University Press, Oxford.

Bergmann, C. (1847) Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, **3,** 595–708.

Bjordal, H., Cole, S.R. & Parkin, D.T. (1986) Genetic differentiation among some populations of the house sparrow, *Passer domesticus*, from southwestern Norway. *Hereditas*, **105,** 107–114.

Blackburn, T.M. & Gaston, K.J. (1996a) Spatial patterns in the body sizes of bird species in the New World. *Oikos*, **77,** 436–446.

Blackburn, T.M. & Gaston, K.J. (1996b) Spatial patterns in the geographic range sizes of bird species in the New World. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **351,** 897–912.

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*. Blackwell Publishing, Oxford.

Blackburn, T.M. & Hawkins, B.A. (2004) Bergmann's rule and the mammal fauna of northern North America. *Ecography*, **27,** 715–724.

Blackburn, T.M. & Ruggiero, A. (2001) Latitude, elevation and body mass variation in Andean passerine birds. *Global Ecology and Biogeography*, **10,** 245–259.

Blackburn, T.M., Gaston, K.J. & Loder, N. (1999a) Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions*, **5,** 165–174.

Blackburn, T.M., Gaston, K. J., Quinn, R.M. & Gregory, R.D. (1999b) Do local abundances of British birds change with proximity to range edge? *Journal of Biogeography*, **26,** 493–505.

Blanckenhorn, W.U. & Demont, M. (2004) Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? *Integrative and Comparative Biology*, **44,** 413–424.

Blanckenhorn, W.U., Stillwell, R.C., Young, K.A., Fox, C.W. & Ashton, K.G. (2006) When Rensch meets Bergmann: does sexual size dimorphism change systematically with latitude? *Evolution*, **60,** 2004–2011.

Blem, C.R. (1974) Geographic variation of thermal conductance in the house sparrow *Passer domesticus*. *Comparative Biochemistry and Physiology A*, **47,** 101–108.

Blows, M.W. & Hoffmann, A.A. (2005) A reassessment of genetic limits to evolutionary change. *Ecology*, **86,** 1371–1384.

Böhning-Gaese, K., Halbe, B., Lemoine, N. & Oberrath, R. (2000) Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. *Evolutionary Ecology Research*, **2,** 823–839.

Brewer, A.M. & Gaston, K.J. (2002) The geographical range structure of the holly leaf-miner. I. Population density. *Journal of Animal Ecology*, **71,** 99–111.

Brewer, A.M. & Gaston, K.J. (2003) The geographical range structure of the holly leaf-miner. II. Demographic rates. *Journal of Animal Ecology*, **72,** 82–93.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *The American Naturalist*, **124,** 255–279.

Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago, IL.

Brown, J.H. & Lee, A.K. (1969) Bergmann's rule and climatic adaptation in. woodrats (*Neotoma*). *Evolution*, **23,** 329–338.

Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996) The geographic range: size, shape, boundaries and internal structure. *Annual Review of Ecology and Systematics*, **27,** 597–623.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85,** 1771–1789.

Bubliy, O.A., Riihimaa, A., Norry, F.M. & Loeschcke, V. (2002) Variation in resistance and acclimation to low-temperature stress among three geographical strains of *Drosophila melanogaster*. *Journal of Thermal Biology*, **27,** 337–344.

Bumpus, H.C. (1899) The elimination of the unfit as illustrated by the introduced sparrow, *Passer domesticus*. *Biology Lectures, Marine Biology Laboratory, Woods Hole*, 209–226.

Cardillo, M. (1999) Latitude and rates of diversification in birds and butterflies. *Proceedings of the Royal Society B: Biological Sciences*, **266,** 1221–1225.

Cardillo, M. (2002a) The life-history basis of latitudinal diversity gradients: how do species traits vary from the poles to the equator? *Journal of Animal Ecology*, **71,** 79–87.

Cardillo, M. (2002b) Body size and latitudinal gradients in regional diversity of New World birds. *Global Ecology and Biogeography*, **11,** 59–65.

Cartron, J.-L.E., Kelly, J.F. & Brown, J.H. (2000) Constraints on patterns of covariation: a case study in strigid owls. *Oikos*, **90,** 381–389.

Ceballos, G., Ehrlich, P.R., Soberòn, J., Salazar, I. & Fay, J.P. (2005) Global mammal conservation: what must we manage? *Science*, **309,** 603–607.

Chown, S.L. & Gaston, K.J. (1999) Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. *Biological Reviews*, **74,** 87–120.

Chown, S.L. & Klok, C.J. (2003) Altitudinal body size clines: latitudinal effects associated with changing seasonality. *Ecography*, **26,** 445–455.

Chown, S.L. & Terblanche, J.S. (2007) Physiological diversity in insects: ecological and evolutionary contexts. *Advances in Insect Physiology*, **33,** 50–152.

Chown, S.L., Addo-Bediako, A. & Gaston, K.J. (2002) Physiological variation in insects: large-scale patterns and their implications. *Comparative Biochemistry and Physiology B*, **131,** 587–602.

Clegg, S.M. & Owens, I.P.F. (2002) The 'island rule' in birds: medium body size and its ecological explanation. *Proceedings of the Royal Society B: Biological Sciences*, **269,** 1359–1365.

Cohan, F.M. & Graf, J. (1985) Latitudinal cline in *Drosophila melanogaster* for knockdown resistance to ethanol fumes and for rates of response to selection for further resistance. *Evolution*, **39,** 278–293.

Collinge, J.E., Hoffmann, A.A. & McKechnie, S.W. (2006) Altitudinal patterns for latitudinally varying traits and polymorphic markers in *Drosophila melanogaster* from eastern Australia. *Journal of Evolutionary Biology*, **19,** 473–482.

Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2005) The mid-domain effect: there's a baby in the bathwater. *The American Naturalist*, **166,** E149–E154.

Cooper, C.B., Hochachka, W.M., Butcher, G. & Dhondt, A.A. (2005) Seasonal and latitudinal trends in clutch size: thermal constraints during laying and incubation. *Ecology*, **86,** 2018–2031.

Cooper, C.B., Hochachka, W.M., Phillips, T.B. & Dhondt, A.A. (2006) Geographical and seasonal gradients in hatching failure in Eastern Bluebirds *Sialia sialis* reinforce clutch size trends. *Ibis*, **148,** 221–230.

Cousins, S.H. (1989) Species richness and the energy theory. *Nature*, **340,** 350–351.

Crozier, L. & Dwyer, G. (2006) Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. *The American Naturalist*, **167,** 853–866.

Crozier, L. & Zabel, R.W. (2006) Climate impacts at multiple scales: evidence for differential population responses in juvenile Chinook salmon. *Journal of Animal Ecology*, **75,** 1100–1109.

Cruz, F.B., Fitzgerald, L.A., Espinoza, R.E. & Schulte, J.A., II (2005) The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a clade of South American lizards. *Journal of Evolutionary Biology*, **18,** 1559–1574.

Curnutt, J.L., Pimm, S.L. & Maurer, B.A. (1996) Population variability of sparrows in space and time. *Oikos*, **76,** 131–144.

Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist*, **137,** 27–49.

Cushman, J.H., Lawton, J.H. & Manly, B.F.J. (1993) Latitudinal patterns in European ant assemblages: variation in species richness and body-size. *Oecologia*, **95,** 30–37.

Darlington, P.J. (1957) *Zoogeography, the geographical distribution of animals*. John Wiley & Sons, New York.

David, J.R. & Bocquet, C. (1975) Similarities and differences in latitudinal adaptation of two *Drosophila* sibling species. *Nature*, **257,** 588–591.

van Delden, W. & Kamping, A. (1997) Worldwide latitudinal clines for the alcohol dehydrogenase polymorphism in

Drosophila melanogaster: what is the unit of selection? *Environmental stress, adaptation and evolution* (ed. by R. Bijlsma and V. Loeschcke), pp. 97–115. Birkhäuser, Basel.

Doherty, P.F., Boulinier, T. & Nichols, J.D. (2003) Local extinction and turnover rates at the edge and interior of species' ranges. *Annales Zoologici Fennici*, **40,** 145–153.

Drakare, S., Lennon, J.J. & Hillebrand, H. (2006) The imprint of the geographical, evolutionary and ecological context on species–area relationships. *Ecology Letters*, **9,** 215–227.

Dunham, A.E. (1993) Population responses to environmental change: Operative environments, physiologically structured models, and population dynamics. *Biotic interactions and global change* (ed. by P.M. Kareiva, J.G. Kingsolver and R.B. Huey), pp. 95–119. Sinauer, Sunderland, MA.

Dyer, M.I., Pinowski, J. & Pinowska, B. (1977) Populations dynamics. *Granivorous birds in ecosystems: their evolution, populations, energetics, adaptations, impact and control* (ed. by J. Pinowski and S.C. Kendeigh), pp. 53–105. Cambridge University Press, Cambridge.

Economo, E.P., Kerkhoff, A.J. & Enquist, B.J. (2005) Allometric growth, life-history invariants and population energetics. *Ecology Letters*, **8,** 353–360.

Enquist, B.J. & Niklas, K.J. (2001) Invariant scaling relations across tree-dominated communities. *Nature*, **410,** 655–660.

Evans, K.L., Duncan, R.P., Blackburn, T.M. & Crick, H.Q.P. (2005a) Investigating geographical variation in clutch size using a natural experiment. *Functional Ecology*, **19,** 616–624.

Evans, K.L., Warren, P.H. & Gaston, K.J. (2005b) Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, **80,** 1–25.

Evans, K.L., Greenwood, J.J.D. & Gaston, K.J. (2005c) The contribution of common and rare species to species–energy relationships. *Biology Letters*, **1,** 87–90.

Evans, K.L., James, N.A. & Gaston, K.J. (2006a) Abundance, species richness and energy availability in the North American avifauna. *Global Ecology and Biogeography*, **15,** 372–385.

Evans, K.L., Jackson, S.F., Greenwood, J.J.D. & Gaston, K.J. (2006b) Species traits and the form of individual species–energy relationships. *Proceedings of the Royal Society B: Biological Sciences*, **273,** 1779–1787.

Farrell-Gray, C.C. & Gotelli, N.J. (2005) Allometric exponents support a 3/4-power scaling law. *Ecology*, **86,** 2083–2087.

Fleischer, R.C. & Johnston, R.F. (1982) Natural selection on body size and proportions in house sparrows. *Nature*, **298,** 747–749.

Fleming, I.A. & Gross, M.T. (1990) Latitudinal clines: a trade-off between egg number and size in Pacific Salmon. *Ecology*, **71,** 1–11.

Foster, J.B. (1964) The evolution of mammals on islands. *Nature*, **202,** 234–235.

Fox, C.W. & Czesak, M.E. (2000) Evolutionary ecology of progeny size in arthropods. *Annual Review of Entomology*, **51,** 341–369.

Frazier, M.R., Huey, R.B. & Berrigan, D. (2006) Thermodynamics constrains the evolution of insect population growth rates: 'Warmer is better'. *The American Naturalist*, **168,** 512–520.

Freckleton, R.P., Harvey, P.H. & Pagel, M. (2003) Bergmann's rule and body size in mammals. *The American Naturalist*, **161,** 821–825.

Frydenberg, J., Hoffmann, A.A. & Loeschcke, V. (2003) DNA sequence variation and latitudinal associations in *hsp23*, *hsp26* and *hsp27* from natural populations of *Drosophila melanogaster*. *Molecular Ecology*, **12,** 2025–2032.

Gaston, K.J. (1998) Species-range size distributions: products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **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 University Press, Oxford.

Gaston, K.J. & Blackburn, T.M. (1996) 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. (1999) Macroecology: a critique. *Oikos*, **84,** 353–368.

Gaston, K.J. & Blackburn, T.M. (2000). *Pattern and process in macroecology*. Blackwell Science, Oxford.

Gaston, K.J., Blackburn, T.M. & Spicer, J.I. (1998) Rapoport's rule: time for an epitaph? *Trends in Ecology & Evolution*, **13,** 70–74.

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., Davies, R.G., Orme, C.D.L., Olson, V.A., Thomas, G.H., Ding, T.-S., Rasmussen, P.C., Lennon, J.J., Bennett, P.M., Owens, I.P.F. & Blackburn, T.M. (2007) Spatial turnover in the global avifauna. *Proceedings of the Royal Society B: Biological Sciences*, **274,** 1567–1574.

Gibert, P. & Huey, R.B. (2001) Chill-coma temperature in *Drosophila*: effects of developmental temperature, latitude, and phylogeny. *Physiological and Biochemical Zoology*, **74,** 429–434.

Gilchrist, G.W. (1995) Specialist and generalist in changing environments. I. Fitness landscapes of thermal sensitivity. *The American Naturalist*, **146,** 252–270.

Gillman, L.N. & Wright, S.D. (2006) The influence of productivity on the species richness of plants: a critical assessment. *Ecology*, **87,** 1234–1243.

Gloger, C.L. (1883) *Das Abandern der Vogel durch Einfluss des Klimas*. A. Schulz, Breslau.

Gockel, J., Robinson, S.J.W., Kennington, W.J., Goldstein, D.B. & Partridge, L. (2002) Quantitative genetic analysis of variation in body size in *Drosophila melanogaster*. *Heredity*, **89,** 145–153.

Graves, G.R. & Rahbek, C. (2005) Source pool geometry and the assembly of continental avifaunas. *Proceedings of the National Academy of Sciences USA*, **102,** 7871–7876.

Green, D.M., Sharbel, T.F., Kearsley, J. & Kaiser, H. (1996) Postglacial range fluctuation, genetic subdivision and speciation in the western North American spotted frog complex, *Rana pretiosa*. *Evolution*, **50,** 374–390.

Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T.-S., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L. & Owens, I.P.F. (2006) The global distribution and conservation of rare and threatened vertebrates. *Nature*, **444,** 93–96.

Halsall, M., Walters, R.J., Telfer, M. & Hassall, M.R.J. (2005) Why does a grasshopper have fewer, larger offspring at its range limits? *Journal of Evolutionary Biology*, **19,** 267–276.

Harvey, P.H. & Pagel, M.D. (1991) *The comparative method in evolutionary biology*. Oxford University Press, Oxford.

van der Have, T.M. & de Jong, G. (1996) Adult size in ectotherms: temperature effects on growth and differentiation. *Journal of Theoretical Biology*, **183,** 329–340.

Hawkins, B.A. (1995) Latitudinal body-size gradients for the bees of the eastern United States. *Ecological Entomology*, **20,** 195–198.

Hawkins, B.A. & Diniz-Filho, J.A.F. (2006) Beyond Rapoport's rule: evaluating range size patterns of New World birds in a two-dimensional framework. *Global Ecology and Biogeography*, **15,** 461–469.

Hawkins, B.A. & Lawton, J.H. (1995) Latitudinal gradients in butterfly body sizes: is there a general pattern? *Oecologia*, **102,** 31–36.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water and broad-scale geographic patterns of species richness. *Ecology*, **84,** 3105–3117.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2006) Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *Journal of Biogeography*, **33,** 770–780.

Heibo, E., Magnhagen, C. & Vøllestad, L.A. (2005) Latitudinal variation in life-history traits in Eurasian perch. *Ecology*, **86,** 3377–3386.

Heino, J. (2005) Functional biodiversity of macroinvertebrate assemblages along major ecological gradients of boreal headwater streams. *Freshwater Biology*, **50,** 1578–1587.

Hengeveld, R. & Haeck, J. (1982) The distribution of abundance. I. Measurements. *Journal of Biogeography*, **9,** 303–316.

Herfindal, I., Solberg, E.J., Sæther, B.-E., Høgda, K.A. & Andersen, R. (2006) Environmental phenology and geographical gradients in moose body mass. *Oecologia*, **150,** 213–224.

Hillebrand, H. (2004a) On the generality of the latitudinal diversity gradient. *The American Naturalist*, **163,** 192–211.

Hillebrand, H. (2004b) Strength, slope and variability of marine latitudinal gradients. *Marine Ecology Progress Series*, **273,** 251–267.

Hodkinson, I.D. (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews*, **80,** 489–513.

Hoffmann, A.A., Hallas, R., Sinclair, C. & Mitrovski, P. (2001) Levels of variation in stress resistance in *Drosophila* among strains, local populations, and geographic regions: patterns for desiccation, starvation, cold resistance, and associated traits. *Evolution*, **55,** 1621–1630.

Hoffmann, A.A., Anderson, A. & Hallas, R. (2002) Opposing clines for high and low temperature resistance in *Drosophila melanogaster*. *Ecology Letters*, **5,** 614–618.

Hoffmann, A.A., Sørensen, J.G. & Loeschcke, V. (2003) Adaptation of *Drosophila* to temperature extremes: bringing together quantitative and molecular approaches. *Journal of Thermal Biology*, **28,** 175–216.

Huey, R.B., Berrigan, D., Gilchrist, G.W. & Herron, J.C. (1999) Testing the adaptive significance of acclimation: a strong inference approach. *American Zoologist*, **39,** 323–336.

Hunt, G., Roy, K. & Jablonski, D. (2005) Species-level heritability reaffirmed: a comment on 'On the heritability of geographic range sizes'. *The American Naturalist*, **166,** 129–135.

Hurlbert, A.H. (2004) Species-energy relationships and habitat complexity in bird communities. *Ecology Letters*, **7,** 714–720.

Hutchison, D.W. (2003) Testing the central/peripheral model: analyses of microsatellite variability in the eastern collared lizard (*Crotaphytus collaris collaris*). *American Midland Naturalist*, **149,** 148–162.

Ives, A.R. & Gilchrist, G.C. (1993) Climate change and ecological interactions. *Biotic interactions and global change* (ed. by P.M. Kareiva, J.G. Kingsolver and R.B. Huey), pp. 120–146. Sinauer, Sunderland, MA.

Ives, A.R. & Klopfer, E.D. (1997) Spatial variation in abundance created by stochastic temporal variation. *Ecology*, **78,** 1907–1913.

Jablonski, D. (1987) Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. *Science*, **238,** 360–363.

James, F.C. (1970) Geographic size variation in birds and its relationship to climate. *Ecology*, **51,** 365–390.

James, A.C. & Partridge, L. (1995) Thermal evolution of rate of larval development in *Drosophila melanogaster* in laboratory and field populations. *Journal of Evolutionary Biology*, **8,** 315–330.

James, A.C., Azevedo, R.B.R. & Partridge, L. (1997) Genetic and environmental responses to temperature of *Drosophila melanogaster* from a latitudinal cline. *Genetics*, **146,** 881–890.

Jenkins, A.R. & Hockey, P.A.R. (2001) Prey availability influences habitat tolerance: an explanation for the rarity of peregrine falcons in the tropics. *Ecography*, **24,** 359–367.

Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, **297,** 1548–1551.

Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology & Evolution*, **19,** 101–108.

Johnston, R.F. (1969) Character variation and adaptation in European sparrows. *Systematic Zoology*, **18,** 206–231.

Johnston, R.F. & Klitz, W.J. (1977) Variation and evolution in a granivorous bird: the house sparrow. *Granivorous birds in ecosystems: their evolution, populations, energetics, adaptations, impact and control* (ed. by J. Pinowski and S.C. Kendeigh), pp. 15–51. Cambridge University Press, Cambridge.

Johnston, R.F. & Selander, R.K. (1964) House sparrows: rapid evolution of races in North America. *Science*, **144,** 548–550.

Johnston, R.F. & Selander, R.K. (1973) Evolution in the house sparrow. III. Variation in size and sexual dimorphism in Europe and North and South America. *The American Naturalist*, **107,** 373–390.

Jonas, C.S. & Geber, M.A. (1999) Variation among populations of *Clarkia unguiculata* (Onagraceae) along altitudinal and latitudinal gradients. *American Journal of Botany*, **86,** 333–343.

Jones, J., Gibb, C.E., Millard, S.C., Barg, J.J., Girvan, M.K., Veit, M.L., Friesen, V.L. & Robertson, R.J. (2005) Multiple selection pressures generate adherence to Bergmann's rule in a Neotropical migratory songbird. *Journal of Biogeography*, **32,** 1827–1833.

de Jong, G. & Bochdanovits, Z. (2003) Latitudinal clines in *Drosophila melanogaster*: body size, allozyme frequencies, inversion frequencies, and the insulin-signalling pathway. *Journal of Genetics*, **83,** 207–223.

Jordan, D.S. (1891) *Temperature and vertebrae: a study in evolution*. Wilder-Quarter Century Books, New York.

Kaspari, M. (2005) Global energy gradients and size in colonial organisms: worker mass and worker number in ant colonies. *Proceedings of the National Academy of Sciences USA*, **102,** 5079–5083.

Kaspari, M., Yuan, M. & Alonso, L. (2003) Spatial grain and the causes of regional diversity gradients in ants. *The American Naturalist*, **161,** 459–477.

Katti, M. & Price, T.D. (2003) Latitudinal trends in body size among over-wintering leaf warblers (genus *Phylloscopus*). *Ecography*, **26,** 69–79.

Kendeigh, S.C. (1976) Latitudinal trends in the metabolic adjustments of the House Sparrow. *Ecology*, **57,** 509–519.

Kingsolver, J.G. (1989) Weather and the population dynamics of insects: integrating physiological and population ecology. *Physiological Zoology*, **62,** 314–334.

Klok, C.J. & Chown, S.L. (2003) Resistance to temperature extremes in sub-Antarctic weevils: interspecific variation, population differentiation and acclimation. *Biological Journal of the Linnean Society*, **78,** 401–414.

Klok, J., Chown, S.L. & Gaston, K.J. (2003) The geographical range structure of the holly leaf-miner. III. Cold hardiness physiology. *Functional Ecology*, **17,** 858–868.

Knouft, J.H. (2002) Regional analysis of body size and population density in stream fish assemblages: testing predictions of the energetic equivalence rule. *Canadian Journal of Fisheries and Aquatic Sciences*, **59,** 1350–1360.

Knouft, J.H. (2004) Latitudinal variation in the shape of the species body size distribution: an analysis using freshwater fishes. *Oecologia*, **139,** 408–417.

Koenig, W.D. (1984) Geographic variation in clutch size in the northern flicker (*Colaptes auratus*): support for Ashmole's hypothesis. *The Auk*, **101,** 698–706.

Koons, D.N., Grand, J.B. & Arnold, J.M. (2006) Population momentum across vertebrate life histories. *Ecological Modelling*, **197,** 418–430.

van Kooten, T., de Roos, A.M. & Persson, L. (2004) Local foraging and limited mobility: dynamics of a size-structured consumer population. *Ecology*, **85,** 1979–1991.

Kozłowski, J., Konarzewski, M. & Gawelczyk, A.T. (2003) Cell size as a link between noncoding DNA and metabolic rate scaling. *Proceedings of the National Academy of Sciences USA*, **100,** 14080–14085.

Kozłowski, J., Czarnoleski, M. & Dańko, M. (2004) Can optimal resource allocation models explain why ectotherms grow larger in cold? *Integrative and Comparative Biology*, **44,** 480–493.

Kulesza, G. (1990) An analysis of clutch-size in New World passerine birds. *Ibis*, **132,** 407–422.

Lack, D. (1947) The significance of clutch-size. Part I – Intraspecific variations. *Ibis*, **89,** 302–352.

Lack, D. (1948) The significance of clutch-size. Part III – Some interspecific comparisons. *Ibis*, **90,** 25–45.

Lardies, M.A. & Bozinovic, F. (2006) Geographic covariation between metabolic rate and life-history traits. *Evolutionary Ecology Research*, **8,** 455–470.

Lawton, J.H. (1993) Range, population abundance and conservation. *Trends in Ecology & Evolution*, **8,** 409–413.

Lawton, J.H. (1999) Are there general laws in ecology? *Oikos*, **84,** 177–192.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2004) Contribution of rarity and commonness to patterns of species richness. *Ecology Letters*, **7,** 81–87.

Letcher, A.J. & Harvey, P.H. (1994) Variation in geographical range size among mammals of the Palearctic. *The American Naturalist*, **144,** 30–42.

Lincoln, R.J., Boxshall, G.A. & Clark, P.F. (1982) *A dictionary of ecology, evolution and systematics*. Cambridge University Press, Cambridge.

Lindstedt, S.L. & Boyce, M.S. (1985) Seasonality, fasting endurance, and body size in mammals. *The American Naturalist*, **125,** 873–878.

Litzgus, J.D., DuRant, S.E. & Mousseau, T.A. (2004) Clinal variation in body and cell size in a widely distributed vertebrate endotherm. *Oecologia*, **140,** 551–558.

Lomolino, M.V. (1985) Body size of mammals on islands: the island rule re-examined. *The American Naturalist*, **125,** 310–316.

Lomolino, M.V. (1996) Investigating causality of nestedness of insular communities: selective immigrations or extinctions? *Journal of Biogeography*, **23,** 699–703.

Lomolino, M.V., Riddle, B.R. & Brown, J.H. (2006a) *Biogeography*, 3rd edn. Sinauer, Sunderland, MA.

Lomolino, M.V., Sax, D.F., Riddle, B.R. & Brown, J.H. (2006b) The island rule and a research agenda for studying ecogeographical patterns. *Journal of Biogeography*, **33,** 1503–1510.

Lutz, F.E. (1921) Geographic average, a suggested method for the study of distribution. *American Museum Novitates*, **5,** 1–7.

Lynch, M. & Gabriel, W. (1987) Environmental tolerance. *The American Naturalist*, **129,** 283–303.

Makarieva, A.M., Gorshkov, V.G. & Li, B.L. (2005) Temperature-associated upper limits to body size in terrestrial poikilotherms. *Oikos*, **111,** 425–436.

Marquet, P.A., Fernández, M., Navarrete, S.A. & Valdovinos, C. (2004) Diversity emerging: toward a deconstruction of biodiversity patterns. *Frontiers of biogeography: new directions in the geography of nature* (ed. by M.V. Lomolino and L.R. Heaney), pp. 191–209. Sinauer Associates, Sunderland, MA.

Martin, T.E. (1987) Food as a limit on breeding birds – a life-history perspective. *Annual Review of Ecology and Systematics*, **18,** 453–487.

Martin, T.E., Martin, P.R., Olson, C.R., Heidinger, B.J. & Fontaine, J.J. (2000) Parental care and clutch sizes in North and South American birds. *Science*, **287,** 1482–1485.

Martin, L.B., II, Pless, M., Svoboda, J. & Wikelski, M. (2004) Immune activity in temperate and tropical house sparrows: a common-garden experiment. *Ecology*, **85,** 2323–2331.

Martin, L.B., II, Gilliam, J., Han, P., Lee, K. & Wikelski, M. (2005) Corticosterone suppresses cutaneous immune function in temperate but not tropical House Sparrows, *Passer domesticus*. *General and Comparative Endocrinology*, **140,** 126–135.

Martinez-Meyer, E., Peterson, A.T. & Hargrove, W.W. (2004) Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecology and Biogeography*, **13,** 305–314.

Mayr, E. (1956) Geographical character gradients and climatic adaptation. *Evolution*, **10,** 105–108.

McKechnie, A.E. & Wolf, B.O. (2004) The allometry of avian basal metabolic rate: good predictions need good data. *Physiological and Biochemical Zoology*, **77,** 502–521.

McNab, B.K. (1971) On the ecological significance of Bergmann's rule. *Ecology*, **52,** 845–854.

Meiri, S. & Dayan, T. (2003) On the validity of Bergmann's rule. *Journal of Biogeography*, **30,** 331–351.

Meiri, S., Dayan, T. & Simberloff, D. (2004a) Carnivores, biases and Bergmann's rule. *Biological Journal of the Linnean Society*, **81,** 579–588.

Meiri, S., Dayan, T. & Simberloff, D. (2004b) Body size of insular carnivores: little support for the island rule. *The American Naturalist*, **163,** 469–479.

Meiri, S., Simberloff, D. & Dayan, T. (2005) Insular carnivore biogeography: island area and mammalian optimal body size. *The American Naturalist*, **165,** 505–514.

Micheli, F. & Halpern, B.S. (2005) Low functional redundancy in coastal marine assemblages. *Ecology Letters*, **8,** 391–400.

Millien, V., Lyons, K.S., Olson, L., Smith, F.A., Wilson, A.B. & Yom-Tov, Y. (2006) Ecotypic variation in the context of global climate change: revisiting the rules. *Ecology Letters*, **9,** 853–869.

Mitrovski, P. & Hoffmann, A.A. (2001) Postponed reproduction as an adaptation to winter conditions in *Drosophila melanogaster*: evidence for clinal variation under semi-natural conditions. *Proceedings of the Royal Society B: Biological Sciences*, **268,** 2163–2168.

Mittelbach, G.C., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82,** 2381–2396.

Mittelbach, G.C., Steiner, C.F. & Scheiner, S.M. (2003) What is the observed relationship between species richness and productivity? Reply. *Ecology*, **84,** 3390–3395.

Murdoch, W.W. (1993) Individual-based models for predicting effects of global change. *Biotic interactions and global change* (ed. by P.M. Kareiva, J.G. Kingsolver and R.B. Huey), pp. 147–162. Sinauer, Sunderland, MA.

Murphy, E.C. (1978) Breeding ecology of house sparrows: spatial variation. *The Condor*, **80,** 180–193.

Murphy, E.C. (1985) Bergmann's rule, seasonality, and geographic variation in body size of house sparrows. *Evolution*, **39,** 1327–1334.

Murphy, H.T., van der Wal, J. & Lovett-Doust, J. (2006) Distribution of abundance across the range in eastern North American trees. *Global Ecology and Biogeography*, **15,** 63–71.

Newton, I. & Dale, L. (1996) Relationship between migration and latitude among west European birds. *Journal of Animal Ecology*, **65,** 137–146.

Olalla-Tárraga, M.Á., Rodríguez, M.Á. & Hawkins, B.A. (2006) Broad-scale patterns of body size in squamate reptiles of Europe and North America. *Journal of Biogeography*, **33,** 781–793.

Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V., Webster, A.J., Ding, T.-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J. & Owens, I.P.F. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature*, **436,** 1016–1019.

Orme, C.D.L., Davies, R.G., Olson, V.A., Thomas, G.H., Ding, T.-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Owens, I.P.F., Blackburn, T.M. & Gaston, K.J. (2006) Global patterns of geographic range size in birds. *PLoS Biology*, **4,** 1276–1283.

Parkin, D.T. & Cole, S.R. (1985) Genetic differentiation and rates of evolution in some introduced populations of the House Sparrow, *Passer domesticus* in Australia and New Zealand. *Heredity*, **54,** 15–23.

Partridge, L., Barrie, B., Fowler, K. & French, V. (1994) Evolution and development of body size and cell size in *Drospophila melanogaster* in response to temperature. *Evolution*, **39,** 1327–1334.

Pautasso, M. & Gaston, K.J. (2005) Resources and global avian assemblage structure in forests. *Ecology Letters*, **8,** 282–289.

Pfenninger, M. (2004) Comparative analysis of range sizes in Helicidae s.l. (Pulmonata, Gastropoda). *Evolutionary Ecology Research*, **6,** 359–376.

Philippart, C.J.M., Henderson, P.A., Johannessen, T., Rijnsdorp, A.D. & Rogers, S.I. (1998) Latitudinal variation in fish recruits in Northwest Europe. *Journal of Sea Research*, **39,** 69–77.

Phillimore, A.B., Orme, C.D.L., Davies, R.G., Hadfield, J.D., Reed, W.J., Gaston, K.J., Freckleton, R.P. & Owens, I.P.F. (2007) Biogeographical basis of recent phenotypic divergence among birds: a global study of subspecies richness. *Evolution*, **61,** 942–957.

Pinowski, J. & Kendeigh, S.C. (eds) (1977) *Granivorous birds in ecosystems: their evolution, populations, energetics, adaptations, impact and control*. Cambridge University Press, Cambridge.

Post, E. (2005) Large-scale spatial gradients in herbivore population dynamics. *Ecology*, **86,** 2320–2328.

Powell, J.R. (1997) *Progress and prospects in evolutionary biology. The Drosophila model*. Oxford University Press, Oxford.

de Queiroz, A. & Ashton, K.G. (2004) The phylogeny of a species-level tendency: species heritability and possible deep origins of Bergmann's rule in tetrapods. *Evolution*, **58,** 1674–1684.

Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, **18,** 200–205.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, **8,** 224–239.

Rahbek, C., Gotelli, N.J., Colwell, R.K., Entsminger, G.L., Rangel, T.F.L.V.B. & Graves, G.R. (2006) Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proceedings of the Royal Society B: Biological Sciences*, **274,** 165–174.

Rako, L., Anderson, A.R., Sgrò, C.M., Stocker, A.J. & Hoffmann, A.A. (2006) The association between inversion In(3R)Payne and clinally varying traits in *Drosophila melanogaster*. *Genetica*, **128,** 373–384.

Rapoport, E.H. (1982) *Areography: geographical strategies of species*. Pergamon, Oxford.

Ray, C. (1960) The application of Bergmann's and Allen's rules to the poikilotherms. *Journal of Morphology*, **106,** 88–108.

Real, R., Barbosa, A.M., Porras, D., Kin, M.S., Marquez, A.L., Guerrero, J.C., Palomo, L.J., Justo, E.R. & Vargas, J.M. (2003) Relative importance of environment, human activity and spatial situation in determining the distribution of terrestrial mammal diversity in Argentina. *Journal of Biogeography*, **30,** 939–947.

Reed, R.N. (2003) Interspecific patterns of species richness, geographic range size, and body size among New World venomous snakes. *Ecography*, **26,** 107–117.

Reid, J.M., Monaghan, P. & Ruxton, G.D. (2000) Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. *Proceedings of the Royal Society B: Biological Sciences*, **267,** 37–41.

Rensch, B. (1938) Some problems of geographical variation and species-formation. *Journal of the Proceedings of the Linnean Society*, **150,** 275–285.

Ricklefs, R.E. & Wikelski, M. (2002) The physiology/life history nexus. *Trends in Ecology & Evolution*, **17,** 462–468.

Rinde, E. & Sjotun, K. (2005) Demographic variation in the kelp *Laminaria hyperborea* along a latitudinal gradient. *Marine Biology*, **146,** 1051–1062.

Rodríguez, M.Á., López-Sañudo, I.L. & Hawkins, B.A. (2006) The geographic distribution of mammal body size in Europe. *Global Ecology and Biogeography*, **15,** 173–181.

Roff, D. (1980) Optimizing development time in a seasonal environment: the 'ups and downs' of clinal variation. *Oecologia*, **45,** 202–208.

Roff, D. (2002) *Life history evolution*. Sinauer, Sunderland, MA.

Rohde, K., Heap, M. & Heap, D. (1993) Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. *The American Naturalist*, **142,** 1–16.

Rohmer, C., David, J.R., Moreteau, B. & Joly, D. (2004) Heat induced male sterility in *Drosophila melanogaster*: adaptive genetic variations among geographic populations and role of the Y chromosome. *Journal of Experimental Biology*, **207,** 2735–2743.

Rosenzweig, M.L. (1968) Net primary productivity of terrestrial communities: prediction from climatological data. *The American Naturalist*, **102,** 67–74.

Roy, K. & Martien, K.K. (2001) Latitudinal distribution of body size in north-eastern Pacific marine bivalves. *Journal of Biogeography*, **28,** 485–493.

Ruggiero, A. & Lawton, J.H. (1998) Are there latitudinal and altitudinal Rapoport effects in the geographic ranges of Andean passerine birds? *Biological Journal of the Linnean Society*, **63,** 283–304.

Sagarin, R.D. & Gaines, S.D. (2002) The 'abundant centre' distribution: to what extent is it a biogeographic rule? *Ecology Letters*, **5,** 137–147.

Sagarin, R.D., Gaines, S.D. & Gaylord, B. (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology & Evolution*, **21,** 524–530.

Sanz, J.J. (1999) Does daylength explain the latitudinal variation in clutch size of pied flycatchers *Ficedula hypoleuca*? *Ibis*, **141,** 100–108.

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,** E429–E441.

Schmidt, P.S., Matzkin, L., Ippolito, M. & Eanes, W.F. (2005) Geographic variation in diapause incidence, life-history traits, and climatic adaptation in *Drosophila melanogaster*. *Evolution*, **59,** 1721–1732.

Sezgin, E., Duvernell, D.D., Matzkin, L.M., Duan, Y.H., Zhu, C.T., Verrelli, B.C. & Eanes, W.F. (2004) Single-locus latitudinal clines and their relationship to temperate adaptation in metabolic genes and derived alleles in *Drosophila melanogaster*. *Genetics*, **168,** 923–931.

Sgrò, C.M., Magiafoglou, A., Faine, L. & Hoffmann, A.A. (2006) Absence of clinal variation in virgin retention capacity in Australian *Drosophila melanogaster*. *Evolutionary Ecology*, **20,** 407–413.

Sibly, R.M. & Calow, P. (1986) *Physiological ecology of animals. An evolutionary approach*. Blackwell Scientific Publications, Oxford.

Simberloff, D.S. & Connor, E.F. (1979) Q-mode and R-mode analyses of biogeographic distributions: null hypotheses based on random colonization. *Contemporary quantitative ecology and related econometrics* (ed. by G.P. Patil and M. Rosenzweig), pp. 123–138. International Co-operative Publishing House, Fairland, MD.

Singh, R.S. & Long, A.D. (1992) Geographic variation in *Drosophila* – from molecules to morphology and back. *Trends in Ecology & Evolution*, **7,** 340–345.

Skutch, A.F. (1949) Do tropical birds rear as many young as they can nourish? *Ibis*, **91,** 430–455.

Spicer, J.I. & Gaston, K.J. (1999) *Physiological diversity and its ecological implications*. Blackwell Science, Oxford.

Stahl, J.T. & Oli, M.K. (2006) Relative importance of avian life-history variables to population growth rate. *Ecological Modelling*, **198,** 23–39.

Starostová, Z., Kratochvíl, L. & Frynta, D. (2005) Dwarf and giant geckos from the cellular perspective: the bigger the animal, the bigger its erythrocytes? *Functional Ecology*, **19,** 744–749.

Stevens, G.C. (1989) The latitudinal gradient in geographical range: how so many species co-exist in the tropics. *The American Naturalist*, **133,** 240–256.

Stevens, R.D., Cox, S.B., Strauss, R.E. & Willig, M.R. (2003) Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. *Ecology Letters*, **6,** 1099–1108.

Stoleson, S.H. & Beissinger, S.R. (1999) Egg viability as a constraint on hatching synchrony at high ambient temperatures. *Journal of Animal Ecology*, **68,** 951–962.

Summers-Smith, J.D. (1988) *The sparrows*. Poyser, Calton.

Symonds, M.R.E., Christidis, L. & Johnson, C.N. (2006) Latitudinal gradients in abundance, and the causes of rarity in the tropics: a test using Australian honeyeaters (Aves: Meliphagidae). *Oecologia*, **149,** 406–417.

Thorson, G. (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews*, **25,** 1–45.

Threadgold, L.T. (1960) A study of the annual cycle of the house sparrow at various latitudes. *The Condor*, **62,** 190–201.

Umina, P.A., Weeks, A.R., Kearney, M.R., McKechnie, S.W. & Hoffmann, A.A. (2005) A rapid shift in a classic clinal pattern in *Drosophila* reflecting climate change. *Science*, **308,** 691–693.

Van't Land, J., Van Putten, W.F., Villarroel, H., Kamping, A. & Van Delden, W. (2000) Latitudinal variation for two enzyme loci and an inversion polymorphism in *Drosophila melanogaster* from Central and South America. *Evolution*, **54,** 201–209.

Verrelli, B.C. & Eanes, W.F. (2001) Clinal variation for amino acid polymorphisms at the *Pgm* locus in *Drosophila melanogaster*. *Genetics*, **157,** 1649–1663.

Voituron, Y., Mouquet, N., de Mazancourt, C. & Clobert, J. (2002) To freeze or not to freeze? An evolutionary perspective on the cold-hardiness strategies of overwintering ectotherms. *The American Naturalist*, **160,** 255–270.

Vucetich, J.A. & Waite, T.A. (2003) Spatial patterns of demography and genetic processes across the species' range: null hypotheses for landscape conservation genetics. *Conservation Genetics*, **4,** 639–645.

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G.C., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. (1999) The relationship between net primary productivity and species richness. *Annual Review of Ecology and Systematics*, **30,** 257–300.

Walters, R.J. & Hassall, M. (2006) The temperature-size rule in ectotherms: may a general explanation exist after all? *The American Naturalist*, **167,** 510–523.

Webb, T.J. & Gaston, K.J. (2003) On the heritability of geographic range sizes. *The American Naturalist*, **161,** 553–566.

Webb, T.J. & Gaston, K.J. (2005) Heritability of geographic range sizes revisited: a reply to Hunt *et al. The American Naturalist*, **166,** 136–143.

Weeks, A.R., McKechnie, S.W. & Hoffmann, A.A. (2002) Dissecting adaptive clinal variation: markers, inversions and size/stress associations in *Drosophila melanogaster* from a central field population. *Ecology Letters*, **5,** 756–763.

West, G.B., Brown, J.H. & Enquist, B.J. (2001) A general model for ontogenetic growth. *Nature*, **413,** 628–631.

Whittaker, R.J. & Heegaard, E. (2003) What is the observed relationship between species richness and productivity? Comment. *Ecology*, **84,** 3384–3390.

Wu, Z.J., Li, Y.M. & Murray, B.R. (2006) Insular shifts in body size of rice frogs in the Zhoushan Archipelago, China. *Journal of Animal Ecology*, **75,** 1071–1080.

Yom-Tov, Y. (1994) Clutch size of passerines at mid-latitudes – the possible effect of competition with migrants. *Ibis*, **135,** 161–165.

Yom-Tov, Y. & Geffen, E. (2006) Geographic variation in body size: the effects of ambient temperature and precipitation. *Oecologia*, **148,** 213–218.

Yom-Tov, Y., Christie, M.I. & Iglesias, G.J. (1994) Clutch size in passerines of southern South America. *The Condor*, **96,** 170–177.

Zapata, F.A., Gaston, K.J. & Chown, S.L. (2003) Mid-domain models of species richness gradients: assumptions, methods and evidence. *Journal of Animal Ecology*, **72,** 677–690.

BIOSKETCHES

Kevin J. Gaston has research interests in the fields of biodiversity, conservation biology and macroecology, with particular emphasis on the ecologies of rare organisms, the structure of geographical ranges and patterns in species richness.

Steven L. Chown works in the fields of macroecology, evolutionary physiology and community ecology. He has a long-standing interest in the ecology, physiology and evolution of the biotas of the islands of the Southern Ocean.

Karl L. Evans has research interests that span a range of ecological and conservation topics, including spatial patterns in biodiversity (particularly species–energy relationships) and urban ecology.

Editor: Glen MacDonald

Special Issue: This article arose from a paper prepared for the third biennial meeting of the International Biogeography Society, held in Puerto de la Cruz, Tenerife, Canary Islands, 9–13 January 2007.