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The distribution of species range size: a stochastic process

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The major role played by environmental factors in determining the geographical range sizes of species raises the possibility of describing their long-term dynamics in relatively simple terms, a goal which has hitherto proved elusive. Here we develop a stochastic differential equation to describe the dynamics of the range size of an individual species based on the relationship between abundance and range size, derive a limiting stationary probability model to quantify the stochastic nature of the range size for that species at steady state, and then generalize this model to the species-range size distribution for an assemblage. The model fits well to several empirical datasets of the geographical range sizes of species in taxonomic assemblages, and provides the simplest explanation of species-range size distributions to date.

Keywords: geographical range size; macroecology; stochasticity; temporal dynamics

1. INTRODUCTION

Species differ enormously in the sizes of their geographical ranges. Some are narrowly distributed, and others occur over areas that may be many orders of magnitude larger (Brown *et al.* 1996; Gaston 1996). For a given taxonomic assemblage, the frequency distribution of species range sizes (the species-range size distribution) tends to be strongly right-skewed, with the smallest size class being the modal one. That is, most species are rather restricted in their geographical occurrence, and only a few are widespread (Anderson 1977, 1984*a,b*; Pagel *et al.* 1991; Gaston 1994, 1996, 1998; Brown *et al.* 1996; Gaston & Chown 1999).

Much of the discussion of the determinants of the shape of species-range size distributions has focused on the roles of speciation and extinction processes (e.g. Anderson 1985; Flessa & Thomas 1985; Chown 1997; Gaston 1998; Gaston & Chown 1999). Speciation adds new ranges and, depending on its mode, may reduce the sizes of those of the ancestral species (e.g. through vicariance). Extinction removes ranges. Although they clearly determine the number of species that are extant at any one time, it is unlikely, however, that these processes are sufficient themselves to explain the species-range size distributions that are actually observed. Rather, the form of these distributions will be set principally by the temporal dynamics (expansions and contractions) of the range sizes of species between their first appearance and their ultimate demise (Webb & Gaston 2000). These dynamics in turn will be determined by the environmental tolerances and capacities of species (and the effects of selection on these features), how abiotic and biotic conditions change, and how species are able to respond to these changes (e.g. dispersal and colonization abilities). Indeed, the influence of

environmental changes on geographical ranges is well established, with local populations being founded and lost, and range limits moving as conditions alter in ecological, let alone evolutionary, time (Burton 1995, 2001; Spicer & Gaston 1999; Dynesius & Jansson 2000; Hewitt 2000).

The importance of environmental factors, and the ability of species to respond, in influencing geographical range sizes raises the possibility of developing a stochastic theory of species-range size distributions. At any one time, the majority of species will have passed beyond the strongly determinate phase of range expansion associated with their initial geographical spread, and the colonization of, and establishment in, new habitats (figure 1). Subsequent changes in range size will reflect both non-random and random temporal variations in the environment. The consequences of both are, however, difficult to predict. Even non-random environmental changes may have complex effects because these changes are themselves spatially heterogeneous and temporally complex (with cycles commonly acting on several time-scales in addition to any broader directional trends), and because for any given species the individuals on which they are acting commonly exhibit both phenotypic and genotypic variation, and thus different responses to a particular alteration of conditions (Spicer & Gaston 1999). Thus, even when local population dynamics and shifts of particular range boundaries may be interpretable in terms of local conditions, changes in the size of whole ranges may often appear essentially stochastic (see § 5).

In this study we first develop a stochastic differential equation (SDE) to describe the dynamics of the range size of an individual species. Based on this SDE, a limiting stationary probabilistic model is derived to quantify the stochastic nature of the range size for that species at steady state. This model is then generalized to the species-range size distribution for an assemblage on the assumption that each individual species follows a similar stochastic process to that shown in figure 1, but equilibrium range sizes vary

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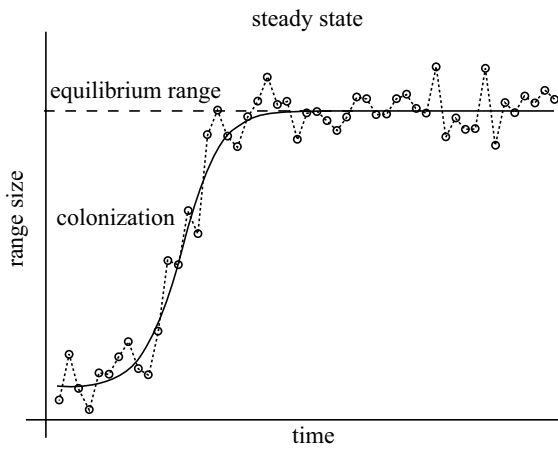


Figure 1. Dynamics of range size. The dashed curve shows the stochastic dynamics of the range size of a species, whereas the smooth solid curve shows the deterministic growth. At a certain point, the range reaches a dynamic equilibrium about which its size fluctuates.

from one species to another. The model is finally tested using several empirical datasets of the geographical range sizes of species in taxonomic assemblages.

2. MODEL

(a) SDE of range size

Let $x(t)$ be the abundance of a population at time t . The dynamics of $x(t)$ are traditionally modelled with an ordinary differential equation, such as the logistic growth model,

$$dx(t) = rx(t) \left(1 - \frac{x(t)}{k} \right) dt, \tag{2.1}$$

where r is the specific growth rate and k is the environmental carrying capacity supporting the population at $x(\infty)$, i.e. the population approaches k as $t \rightarrow \infty$.

In reality, populations seldom grow in a deterministic manner, but rather in a stochastic one. An approach to modelling stochastic growth is to view the specific growth rate r as being subject to stochastic environmental fluctuations, which is equivalent to adding a white noise term to equation (2.1) (e.g. May 1974),

$$dx(t) = rx(t) \left(1 - \frac{x(t)}{k} \right) dt + \sigma x(t) dw(t), \tag{2.2}$$

where $dw(t)$ is Gaussian white noise with $N(0,dt)$. Here, at steady state (i.e. as $t \rightarrow \infty$) the population fluctuates along the deterministic equilibrium k . This gives rise to a gamma probability distribution for the population (Dennis & Costantino 1988).

The relationship between the abundance $x(t)$ and the range size $y(t)$ of a species can be expressed in terms of a power model (Gaston 1994; Leitner & Rosenzweig 1997; Harte *et al.* 2001),

$$y(t) = ax(t)^b, \tag{2.3}$$

where a and b are parameters. Both abundance $x(t)$ and range size $y(t)$ are random variables and dependent on time in equation (2.3). The SDE for $y(t)$ can therefore be

derived according to the following transformation (transforming $x(t)$ to $y(t)$) for the Ito stochastic differential (Karlin & Taylor 1981, p. 347)

$$dy(t) = \left[\frac{\partial y(t)}{\partial x(t)} rx(t) \left(1 - \frac{x(t)}{k} \right) + \frac{\partial y(t)}{\partial t} + \frac{1}{2} \frac{\partial^2 y(t)}{\partial x(t)^2} \sigma^2 x(t)^2 \right] dt + \frac{\partial y(t)}{\partial x(t)} \sigma x(t) dw(t). \tag{2.4}$$

Substituting the appropriate derivatives of equation (2.3) and further replacing $dx(t)/dt$ by equation (2.2), we arrive at an SDE for range size,

$$dy(t) = y(t) \left[\frac{4\beta r + (1 - \beta)\sigma^2}{2\beta^2} - \frac{2r\alpha}{\beta k} y(t)^\beta \right] dt + \frac{2\sigma}{\beta} y(t) dw(t), \tag{2.5}$$

where, in terms of the parameters in equation (2.3), $\alpha = \left(\frac{1}{a} \right)^{\frac{1}{b}}$ and $\beta = \frac{1}{b}$.

This SDE (equation (2.5)) describes the stochastic dynamics of the range size of a species, and is of the logistic type, with a trajectory as shown in figure 1.

(b) Steady-state probabilistic distribution of range size

If $\sigma = 0$, the SDE (equation (2.5)) becomes a deterministic differential equation. When time is sufficient, the range size $y(t)$ of a species will reach a stable equilibrium (figure 1), $y(\infty) = (k/\alpha)^{1/\beta}$. In the stochastic setting, $\sigma > 0$, the range size of the species fluctuates above and below this equilibrium. Therefore, at the steady state, the range size approaches an approximately limiting, stationary probabilistic distribution of the form

$$f(y) = \varphi \exp \left[\frac{2}{\sigma^2} \int \frac{g(y)}{y} dx - 2 \log(y) \right], \quad y > 0, \tag{2.6}$$

for an SDE $dy = yg(y)dt + \sigma y dw(t)$ (see Dennis & Costantino 1988). φ is a constant that makes equation (2.6) a probability density function (PDF), i.e. the integration of $f(y)$ over the support of y equals 1.

Applying equation (2.6) to the SDE of equation (2.5), results in the stationary PDF for range size y

$$f(y) = \varphi y^{\frac{\beta r}{\sigma^2} - \frac{\beta}{4} - \frac{7}{4}} \exp \left(- \frac{\alpha r}{\sigma^2 k} y^\beta \right), \quad 0 < y < \infty. \tag{2.7}$$

Solving for constant φ by setting the integration of equation (2.7) over $0 < y < \infty$ to be 1, we obtain a stationary distribution for the range size y of a species that is a generalized gamma distribution

$$f(y) = \frac{\beta \left(\frac{c}{k} \right)^\delta}{\Gamma(\delta)} y^{\beta\delta - 1} \exp \left(- \frac{c}{k} y^\beta \right), \quad y > 0, \tag{2.8}$$

where $\delta = \frac{r}{\sigma^2} - \frac{3}{4\beta} - \frac{1}{4}$ and $c = \frac{\alpha r}{\sigma^2}$.

The PDF (equation (2.8)) describes the steady-state distribution of range size for a species that fluctuates above and below the equilibrium range (figure 1). δ and β are the two parameters determining the shape of the distribution. The shape of $f(y)$ shifts from monotonically

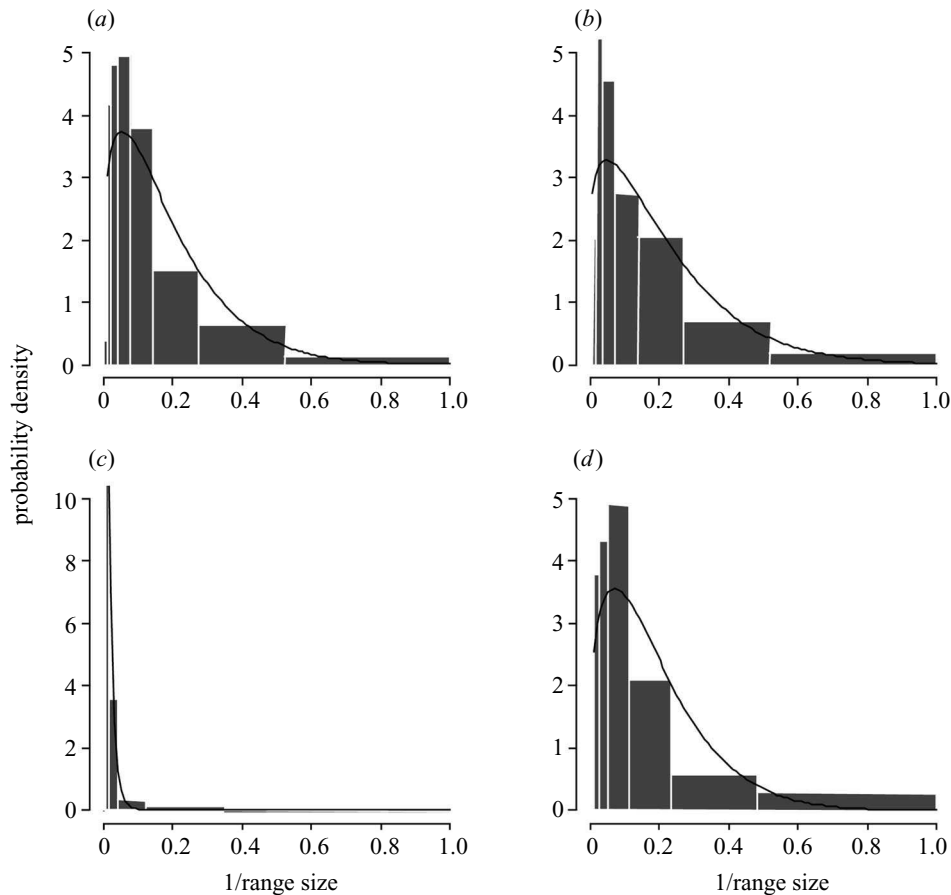


Figure 2. The probability densities for the inverse range sizes of species to illustrate the validity of the exponential assumption for equation (2.9). The smooth curves are the fittings of the Weibull distribution to the inverse of range sizes for four assemblages: (a) bumble-bees; (b) New World birds (overall); (c) primates; (d) woodpeckers. See § 4 for descriptions of the datasets.

decreasing to unimodal when δ (or β) varies from small to large. On the other hand, c/k is a position parameter. A small k (the carrying capacity) (or a large c) leads the distribution to be concentrated in the small range classes, whereas a large k makes the distribution more evenly distributed from small to large range classes. If there were time-series of measurements of the range size of a species, the data would be expected to follow this distribution. Unfortunately, such data are not available.

There is variation between species in the growth rate of range size, reflecting differences in their population growth rates. This variation has been accounted for in the SDE (2.2) through the stochastic term, and thus in equation (2.5). If all species had the same equilibrium range size, equation (2.8) would be sufficient to describe the distribution of range sizes for a species assemblage. However, in reality, there is also variation between species in the equilibrium range size, resulting from differences in equilibrium population k . Variation in equilibrium range size can be accounted for by considering the carrying capacity k in equation (2.8) to be a random variable. To simplify, here we assume the inverse of k to follow an exponential distribution

$$f\left(z = \frac{1}{k}\right) = \lambda \exp(-\lambda z), \quad z > 0. \quad (2.9)$$

This assumption is simple yet not unreasonable. This

can be approximately corroborated because if we assume that the observed range size of each species had indeed reached the deterministic equilibrium, the inverse of these range sizes (i.e. $1/y$) would be expected to follow the Weibull distribution. The Weibull distribution is derived through variable transformation according to equation (2.3) at $x(t) = k$. We have found this to be the case for several datasets (including those employed below; see figure 2), probably reflecting the pattern of resource partitioning among the species in an assemblage (see § 5).

A compound distribution of equation (2.8) can be constructed by assuming the exponential distribution of equation (2.9) for $1/k$

$$f(y) = \frac{\beta c^\delta}{\Gamma(\delta)} y^{\beta\delta-1} \int_0^\infty z^\delta \exp(-cy^\beta z) \lambda \exp(-\lambda z) dz. \quad (2.10)$$

The integration in equation (2.10) leads to the distribution

$$f(y) = \beta \delta \phi \frac{y^{\beta\delta-1}}{(\phi + y^\beta)^{\delta+1}}, \quad y > 0 \quad (2.11)$$

where $\phi = \lambda/c$. This is the PDF of a Pearson type VI distribution and it accounts for the stochastic effects on the growth rate of range size and for variation in the equilibrium range sizes of an assemblage of species. As for the distribution of typical range size data, equation (2.11) can

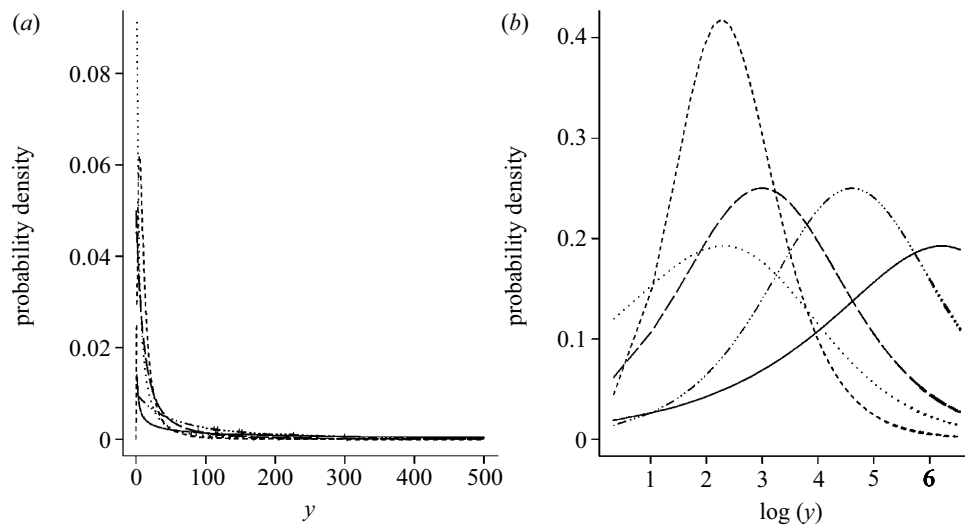


Figure 3. Shapes of the probability model (equation (2.11)) for five numerical examples. (a) The probability density functions for the original data (solid line, $\beta = 1.0, \delta = 0.5, \phi = 1000$; dotted line, $\beta = 1.0, \delta = 0.5, \phi = 20$; long dashes, $\beta = 1.0, \delta = 1.0, \phi = 20$; dot and dashed line, $\beta = 1.0, \delta = 1.0, \phi = 100$; dashed line, $\beta = 1.5, \delta = 1.5, \phi = 20$). The curves are strongly right-skewed, except in the fifth case (dashed line) which has a mode at $y = 5$. (b) The corresponding densities for the log-transformed data.

Table 1. The maximum-likelihood estimates of the parameters of equation (2.11) (\pm s.e.) and the results of KS and χ^2 goodness-of-fit tests to 10 range size datasets.

data	β (s.e.)	δ (s.e.)	ϕ (s.e.)	p -value (KS test)	p -value (χ^2 -test)
bumble-bees	1.603 (0.0652)	1.137 (0.197)	23.169 (0.687)	0.25	0.38
New World birds (breed)	1.607 (0.0188)	1.120 (0.0291)	17.738 (0.407)	0.00	0.00
New World birds (overall)	1.464 (0.0185)	1.309 (0.0302)	11.700 (0.399)	0.00	0.00
Procellariiforms	1.811 (0.0396)	0.493 (0.0344)	5000.001 (757.079)	0.48	0.12
mammals	0.903 (0.0369)	0.543 (0.269)	448.531 (2.026)	0.24	0.88
primates	1.780 (0.0351)	0.303 (0.338)	941 239.652 (86.334)	0.48	0.88
suckers	0.644 (0.112)	1.471 (1.013)	1137.978 (6.572)	0.43	0.20
sunfishes	0.740 (0.371)	2.975 (0.500)	5000.027 (928.477)	0.24	0.09
wildfowl	2.192 (0.0827)	0.441 (0.106)	1248.085 (13.044)	0.086	0.0038
woodpeckers	1.866 (0.0906)	0.904 (0.0820)	51.478 (6.332)	0.35	0.86

show a mode at very small range sizes and be strongly skewed to the right (figure 3).

3. PARAMETER ESTIMATION AND GOODNESS-OF-FIT

The maximum-likelihood estimates of the parameters of equation (2.11) are easy to compute. Given observed range sizes for n species $y = \{y_1, y_2, \dots, y_n\}$, the joint PDF of equation (2.11) is $f(y)$. The log-likelihood function of equation (2.11) is

$$l(\beta, \delta, \phi; y) = \sum_{i=1}^n \log(f(y_i)). \tag{3.1}$$

The maximum-likelihood estimates of the three parameters (β, δ, ϕ) are obtained by maximizing the log-likelihood function (equation (3.1)). The maximization of the likelihood function is evaluated using the iterative Newton–Raphson method, and the Hessian matrix used in the Newton–Raphson method (constructed from the second-order derivatives of the log-likelihood function) is used to derive the asymptotic standard errors for the estimates.

The goodness-of-fit of the model to the observed range data is tested using both the Kolmogorov–Smirnov (KS) test and the χ^2 -test. The null hypothesis is: does the sample arise from the hypothesized distribution (equation (2.11))? For continuous data, the KS test is generally more powerful than the χ^2 -test and is more likely to reject the null hypothesis.

4. EMPIRICAL EVALUATION OF THE STOCHASTIC MODEL

(a) Data

We have acquired geographical range size data for 10 assemblages of species covering a wide range of taxonomic groups (details of the varied methods employed for the calculation of range sizes are provided in the references cited): (i) bumble-bees—global overall range sizes of 241 species (P. H. Williams, unpublished data; Gaston 1996); (ii) New World birds—breeding range sizes for 3901 species (Blackburn & Gaston 1996); (iii) New World birds—overall range sizes for 3906 species (Blackburn & Gaston 1996); (iv) Procellariiform seabirds—global overall range sizes for 108 species (Chown *et al.* 1998; Gaston & Chown

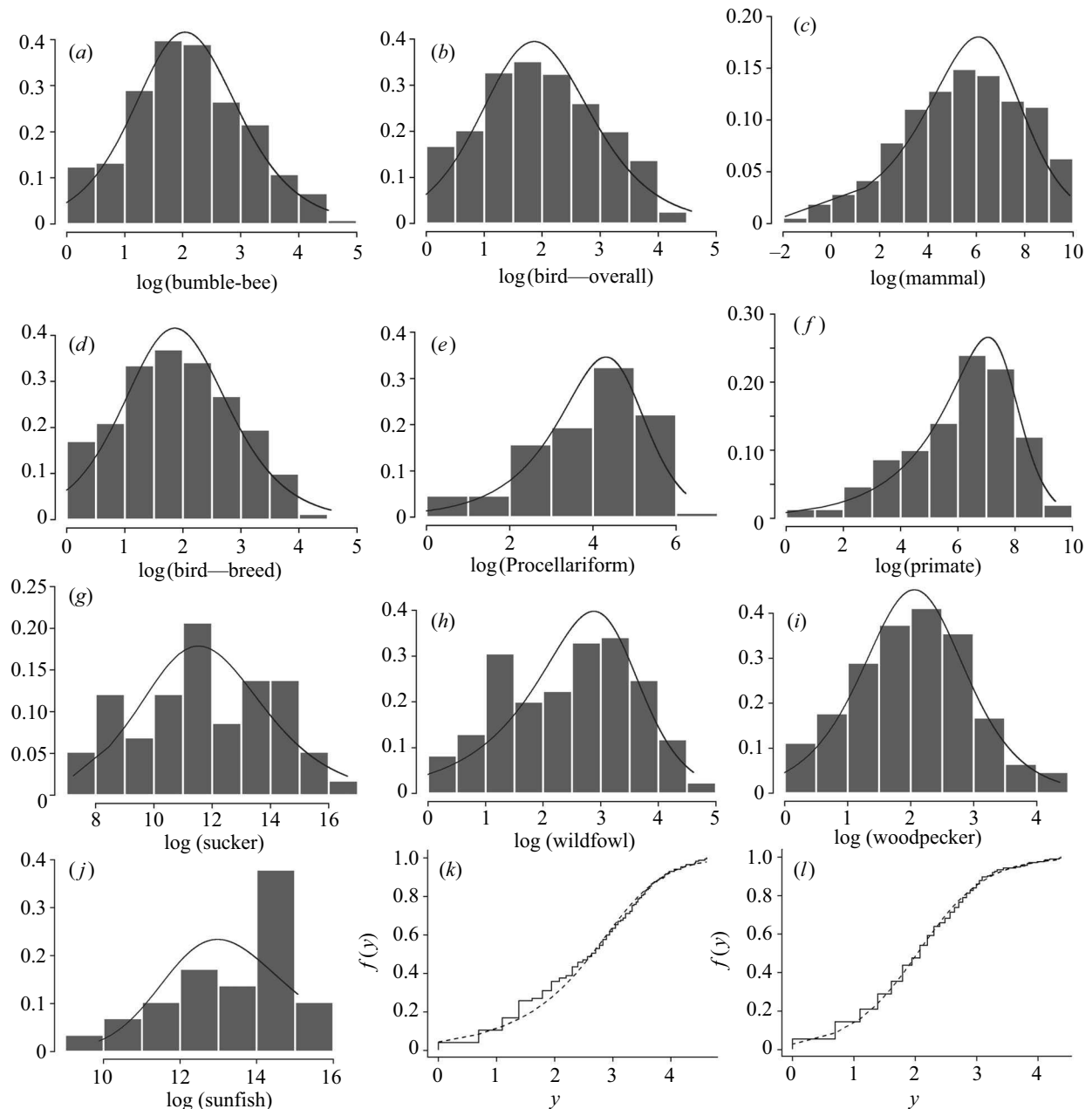


Figure 4. (a–j) The log-transformed observed (histograms) and fitted (smooth curves) PDFs for the 10 empirical datasets. (k,l) The CDFs $f(y)$, on which the KS test is based, for the wildfowl and woodpecker data, respectively. The stepped curves are the empirical $f(y)$, while the dashed curves are the hypothetical (estimated) $f(y)$.

1999); (v) North American nonaquatic mammals—overall range sizes for 523 species (Pagel *et al.* 1991); (vi) primates—global overall range sizes for 150 species (Wolfheim 1983); (vii) North American suckers—overall range sizes for 58 species (Pyron 1999); (viii) North American sunfishes—overall range sizes for 29 species (Pyron 1999); (ix) wildfowl—breeding range sizes of 170 species (Webb *et al.* 2001); and (x) woodpeckers—global overall range sizes of 214 species (Blackburn *et al.* 1998).

(b) Results

For the majority of the datasets, the fit of equation (2.11) to the range size distributions was quite satisfactory. Although the results of the KS test and of the χ^2 goodness-of-fit test were not necessarily in full agreement in every case, for only two datasets (both for New World

birds) did both tests fail (table 1). The rejection of these two datasets by the KS test is in a large part due to the large number of species (more than 3900). With such a large sample, even a small difference between the observed cumulative distribution function (CDF) and the hypothetical CDF would result in the rejection of the null hypothesis, although the largest difference between the two CDFs for the datasets is *ca.* 0.07. Given the difficulty of measuring range sizes for so many species at such a large scale, it is almost inevitable that there are a few 'outlier' species. A third dataset (that for wildfowl) marginally passed the KS test but failed the χ^2 -test, which is obviously caused by the unexpectedly high number of species in the third class of the range size distribution (see the PDF for wildfowl of figure 4). A similar explanation applies to the sunfish data, which passed the KS test but

marginally met the χ^2 -test owing to the excessive number of species in the sixth class of the range size distribution (table 1; figure 4). In these cases poor fits are for datasets that do not exhibit a simple frequency distribution, often because the numbers of species per class (and thus overall) are rather low. Nevertheless, regardless of the statistical tests, equation (2.11) captures the overall shape of the distributions for all of the datasets, with a close match in the position of the mode and in the direction of any skew (figure 4).

(c) *Derivation of the range size–abundance power model*

The derivation of equation (2.11) is based on the power model (equation (2.3)) for the relationship between range size and population size. The derivation can be reversed, so as to derive the power model from the probabilistic model (equation (2.11)). The parameters a and b of equation (2.3) can be computed from the three parameters (β , δ and c) of equation (2.11) as

$$a = \left(\frac{4\beta\delta + \beta + 3}{4\beta c} \right)^{\frac{1}{\beta}} \quad \text{and} \quad b = \frac{1}{\beta}.$$

Whilst β and δ can be read directly from equation (2.11), c can only be obtained if we know either r and σ of the stochastic logistic equation (2.2) (see notation for equation (2.8)) or λ of equation (2.9) (see notation for equation (2.11)). Unfortunately, neither set of parameters is readily determined given a set of range size data. Furthermore, a is a factor that converts abundance (x) into a range size for a species. It has to depend on the measurement unit (e.g. m², km² or ha) used for the observed range sizes and the activity range of individuals (e.g. m² may be an appropriate measurement unit for plants, but may not be so for animals). Nevertheless, from equation (2.11) we can at least obtain the exponent of equation (2.3). In other words, we at least are able to predict the observed range sizes up to a proportion: $y \propto x^b$. For example, for the wildfowl data, the maximum-likelihood estimates of the two parameters in equation (2.11) are: $\beta = 2.192$, $\delta = 0.441$ (see ‘wildfowl’ in table 1). From these values, equation (2.3) is obtained as

$$y = 1.015c^{-0.456} x^{0.456} = ax^{0.456} \propto x^{0.456}. \quad (4.1)$$

Although we know the range sizes for the wildfowl in figure 4 are measured as the number of grid cells occupied, with each cell being ca. 611 000 km², it is still not clear how the conversion factor a should be determined. Nevertheless, if the stochastic model (equation (2.11)) is reasonable, it is expected that the range sizes predicted based on equation (4.1) should be linearly related to the observed range sizes used to parametrize equation (2.11); i.e. equation (4.1) predicts the observed range sizes up to $y \propto x^{0.456}$. This can be tested because independent estimates have been made of the global population size (x) of each of the wildfowl species (see Webb *et al.* (2001) and references therein). Figure 5 shows that the power model (equation (4.1)) predicts the observed range sizes for the wildfowl extraordinarily well, even though in terms of the results of both the KS test and the χ^2 -test, equation (2.11) does not provide a particularly good fit (table 1).

5. DISCUSSION

The stochastic hypothesis of range size dynamics is generally upheld by the results reported in this study. In particular, equation (2.11) seems to capture reasonably well the pattern of variation in range sizes of species in a taxonomic assemblage.

The formulation of equation (2.11) makes several significant assumptions. First, it assumes a power model for the relationship between population size and range size. The power model has been widely used for describing the range size–abundance relationship (Gaston 1994; Leitner & Rosenzweig 1997; Harte *et al.* 2001), although it is only one of a number of models that have been employed in this context (He *et al.* 2002; Holt *et al.* 2002). The simplicity of the power model allows the derivation of an explicit stationary probabilistic density function for range size that would be difficult to achieve with more complex formulations. However, over the ranges of variation in abundances commonly observed, different range size–abundance models are frequently not strongly differentiated; the power model captures the form of real range size–abundance relationships well (Holt *et al.* 2002), and we would not anticipate the use of alternatives to change markedly the conclusions drawn herein. Where fits to empirical data are less good, the principal weakness of the power model is likely to lie in overestimating the range sizes of species that have large population sizes (which may often aggregate more strongly than the model indicates), and with possibly some underestimation at small population sizes (Holt *et al.* 2002). Nonetheless, for the one dataset for which such a test is possible, the wildfowl, the form of the power law range size–abundance relationship assumed from equation (2.11) makes for a reasonable prediction of observed range sizes, particularly given that global estimates of the population sizes of these species are inevitably only approximate (though doubtless better than for any other group of at least moderate species richness), and the range sizes are measured in quite a crude fashion (which is invariably the case at global scales).

Second, equation (2.11) is derived on the assumption that the range sizes of species are at equilibrium with the environment, in as much as whilst range sizes vary, they do so about some equilibrium level. This assumption may break down in the face of strong directional change in environmental conditions (e.g. climate change, habitat destruction (see Parmesan 1996; Burgman & Lindenmayer 1998; Parmesan *et al.* 1999; Channell & Lomolino 2000)), or in the face of phenotypic or genotypic changes that enable a species to utilize previously unexploited resources and thereby colonize fresh areas (see Lewontin & Birch (1966) for a rare possible empirical example of the latter). The former is the more significant concern, and in the extreme could undermine the model. However, ‘natural’ directional changes in environmental conditions (especially climate) may often result in the geographical ranges of species shifting in location rather than necessarily responding with systematic changes in extent, and there is evidence that species in some assemblages have retained quite stable range sizes over long periods (e.g. Jablonski 1987; Riddle 1996). This may make the

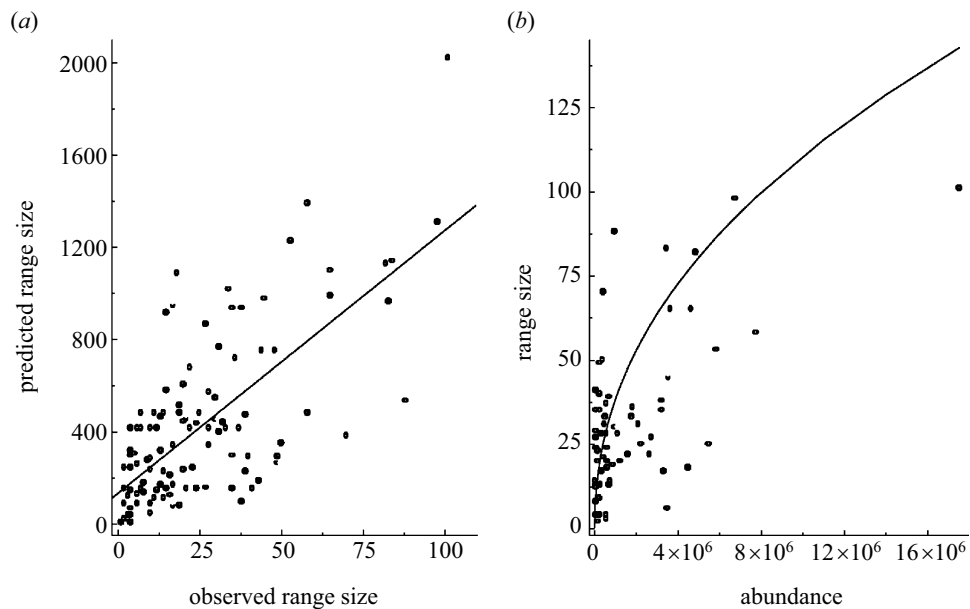


Figure 5. (a) The predicted range sizes versus the observed range sizes for 170 wildfowl species. The prediction was made from $y = x^{0.456}$ of equation (4.1). The line is the regression of the predicted on the observed range sizes. (b) The observed and predicted range–abundance relationships. The prediction (the smooth curve) is that of equation (4.1), arbitrarily setting $a = 0.0707$ ($y = 0.0707x^{0.456}$).

equilibrium assumption more appropriate than it may seem at first.

Human activities have undoubtedly exerted marked directional changes in the geographical range sizes of species, although the extent to which these forces are fundamentally different from those that have shaped range size distributions in the past remains unclear (for discussion see Gaston & Blackburn (2000)). Certainly these activities have eradicated some species from large proportions of their distributions (primarily through habitat destruction), and have opened up novel opportunities for others to extend their distributions (primarily through habitat change and accidental or intentional introductions (Lockwood & McKinney 2001)). However, the majority have not been strongly influenced in this way; their ranges instead have been subjected to increasing fragmentation whilst maintaining their broad extent of distribution. Given that it is this broad extent that is being modelled here, once again the equilibrium assumption may not be an unreasonable first approximation.

The third significant element of equation (2.11) is that it is derived on the assumption that carrying capacity k is a random variable. For simplicity, population dynamics models usually assume k is a constant. In reality, however, this is unlikely to be the case because the equilibrium population level is subject to a wealth of, often stochastic, factors. For an assemblage, k obviously varies from species to species, reflecting the different capabilities in sharing (partitioning) resources. Therefore, the assumption of a random k is reasonable at both population and assemblage levels. The importance of stochasticity in explaining range size–abundance patterns is also emphasized by Hanski (1982), although our results do not necessarily support his bimodal distribution of range sizes. An important difference between our approach and Hanski's core–satellite model is that the former explicitly takes account of population dynamics while the latter considers species coloniz-

ation and extinction processes. Following an argument that has more usually been applied to species–abundance distributions (but also non-biological systems, such as the gross national products of different countries), the frequency distribution of carrying capacities can be explained in terms of the action of multiplicative factors and the central limit theorem. If the carrying capacity of each species is a consequence of multiple factors operating essentially independently, and the differences between these capacities are expressed as differences in exponential growth, then one might expect that a right-skewed distribution of species carrying capacities would tend to result, with those for most species tending to be rather small and those of only a small proportion tending to be large (MacArthur 1957; May 1975; Gotelli & Graves 1996; but see Pielou 1975). This makes a great deal of biological sense, in as much as most of the resource bases exploited, and environmental spaces occupied, by species tend to be limited, and only a few tend to be extensive. However, the details of the shape of carrying capacity distributions is extremely difficult to establish, likely to vary from one taxon to another, and any assumptions regarding its form are ultimately somewhat speculative.

The stochastic hypothesis of range size dynamics seems to provide a reasonable prediction of variation in geographical range sizes amongst the species in a taxonomic assemblage. Of course, this does not mean that the processes embodied in the model necessarily give rise to the patterns of variation that are observed. If they do not, the fit of model and data suggest that at worst the actual processes are quite well characterized by the stochastic hypothesis.

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REFERENCES

- Anderson, S. 1977 Geographic ranges of North American terrestrial mammals. *Am. Mus. Novitates* **2629**, 1–15.
- Anderson, S. 1984a Geographic ranges of North American birds. *Am. Mus. Novitates* **2785**, 1–17.
- Anderson, S. 1984b Areography of North American fishes, amphibians and reptiles. *Am. Mus. Novitates* **2802**, 1–16.
- Anderson, S. 1985 The theory of range-size (RS) distributions. *Am. Mus. Novitates* **2833**, 1–20.
- Blackburn, T. M. & Gaston, K. J. 1996 Spatial patterns in the geographic range sizes of bird species in the New World. *Phil. Trans. R. Soc. Lond. B* **351**, 897–912.
- Blackburn, T. M., Gaston, K. J. & Lawton, J. H. 1998 Patterns in the geographic ranges of the world's woodpeckers. *Ibis* **140**, 626–638.
- Brown, J. H., Stevens, G. C. & Kaufman, D. M. 1996 The geographic range: size, shape, boundaries and internal structure. *A. Rev. Ecol. Syst.* **27**, 597–623.
- Burgman, M. A. & Lindenmayer, D. B. 1998 *Conservation biology for the Australian environment*. Chipping Norton, UK: Surrey Beatty.
- Burton, J. F. 1995 *Birds and climate change*. London: Christopher Helm.
- Burton, J. F. 2001 The response of European insects to climate change. *Br. Wildl.* **12**, 188–198.
- Channell, R. & Lomolino, M. V. 2000 Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. *J. Biogeogr.* **27**, 169–179.
- Chown, S. L. 1997 Speciation and rarity: separating cause from consequence. In *The biology of rarity: causes and consequences of rare-common differences* (ed. W. E. Kunin & K. J. Gaston), pp. 91–109. London: Chapman & Hall.
- Chown, S. L., Gaston, K. J. & Williams, P. H. 1998 Global patterns in species richness of pelagic seabirds: the Procellariiformes. *Ecography* **21**, 342–350.
- Dennis, B. & Costantino, R. 1988 Analysis of steady-state populations with the Gamma abundance model: application to *Tribolium*. *Ecology* **69**, 1200–1213.
- Dynesius, M. & Jansson, R. 2000 Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proc. Natl Acad. Sci. USA* **97**, 9115–9120.
- Flessa, K. W. & Thomas, R. H. 1985 Modeling the biogeographic regulation of evolutionary rates. In *Phanerozoic diversity patterns: profiles in macroevolution* (ed. J. W. Valentine), pp. 355–376. Princeton University Press.
- Gaston, K. J. 1994 *Rarity*. London: Chapman & Hall.
- Gaston, K. J. 1996 Species-range-size distributions: patterns, mechanisms and implications. *Trends Ecol. Evol.* **11**, 197–201.
- Gaston, K. J. 1998 Species-range size distributions: products of speciation, extinction and transformation. *Phil. Trans. R. Soc. Lond. B* **353**, 219–230.
- Gaston, K. J. & Blackburn, T. M. 2000 *Pattern and process in macroecology*. Oxford: Blackwell Science.
- Gaston, K. J. & Chown, S. L. 1999 Geographic range size and speciation. In *Evolution of biological diversity* (ed. A. E. Magurran & R. M. May), pp. 236–259. Oxford University Press.
- Gotelli, N. J. & Graves, G. R. 1996 *Null models in ecology*. Washington DC: Smithsonian Institution Press.
- Hanski, I. 1982 Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* **38**, 210–221.
- Harte, J., Blackburn, T. & Ostling, A. 2001 Self-similarity and the relationship between abundance and range size. *Am. Nat.* **157**, 374–386.
- He, F., Gaston, K. J. & Wu, J. 2002 On species occupancy–abundance models. *Ecoscience* **9**, 119–126.
- Hewitt, G. 2000 The genetic legacy of the Quaternary ice ages. *Nature* **405**, 907–913.
- Holt, A. R., Gaston, K. J. & He, F. 2002 Occupancy–abundance relationships and spatial distribution. *Basic Appl. Ecol.* **3**, 1–13.
- Jablonski, D. 1987 Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. *Science* **238**, 360–363.
- Karlin, S. & Taylor, H. M. 1981 *A second course in stochastic processes*. Orlando, FL: Academic.
- Leitner, W. A. & Rosenzweig, M. L. 1997 Nested species-area curves and stochastic sampling: a new theory. *Oikos* **79**, 503–512.
- Lewontin, R. C. & Birch, L. C. 1966 Hybridization as a source of variation for adaptation to new environments. *Evolution* **20**, 315–336.
- Lockwood, J. L. & McKinney, M. L. (eds) 2001 *Biotic homogenization: the loss of diversity through invasion and extinction*. New York: Kluwer/Plenum.
- MacArthur, R. H. 1957 On the relative abundance of bird species. *Proc. Natl Acad. Sci. USA* **43**, 293–295.
- May, R. M. 1974 *Stability and complexity in model ecosystems*. Princeton University Press.
- May, R. M. 1975 Patterns of species abundance and diversity. In *Ecology and evolution of communities* (ed. M. L. Cody & J. M. Diamond), pp. 81–120. Cambridge, MA: Harvard University Press.
- Pagel, M. P., May, R. M. & Collie, A. R. 1991 Ecological aspects of the geographic distribution and diversity of mammalian species. *Am. Nat.* **137**, 791–815.
- Parmesan, C. 1996 Climate and species' range. *Nature* **382**, 765–766.
- Parmesan, C. (and 12 others) 1999 Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**, 579–583.
- Pielou, E. C. 1975 *Ecological diversity*. New York: Wiley.
- Pyron, M. 1999 Relationships between geographical range size, body size, local abundance, and habitat breadth in North American suckers and sunfishes. *J. Biogeogr.* **26**, 549–558.
- Riddle, B. R. 1996 The historical assembly of continental biotas: Late Quaternary range-shifting, areas of endemism, and biogeographic structure in the North American mammal fauna. *Ecography* **21**, 437–446.
- Spicer, J. I. & Gaston, K. J. 1999 *Physiological diversity and its ecological implications*. Oxford: Blackwell Science.
- Webb, T. J. & Gaston, K. J. 2000 Geographic range size and evolutionary age in birds. *Proc. R. Soc. Lond. B* **267**, 1843–1850.
- Webb, T. J., Kershaw, M. & Gaston, K. J. 2001 Rarity and phylogeny in birds. In *Biotic homogenization: the loss of diversity through invasion and extinction* (ed. J. L. Lockwood & M. L. McKinney), pp. 57–80. New York: Kluwer/Plenum.
- Wolfheim, J. H. 1983 *Primates of the world: distribution, abundance and conservation*. Seattle, WA: University of Washington Press.

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