

Areas, cradles and museums: the latitudinal gradient in species richness

Steven L. Chown and Kevin J. Gaston

Rosenzweig^{1,2} has added much needed focus to discussions of the mechanisms that generate latitudinal gradients in taxon richness. His championing of the importance of geographic area as the primary determinant of this almost ubiquitous pattern in biodiversity stands in stark contrast to recurrent statements that numerous factors might be responsible and that it is not clear in practice which are the most significant³. Building on work by Terborgh⁴, Rosenzweig's¹ essential argument is that because the tropics north and south of the equator abut, they have a larger climatically similar total surface area than any other ecoclimatic zone. This results in larger mean geographic range sizes of species in the tropics, which translates into higher speciation rates (presuming larger ranges have higher probabilities of speciation) and lower extinction rates (presuming larger ranges have lower probabilities of extinction). Consequently, tropical regions have greater numbers of species and higher taxa than extratropical ones.

To date, beyond Rosenzweig's publications, there has been limited critical appraisal of this important 'area model'. Rohde^{5,6} suggested that several lines of evidence fail to provide support, but these points were convincingly rejected⁷. Although several other studies have claimed to test assumptions or predictions of the model⁸⁻¹¹, these tests have been either weak or tangential.

At the heart of the area model lie three macroecological and macroevolutionary assumptions: a positive relationship between the geographic range size of a species and the size of an ecoclimatic zone; a positive relationship between the geographic range size of a species and the likelihood of its speciation; and a negative relationship between the geographic range size of a species and its likelihood of extinction². We will consider each of these assumptions in turn.

Range size and area

If numbers of species are equal, the area model predicts that the geographic range sizes of species in the tropics should be larger than those in ecoclimatic zones at higher latitudes. By definition, these preconditions do not exist. With greater numbers of species in the tropics, the area model makes no precise prediction about the nature of the observed latitudinal pattern in range size. The existence of a Rapoport effect (a decline in mean or median latitudinal extent towards lower latitudes^{12,13}) does not falsify the area model, although the mechanistic basis of the effect might modulate it – a point to which we will return. Neither

Although numerous factors are postulated to be responsible for the gradient of increasing taxon richness towards lower latitudes, it has recently been suggested that the primary determinant is geographic area. This area model is appealing in its logic, but there is little empirical evidence to support it and several other mechanisms might also interact to obscure its effects. Nonetheless, the model has highlighted several fundamental issues concerning range size, speciation and extinction that, despite their considerable significance, remain poorly understood.

Steven Chown is at the Dept of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa (slchown@zoology.up.ac.za); and Kevin Gaston is at the Biodiversity and Macroecology Group, Dept of Animal and Plant Sciences, University of Sheffield, Sheffield, UK S10 2TN (k.j.gaston@sheffield.ac.uk).

the existence of the inverse relationship nor the absence of any latitudinal gradient in latitudinal extent¹³ provide any comment on the model. Unfortunately, this means that the first pivotal relationship for the area model is virtually impossible to test. The occurrence of species with a larger maximum range size in larger biogeographic regions^{14,15} might be suggestive, but little more.

Range size and speciation

The second relationship underpinning the area model is a positive one between the likelihood of speciation and a species' geographic range size. Assuming speciation is allopatric, species with larger ranges are more likely to undergo speciation because their likelihood of being bisected by a

barrier is higher. This assertion is true of barriers that are 'moats' (which surround their isolates) but not of those that are 'knives' (which have beginnings and ends), because at the largest range sizes the knives would be engulfed¹⁶. Thus, the probability of speciation resulting from knives (probably the more common barrier type) should peak at intermediate range sizes. However, Rosenzweig² argues that few species have geographic ranges that are so large that reducing them would make them an easier target for barriers. Therefore, speciation probability should increase with range size in this case too.

How general this conclusion is depends on the frequency distribution of barrier sizes. If large barriers are rare, as seems likely to be the case¹⁷, then a full, peaked function for the relationship between speciation and geographic range size might actually be more appropriate (Fig. 1). Such a peaked function has been discussed elsewhere¹⁸ and might explain the strong dichotomy in historical and current opinion concerning the relationship between geographic range size and speciation probability (a debate dating at least to Darwin; reviewed in Ref. 17).

Additional evidence for a peaked function between the probability of speciation and geographic range size, rather than a positive function, comes from the generally positive interspecific relationship between population size and range size. Here, population size increases at a disproportionately faster rate with increasing range size and thus local density also increases with increasing range size¹⁹. Consequently, density-dependent dispersal probability tends to increase the cohesion of ranges disproportionately with increases in their size. This might occur in two ways. First, higher densities result in more individuals moving between disjunct populations on a purely probabilistic basis, thus increasing gene flow and lowering

speciation probability. Second, gene flow from populations at a range centre can act as a powerful inhibitor of change in more peripheral populations, thus precluding speciation^{20–23}. Indeed, Gavrillets *et al.*²⁴ have modelled patterns of parapatric speciation and have found that the positive effects of geographic range size on the likelihood of speciation are overwhelmed by negative effects of population density and dispersal ability, such that species with smaller range sizes have higher speciation rates²⁵.

Range size and extinction

The third assumption central to the area model is a positive relationship between time to extinction and geographic range size. The rationale is that large ranges should buffer species from extinction by reducing the probability of range-wide catastrophes, and that large population sizes should minimize the chance that a species goes extinct for stochastic reasons. There is a considerable amount of widely cited evidence, from various palaeontological assemblages, that larger ranges have a reduced risk of extinction^{20,26–30}. However, a variety of factors can lead to this relationship appearing stronger than it actually is or might confound it.

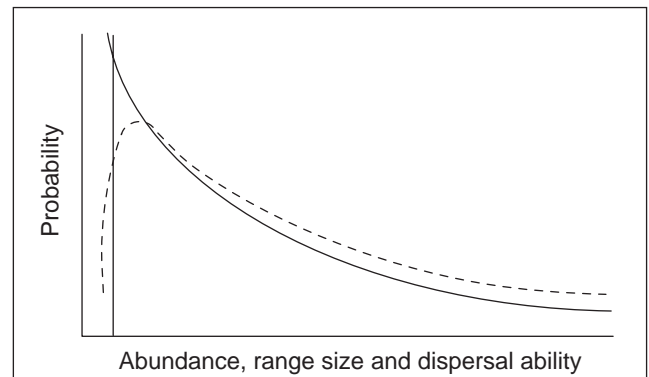
First, the positive correlation between density and range size means that widely distributed species tend to be locally more abundant, and are thus more likely to be recorded in the fossil record. Consequently, they might appear to persist for longer than less widely distributed species.

Second, estimates of the allochronic extent of occurrence (i.e. summing the spatial extent of localities – often the number of provinces – over the total geological duration of a species or the geological period under investigation¹⁷) might confound the relationship between range size and risk of extinction. Where studies are explicit about the way in which range size has been calculated, this is often done using a measure of the allochronic extent of occurrence. Such an estimate would provide a reliable indication of the range size of a species only if it could be demonstrated that, subsequent to speciation, species rapidly attain the range size that will characterize them for the bulk of their geological duration, and that these ranges do not shift their geographic position (Box 1). Palaeontologists have sought to overcome this last problem by estimating the range sizes of Recent taxa (especially species)

Box 1. Range transformation

Models of the relationships between geographic range size and the probabilities of speciation and/or extinction would be straightforward to construct if the ranges of species were static in area. However, they are not. Not only are ranges likely to decrease in size at speciation, thus increasing extinction probability (perhaps the fate of most nascent species), but also subsequent range transformation might precipitate a continuous change in the speciation and extinction probability of a species through time. At least seven range transformation scenarios have been mooted in the literature:

- Age and area:** a trajectory of steadily increasing size.
- Age and area with positional shift:** essentially a combination of the stasis with positional shift, and the age and area models; this model conforms to a taxon-pulse concept.
- Cyclic:** this model is similar to the previous one, but species ranges fragment as the species divides up into subspecies and eventually species. This is essentially equivalent to a taxon cycle.
- Idiosyncratic:** ranges assume any size and position, and these change regularly, in no ordered manner, over the lifetime of a species.
- Stasis:** an unrealistic model.
- Stasis after a rapid early range expansion:** the model favoured by Jablonski²⁹. After speciation, species rapidly attain their characteristic range size, which they maintain until just before extinction.
- Stasis with positional shift:** here, range size remains constant, but the position of the range changes.



Trends in Ecology & Evolution

Fig. 1. Speciation probability as a function of geographic range size, showing the full, peaked relationship (speciation, broken line; extinction, unbroken line) that can be expected if the frequency distribution of barrier sizes is right skewed. Modified, with permission, from Ref. 18.

and then examining their persistence back through the fossil record. Unfortunately, the temporal dynamics of range sizes, throughout the duration of the taxa concerned, are still likely to confound conclusions.

Third, documented relationships between time to extinction and range size, which concern taxa above the species level, are problematic. Even if a positive relationship is demonstrated between the geographic range size of a higher taxon and its likelihood of persistence, the relationship might well be of limited relevance at the species level. This could be a consequence of different extinction patterns for species and higher taxa during extinction events of different magnitude or because range size variance is partitioned to a large extent at the species level¹⁷. In the latter case, summing species ranges to generate those for genera (or other higher taxa) might provide insufficient insight into relationships at the species level.

Despite these problems with the existing empirical evidence, it seems reasonable to assume that species persistence increases with range size, at least during periods of background extinction rates – there might be no relationship during mass extinction events²⁸. Perversely, the lower extinction risk of species with larger range sizes could also generate a positive relationship between the likelihood of speciation and geographic range size viewed over long timescales. A peaked function relating range size and speciation probability is essentially based on a static or instantaneous assessment of speciation probability. It does not take into account the relationship between persistence and geographic range size. If there is a reasonably strong positive relationship between time to extinction and range size for species, then range size and likelihood of speciation could show the positive relationship suggested by Rosenzweig. In other words, even though the instantaneous likelihood of speciation might show a peaked function, because the largest ranges have the longest persistence times and thus a greater lifetime probability of undergoing a speciation event, the full relationship might, in fact, be positive.

Apparently, only Wagner and Erwin³¹ have set out to test these relationships empirically. They found that, in two out of three case studies, species with larger ranges were likely to leave more descendants and that, in all three cases, species that persisted for longer were likely to leave more descendants. The relationship between the instantaneous rate of speciation (which is likely to be peaked) and the number of descendants left by a lineage over time (which

might assume some other function) will require more attention if it is to be resolved in the context of the area model. Recent work suggesting that speciation is sufficient to reduce the likelihood of another such event in a given ancestral species³² is particularly relevant in this regard.

The tropics as a museum

If species with larger geographic range size are more persistent and such range sizes are typical of the tropics, then the tropics should act as a museum of diversity, with low extinction rates. In other words, taxa should be considerably older in the tropics. Of course, this discounts any effect of speciation on range sizes and on species persistence. Nonetheless, authors such as Stebbins³³ argued in favour of the tropics as a museum. Recently, the New World and African avifaunas have provided more rigorous evidence³⁴ for the tropics housing older species. This also appears to be the case for higher taxa in the New World birds³⁵. Here, mean tribe-age declines from the equator towards higher latitudes, particularly in the northern hemisphere; this appears to be the consequence of the colonization of higher latitudes by younger taxa following glaciation-induced extinctions of the previously incumbent avifauna. However, note that higher taxa might generate many new species without giving rise to a new higher group³⁶.

Paradoxically, although the tropics could be acting as a museum because of longer persistence times³⁴, this pattern could also be the consequence of: high unrecorded extinction rates (Box 2); evolutionary senescence and, therefore, the absence of speciation in some taxa (which might ultimately also mean longer persistence times); or latitudinal differences in speciation models (Fig. 2). Indeed, declining skewness of the tribal-age-frequency distribution with latitude in the northern hemisphere and, therefore, the apparent absence of older New World avian tribes in the northern hemisphere, could be a consequence of any of these mechanisms. However, insufficient time for significant speciation at higher latitudes since the last Neogene glaciation³⁷, the steep cline in mean age of tribes and an absence of any firm evidence for latitudinal differences in speciation models suggest that immigration of younger tribes to higher latitudes and unrecorded extinctions in the tropics are responsible for this pattern. Thus, there is some evidence for the tropics as a museum, albeit one whose collections, at least from a northern perspective, were fortuitously spared destruction.

Such a pattern of low extinction rates in the tropics, and the converse in the extratropics, is predicted by most models examining differences in evolutionary rates as a means to account for differences in diversity between these areas³⁸. However, as for predictions regarding range size, these models are also confounded by equilibrational differences in rates, with equilibrational extinction rates generally being higher in the tropics. Extinction rates might also appear higher because of high species richness in the tropics³⁹, although in some cases the converse might actually be true.

The tropics as a cradle

Conversely, the tropics can also be viewed as a cradle of diversity, with high origination rates^{3,30,33,38,40-42}. The two views need not be mutually exclusive, which greatly complicates indirect methods of determining whether the tropics do indeed act as a cradle. The most convincing evidence derives from elegant analyses performed by Jablonski⁴⁰. Using post-Paleozoic benthic marine invertebrates, he demonstrated that significantly more first fossil appearances of orders occur in tropical latitudes than would be

Box 2. The missing branches problem

Missing taxa in phylogenies pose a potentially significant problem for estimating taxon age in different regions. Figure I shows a hypothetical phylogeny of two tropical taxa (A, B) and two extratropical taxa (C, D), with speciation events taking place at times X and Y before the present (0). Should B become extinct by chance (broken line), then in the absence of knowledge of this event the observed age of the taxon containing A is Y rather than X, therefore making the tropical clade appear older. *Redrawn, with permission, from Ref. 35.*

This 'missing branches problem' has significant implications for virtually all analyses in which phylogenies are used to estimate parameters, such as the age of a taxon, internode durations, extinction rates and speciation rates. In this respect, two types of missing branches can be distinguished. The first occurs where the extant taxa have not been sampled for a phylogeny and the second occurs when it is not known whether there are missing taxa (i.e. taxa that have gone extinct and remain unrecorded). An example of these problems is provided by the rails (*Rallidae*)⁴⁹. Ways to overcome these problems are currently being investigated⁵⁰.

expected from sampling bias alone. Although such elevated ordinal originations do not necessarily mean that speciation rates must be highest in this region⁴⁰, they certainly suggest that this might be the case.

Other studies have also claimed to provide support for higher origination rates in the tropics, based on an indirect method involving comparison of frequency distributions of the ages of fossil assemblages from different latitudes^{30,41}. The authors argue that because assemblages from the tropics are younger, there must be a greater rate of origination there. For example, Flessa and Jablonski³⁰ concluded that there is considerable support for higher turnover and, therefore, higher origination rates of Recent marine bivalve genera (and other marine groups) in the tropics compared with in temperate regions. However, interpretation of such analyses must be made cautiously because temperate and tropical fossil records might not be comparable.

In particular, tropical records might be poorer, with the average persistence of taxa appearing to be younger,

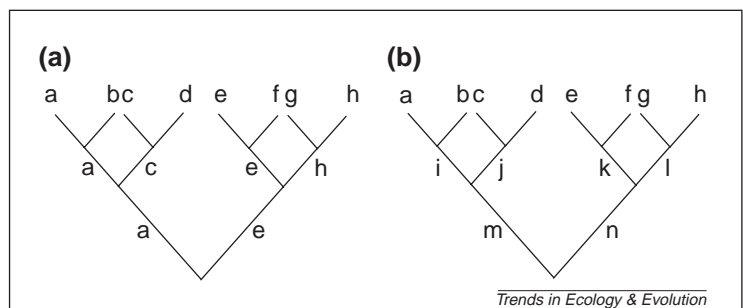


Fig. 2. Two hypothetical phylogenies with the same number of speciation events (seven events). All branch lengths represent five million years (My). In phylogeny (a) speciation is via cladogenesis with ancestral persistence, while in (b) speciation is via cladogenesis without ancestral persistence. The median taxon age is between five and 10 My in (a) and is five My in (b). Thus, latitudinal differences in the mode of speciation can cause differences in species-age frequency distributions (see also Ref. 38 for a discussion of latitudinal differences in models of diversification).

for several reasons. The tropical fossil record is more poorly explored than the temperate one^{40,43} and tropical climates usually provide poorer preservation than temperate climates⁴³. Thus, differences in both taphonomic setting and spatial asymmetry of fossil localities might result in tropical taxa appearing slightly younger than their temperate counterparts, especially given the decline in the likelihood of fossil recovery with time⁴³. Lyellian percentages (i.e. the proportion of a fossil fauna consisting of living species) have been used in some analyses in an attempt to overcome these issues, but the outcomes are often equivocal³⁰.

Equally, if the tropics are acting as both a museum and as a cradle, then no difference between age–frequency distributions might be observed. In other words, if origination rates are high and extinction rates are low in the tropics, and the converse is true in extratropical regions, then the two age–frequency distributions might be extremely similar, with the exception that diversity will be higher in the tropics. Indeed, in the study by Flessa and Jablonski³⁰ the frequency distributions of ages of tropical and extratropical bivalves did not differ significantly, although their median ages did under certain conditions.

Some authors have argued that higher speciation rates in the tropics have more to do with greater effective evolutionary time (e.g. shorter generation times) than with the larger geographic area of this region³. However, the relationship between evolutionary rate and generation time remains the subject of considerable debate⁴⁴.

A major hurdle

In addition to the three macroecological and macroevolutionary patterns the area model assumes, it also requires that the ecoclimatic zones decline in area moving from the equator towards the poles. However, they do not do so, at least not in terrestrial systems of the northern hemisphere. Here, the tundra region is larger than the other extratropical regions, which in themselves show little variation in total surface area, although they remain much smaller than the tropics¹. Three possible explanations have been proposed for why a latitudinal species-richness gradient might be expressed: first, low productivity at high latitudes reduces the species richness they would gain as a result of area alone^{2,9}. Second, zonal bleeding of tropical species into extratropical regions smooths out species-richness gradients⁷. Third, climatic variability at high latitudes increases the area of ecoclimatic zones that individual species can actually occupy¹².

In favour of the first explanation, there is a reasonable body of evidence indicating a strong monotonic relationship between productivity (or more accurately a surrogate for productivity) and diversity in terrestrial systems at geographic scales⁴⁵. However, some studies have shown either that this relationship is explained better by other variables or that it is highly nonlinear. Nonetheless, variation in productivity is regularly identified as an important correlate of species richness, often to the exclusion of other potential explanatory variables⁴⁵. The second explanation is accorded considerable importance by Rosenzweig⁷. To date, the one study that has been performed on zonal bleeding has provided support for it⁸.

The third hypothesis regarding climatic variability is also quite plausible. Stevens¹² suggested that a Rapoport effect is the consequence of a relatively straightforward mechanism. Individuals at higher latitudes encounter a wider temporal range of climatic conditions (e.g. greater extremes in temperature) than their more tropical counterparts. Thus, species to which these individuals belong have broader tolerances enabling them to achieve wider ranges. Because the

microhabitat requirements of these high-latitude organisms are not narrowly defined, the rescue or mass effect that leads to coexistence of high numbers of species does not occur in these areas. Consequently, they have lower species richness than more tropical areas. Although it appears that the Rapoport effect might be a more local than general phenomenon^{13,46}, the mechanism thought to be responsible for it has some significant, although poorly explored, nuances that might well be extremely important in accounting for the lack of a consistent relationship between diversity and the size of ecoclimatic regions.

Of most interest is the relationship between the mean and variability in climatic conditions. Terborgh⁴ showed that mean temperatures remain virtually constant between 25°N and 25°S. Combining this pattern with variation in surface area essentially generates a strongly peaked plot of the Earth's surface between 1°C isotherms centred on equatorial latitudes. This means that, for a substantial band about the equator, the temporal average of climatic conditions remains relatively constant. Thus, even if the temporal variability in temperature declines towards the equator, species at these latitudes should be able to occupy a disproportionately large latitudinal extent. Therefore, species at low latitudes might lose the potential to occupy broad latitudinal extents because individuals do not have to be able to withstand high temporal variance in climatic conditions. However, they regain some of this potential because mean conditions stabilize at low latitudes; thus, the latitudinal extent available to them is greater. Species at low latitudes might have large ranges for geographic reasons, whereas those at high latitudes might have large ranges for climatic reasons.

Therefore, for extratropical species any barriers posed by climatic conditions are likely to be less important than similar barriers are to tropical species; therefore, the speciation rate will decline. In addition, because of larger variation in patch quality at high latitudes (as a consequence of seasonal variation), species at higher latitudes probably move larger distances, thus reducing the impacts of barriers. This movement is also likely to have been exacerbated by the effects of glaciations^{46,47}, thus reducing the likelihood of speciation even further.

Conclusions

The area model assumes not only that latitudinal gradients in richness can be generated by differences in ecoclimatic area, but also that they must. The effect of area on species richness is so important that it is almost inconceivable that it does not have a major role in determining these gradients. In principle, we agree. However, we caution that support for at least two of the three relationships underlying the area model is scanty or in the opposite direction and, in the case of the relationship between geographic range size and ecoclimatic area, perhaps impossible to accumulate empirically. Furthermore, the mechanisms modulating the area model might obscure its effects in many circumstances. The influence of productivity on taxon richness is especially significant in this regard and the subtleties of this relationship are increasingly being explored^{9,45}.

A second modulating mechanism that might significantly affect the interaction between range size and speciation probability at geographic scales is the major difference in the mechanisms promoting large range sizes in the tropics (geographic area) and in more polar (climate) regions⁴⁸. Finally, the existence of equilibrium diversities or, more importantly, latitudinal variation in such equilibrium conditions, is an assumption frequently made with regard

to the area model. Despite some evidence in favour of equilibrium conditions^{2,7,39}, their existence has often been questioned^{3,6}. Thus, like so many of the other processes underlying the area model, both the existence of equilibrium conditions and its implications, with regard to the way in which the latitudinal diversity gradient in species richness has arisen³⁹, merit further explicit investigation.

Despite these caveats, the area model is an important, although in many instances perhaps not sufficient, explanation for latitudinal patterns in taxon richness. Therefore, analyses examining geographic variation in taxon richness cannot afford to ignore the model and its nuances. More importantly, Rosenzweig's² championing of the area model has served to highlight several basic issues concerning range size, speciation and extinction that remain poorly understood despite their considerable significance.

Acknowledgements

We thank D. Jablonski, M. McGeoch, E. Stam and three anonymous referees for useful comments on this article; A. Rodrigues for discussion; and J. Barendse for drawing the figures. S.L.C. is funded by the South African National Research Foundation and the University of Pretoria. K.J.G. is a Royal Society University Research Fellow. The Royal Society generously funded a research visit by K.J.G. to South Africa, during which parts of this article were written.

References

- Rosenzweig, M.L. (1992) Species diversity gradients: we know more and less than we thought. *J. Mammal.* 73, 715–730
- Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*, Cambridge University Press
- Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65, 514–527
- Terborgh, J. (1973) On the notion of favorableness in plant ecology. *Am. Nat.* 107, 481–501
- Rohde, K. (1997) The larger area of the tropics does not explain latitudinal gradients in species diversity. *Oikos* 79, 169–172
- Rohde, K. (1998) Latitudinal gradients in species diversity. Area matters, but how much? *Oikos* 82, 184–190
- Rosenzweig, M.L. and Sandlin, E.A. (1997) Species diversity and latitudes: listening to area's signal. *Oikos* 80, 172–176
- Blackburn, T.M. and Gaston, K.J. (1997) The relationship between geographic area and the latitudinal gradient in species richness in New World birds. *Evol. Ecol.* 11, 195–204
- Roy, K. *et al.* (1998) Marine latitudinal diversity gradients: tests of causal hypotheses. *Proc. Natl. Acad. Sci. U. S. A.* 95, 3699–3702
- Willig, M.R. and Lyons, S.K. (1998) An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the New World. *Oikos* 81, 93–98
- Qian, H. and Ricklefs, R.E. (1999) A comparison of the taxonomic richness of vascular plants in China and the United States. *Am. Nat.* 154, 160–181
- Stevens, G.C. (1989) The latitudinal gradient in geographic range: how so many species coexist in the tropics. *Am. Nat.* 133, 240–256
- Gaston, K.J. *et al.* (1998) Rapoport's rule: time for an epitaph? *Trends Ecol. Evol.* 13, 70–74
- Pagel, M.D. *et al.* (1991) Ecological aspects of the geographical distribution and diversity of mammalian species. *Am. Nat.* 137, 791–815
- Smith, F.D.M. *et al.* (1994) Geographical ranges of Australian mammals. *J. Anim. Ecol.* 63, 441–450
- Rosenzweig, M.L. (1978) Geographical speciation: on range size and the probability of isolate formation. In *Proceedings of the Washington State University Conference on Biomathematics and Biostatistics* (Wolkind, D., ed.), pp. 172–194, Washington State University Press
- Gaston, K.J. and Chown, S.L. (1999) Geographic range size and speciation. In *Evolution of Biological Diversity* (Magurran, A. and May, R.M., eds), pp. 236–259, Oxford University Press
- Chown, S.L. (1997) Speciation and rarity: separating cause from consequence. In *The Biology of Rarity* (Kunin, W.E. and Gaston, K.J., eds), pp. 91–109, Chapman & Hall
- Gaston, K.J. (1996) The multiple forms of the interspecific abundance–distribution relationship. *Oikos* 75, 211–220
- Hansen, T.A. (1978) Larval dispersal and species longevity in Lower Tertiary gastropods. *Science* 199, 886–887
- Jablonski, D. and Lutz, R.A. (1983) Larval ecology of marine benthic invertebrates: paleobiological implications. *Biol. Rev.* 58, 21–89
- García-Ramos, G. and Kirkpatrick, M. (1997) Genetic models of adaptation and gene flow in peripheral populations. *Evolution* 51, 21–28
- Gavrilets, S. *et al.* (1998) Rapid parapatric speciation on holey adaptive landscapes. *Proc. R. Soc. London Ser. B* 265, 1483–1489
- Gavrilets, S. *et al.* Patterns of parapatric speciation. *Evolution* (in press)
- Stanley, S.M. (1986) Population size, extinction and speciation: the fission effect in Neogene Bivalvia. *Paleobiology* 12, 89–110
- Jackson, J.B.C. (1974) Biogeographic consequences of eurytopy and stenotopy among marine bivalves and their evolutionary consequences. *Am. Nat.* 108, 541–560
- Flessa, K.W. and Thomas, R.H. (1985) Modelling the biogeographic regulation of evolutionary rates. In *Phanerozoic Diversity Patterns. Profiles in Macroevolution* (Valentine, J.W., ed.), pp. 355–376, Princeton University Press
- Jablonski, D. (1986) Background and mass extinctions: the alternation of macroevolutionary regimes. *Science* 231, 129–133
- Jablonski, D. (1987) Heritability at the species level: analysis of geographic ranges of Cretaceous molluscs. *Science* 238, 360–363
- Flessa, K.W. and Jablonski, D. (1996) The geography of evolutionary turnover: a global analysis of extant bivalves. In *Evolutionary Paleobiology* (Jablonski, D. *et al.*, eds), pp. 376–397, Chicago University Press
- Wagner, P.J. and Erwin, D.H. (1995) Phylogenetic patterns as tests of speciation models. In *New Approaches to Speciation in the Fossil Record* (Erwin, D.H. and Anstey, R.L., eds), pp. 87–122, Columbia University Press
- Pearson, P.N. (1998) Speciation and extinction asymmetries in paleontological phylogenetics: evidence for evolutionary progress? *Paleobiology* 24, 305–335
- Stebbins, G.L. (1974) *Flowering Plants: Evolution Above the Species Level*, Belknap
- Fjeldså, J. (1994) Geographical patterns for relict and young species of birds in Africa and South America and implications for conservation priorities. *Biodiv. Conserv.* 3, 207–226
- Gaston, K.J. and Blackburn, T.M. (1996) The tropics as a museum of biological diversity: an analysis of the New World avifauna. *Proc. R. Soc. London Ser. B* 263, 63–68
- Jablonski, D. and Bottjer, D.J. (1991) Environmental patterns in the origins of higher taxa: the post-Paleozoic fossil record. *Science* 252, 1821–1833
- Klicka, J. and Zink, R.M. (1999) Pleistocene effects on North American songbird evolution. *Proc. R. Soc. London Ser. B* 266, 695–700
- Stenseth, N.C. (1984) The tropics: cradle or museum? *Oikos* 43, 417–420
- Wei, K.-Y. and Kennett, J.P. (1986) Taxonomic evolution of Neogene planktonic Foraminifera and paleoceanographic relations. *Paleoceanography* 1, 67–84
- Jablonski, D. (1993) The tropics as a source of evolutionary novelty through geological time. *Nature* 364, 142–144
- Stehli, F.G. *et al.* (1969) Generation and maintenance of gradients in taxonomic diversity. *Science* 164, 947–949
- Sepkoski, J.J. (1999) Rates of speciation in the fossil record. In *Evolution of Biological Diversity* (Magurran, A. and May, R.M., eds), pp. 260–282, Oxford University Press
- Smith, A.B. (1994) *Systematics and the Fossil Record: Documenting Evolutionary Patterns*, Blackwell Science
- Cardillo, M. (1999) Latitudinal rates of diversification in birds and butterflies. *Proc. R. Soc. London Ser. B* 266, 1221–1225
- Waide, R.B. *et al.* (1999) The relationship between productivity and species richness. *Annu. Rev. Ecol. Syst.* 30, 257–300
- Roy, K. *et al.* (1996) Scales of climatic variability and time averaging in Pleistocene biotas: implications for ecology and evolution. *Trends Ecol. Evol.* 11, 458–463
- Coope, G.R. (1995) Insects in ice age environments: why so little extinction? In *Extinction Rates* (Lawton, J.H. and May, R.M., eds), pp. 55–74, Oxford University Press
- Gaston, K.J. and Chown, S.L. (1999) Why Rapoport's rule does not generalise. *Oikos* 84, 309–312
- Trewick, S.A. (1997) Flightlessness and phylogeny amongst endemic rails (Aves: Rallidae) of the New Zealand region. *Philos. Trans. R. Soc. London Ser. B* 352, 429–446
- Paradis, E. (1997) Assessing temporal variations in diversification rates from phylogenies: estimation and hypothesis testing. *Proc. R. Soc. London Ser. B* 264, 1141–1147