PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 1998 **353**, 219-230
doi: 10.1098/rstb.1998.0204

The Royal Society

Species-range size distributions: products of speciation, extinction and transformation

Kevin J. Gaston

Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK (`k.j.gaston@sheffield.ac.uk`)

One basic summary of the spatial pattern of biodiversity across the surface of the Earth is provided by a species-range size distribution, the frequency distribution of the numbers of species exhibiting geographic ranges of different sizes. Although widely considered to be approximately log-normal, increasingly it appears that across a variety of groups of organisms this distribution systematically departs from such a form. Whatever its detailed shape, however, the distribution must arise as a product of three processes, speciation, extinction and transformation (the temporal dynamics of the range sizes of species during their life times). Considering the role potentially played by each of these processes necessitates drawing on information from a diverse array of research fields, and highlights the possible role of geographic range size as a common currency uniting them.

Keywords: speciation; transformation; geographic ranges; extinction; macroecology

1. INTRODUCTION

No species is distributed ubiquitously across the Earth. Nonetheless, global geographic range sizes still vary by at least some 12 orders of magnitude (Brown *et al*. 1996). At one extreme lie those species constrained by ecology or by history to occupy small isolated islands of habitat or very scarce sets of environmental conditions. Human activity increasingly plays a role in this constraint, but undoubtedly very many species would never have been widely distributed even in its absence. At the other extreme lie those species which are distributed across multiple biogeographic regions. Such widespread occurrence appears more frequent among marine than terrestrial species, although particularly in the case of the latter it has doubtless become more common also as a consequence of human activity (facilitating the movement of species across otherwise largely impassable barriers).

The tendency for marine species on average to be more widely distributed than terrestrial (Rapoport 1994) is associated with a lower species richness in marine than terrestrial systems (May 1994; Gaston & Williams 1996). This reflects a more general observation that variation in geographic distribution is related to many other large-scale spatial patterns of biodiversity. Latitudinal, altitudinal and depth gradients, as well as patterns of hotspots, turnover and complementarity, all follow from the fact that species exhibit ranges of differing geographic extent, which are then distributed non-randomly across the landscape and through the media which envelop it.

The interspecific variance in geographic range sizes has stimulated a host of investigations of the constraints on the occurrences of more narrowly distributed species and of the mechanisms which enable the more widely distributed to become so (e.g. for references and reviews, see Woodward 1987; Hengeveld 1990). This contrasts with the relative paucity of interest that has been directed toward broad interspecific patterns in the determinants and consequences of this variation (for reviews, see Kunin & Gaston 1993, 1997; Gaston 1994*a*; Brown 1995). Perhaps the most basic summary of, and pattern in, the variation of geographic range sizes exhibited by a taxonomic assemblage is the species-range size distribution (the frequency distribution of species with different range sizes) and its associated statistics. In stark contrast to the closely related species-abundance distribution there have been only a comparative handful of studies concerned with species-range size distributions (Gaston 1996*a*).

In this paper I consider the form of, and some of the mechanisms underlying, species-range size distributions. In so doing, I will essentially be exploring one viewpoint on the generation of spatial and temporal patterns in biodiversity. Throughout, discussion will be centred on the entire geographic range sizes of species. The frequency distributions of the occurrences of species over smaller areas have been the subject of substantial interest (e.g. Hanski 1982; Gotelli & Simberloff 1987; Williams 1988; Gaston & Lawton 1989; Collins & Glenn 1990; Maurer 1990; Gotelli 1991; Tokeshi 1992; Gaston 1994*a*). They may, however, take a rather different form from distributions based on entire geographic range sizes, with doubtless an interesting interplay between the two, and will not be addressed herein.

2. THE FORM OF THE DISTRIBUTION

The frequency distribution of the geographic range sizes of species in a taxonomic assemblage tends to be unimodal with a strong right-skew. That is, most species have relatively small range sizes, and a few have relatively large ones (figure 1; e.g. Willis 1922; Freitag 1969; Anderson 1977, 1984*a*,*b*, 1985; Rapoport 1982; McAllister *et al*. 1986; Schoener 1987; Pomeroy & Ssekabiira 1990; Pagel *et al*. 1991; Gaston 1994*a*, 1996*a*; Brown 1995; Roy *et al*. 1995;

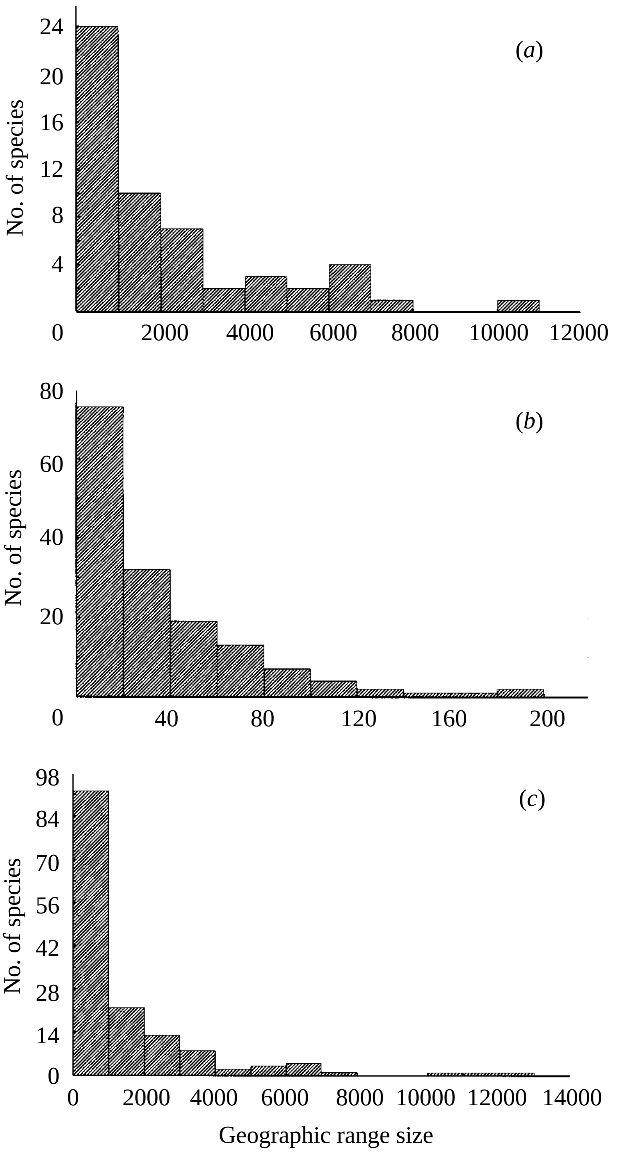

Figure 1. Species-range size distributions for: (*a*) *Harpalus* beetles in North America (maximum extent, km); (*b*) wildfowl worldwide (number of 611 000 km^2 cells occupied); and (*c*) primates worldwide (1000s km^2). From unpublished analyses and data in Noonan (1990) and Wolfheim (1983).

Blackburn & Gaston 1996; Brown *et al*. 1996; Hughes *et al*. 1996). Indeed, in virtually all published species-range size distributions in which range size is untransformed, the most left-hand range size class is also the modal class. These distributions tend toward an approximately normal distribution when geographic range sizes are subject to a logarithmic transformation (e.g. Anderson 1984*a*,*b*; McAllister *et al*. 1986; Pagel *et al*. 1991; Gaston 1994*a*, 1996*a*; Blackburn & Gaston 1996; Brown *et al*. 1996; Hughes *et al*. 1996). This implies that there are not simply disproportionately fewer species with large range sizes, but also with very small ones.

How adequate a description of species-range size distributions a log-normal distribution actually provides remains at present an open question. First, few studies have actually formally tested for significant departure from this model. Second, there have been growing hints that under a logarithmic transformation, species-range size distributions for at least some assemblages are, in some cases quite markedly, left-skewed (hereafter referred to as a left log-skew; Ruggiero 1994; Blackburn & Gaston 1996; Brown *et al*. 1996; Gaston & Blackburn 1997*b*). A perusal of published distributions suggests that this phenomenon may be widespread, a view which is supported by formal analyses of several data sets, although the coefficient of skewness is not always statistically significant (table 1).

If, as seems likely, a left log-skew is a general feature of species-range size distributions, this pattern could potentially simply be an artefact of the ways in which such distributions are assembled, with underlying distributions being log-normal. First, it could perhaps result from the rather crude fashion in which geographic range sizes are typically measured. The range sizes of species tend to be quantified either in terms of the approximate area contained within the geographic limits to their occurrence (an extent of occurrence measure) or in terms of an estimate of the numbers of cells in which a species has been recorded of a grid layed over a map of the region in which it occurs (an area of occupancy measure; both terms, *sensu* Gaston 1991, 1994*b*). For any given species, the former measure will tend to be larger than the latter, as it incorporates more areas in which individuals do not actually occur. However, in practice most assessments of either quantity are sufficiently crude that the true areal occurrence of a species is markedly overestimated. The proportional overestimation is unlikely to be similar for species of all range sizes, possibly distorting species-range size distributions markedly (Gaston *et al*. 1996). The variety of range size measures used by the studies in table 1 suggest that this is not a cause of the left log-skew, unless such distortions are shared by all such measures.

Second, many published species-range size distributions concern continental faunas. They may thus be truncated in one of two ways. Either those species in a taxonomic group whose ranges extend beyond the bounds of the continent are excluded from consideration, or their range sizes are measured only on the continent. Again such constraints may markedly distort species-range size distributions. However, such effects plainly cannot explain all left log-skewed distributions because these are also exhibited by global assemblages (table 1), and by assemblages of species endemic to continents (figure 2).

Third, the left log-skew may perhaps be a consequence of the impact of human activities on the occurrences of species, either in recent or prehistoric times, particularly in terms of increased levels of local extinction. This is difficult to discount for any assemblage. However, if this alone is the cause of the skew it would require that humans acted on the ranges of species in a rather different fashion from other agents of limitation (perhaps through the strong tendency to fragment ranges).

Assuming, as seems likely, that it is real and not an artefact, then the left log-skew pattern of species-range size distributions is reminiscent of species-abundance distributions at geographic scales, which have also been found to be left-skewed under logarithmic transformation, at least where the very rarest species have been censused adequately (Nee *et al*. 1991; Gaston 1994*a*; Gregory 1994;

Table 1. *The coefficients of skewness* (g_1) *associated with the species-range size distributions of various assemblages*

(In all cases, geographic range sizes are logarithmically (base 10) transformed. or, overall range; br, breeding range. Measure is that used to quantify range size: m, maximum linear extent; b, area within boundary; c, number of grid cells occupied; n.s., not significantly different from zero; $^{*}\,p<0.05$, $^{**}\,p<0.01$, and $^{***}\,p<0.001$.)

		measure	*n*	skewness	source
Harpalus carabids	N. America	b	54	-1.202^{***}	data in Noonan (1990)
Nebria carabids	N. America	m	55	$-0.350^{\text{n.s.}}$	data in Kavanaugh (1985)
bumblebees	global	c	241	$-0.034^{\text{n.s.}}$	P. H. Williams (unpublished data)
procellariiforms	global	c	108	-0.857^{***}	Gaston & Chown (unpublished data)
wildfowl	global (or)	c	154	$-0.36^{\text{n.s.}}$	Gaston & Blackburn (1996)
wildfowl	global (br)	c	154	$-0.31^{\text{n.s.}}$	Gaston & Blackburn (1996)
rails	global	c	132	$-0.750^{\text{n.s.}}$	data in del Hoyo *et al.* (1996)
woodpeckers	global	c	214	$-0.07^{\text{n.s.}}$	Blackburn *et al.* (1998)
birds	New World	c	3901	-0.585^{***}	Gaston & Blackburn (1997*b*)
ciconiiformes	New World	c	387	-0.923^{***}	Gaston & Blackburn (1997*b*)
sub-oscine passerines	New World	c	1107	-0.590^{***}	Gaston & Blackburn (1997*b*)
oscine passerines	New World	c	1158	-0.544^{***}	Gaston & Blackburn (1997*b*)
birds	Australia	c	573	-0.575^{***}	data in Blakers *et al.* (1984)
endemic birds	Australia	c	320	-0.531^{***}	data in Blakers *et al.* (1984)
primates[†]	global	b	148	-0.493^{*}	data in Wolfheim (1983)
bats	S. America	b	187	-0.825^{***}	Ruggiero (1994)
marsupials	S. America	b	77	$0.235^{\text{n.s.}}$	Ruggiero (1994)
edentates	S. America	b	28	$-0.472^{\text{n.s.}}$	Ruggiero (1994)
primates	S. America	b	57	$-0.385^{\text{n.s.}}$	Ruggiero (1994)
carnivores	S. America	b	43	-1.255^{**}	Ruggiero (1994)
artiodactyls	S. America	b	18	$0.177^{\text{n.s.}}$	Ruggiero (1994)
hystriocognath rodents	S. America	b	122	0.499^{*}	Ruggiero (1994)

[†] Data missing for a few very restricted species.

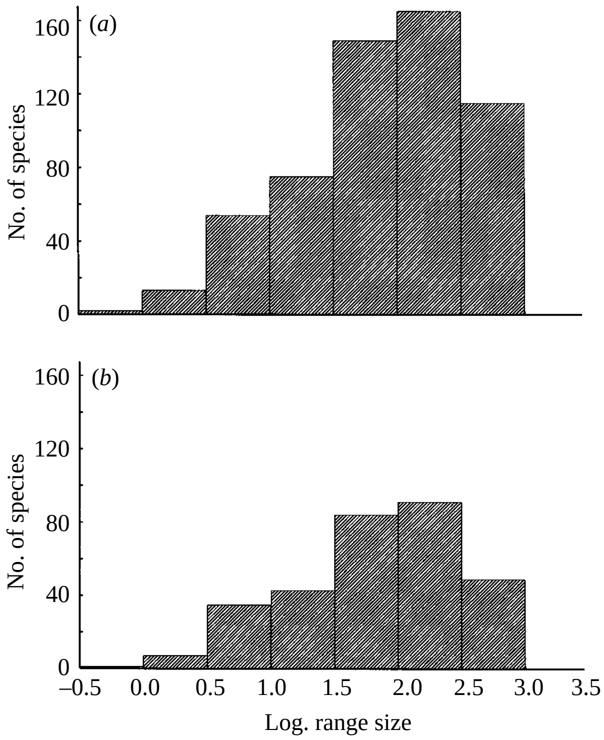

Figure 2. Species-range size distributions for birds in Australia: (*a*) all species; and (*b*) endemic species only. Seabirds and introductions are excluded in both cases. Data from Blakers *et al.* (1984).

Gaston *et al.* 1998). Given that species-body size distributions for geographic scale assemblages tend to be right-skewed under logarithmic transformation (Brown & Nicoletto 1991; Maurer *et al.* 1992; Brown *et al.* 1993; Blackburn & Gaston 1994), this would imply that none of the distributions of the three primary macroecological variables (abundance, range size, body size) for assemblages at large spatial scales are distributed strictly according to a log-normal.

In the case of species-abundance distributions, the left log-skew has been explained in terms of niche apportionment models, in which the abundances of species are considered to be associated with different processes of niche division (Nee *et al.* 1991; Tokeshi 1996). Models in which successive niche division tends to be higher for species with larger niches or higher abundances appear to fit particularly well, and Tokeshi (1996) has associated this with the greater likelihood that both higher abundances and larger geographic range sizes are more likely to generate new species (a point to which I shall return later). In so doing he raises a potential connection between the processes determining species-abundance and species-range size distributions, particularly because there is generally a positive (albeit not especially strong) interspecific relationship between abundance and range size (Hanski 1982; Brown 1984; Gaston & Lawton 1990; Hanski *et al.* 1993; Gaston 1994*a*, 1996*b*; Gotelli & Graves 1996; Gaston *et al.* 1997). However, if applicable at large spatial scales, niche apportionment models can only be acting as caricatures of the processes moulding species-abundance distributions. At such scales ultimately these distributions must be products of speciation, extinction and the temporal dynamics of the abundances of individual species. Similar processes must also ultimately determine the form of the frequency distributions of the geographic range sizes of species.

3. MECHANISMS

(a) *Speciation*

Speciation generates new species and hence additional geographic ranges, adding to a species-range size distribution. Its influence on such a distribution is, however, more complex, and depends fundamentally on the geographic mode of speciation. If we assume that speciation is predominantly allopatric, whilst acknowledging that other forms are probably more frequent or important than has often been claimed in the past (Tauber & Tauber 1989; Ripley & Beehler 1990; Schliewen *et al*. 1994; Rosenzweig 1995), then there are two essential issues to consider. First, we need to know whether species with geographic ranges of particular sizes are more likely to speciate than are those with ranges of other sizes. Second, we need to know the frequency of different asymmetries in the division of ancestral ranges as a product of speciation.

(i) *Probability of speciation*

The idea that species with larger geographic range sizes have a greater probability of speciation dates at least to Darwin (1859), and continues to attract support (e.g. Marzluff & Dial 1991; Wagner & Erwin 1995; Tokeshi 1996). Rosenzweig (1975, 1978, 1995) argues that on a purely probabilistic basis, species with larger geographic range sizes are more likely to undergo speciation, because the likelihood of their ranges being bisected by a barrier is greater than for a small range size. Differentiating, as Rosenzweig does, between two kinds of barriers, 'knives' (which have beginnings and ends) and 'moats' (which surround their isolates), then strictly this assertion is only true of moats. Very large ranges will tend to engulf knives, such that they do not engender speciation, and the probability of division will have a peak at intermediate range sizes. Rosenzweig (1995) argues that this is unlikely to occur because there are no, or virtually no, species with ranges so large that reducing them would make them an easier target for barriers. However, this view depends critically on the frequency distribution of barrier size. If most barriers are small-to-intermediate in size, relative to the range sizes of widespread species, then intermediate-sized ranges may indeed have a higher probability of speciation. Such an effect would be enhanced because barriers seem far more likely to take the form of knives than of moats.

In support of the view that species with small-to-intermediate range sizes are more likely to speciate than are those with larger range sizes, it has been argued that widespread and abundant taxa may often possess well-developed dispersal abilities (perhaps associated with them becoming widespread) and should as a consequence have a strong proclivity to maintain gene flow among populations, which will tend to inhibit speciation (e.g. Mayr 1963, 1988; Stanley 1979). Narrowly distributed and locally rare taxa with poor dispersal abilities (and patchy populations which may tend to form isolates) will tend to have higher speciation rates. The extent to which widely distributed species do indeed tend to have greater dispersal abilities remains debatable (e.g. Levinton 1988; Palumbi 1994; Gaston & Kunin 1997*a*).

In a similar vein, Chown (1997) proposes that rare, but not the rarest, species have the highest probability of speciation. Based on Stanley's (1986) 'fission effect' model, Chown envisages that speciation is a peaked function of geographic range size, which rises rapidly at small range sizes and then progressively subsides towards large range sizes. This is a substantial modification of the original fission effect model, which was intended to capture how the relative rates of speciation and extinction varied with the mean population size across all the species in an assemblage. However, equating geographic range size with population size, the underlying relationship between speciation rate and range size is not dissimilar to the full relationship modelled by Rosenzweig (1978, 1995) when the truncation effects he postulates are ignored.

A complication to assertions that small-to-intermediate range sizes are more likely to undergo speciation arises from the reduced probability of extinction associated with larger range sizes (see §3(*c*)). If species with larger range sizes are likely to persist for longer, this may enhance their probability of speciation. Even if species with smaller range sizes have a greater likelihood of speciation per unit time, species with larger ranges could potentially still be more likely to leave descendants.

I am aware of only one explicit attempt empirically to test the relationship between geographic range size and likelihood of speciation. Wagner & Erwin (1995) find that in analyses of two Neogene clades of Foraminifera and an Ordovician family of gastropods, species with larger geographic ranges are likely to leave more descendants in two cases but not in the third, and in all three cases species that have persisted for longer are likely to leave more descendants (the patterns are not consistent between cladogenetic and anagenetic modes of speciation). In the gastropod case (for which data are provided) the partial correlation between number of descendants (dependent variable) and range size, controlling for differences in longevity, is not significant ($r = 0.005$, $n = 45$, n.s.).

Regardless of whether speciation is more probable for species with small, intermediate or large range sizes, speciation will result (initially, but not necessarily eventually, see below) in the disproportionate addition to a species-range size distribution of range sizes towards smaller sizes than that of the ancestral species.

(ii) *Asymmetry of range division*

If it is ancestral species with relatively small geographic range sizes which are most likely to speciate, then the importance of the asymmetry of range division for an understanding of the form of species-range size distributions is markedly lessened. The products of any range division can only be two small ranges (be they two daughters, or a daughter and its ancestor if the latter persists). If species with large geographic range sizes are more likely to speciate, depending on the asymmetry of division, the outcome may span one large and one small range size through to two ranges each half the size of that of the ancestor at speciation. If we continue to regard patterns of speciation in terms of simple random events then, even with species with small range sizes being the more likely to speciate, the most likely immediate products of speciation are two species one of which is more widely distributed than is the other. A perfect 50:50 split is highly improbable.

The question of the degree of asymmetry in the range sizes of sister groups, immediately post-speciation, is closely related to the issue of whether allopatric speciation is best typified by a peripheral isolation model or by a vicariance model. In the former, peripheral isolates form by waif dispersal (establishment of a new population through long-distance movement across a barrier), micro-vicariance (physical division of a previously continuous distribution) or range retraction (causing peripheral populations to become isolated; Frey 1993). Here, the relatively widespread ancestral species is likely to change little while the peripheral isolate diverges (Glazier 1987). In the vicariance model, a subdivision of the range of an ancestral species occurs, such that there is cessation of contact between the two subpopulations, giving rise to new species. Here, both daughters of the ancestral range are likely to diverge, and the ancestral species will cease to exist. The two models are plainly very closely related, and may in some sense be seen as constituting points on a continuum of speciation processes. However, vicariant speciation may potentially result in any degree of asymmetry in the initial range sizes of daughter species, and is often portrayed as generating very similar-sized ranges. In contrast, peripheral isolation results, immediately post-speciation, in a highly asymmetrical split.

Both peripheral isolation (e.g. Kavanaugh 1979; Ripley & Beehler 1990; Levin 1993; Chesser & Zink 1994) and vicariance models (e.g. Cracraft 1982, 1986; Cracraft & Prum 1988; Lynch 1989) have significant support. The relative frequency of the two modes of speciation remains a point of some contention (e.g. see Bush 1975; Barton & Charlesworth 1984; Mayr 1988; Lynch 1989; Brooks & McLennan 1993; Frey 1993; Ripley & Beehler 1993; Chesser & Zink 1994; Taylor & Gotelli 1994; Wagner & Erwin 1995). Resolution of the issue rests in major part on the extent of post-speciational change in geographic range sizes (see §3(*b*)). This will to a marked degree determine the extent to which the present-day distributions of species can be used to reconstruct past patterns of speciation (Lynch 1989; Brooks & McLennan 1991). If dispersal is important, then it may entirely obscure the relative positions of, say, sister taxa at the time of their divergence. If it is not important then this will not be a problem.

Simplifying matters greatly, the probable patterns of gain and loss of small (S), intermediate (I) and large (L) range sizes can be determined under peripheral isolation and vicariance modes of speciation, if large ranges or small/intermediate ranges have the greater probability of speciation (table 2). The patterns vary perhaps most markedly in the loss of large ranges when speciation is by vicariance and large ranges have a greater likelihood of speciation.

Table 2. *Probable patterns of gain and loss of small (S), intermediate (I) and large (L) range sizes under peripheral isolation and vicariance modes of speciation, if large ranges or small/intermediate ranges have the greater probability of speciation (and ignoring subsequent range size transformation)*

greater probability of speciation	peripheral isolation		vicariance	
	gain	loss	gain	loss
large ranges	S	—	S/I	L
small/intermediate ranges	S	I?	S	S/I

(b) *Transformation*

The influence of speciation on the shape of species-range size distributions will rest in large part on the form the temporal dynamics of the sizes of the ranges of species subsequently take over their lifetimes (here termed 'transformations', to avoid possible confusion with other elements of the temporal dynamics of ranges). Plainly if ranges tended to remain very similar in size to those they initially attained, then speciation would be of far more importance than if they dramatically increased (or decreased) in range size shortly after (or at least on a far faster time-scale than that on which speciation operates). Speciation and transformation are not entirely independent; if an ancestral species persists after a speciation event (e.g. by peripheral isolation), the range size of that species will be reduced by that event. However, for the purposes of this discussion this complication will largely be ignored. Plainly its significance will rest on the predominant mode of speciation.

Several models of transformation have, explicitly or implicitly, been discussed (see, also, Gaston & Kunin 1997*b*; Gaston & Blackburn 1997*a*). I will consider five, although these are not, as we shall see, necessarily of equivalent status.

(i) *Models*

Stasis I: the simplest model of range size change is one of stasis, in which the range size of a species changes little post-speciation, either until the species disappears as a result of cladogenesis or until a rapid decline to extinction (figure 3*a*). This model is plainly unrealistic. If it operated then geographic range sizes would be expected to have declined steadily, and rather rapidly, through evolutionary time, as speciation progressively subdivided them. This is not to say that mean range size may not indeed have declined through time, it seems inevitable that for terrestrial organisms declines will have accompanied continental breakup, and that, more generally, declines may have accompanied increases in species richness.

As previously noted, our ability to reconstruct past speciation events will often depend in large part on the extent of deviation from the stasis I model. Departure may, however, under some circumstances be substantial without necessarily greatly influencing reconstructions. For example, the geographic ranges of daughter species either side of a major barrier (e.g. continental separation) may change dramatically after a vicariant speciation event without necessarily obscuring that event, provided that in spreading neither daughter species crosses the barrier.

Stasis II: an alternative model of stasis is one in which post-speciation the range size of a daughter species increases rapidly, remains approximately at this level for the bulk of its existence, and then either declines rapidly to extinction or simply ceases to exist through vicariant speciation (figure 3*b*). Such a model has been argued to

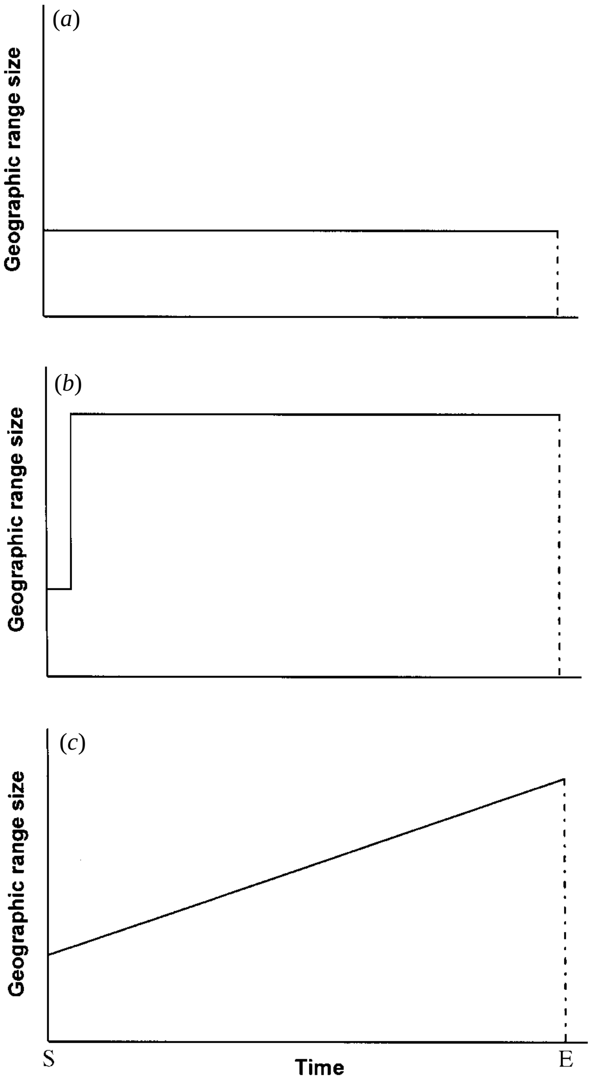

Figure 3. Three models of the temporal dynamics of the geographic range sizes of species (see text for details). (*a*) Stasis I, (*b*) stasis II, and (*c*) age and area. Solid lines represent the trajectory of range size from speciation (S) to extinction (E), with the latter either occurring through vicariant speciation or a decline in range size to zero (dashed line).

reflect well the dynamics of the geographic range sizes of species of Late Cretaceous molluscs, because the distribution of range sizes of those species that originated in the two million years preceding the end-Cretaceous extinction (whose geologic durations were thus truncated) is statistically indistinguishable from that of the species originating in the previous 14 million years (Jablonski 1987). Additional tests of this model are lacking and would be highly desirable.

This stasis II model would require that species be able to spread very rapidly postspeciation. An explicit test is difficult, but some indication of potential rates of spread may be given by the results of introducing species to areas in which historically they have not occurred (e.g. continents which lie outside their native distributions) or by human alteration of conditions enabling them to do so. In such cases rates of spread can indeed be high, with large areas being invaded in matters of decades (e.g. Wing 1943; Lynch 1989; Hengeveld 1989; Grosholz 1996; Veit & Lewis 1996; Williamson 1996).

Perceptions of the extent to which the geographic range sizes of species may remain approximately constant for long periods may have been unduly influenced by studies of the ranges of north temperate species post glaciation, which tend to exhibit great dynamism (although even then often punctuated by perhaps long periods of stasis; e.g. Woods & Davis 1989; Dennis 1993; Burton 1995; Coope 1995). These may be far from typical of all species, and it is frequently not clear to what extent such dynamism is reflected in changes in range size rather than simply range shifts.

Age and area: Willis (1922) argued that the geographic ranges of species followed a trajectory of steadily increasing size the longer they persisted, presumably culminating with a rapid decline to extinction or disappearance through cladogenesis (figure 3*c*). That is, there is a positive intraspecific relationship between evolutionary age and range size. The age and area hypothesis underwent vigorous debate, and was widely rejected (e.g. Gleason 1924; Stebbins & Major 1965; Stebbins 1978). In its simplest form it cannot be correct because there are ample examples of young species that are widely distributed and old species that are very restricted in their distribution. Nonetheless, it continues to be maintained in some circles that there is a broad positive interspecific correlation between age and area (although such a pattern need not follow from an intraspecific age and area relationship), albeit not necessarily of strong predictive value (McLaughlin 1992), and some recent analyses have reported such a pattern, at least among small numbers of closely related species (Taylor & Gotelli 1994).

Cyclic: the dynamics of the geographic range sizes of species have been regarded by some as essentially cyclic (e.g. Dillon 1966). This is most explicitly expressed in the concept of the taxon cycle (initially proposed for insular faunas but later generalized to mainland ones; Wilson 1961; Ricklefs & Cox 1972, 1978). Here, a newly evolved species expands its range (stage I), to become widespread (stage II), this range then fragments due to local extinctions (stage III), and the species becomes restricted to a small area (stage IV) (Ricklefs & Cox 1972, 1978).

Depending on the relative duration of these stages, this model could be closely caricatured by some that have already been mentioned. For example, if stage II were to be dominant, the taxon cycle would equate to the stasis II model, whereas if stage I were to be dominant the cycle would equate to an age and area model.

Evidence has been produced both in support of (Ricklefs & Cox 1972; Glazier 1980; Rummel & Roughgarden 1985; Roughgarden & Pacala 1989) and against (Pregill & Olson 1981; Liebherr & Hajek 1990; Losos 1992) the existence of taxon cycles for particular assemblages; the observed pattern is likely to be determined by the geographic pattern of isolation. Likewise, other essentially cyclic models have variously been postulated, supported and rejected (e.g. Erwin 1985; Liebherr & Hajek 1990). It certainly seems unlikely that any single cyclic model is of very general applicability.

Idiosyncratic: there need, of course, be no general pattern of change in the geographic range sizes of species

Table 3. *Spearman rank correlations between the range sizes of sister species (sharing a terminal bifurcation), assuming that they are of equal age, and based on arbitrary sequencing of species in each pair*

	No. pairs	r_s
Harpalus carabids	10	0.515^{NS}
leopard frogs	7	0.643^{NS}
albatrosses	6	0.170^{NS}
passerine birds	18	0.220^{NS}
birds	18	0.647^{**}
dabbling ducks	16	0.275^{NS}

Data sources: Madge & Burn (1988), Lynch (1989), Noonan (1990), Livezey (1991), del Hoyo *et al.* (1992), Chesser & Zink (1994), Nunn *et al.* (1996).

between speciation and extinction. Different species may exhibit entirely idiosyncratic trajectories. This would seem in keeping with the continual adaptation and change that may result from responding to the demands of the Red Queen (Van Valen 1973; Ricklefs & Latham 1992), and with the changes in the distributions of some species over the past few decades (e.g. Frey 1992; Burton 1995; Parmesan 1996). If such a pattern prevails then one might expect to see little similarity in the geographic range sizes of closely related species, unless the traits which influence range size are strongly phylogenetically conserved, in which case in climatically and ecologically similar regions the distributions of close relatives might be expected to fluctuate in parallel (Ricklefs & Latham 1992).

There are two lines of evidence regarding the similarity of geographic range sizes of closely related species. First, a significant positive correlation has been documented between the geographic range sizes of closely related species of Late Cretaceous molluscs, from which Jablonski (1987) inferred that range size is heritable at the species level (see, also, Ricklefs 1989; Ricklefs & Latham 1992). However, examination of a few contemporary data sets based on sister species does not uphold this as a generality, albeit all have comparatively small sample sizes (table 3); although note that all the correlations are positive. These results could potentially be reconciled if the geographic range sizes of species are highly labile over their lifetimes such that at any one time closely related species do not have very similar range sizes, but that when this variation is effectively summed over periods of evolutionary or geological time (as inevitably occurs in the fossil record) then strong phylogenetic patterns of interspecific variation in range sizes become apparent. Equally, the results for Late Cretaceous molluscs simply may not generalize.

Second, it also appears that most of the variation in the geographic range sizes of species is explained at low taxonomic levels (Arita 1993; Brown 1995; Gaston & Blackburn 1997*b*; for similar results for range sizes at mesoscales, see Hodgson 1993; Peat & Fitter 1994; Kelly & Woodward 1996). Indeed, for several data sets the majority of variation is explained at the level of species within genera (figure 4). This contrasts with many life history variables, where little variation is explained at this level (e.g. Read & Harvey 1989; Harvey & Pagel 1991). However, this is not to say that higher taxonomic levels are not important, as they may still account for reasonable amounts of variation (figure 4; Cotgreave & Pagel 1997).

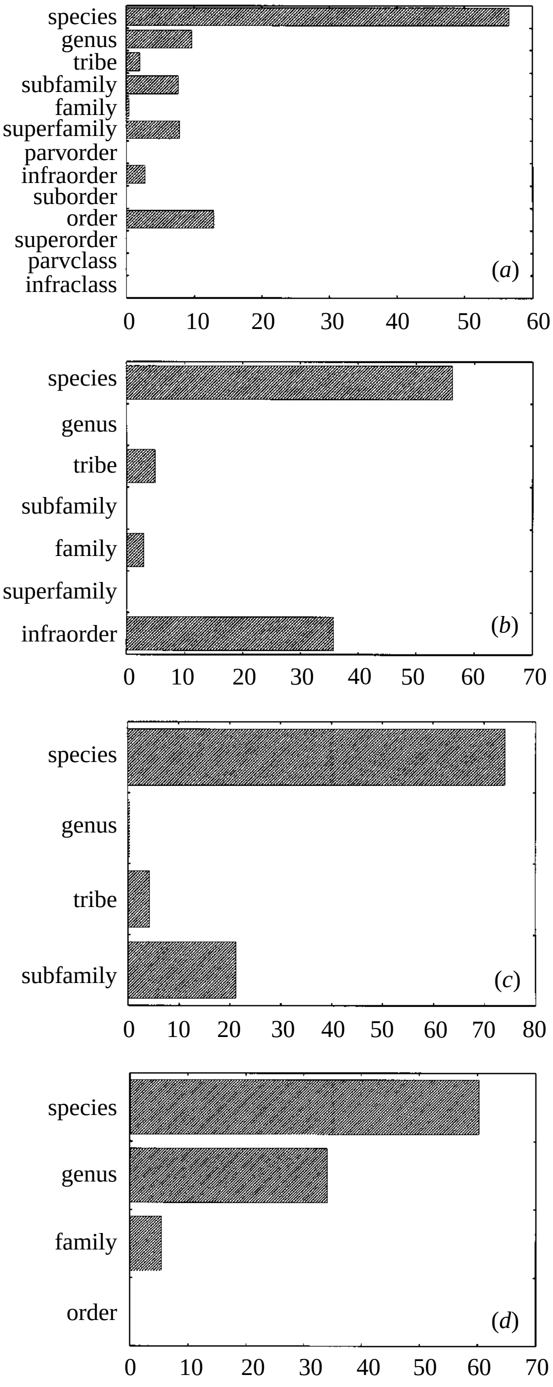

Figure 4. The proportion of variation in the geographic range sizes (logarithmically transformed) of species that is explained at different taxonomic levels for: (*a*) New World birds; (*b*) wildfowl; (*c*) woodpeckers; and (*d*) regular sea urchins. From: Gaston & Blackburn (1997*b*), Blackburn *et al.* (1998), and data in Emlet (1995) and Kier & Lawson (1978).

Overall, the weight of evidence suggests that range sizes are not strongly phylogenetically conserved, possibly favouring an idiosyncratic model of range size dynamics. However, such a pattern could equally fit several other models of such dynamics. For example, if closely related species each followed a stasis II-type model, but the maximum range sizes achieved were rather different.

In considering the potential validity of an idiosyncratic model it should be borne in mind that, if for an individual species this tends to result in the maintenance of an average range size of similar size to that immediately after its speciation, then as with the stasis I model the average range size across species may be expected to decline markedly with evolutionary time.

(ii) *Synthesis*

In summation, there is limited evidence in support of several possible models of the long-term dynamics of range sizes, but we do not appear at the present time to be in a position to conclude which are the most important. Such a conclusion seems at odds with, for example, the claims of vicariance biogeography, in which dispersal is rejected as a first-order explanation of the distribution of a group, in favour of one based on vicariance (Wiley 1988).

(c) ***Extinction***

The form of a species-range size distribution is not only potentially influenced by the addition of new ranges through speciation and the transformation of range sizes through temporal dynamics, but also by the loss of ranges through extinction, and hence by the duration for which species with different geographic range sizes persist. As with transformation, the role of extinction in shaping species-range size distributions is intimately associated with the predominant pattern of speciation. If speciation occurs primarily by vicariance, then speciation events may be accompanied by extinction (pseudo-extinction, *sensu* Wagner & Erwin 1995) of the ancestral species (Brooks & McLennan 1991). This would mean that, ignoring other extinction events, the relationship between probability of extinction and range size would be the same as that between the probability of speciation and range size.

There is empirical evidence for a positive relationship between time to extinction and range size for various paleontological species assemblages (Jackson 1974; Hansen 1978, 1980; Stanley 1979; Koch 1980; Jablonski 1986*a*,*b*; Buzas & Culver 1991; Jablonski & Raup 1995). Species with larger range sizes tend to persist for longer (an observation which dates at least to Lamarck; see McKinney 1997). The correlation appears very general, although it is not always especially strong, and may break down during periods of mass extinction (Jablonski 1986*b*; Norris 1991), which should perhaps raise concerns among conservationists given the present highly elevated levels of extinction (May *et al*. 1995). The relationship may also have an artefactual component, because species with larger range sizes have a greater probability of preservation in the fossil record and may thus appear to persist for longer (Russell & Lindberg 1988*a*,*b*; but, see Jablonski 1988).

Assuming, not unreasonably, that it is not simply an artefact, such a pattern may exist for three possible reasons, although often only the first is explicitly stated: (i) species with larger geographic range sizes may be less likely to walk randomly to extinction, and thus they persist for longer; (ii) species with traits which make them less prone to local extinction, and hence able to persist for longer, may also be enabled to maintain larger range sizes because of this extinction resistance; and (iii) species with larger range sizes may have them because they have persisted for longer (there is an age and area relationship; see above).

The first argument, that species with large range sizes are *per se* less likely to become extinct, seems inescapable, if for no other reason than that in a changing environment a widespread species is more likely to be able to continue to persist somewhere than is a narrowly distributed species. There have, however, been few empirical attempts to ascertain whether range size exerts an effect on extinction risk which is independent of local density, perhaps the most important correlate of range size. A positive correlation between geographic range size and persistence may potentially result because widespread species tend to be locally more abundant (i.e. at higher density; see earlier references), and locally more abundant species tend to be less likely to become extinct (e.g. Terborgh & Winter 1980; Pimm *et al*. 1988; Tracy & George 1992). What limited evidence there is suggests, however, that range size may indeed have an independent effect (see Rosenzweig 1995; Gaston & Blackburn 1996; Mace & Kershaw 1997).

As mentioned earlier, although there is some limited evidence for an age and area relationship it is not a general one, and seems unlikely to contribute strongly to a general relationship between geographic range size and persistence.

Whatever determines the relationship between range size and likelihood of extinction, the influence of extinction on species-range size distributions will predominantly be to remove species from the left-hand side of the distribution. If speciation tends to generate large numbers of species with very small range sizes, and extinction probability is greater for species with small ranges, this begs the question of how these incipient species manage to persist. The obvious answer is that many of them probably do not (Gorodkov (1992) suggests most). Indeed, it would seem likely that there is strong selection among newly evolved species (Glazier 1987). The existence of some very general biological differences between narrowly distributed and widely distributed species (Kunin & Gaston 1997) may, in part, be generated by this process, with only those species possessing traits which reduce their vulnerability to extinction persisting at small range sizes.

4. CONCLUSIONS

Charles Darwin (1975) described the study of geographic ranges as 'a grand game of chess with the world for a board'. The game is not a simple one. The pieces—the species—occupy different numbers of squares on the board at different times, they appear and then disappear, and many pieces may occupy the same square at the same time. Moreover, we can only gain glimpses of the past moves. Nonetheless, this is also no idle game. The pattern of moves has resulted in the patterns of biodiversity that we observe today.

The species-range size distribution provides a useful framework for considering how Darwin's 'game of chess' has generated the patterns of biodiversity and for organizing and cataloguing our thoughts about them. Determining how this distribution results requires the answers to questions that have been posed in a variety of fields of study, and whose connections have in the past not often been readily apparent. Indeed, to determine

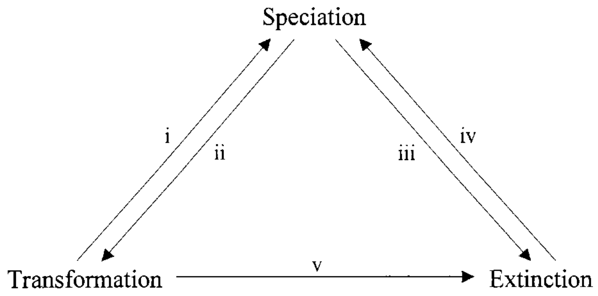

Figure 5. Some interactions between the effects of speciation, transformation and extinction with possible implications for species-range size distributions: (i) temporal changes in range size change the likelihood of speciation; (ii) speciation changes range size; (iii) under some speciation scenarios the ancestral species does not persist after speciation; (iv) lower rates of extinction may increase the likelihood of speciation; and (v) temporal changes in range size change the likelihood of extinction.

the relative importance of the processes of speciation, transformation and extinction in shaping the distribution is to forge a link between questions that are central to the study of ecology and of biogeography, with geographic range size as the common currency. On the one hand, ecology is concerned with the interactions between organisms and their environment (Begon *et al*. 1996), typically at local scales. In particular, in this context, it is concerned with the role of present conditions (abiotic and biotic) in determining distribution (transformation). On the other hand, the origins of biogeography lie in systematics (Myers & Giller 1988), and a more historical, and regional or global, view of the determinants of distributions has been a dominant theme (speciation and extinction).

If the likelihood of speciation and extinction were unbiased with respect to geographic range size and were the dominant processes, and if speciation had relatively little impact on the size of ancestral geographic ranges, then an approximately log-normal species-range size distribution would be predicted to result. However:

(i) Likelihood of speciation is probably not an unbiased function of range size. The form of the bias remains contentious, but the weight of opinion would seem to favour an approximately unimodal relationship, with small to intermediate range sizes having the greatest likelihood of speciation and large and very small range sizes the least likelihood.
(ii) Speciation may have a marked impact on the range sizes of ancestral species, unless it occurs predominantly by peripheral isolation.
(iii) Likelihood of extinction is not an unbiased function of range size. Rather, risk of extinction declines with increasing range size.
(iv) Transformation must influence species-range size distributions to some degree, because the only model which involves no change of range sizes at speciation (a stasis I model) is problematic. The limited evidence for several different models of transformation suggests that the importance of the process in shaping species-range size distributions may be very variable. For example, it would seem likely to be very significant, and to potentially swamp the effects of speciation, in regions experiencing strong environmental change. Here, areas which a species initially occupied may become untenable and new areas may become accessible.

The interactions of speciation, extinction and transformation are potentially complex (figure 5). Their outcome is a species-range size distribution which although sometimes not dissimilar from a log-normal, seems consistently to depart from such a description. This departure may ultimately prove a key to understanding the relative importance of the processes that generate it.

K.J.G. is a Royal Society University Research Fellow. I am grateful to Tim Blackburn, Steven Chown, Bob May, John Spicer, Phil Warren, Mark Williamson and an anonymous referee for helpful discussion and comments, to Bob May for his encouragement to pursue the ideas outlined herein, and to Anne Magurran and Bob May for the invitation to participate in the Royal Society discussion meeting.

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