

On the relationship between range size and local abundance: back to basics

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In many taxa, the sizes of species' geographic ranges and their average local abundances at sites where they occur are positively correlated. We develop a simple population model that predicts this relationship which does not rely upon spatial dynamics. The simple, but fundamental, fact which should link distribution and abundance is that the distribution of species i is given by the number of sites at which its intrinsic rate of increase, $r_i > 0$, whereas its equilibrium local abundance should often vary directly with r_i . Any factor which tends to increase r_i across all sites will simultaneously enlarge the number of sites potentially occupied, and increase abundance at each occupied site. If species differ principally in their response to density-independent factors influencing birth and death rates, but are similar in density-dependence, then in a broad range of circumstances one should observe a range–abundance correlation. The model also predicts particular circumstances in which there is no, or even a negative, correlation between range and abundance. The general occurrence of this correlation in a broad range of taxa may reflect the operation of a number of distinct mechanisms.

Explanations for patterns in the distribution and abundance of species must, ultimately, be reducible to assumptions about how the vital rates of birth, death and dispersal vary in space and time. In recent years an empirical relationship which has received considerable attention is the positive correlation between the size of species' ranges and the mean abundance of those species at occupied sites within their ranges. This correlation has been observed in a wide range of taxa and habitats (e.g. Järvinen and Sammalisto 1976, Hanski 1982, Brown 1984, Gaston and Lawton 1990; see Lawton 1993, Gaston 1994, 1996 for reviews). There is usually considerable scatter in the relationship, suggesting the importance of multiple causal factors, yet the fact that the pattern exists at all has motivated the search for general explanations that transcend the idiosyncrasies of particular systems.

A number of different hypotheses have been suggested that could explain this pattern. Gaston (1994) lists six possible contributory mechanisms. None of

these existing hypotheses has unequivocal support (see Hanski et al. 1993, Lawton 1993, Gaston 1994, for an overview). A major distinction among these hypotheses is between those which emphasise spatial coupling among populations (e.g. metapopulation dynamics), and those which do not. The purpose of this paper is to present a simple, non-spatial mechanism for generating a correlation between species' distributions and abundances.

The basic insight we explore is that if a set of species differ among themselves with respect to their responses to spatially independent, density-independent factors, but are otherwise similar (particularly in their responses to density-dependent processes), they should automatically exhibit a positive correlation between range size and average abundance within occupied sites. The nature of the argument also suggests that the correlation should break down in various well-specified circumstances. Predicting those circumstances under which we would not expect a positive correlation between range and abundance is important, because although the correlation has been described as "almost without exception" (Hanski et al. 1993), situations with no correlation, and some with negative correlations, are known (Gaston and Lawton 1990).

In this paper, we deliberately concentrate on presenting the basic idea. It is not our aim to discuss in detail other hypotheses that may account for range–abundance correlations. However, our idea has some similarities to the hypothesis of Brown (1984), and in the discussion we draw out similarities and differences between Brown's approach, and ours. We also mention the model of Gyllenberg and Hanski (1992), which we take as paradigmatic of hypotheses which emphasise spatial dynamics. Empirical assessments of the adequacy of various hypotheses for explaining distribution–abundance correlations, using British bird and mammal

datasets as test systems, will be provided elsewhere (Blackburn et al. unpubl., Gaston et al. unpubl.).

The basic framework

Over biogeographical time-scales, dispersal is obviously essential for determining the size of species' ranges. However, species differ greatly in the degree to which immigration and emigration matter in determining local abundance (relative to in situ birth and death processes), once a population has become established. Here, we focus on one end of a continuum of potential dispersal effects. Assume that a number of species exist in a biogeographical region, all of which have had sufficient time to disperse to those sites at which they can potentially persist. For a subset of the community (possibly comprising many species), local population dynamics following colonisation into any given site will be driven by local birth and death processes, rather than by dispersal. In this paper, we concentrate on this set of species. For such species, what are the conditions that must be satisfied for one to observe an interspecific correlation between distribution and abundance?

The model described below lays out some logical requirements for an abundance–range size correlation to be observed in the absence of strong effects of spatial dynamics on local abundance. Our model therefore differs fundamentally from metapopulation dynamic models, such as those developed by I. Hanski and colleagues (Gyllenberg and Hanski 1992, Hanski et al. 1993), hereafter referred to as G & H, which also seek to predict abundance–range size plots. We should stress at the outset that these models are not competing hypotheses, but instead may pertain to different subsets of an entire species assemblage.

We assume that population dynamics at each site can be described with reasonable accuracy by simple, deterministic population models. We index species by '*i*', and sites by '*x*'. Because the effects of dispersal can be neglected, the 'range' of a species is precisely that set of sites at which it can deterministically persist. These are those sites where the species intrinsic growth rate r_i (= per capita birth minus per capita death rates, evaluated at densities sufficiently low to ignore density-dependence) exceeds zero (Lawton 1993, 1996).

Because we are interested in what is required for local population dynamics to generate a distribution–abundance correlation, it is useful to begin with a quite simple model. Assume that at low densities, all species have the same spatial pattern of birth rates, with substantial spatial variance among sites in this rate (Lawton 1993, 1996). For each species, let the basal birth rate at low densities at site *x* be $b_0(x)$. Further, assume that intraspecific density-dependence in births is experienced in the same way by each species. For simplicity,

assume that birth rates decline linearly with density, with the strength of density-dependence measured by *u*. Finally, assume each species has a constant, spatially invariant, density-independent death rate d_i . Later, we will relax some of these assumptions.

In the absence of significant migration, the dynamics of species *i* at site *x* is described by a logistic equation:

$$(1/N_i)(dN_i/dt) = (b_0(x) - d_i) - uN_i(x).$$

The equilibrium density of species *i* at site *x* is

$$N_i^*(x) = (b_0(x) - d_i)/u,$$

and its intrinsic rate of increase is $r_i(x) = b_0(x) - d_i$. Hence, the equilibrium population density of species *i* is $N_i^*(x) = r_i(x)/u$, its "carrying capacity" K_i .

As Williamson (1972) and Kuno (1991) have observed, the usual parameterisation of logistic growth in terms of *r* and *K* fosters the misleading impression that density-independent factors influencing birth and death rates have no effect upon equilibrium population size. Yet most mechanistic models of population dynamics reveal that changes in such factors can simultaneously alter the rate of population growth when rare, and equilibrium population size when common (e.g. the resource-consumer model of MacArthur (1972)). Thus, a species' carrying capacity in a given environment in general is not a fixed quantity, independent of the factors influencing its capacity for increase when rare.

The simple, but fundamental, fact which links distribution and abundance in the above model is that distribution is given by the number of sites at which $r_i > 0$, whereas at equilibrium, local abundance varies directly with r_i . Any factor which tends to increase r_i across all sites will simultaneously enlarge the number of sites potentially occupied, and increase abundance at each occupied site. Although this statement seems rather obvious, it is a hypothesis, not a fact or truism. Different taxa are likely to fit the model assumptions to differing extents, and even when they do, a positive correlation between local abundance and range size does not inevitably arise, as we show below.

Formal development of a simple model

Assume we can rank-order the *m* available sites (for all species) by basal birth rate, i.e., $b_0(1) > b_0(2) > \dots > b_0(m)$. Likewise, we rank-order species by their density-independent death rates, such that $d_1 < d_2 < \dots < d_n$. Any site occupied by the species with highest death rate can also be occupied by any lower-ranked species, but not conversely. This leads to nested distributions, with species *i* encompassing the range of all higher-ranked species – a not unrealistic scenario in some systems (e.g.

Patterson 1987, Cutler 1991, Cook and Quinn 1995, and references therein). Below, we will relax this particular assumption.

At each site occupied by both species i and $i + 1$, species i will have the higher equilibrium abundance: $N_i^*(x) > N_{i+1}^*(x)$ if $d_i < d_{i+1}$. This is one step towards generating a positive correlation between mean abundance across sites occupied, and number of sites occupied, but it is not quite enough. The final ingredient needed is a specification of the availability of sites with different birth rates.

As an illustrative case, assume that one can order sites along a gradient, such that $b_0(x) = b_0 - s|x|$, where s measures the 'sharpness' of the gradient in birth rates. This assumption, in effect, is equivalent to assuming that different habitat types (as assessed operationally by realised birth rates) are equally available. The range limit for species i is determined by identifying the largest value of the gradient position, $|x|$, such that the per capita growth rate at x is just equal to zero, or:

$$r_{0i} = b_0 - s|x| - d_i, \text{ or } |x| = (b_0 - d_i)/s.$$

Call this value of x ' R ', a measure of range size (R is the distance from the point on the gradient with the highest density, to the point of zero density).

The average density over the entire range, which we denote $\langle N_i \rangle$, is clearly $1/2$ the maximal local density, so

$$\langle N_i \rangle = (1/2)(b_0 - d_i)/u = (1/2)(s/u)R.$$

Hence, given that species differ solely in rates of density-independent mortality, have similar spatial variation in birth rates, and different habitats are equally available (say along a smooth environmental gradient along a spatial transect), one predicts that range size and mean local abundance will be *directly* proportional.

A graphical version, and elaborations

Fig. 1 provides a graphical version of the above model. Fig. 1a displays birth rates at low density, declining linearly away from an optimal position on the gradient, for each of two species with different death rates. The range is determined by the need for births to exceed deaths. Assuming that the strength of density-dependence, u , is uniform across this gradient leads to the positive distribution-abundance relation shown in Fig. 1b.

The above conclusion is considerably more general than the specific model used to generate it. For instance, we could have assumed that species differed by a constant amount in their basal birth rates, across sites, or by fixed amounts in both birth and death rates, with no effect whatsoever on the basic conclusion. Fig.

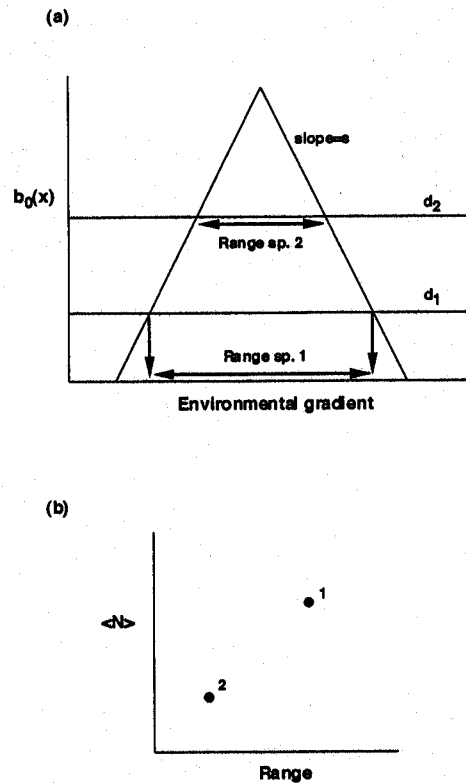


Fig. 1. a) Birth rates (b_0) at low density at each site (x) along an environmental gradient decline linearly (with slope s) away from the optimum site, with the same gradient s for all species. Species 1 and 2 have different density-independent death rates (d_1 and d_2), giving rise to b) a positive relationship between mean abundance ($\langle N \rangle$) and range size.

2 shows a graphical example of two species with equal density-independent death rates, but a spatially uniform difference in birth rates (for all sites where births are non-zero). Once again, one would predict the range-abundance relation of Fig. 1b. (For illustrative purposes, we have displayed triangular species responses to

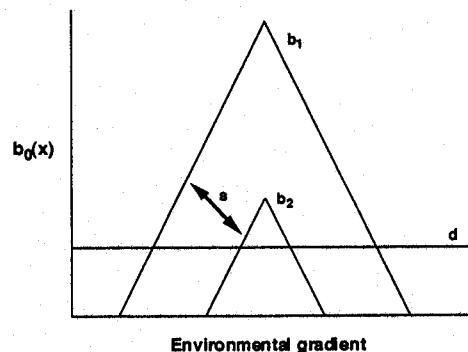


Fig. 2. Species 1 and 2 have the same density-independent death rate, but a spatially uniform (s is constant) difference in birth rates. This gives rise to the same positive relationship between mean abundance ($\langle N \rangle$) and range size as in Fig. 1b.

spatial variation in the figures; one could substitute rounded, unimodal responses without changing our qualitative conclusions.)

Similarly, varying the form of density-dependence in the model can be quantitatively important, but does not alter the principal conclusion that distribution and abundance should be correlated – provided all species experience intraspecific density-dependence in the same way.

Note that these figures need not indicate an actual spatial structure in birth and death rates; the x -axis could denote an abstract ordering of sites that in reality are arranged in a complex spatial mosaic of habitats of varying quality (Lawton 1996). It matters only that the sites vary in quality and that they can be ranked as shown in Figs 1 and 2. Moreover, although the above model assumes a linear relationship of gradient position and demographic rates, it is clear that mild non-linearities do not affect the basic conclusion (see also below). Thus, real geographic ranges may show multiple abundance peaks (summary of examples in Lawton 1993, 1996), yet in some abstract environment space nonetheless show a unimodal response in their basic demographic rates to environmental variation.

Moreover, it is not essential that all species reach their maximal birth rate at the same point along an environmental gradient. Fig. 3 shows a set of species which experience maximal birth rates at different points along a smooth gradient, but with the same pattern of spatial decline in each as one moves away from this maximum (i.e. they have equal s). Variation in density-independent mortality among species will necessarily generate a distribution–abundance correlation, provided all habitats are equally available and density dependence is uniform across species.

At the outset, we assumed that each species was present at all those sites at which it could potentially persist. One could assume that the determination of range occupancy is in part stochastic. If this leads to only a fraction p of occupiable sites being actually occupied by a given species, this does not affect our conclusions, provided that all species have roughly the same proportional reduction in their realised ranges below that of their maximal ranges.

Finally, our conclusions should be robust to certain kinds of temporal variation in population growth parameters. If a population with continuous growth (as in the above model) persists, fluctuating between an upper bound and a lower bound displaced from zero (i.e. no local extinctions), its expected long-term growth rate is zero (Levins 1979). Using a bar to denote a long-term average, and applying time-averaging techniques (Levins 1979) to the above model, leads to

$$\bar{r}_i(x) = \bar{b}_i(x) - \bar{d}_i = u\bar{N}_i$$

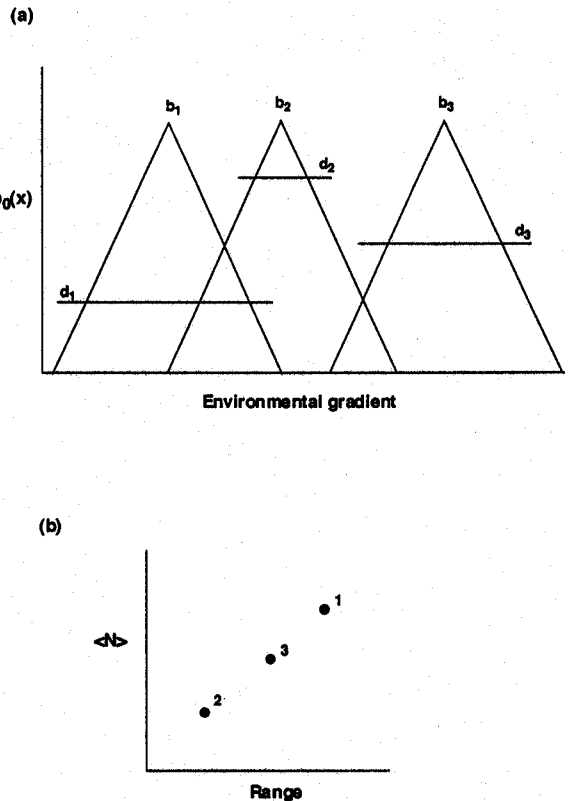


Fig. 3. a) A set of three species experience maximal birth rates (b_1, b_2, b_3) at different points along the environmental gradient, but share the same pattern of spatial decline in birth rate away from the optimum site (s is constant). Each species has a different density-independent death rate (d_1, d_2, d_3), giving rise to b) a positive relationship between mean abundance ($\langle N \rangle$) and range size.

If the strength of density-dependence is temporally constant, we can factor out u , giving

$$\bar{N}_i = (\bar{b}_i(x) - \bar{d}_i)/u.$$

As before, species-specific differences in long-term average density-independent mortality simultaneously affect both range size (which is given by those sites, x , where $r_i(x) > 0$), and the time-average of abundance at those sites occupied. Species-specific differences in density-independent growth rates should tend to produce correlations between range size and mean abundance, even if local populations fluctuate greatly in response to temporal environmental variation.

Some predictions and tests

Given the assumptions in our model, a number of predictions follow. In this section, we list the key assumptions and predictions, together with comments

about the degree to which they appear to accord with available data. Predictions 5–7 define circumstances in which one might *not* observe a positive range–abundance correlation (see above).

1. An explicit assumption of the model is that species with small ranges should also have lower relative maximal growth rates (compared to species with large ranges), averaged across the range. This prediction is also made by G & H's model; possible examples consistent with both models are discussed by Hanski et al. (1993), but data to test this prediction adequately are lacking. As well as these examples, there are indications that insect biological control agents with high r -values also have larger native ranges and are more likely to establish in alien environments (Crawley 1987). This is consistent with our assumptions.

2. If invading species are established at a random point within their feasible range, then their initial growth rates should be a good predictor of their ultimate range size. Critical tests are lacking, although Forcella (1985) noted that the rate of spread of alien weeds in the north-western U.S.A. was positively correlated with the range size the species had attained by 1980. Preliminary data on British alien plants may also be consistent with this prediction (M. J. Crawley, pers. comm.).

3. Our model predicts that erosion of a species' range (for example by habitat destruction) need not be accompanied by a reduction in local abundances at surviving, unaffected sites, whereas this is an explicit prediction of the G&H model. However, if demographic performance declines over most or all parts of a species range – for example, an increase in the death rate or a decrease in the birth rate caused by, inter alia, pollution, climate change, shifting patterns of human exploitation, or generalised habitat degradation – then we also predict synchronous change in a species local abundance *and* its range size. This is interesting, because we know that for common breeding land-birds of the United Kingdom, range size and abundance do tend to decline in synchrony (e.g. Gibbons et al. 1993, Fuller et al. 1995, Gaston et al. unpubl.). Gaston and Curnutt (unpubl.) have also recently shown this phenomenon in a number of North American birds.

4. The model suggests that the range–size abundance correlation should be stronger for ranges measured in terms of 'area of occupancy', than for ranges measured in terms of 'extent of occurrence' (sensu Gaston 1991). That is, the model is concerned with the area over which a species actually occurs, not all areas within the outer geographic bounds of its occurrences (which may include scattered 'sink' populations, maintained by immigration (Pulliam 1988, Lawton 1996), or even empty sites).

Zero or negative range–abundance correlations

The model also suggests several mechanisms which can produce, weak, non-existent or negative correlations between range size and mean local abundance (see Gaston and Lawton (1990) for examples).

5. Species may differ mainly in the strength of local density-dependence, rather than in responses to density-independent factors. In the above model, if u varies among species, but density-independent factors do not, species will have the same range, but different average abundances within their ranges. (In this case, at very low abundances (i.e. with strong density-dependence), a weak range–abundance correlation may arise because of demographic stochasticity.)

Fig. 4 shows several distinct potential patterns of variation among taxa in r and u . In this parameter space, our model assumes that species occupy shaded region (A). By contrast, if taxa fall in the region B, they will vary in local abundance, without any necessary variation in range size at all. Moving shaded region (B) with respect to the vertical axis changes the range size of all the species: as illustrated, all species are narrowly distributed, but move the cloud of points up the y axis and eventually all species would become distributed everywhere. Finally, region C shows the case where r and u are positively correlated, so that equilibrium density is unchanged. In this case, there can be variation in range size, but not in local abundance. If one observes a range-size correlation, we conjecture that variation among taxa and across sites should more closely match A than either B or C. The extent to which density-dependence is similar among populations within a species or across groups of related species is an important and untested question in comparative population ecology.

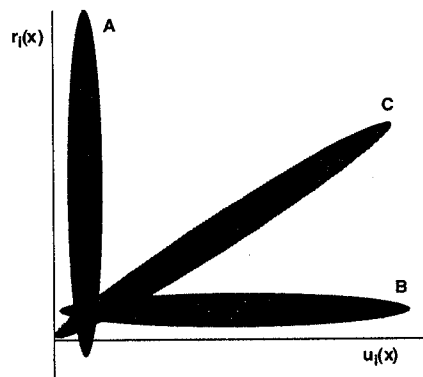


Fig. 4. A graphical illustration of how taxa might occupy parameter space defined by different values of r and u , where $r_i(x)$ is the intrinsic growth rate of species i at site x , and $u_i(x)$ is the strength of density dependence on species i at site x . The shaded regions are different areas of parameter space in which taxa are hypothesised to fall. If taxa occupy shaded region A, then range size is proportional to abundance. If taxa occupy shaded regions B or C, then there is no abundance–range size correlation. Note that r can be negative, but u cannot.

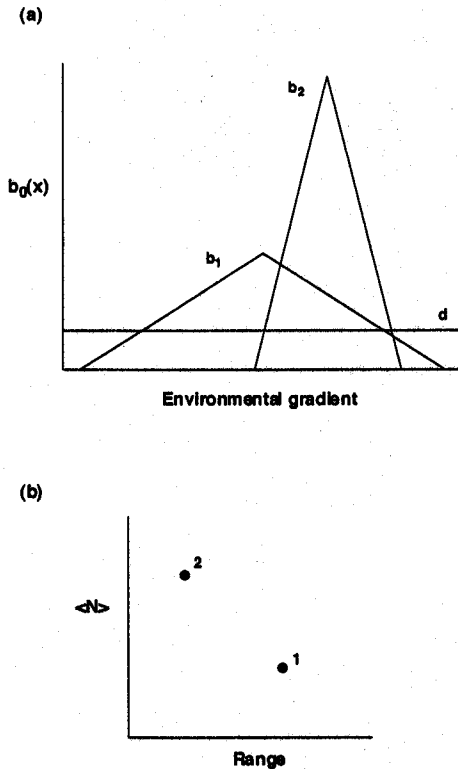


Fig. 5. a) Species 1 and 2 share the same density-independent death rate (d) but show greatly differing patterns of spatial decline in birth rate (b) away from the optimum site (different s). This gives rise to b) a negative correlation between mean abundance ($\langle N \rangle$) and range size.

6. Species may differ in their spatial responses to environmental variation (e.g. differ in s). For example, Fig. 5 shows two species with the same mortality rate, but greatly different spatial patterns in their birth rates. The species with the greater range has the lower mean local abundance.

7. The positive correlation between range and abundance may be weakened, or disappear altogether, if there is great disparity in the availability of habitats of different quality. A numerical example may be helpful here.

Assume there are 100 sites and 2 species. At site 1, the birth rate of both species is 2, and at the other 99 sites the birth rate of both is 1. The strength of density-dependence, u , is 1. Species 1 has a death rate of 0.5 everywhere, whereas species 2 has a death rate of 1.5 everywhere. Both species can persist in site 1; species 1 has an equilibrium density there of 1.5, whereas species 2 has a density of 0.5. At the other 99 sites, species 2 is absent (its intrinsic growth rate is -0.5 , so it goes rapidly extinct whenever a colonising propagule chances to arrive). Species 1 has a positive intrinsic growth rate, and persists with an equilibrium abundance of 0.5 at each of the 99 sites. Its average abun-

dance, across all sites, is very close to 0.5. Hence, for these two species in this particular suite of sites, there is no strong correlation between mean local abundance and number of sites occupied, basically because of great heterogeneity in the availability of sites of different quality.

By contrast, if there are 50 of each site, the mean abundance of species 1 is 1, and its range is 100; the mean abundance of species 2 is still 0.5, and its range is 50. So, with equal habitat availability, a correlation between range size and mean local abundance emerges.

Scale-dependence in predictions

8. One virtue of our hypothesis that the range–abundance correlation reflects differences in species' responses to density-independent factors, for species with otherwise similar responses to environmental variation, is that in principle, it can apply at all spatial scales, from a local mosaic of habitats, up to entire continents. Moreover, one might expect to see similar patterns at different scales for the same assemblages. There is some evidence that this is so (e.g. Bock 1987).

9. However, the assumptions built into the model suggest that we ought to see weaker relationships if we sample progressively larger areas, or if we include progressively larger numbers of species, encompassing increasing taxonomic or trophic diversity in the sample. The reasoning is that increasing spatial and/or taxonomic diversity is surely likely to encompass more variation in density-dependence, and in the spatial responses of density-independent components in basic vital rates. Indeed, all of predictions 5–8 above are more likely to hold if one considers larger spatial scales or taxonomic diversity. This qualitative expectation indeed appears to be what is seen in the documented relationships to date (Gaston 1994).

Discussion

At the outset we noted that it was not our intention to contrast in any detail the various hypotheses which could account for range–abundance correlations (Gaston 1994), but rather to lay out in detail what is needed for such correlations to arise when considering species that are not strongly influenced by dispersal in their local population dynamics. Our hypothesis for range–abundance correlations is non-spatial, in the sense that we did not assume colonisation–extinction dynamics, or effects of immigration on local population size. However, two crucial assumptions we made are that spatial heterogeneity among sites exists in density-independent demographic parameters, and that related species might show qualitative similarities in how they respond to such variation. If all sites are the same, but species differ, then in our model there is no reason to expect a range–abundance correlation.

This differs sharply from the assumptions of hypotheses emphasising spatial dynamics. For instance, Gyllenberg and Hanski's (1992) model assumes that immigration increases local population size and thus decreases the probability of local extinction. This mechanism can lead to a range–abundance correlation in a spatially homogeneous environment for species with similar properties (Hanski 1991, and pers. comm.). Nee et al. (1991) suggest that species with higher local carrying capacities either have lower extinction rates and/or higher colonisation rates, and so at equilibrium should occupy a larger fraction of occupiable sites. This mechanism rests on species differences in a spatially homogeneous environment, but assumes metapopulation dynamics. Our hypothesis requires species differences as well as spatial heterogeneity (not just patchiness), but does not require metapopulation dynamics. Because many populations (possibly a majority) may not behave as classical metapopulations (Harrison 1991, Harrison et al. 1995), our model may be applicable to a wide range of species not accounted for by the mechanisms of G & H and Nee et al. (1991). In other words, the models are complementary, embracing a continuum of possibilities that plausibly exist in the real world.

We suggested a number of predictions that follow from our simple model. Interestingly, many of these predictions also can be derived from the metapopulation models of G & H. We find this encouraging, because it suggests that different regional population structures lead to similar, large-scale patterns in local abundance and size of range, and may account for the robust nature of the pattern across many taxa and biomes (Lawton 1996). Both models can also account for situations in which there is no, or a negative, correlation between range and abundance (Gaston and Lawton 1990), and it is in these more exceptional circumstances that new data may eventually allow us to distinguish between the two models.

Another influential model for the abundance–range size relationship is due to Brown (1984), who proposed that species able to exploit a wide range of resources and/or with wide environmental tolerances (species with broad niches) are likely to achieve high local densities, and to be widespread geographically; the reverse will be true for more specialised species with narrow niches. In general, Brown's model will generate positive range–abundance plots, except if the 'reference habitat' in which populations are censused is rare regionally. Then, zero, or negative correlations are predicted (Gaston and Lawton 1990).

Superficially, Brown's hypothesis seems to be a very different kind of explanation to the model proposed here. In fact, the two approaches may well be complementary ways of thinking about the same problem. Brown (1995) defines a 'broad-niched' species as one that "can tolerate a wide range of physical conditions,

use many different kinds of resources, and survive in the presence of many potential enemies". If these factors vary among sites, it is clear that broad-niched species will be able to occupy a wider range of sites than do narrow-niched species. In our model, we express a similar idea in terms of demographic parameters: a species will have a wide range if it has a $r > 0$ across many sites. Brown further asserts that "the same attributes that enable [this] species to occur in many different habitats over a wide geographic area would also enable it to attain relatively high population densities in many of those places".

The reason that our model is not simply a restatement of Brown's hypothesis is that a species' niche specifies the range of environmental conditions (defined broadly) within which populations of that species can deterministically persist (Hutchinson 1957, Holt and Gaines 1992), or $r > 0$. Yet, given that a population persists at a site, realised abundance also reflects how density-dependence acts there. A species with small r , but weak density-dependence, can obtain enormous local abundances, compared to another species with large r , but intense density-dependence. Spatial variation in r is what determines a species' range. For this to be directly correlated, across species, with local abundances, requires that the strength of density-dependence be similar among species. Brown's niche hypothesis does not directly address the issue of density-dependence. Moreover, despite the intuitive appeal of Brown's model, niche-breadths are notoriously difficult to measure in the field (Colwell and Futuyma 1971). By casting our model in strictly demographic terms, it is, in principle at least, inherently open to empirical tests using census data, unlike Brown's model.

What would be needed further to test our model? The best data to have would be birth and death rates across a range of densities at numerous sites. In most circumstances, this ideal is not practical. Empirical understanding of spatial variation in demographic rates is very poor. For instance, the assumption that birth rates decline towards range edges has not often been tested. A particular sticking point is that one needs to assess density-dependence, and in particular spatial variation in density-dependence, along with maximal growth rates across a range of sites, for a set of species showing a positive correlation between range sizes and abundances. This is obviously a demanding task, but is exactly the sort of large-scale research enterprise that ecologists must now engage in if we are to make a serious attempt to understand major patterns in nature.

A less ambitious, but equally valid approach, may be to look critically at episodes of large-scale changes in rates. This is not practical experimentally, but rates may at times be changed in a broad-scale fashion by 'natural experiments'. Information on changes in the distribution, abundance, survivorship and breeding performance of UK birds, held by the British Trust for

Ornithology, extending back from the present day over several decades, provides one such data set, and is currently being analysed to test the model.

Finally, if after such analyses, one were to conclude that patterns of density-dependence and -independence in local demography did not match our model, the existence of range-abundance correlations might strengthen one's belief that spatial dynamics (e.g. metapopulation dynamics) are pervasive in natural communities.

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