VOLUME 85, NO. 1 MARCH 2010

THE QUARTERLY REVIEW
of BIOLOGY

CAUSALITY OF THE RELATIONSHIP BETWEEN GEOGRAPHIC DISTRIBUTION AND SPECIES ABUNDANCE

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KEYWORDS
distribution-abundance relationships, range-abundance, occupancy-abundance, distribution-density, macroecology, spatial scale

ABSTRACT

The positive relationship between a species' geographic distribution and its abundance is one of ecology's most well-documented patterns, yet the causes behind this relationship remain unclear. Although many hypotheses have been proposed to account for distribution-abundance relationships, none have attained unequivocal support. Accordingly, the positive association in distribution-abundance relationships is generally considered to be due to a combination of these proposed mechanisms acting in concert. In this review, we suggest that much of the disparity between these hypotheses stems from differences in terminology and ecological point of view. Realizing and accounting for these differences facilitates integration, so that the relative contributions of each mechanism may be evaluated. Here, we review all the mechanisms that have been proposed to account for distribution-abundance relationships, in a framework that facilitates a comparison between them. We identify and discuss the central factors governing the individual mechanisms, and elucidate their effect on empirical patterns.

The Quarterly Review of Biology, March 2010, Vol. 85, No. 1

0033-5770/2010/8501-0001$15.00

Introduction

THE POSITIVE RELATIONSHIP between the geographic distribution and abundance of organisms is a recurrent pattern in ecology (Figure 1 and 2) (Andreawartha and Birch 1954; Bock and Ricklefs 1983; Brown and Maurer 1989). Published associations between the two variables are disparate, in part reflecting the diversity of methods used to measure distribution or abundance (Wilson 2008). Likewise, many different mechanisms for governing the underlying relationship have been proposed. Here, we group these associations under the overall term *distribution–abundance relationships*, and argue that, although they may have "multiple forms" (Gaston 1996; Blackburn et al. 2006), these associations constitute a single overall phenomenon. In this unifying context, we emphasize the impact of any given study's ecological viewpoint on the perception of underlying mechanisms. The mechanisms governing the distribution-abundance relationship act at different spatial scales and on different aspects of distribution and abundance, and a consideration of the differential impact of each individual mechanism is necessary for a coherent understanding of the mechanistic basis of these relationships.

The empirical evidence for a positive association between measures of the distribution and abundance of organisms is strong. Positive correlations have been demonstrated for a host of taxa, including birds (e.g., Lacy and Bock 1986), butterflies (e.g., Pollard et al.

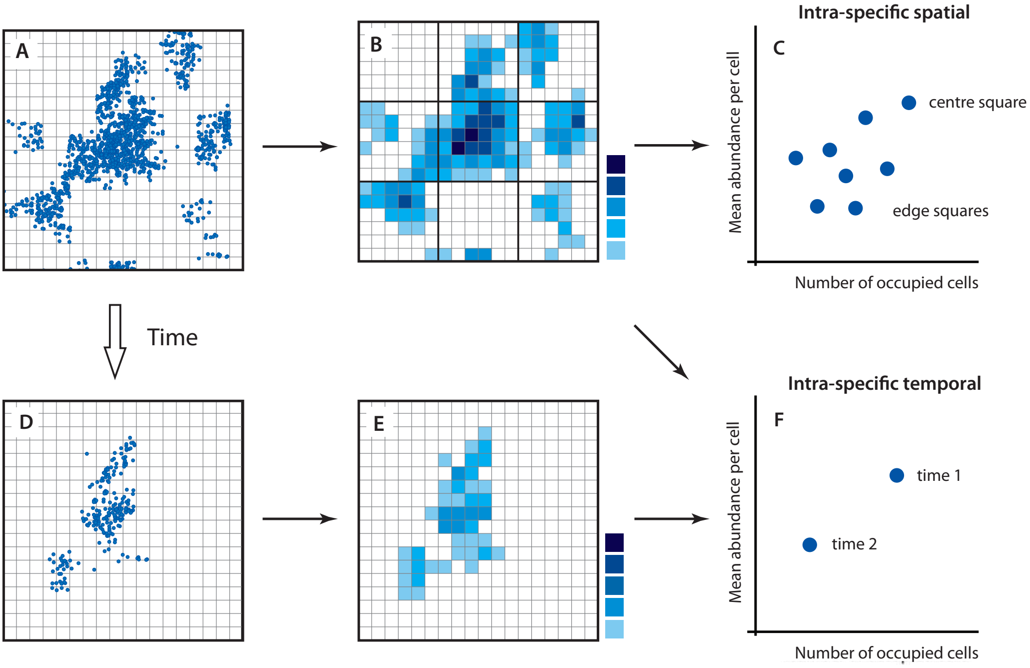

Figure 1. Intraspecific Distribution-Abundance Relationships

A) Shows the spatial location of individuals of a species. For clarity, we demonstrate sampling with uniform grid cells; alternatives include distributed sampling quadrates, or sites defined by habitat characteristics. B) Distribution and abundance are measured, as the presence/absence and population number in each grid cell. On a larger grid (overlaid), the central areas have larger grid cell occupancy. C) The spatial intraspecific relationship: There is a positive correlation between the cell occupancy and mean local abundance across areas from different parts of the range. D) Depicts the same species sampled at a later point in time where the population size has decreased. E) Repeating the sampling process gives a measure of distribution and abundance at this time. F) The temporal intraspecific relationship: integrating the data from (B) and (E) reveals a positive correlation between the distribution and abundance across time.

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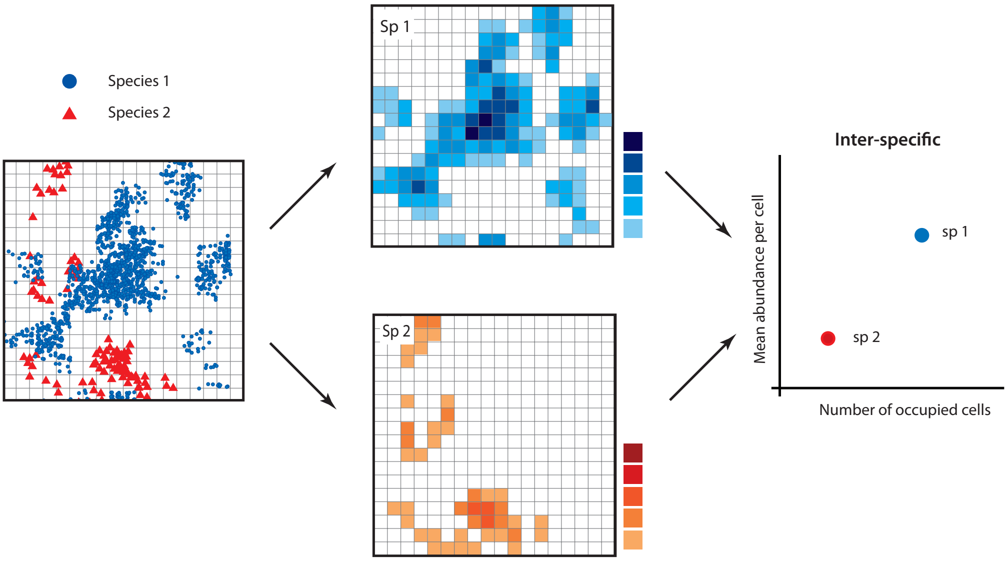

FIGURE 2. THE INTERSPECIFIC DISTRIBUTION-ABUNDANCE RELATIONSHIP

Two co-occurring species are sampled in a similar way to the species in Figure 1. Plotting the distribution and abundance of each species against each other reveals a positive interspecific relationship.
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1995; Conrad et al. 2001), mammals (e.g., Blackburn et al. 1997), and protists (e.g., Holt et al. 2002b); a few studies have also been published on plants (e.g., Thompson et al. 1998; Guo et al. 2000). Although most studies have focused on the terrestrial biome, relationships between distribution and abundance have also been reported in both marine (Foggo et al. 2003) and limnetic (Tales et al. 2004; Heino 2005) biomes, and they have been documented in areas across the planet (although with an overrepresentation of northern temperate regions; for a meta-analysis, see Blackburn et al. 2006). Distribution–abundance relationships have been identified over a large range of spatial scales, from micro-invertebrates in moss fragments on rocks (Gonzalez et al. 1998) to birds from the entire North American continent (Brown and Maurer 1987). Indeed, although exceptions do occur (e.g., Johnson 1998; Paivinen et al. 2005; Reif et al. 2006; Symonds and Johnson 2006), distribution-abundance relationships are so general that they have been proposed as a candidate for an empirical ecological "rule" (Gaston and Blackburn 2003).

Several hypotheses have been proposed to explain the processes linking distribution and abundance (Table 1). However, diversity in terminology and ecological viewpoint has made a straightforward evaluation of these hypotheses difficult, and little consensus currently exists regarding the mechanistic basis of observed distribution–abundance patterns (Gaston et al. 2000).

Up until the beginning of the 1990s, the central tenet was that some species had evolutionary adaptations that made them more successful than others, enabling them to both establish a wide range and a large population size (McNaughton and Wolf 1970; Bock 1987). One of the most influential hypotheses to explain this superiority was originally put forward by Brown (1984) (see Table 1, "resource use"), who related distribution and abundance to the size of the ecological niche of species. Analytical studies from this period generally addressed the effects of the distribution of resources and habitat on the distribution and abundance of species (e.g., O'Connor 1987; Gaston and Lawton 1990; Novotny 1991).

A different perspective, founded in population ecology, was introduced when Hanski and colleagues (1991a; Hanski et al. 1993)

TABLE 1
Proposed hypotheses

Mechanisms/Effects	Original explanation	Distribution measure	Causality	Reference	Comment
Measurement effects					
Sampling bias	Species with low abundances are more likely to be missed by censuses, thus their distributions are underestimated.	Occupied sites	A	Bock and Rickleffs (1983)	Not a mechanism
Phylogeny	Species traits, such as distribution and abundance, are not independent, and may reflect phylogeny rather than ecology.	N/A	N/A	Gaston and Lawton (1997)	Only interspecific relationships; not supported
Range position	If the study area overlaps different parts of species ranges, intraspecific spatial relationships will lead to interspecific relationships.	Range density	N/A	Brown (1984)	Not a biological mechanism
Structural mechanisms					
Resource use	Species that are able to exploit a broader range of resources may acquire larger ranges and also be more locally abundant, as they will have more resources available to them where they occur.	Potential habitat	B	Brown (1984)	Ambiguous empirical support
Resource availability	Species that utilize abundant and widespread resources may themselves become abundant and widespread.	Potential habitat	B	Hanski et al. (1993)	See text
Vital rates	The local abundance and the number of occupied sites of species are both determined by rates of births and deaths among populations: High population growth rate leads to high abundance, as well as to more sites with a positive absolute growth.	Occupied sites	B	Holt et al. (1997)	See text
Unified theory	If the spatial structure of abundance follows a monotonically decreasing relationship from the center of a species' distribution, the extent of the range (i.e., the area where abundance > 0) is larger for more abundant species.	Extent	B	McGill and Collins (2003)	Distribution measure not empirically supported

continued

TABLE 1
(continued)

Mechanisms/Effects	Original explanation	Distribution measure	Causality	Reference	Comment
Dynamic mechanisms					
Metapopulation dynamics	The number of occupied patches and local abundance both influence the number of dispersers, which again influences both occupancy and abundance.	Occupied sites	C	Hanski (1991)	
Density-dependent habitat selection	Individuals in populations with high densities might be driven by intraspecific competition to exploit less suitable habitats, thus increasing the occupancy of the population.	Occupied/potential habitat	A	O'Connor (1987)	See text
Habitat dispersal	Populations with much available habitat may produce sufficient numbers of successful dispersers to inflate local abundances.	Occupied sites	C	Venier and Fahrig (1996)	
Spatial aggregation/nonindependence					
Individual aggregation	A random spatial dispersion of individuals leads to a correlation between local abundance and site occupancy. This relationship is strengthened when individuals are spatially aggregated.	Range density	B/D	Wright (1991), Hartley (1998)	
Self-similarity	The distribution of species is self-similar across a range of scales. Since the density of a species equals the range density at the scale where the average number of individuals per cell equals 1, density and range density will be correlated across scales.	Range density	B/D	Harte et al. (1999)	
Neutral models	Range-abundance relationships are observed in neutral community simulations, but no explicit mechanism has been stated. The causal pathway is through spatial aggregation generated by dispersal limitation.	Range density	B	Bell (2000)	

A: One variable causes the other.
B: Both variables are controlled by another (unmeasured) variable.
C: Both variables affect each other (the effect takes place in the future, since causality can never be simultaneously mutual).
D: There is no causality between the variables.

This table lists all of the hypotheses proposed to explain distribution-abundance relationships. Hypotheses published before 1997 essentially follow Gaston and Lawton (1997).

argued that the geographic distribution and abundance of a species need not be independent measures of its ecological success, but instead could be directly linked to each other through the action of metapopulation dynamics. At the same time, a statistical perspective was added to the discussion of distribution–abundance relationships by Wright (1991), who pointed out that a random spatial distribution pattern of individuals could in itself be predicted to result in a correlation between the two variables.

These different frameworks were not easy to integrate, and analytical studies formulated within one of these hypotheses have tended to ignore the others (e.g,. Nee et al. 1991; Venier and Fahrig 1996; Collins and Glenn 1997; Newton 1997; Hartley 1998; Gregory 1998; Gaston et al. 1998b), with the notable exception concerning a large study of British birds that attempted to test all of the proposed hypotheses (reviewed in Gaston et al. 2000). Recently, a number of comprehensive macroecological theories aimed at explaining the multiplicity of observed diversity patterns in a single theoretical framework have also sought to account for distribution–abundance relationships, notably those of community self-similarity (Harte and Ostling 2001) and neutral theory (Bell 2001; Hubbell 2001).

In all, at least thirteen different hypotheses have been proposed to explain relationships between distribution and abundance (Table 1). The tendency for explanations of general empirical patterns to accumulate mechanistic hypotheses is common in (macro)ecology, and can probably be attributed to difficulties with applying strong inference to ecological theories (McGill et al. 2007). The complementarity and overlap between hypotheses of distribution-abundance relationships mean that a strict Popperian approach of generating specific and identifiable predictions from each hypothesis is not likely to lead to clear-cut empirical tests. In addition, it is very unlikely that any one of these hypotheses will be found to be correct to the exclusion of the others (Gaston and Lawton 1997). The mechanisms are not mutually exclusive, and may often act in concert to give rise to distribution-abundance relationships (Cowley et al. 2001; Holt and Gaston 2003). The concept that several mechanisms may be responsible for creating general ecological patterns (see Chamberlain 1890) is well-established in the study of large-scale species richness gradients (e.g., Rahbek and Graves 2001; Willig et al. 2003; Colwell et al. 2004; Currie et al. 2004) as well as species-area curves (Rosenzweig 1995), as is the observation that the relative importance of factors and their interaction may change with spatial scale (e.g., Rahbek and Graves 2001; Lyons and Willig 2002; see Rahbek 2005 for a review).

The central claim of this review is that the different mechanisms underlying distribution-abundance relationships do not constitute competing hypotheses to be supported or refuted; rather, they are descriptions of processes working at different scales and in different manners to create and modify these relationships. The key to moving from a list of potential hypotheses to a coherent view of the causation of distribution-abundance relationships is to consider the factors that order and differentiate the hypotheses, in order to develop a framework that allows comparisons to be made (Leibold et al. 2004). The factors identified in this paper include spatial scale, type and direction of causality, temporal dynamics, and the measure of distribution and abundance that are implicit in each hypothesis. This alliance of factors also serves to differentiate many of the primary ecological frameworks and worldviews that constitute contemporary ecological thought.

A FRAMEWORK FOR DISTRIBUTION-ABUNDANCE RELATIONSHIPS

Distribution-abundance relationships are studied under a plethora of names: distribution-abundance relationships (Bock 1987; Blanchard et al. 2005), density-distribution relationships (Cowley et al. 2001; Paivinen et al. 2005), abundance-occupancy (or occupancy-abundance) relationships (Gaston et al. 1998b; Freckleton et al. 2006), density range-size relationships (Tales et al. 2004), and range size-abundance relationships (Symonds and Johnson 2006), just to name a few. While this variety in nomenclature reflects the important efforts made to distinguish precisely among different measuring techniques, it has also fragmented the literature, and may have prevented important findings and theoretical developments from coming to the attention of researchers. Accordingly, although accurate nomenclature is important, different names should only be upheld if they describe clearly separate phenomena. Unfortunately, until now it appears that the exact choice of wording tends to reflect each researcher's individual preference, rather than following an exact nomenclature aimed at clarifying the measures in use.

Therefore, we propose reverting to the deliberately general term "distribution-abundance relationships" to indicate any kind of correlation of a measure of range and a measure of abundance; more specific terms that do not contribute to the theoretical understanding of the pattern should be abandoned. This is the term used when the pattern was originally described (Andreawartha and Birch 1954; Brown 1984; Bock 1987), and thus provides consistency with the original literature. This term also allows for studies using nontraditional measures of distribution and abundance—for instance, the specificity and incidence of parasites on birds (Poulin 1999)—to be understood in light of distribution-abundance mechanisms.

Although we propose a general term to encompass all studies relating distribution and abundance, a first priority at the present stage is to establish a clear consensus on exact empirical patterns (Wilson 2008). To this end, a stringent terminology of distribution-abundance relationships is needed, and this requirement should be kept in mind when defining mechanistic hypotheses.

Measures of Abundance

Published studies of distribution-abundance relationships have correlated distribution with either the total population size of the species (e.g., Blackburn et al. 1997; Webb et al. 2007) or the local abundance (i.e., the average abundance at occupied sites; e.g., Hanski and Gyllenberg 1997). The most interesting distribution-abundance relationship ecologically is the relationship between local abundance and distribution (Figure 3). Because population size is the product of occupied area and local abundance, a positive correlation between total population size and distribution inevitably follows; for distribution and population size to be unrelated would require a negative relationship between distributional size and local abundance. Correlations between population size and distribution, therefore, do not require any biological explanation. Although some of the hypothesized mechanisms of distribution-abundance relationships are phrased in terms of population size (e.g., neutral models [Bell 2001] and self-similarity [Harte and Ostling 2001]), these mechanisms are also expected to lead to correlations between local abundance and distribution.

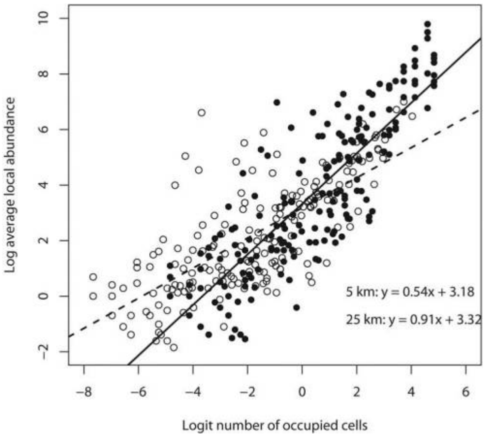

Figure 3. The Relationship between Local Abundance and Proportional Occupany among Danish Birds

Data taken from the Danish breeding bird Atlas (Grell 1998; for a description of data selection, see Borregaard and Rahbek 2006) at the 5x5 km scale (black dots), and subsequently resampled by lumping grid cells to 25x25 km cells (white dots). The slopes are significantly different ($t = 7.14$, $p < 0.001$).

In local scale analyses, abundance can be measured directly using site population counts (e.g., Bibby et al. 1992). This is the preferred method of measurement when data of sufficient quality are available (Blackburn et al. 1997), which may be the case for certain organisms—typically vertebrates and plants—or where the extent of the study area is relatively limited. However, the size of the data set often makes a direct estimation of local abundance impractical, and, in these cases, local abundance is estimated by dividing the total population size of the given domain by the number of occupied sites within that domain (Gaston and Lawton 1990). Although some studies have estimated local abundance by averaging population size over the entire study area (including unoccupied sites—termed the "true mean abundance" by Wilson [2008]), this division by a constant is merely a different scale representation of total population size; therefore, the division of population size by the number of occupied sites is to be preferred (Gaston and Lawton 1990).

It is important to note that the use of averaged local abundances may give rise to a number of issues. Since local abundances are generally not normally distributed (McGill et al. 2007), the average value may not accurately describe species abundance at any specific point on the landscape and should, thus, be interpreted with caution. Furthermore, this approach may lead to spurious inference of distribution-abundance relationships. At large grain sizes, a species usually occupies only a portion of each grid cell. When averaging occurrences over grid cells, one implicitly assumes that the distribution of individuals is uniform—or at least comparable among different species—within each grid cell. If there are differences among species distributions within grid cells (this in itself is a prediction of several of the proposed hypotheses for distribution-abundance relationships), then studies using averaged abundances may in fact be comparing the range density at different scales (i.e., comparing the within-cell occupancy with the across-cells occupancy; see the discussion of self-similarity theory below).

Measures of Distribution

Measures of distribution are fundamentally different from measures of abundance in that distributions are spatial patterns; therefore, comparisons between the two variables are not straightforward. Abundances are counts of individuals within a predefined area, whereas the distribution of a species is essentially a representation of the complex spatial distribution of individuals (see Figure 1) (Brown et al. 1996). This is usually measured as the sum of occupied areas and, as such, is always a function of how areas are defined and delimited. Much of the confusion regarding distribution-abundance relationships comes from the inherent difficulty in relating absolute counts to measurement-dependent distributions.

Importantly, the measurement of species' distributions is strongly dependent upon the scale of extent and the grain size at which they are perceived (Hartley and Kunin 2003; Rahbek 2005). Accordingly, the variety of distribution definitions used in studies of distribution-abundance relationships is even greater than those used for abundance (see Gaston 1996; Blackburn et al. 2006; Wilson 2008). The empirically supported relationship is a correlation of abundance with density of occupied sites or grid cells on a range—a measure termed "range density" by Hurlbert and White (2005). The extent of the distribution is not very well-correlated with local abundance (e.g., Harcourt et al. 2005); a recent meta-analysis showed that studies using extent as the distribution measure generally report no correlation with abundance (Blackburn et al. 2006). This carries the implication that mechanisms proposed to lead only to extent-abundance correlations, such as the unified theory of macroecology (McGill and Collins 2003), are not able to account for observed distribution-abundance relationships.

A consequence of the spatial nature of distribution measures is that abundance and distribution are not expected to scale in the same way. Accordingly, the exact slope of distribution-abundance relationships is scale-specific, and can only be compared between communities censused at the same grain size (He and Gaston 2000b) (see Figure 2). This is further complicated by the fact that the perception of scale varies between organisms (Wiens 1989; Chust et al. 2003; Rahbek 2005). In any one assemblage, the same grain size is likely to be perceived differently by an eagle and a sparrow, for instance (Wiens 1989).

Not all the proposed hypotheses are applicable at all scales. Although the exact scale is rarely explicitly defined in mechanistic hy-

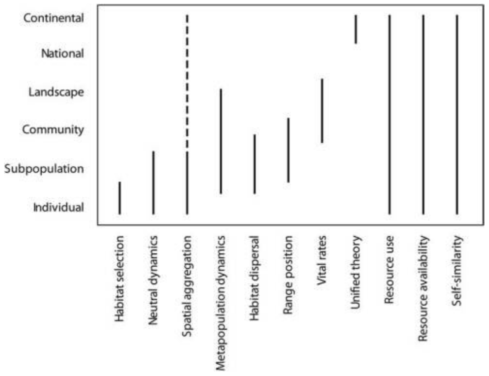

Figure 4. Scale Dependency of the Proposed Mechanistic Hypotheses

Several of the hypotheses assume biological processes that are characteristic of a certain spatial scale. For example, meta-population dynamics depend on dispersal between habitat patches and cannot explain patterns at larger scales, whereas the unified theory concerns distributional extent and is only applicable at the largest scales. Individual aggregation models individuals (dotted line) and is traditionally associated with local scales, although this is not a strict assumption of aggregation theory.

potheses (Collins and Glenn 1997), many of the mechanisms are based on assumptions that are characteristic of biological processes operating at a specific spatial scale of resolution (see Figure 4). Scale issues are of great importance. Analyzing a specific mechanistic hypothesis that is operational within a given range of spatial scales, but using data obtained outside of this range to do so, can seriously confound conclusions. For instance, applying the hypothesis of density-dependent habitat selection (O'Connor 1989) to relationships between the distribution and abundance measured at the spatial resolution of 100x100 km grid cells is clearly flawed. Individuals dispersing as a result of density dependence are likely to disperse into lower quality habitat patches that are interspersed with optimal habitat within the landscape matrix, and these individuals are not likely to affect the distribution of the organism at a larger grain size. A converse example would be interpreting distribution and abundance of butterflies in a set of closely connected forest patches by employing the "vital rates" model (Holt et al. 1997). This model is only applicable at larger scales, where sites may be spaced sufficiently far apart such that dispersal between them can be neglected. Another equally important aspect of spatial dependency is that some mechanisms, rather than acting as competing explanations, describe processes working at different scales. For instance, Brown's (1984) resource use hypothesis acts at a large landscape scale and affects the distribution of potential habitat rather than the distribution of individuals, whereas metapopulation dynamics (Hanski, 1981) determine the individual occupancies in a network of closely connected patches and, hence, act at an organismic scale nested within that of the resource use hypothesis (Storch et al. 2008). Regardless of these scale associations, positive distribution-abundance relationships exist over a wide range of scales and display a certain degree of scale invariance: organisms common and widespread at one scale are generally equally so at any other (e.g., Bock 1987).

Another consequence of the spatial nature of ranges is that distribution measures are proportion data (i.e., the proportion of the study area that is occupied). Because of

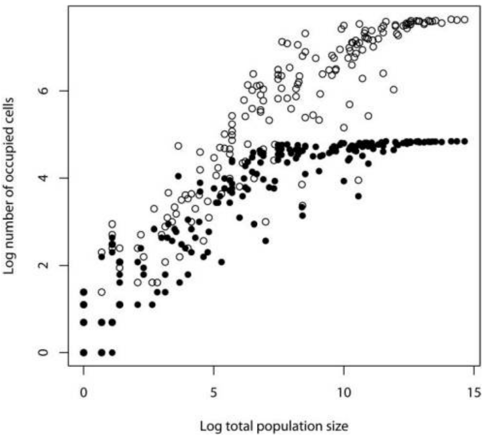

Figure 5. The Effect of Grain Size on Measured Relationships

Log/log plots of occupancy on total population size often exhibit saturation at large grid cell sizes. Data as in Figure 3. A positive relationship between local abundance and distribution is predicted to yield linear slopes of >1 in this type of plot (Blackburn et al. 1997).

this, the linear trend of log-log plots of distribution on population size often shows a flattening at high population sizes, where distribution cannot increase further (Gregory 1995; Gaston et al. 1998c; Webb et al. 2007). This behavior is caused by the grain size or focus of the study rather than by the extent (sensu Scheiner et al. 2000); as grain size decreases, the flattened area moves progressively higher, and the effect almost disappears at the smallest grain size (Figure 5). The claim that this flattening is "a real phenomenon" (Webb et al. 2007) seems to be inaccurate, as it is actually a measurement effect of grain size. Smaller variation of measured distributions among abundant species is a product of poor resolution in this part of the plot. A more appropriate approach is to normalize the distribution values using logit ($\mathrm{logit}(p):=\log(p/(1-p))$ transformation (Hanski and Gyllenberg 1997; Williamson and Gaston 1999), which generally leads to stronger distribution-abundance relationships (Blackburn et al. 2006) and removes the above effect (Figure 3).

SAMPLING BIAS

Spurious relationships between measured distribution and abundance may be created by sampling bias. If species with low densities are more likely to elude detection at sites where they are actually present, they will be registered at fewer sites than more numerous species, and a spurious relationship between distribution and local abundance will result (Bock and Ricklefs 1983; Brown 1984). This organism-specific sampling effect has been demonstrated in empirical studies (e.g., Selmi and Boulinier 2004) and will always contribute to distribution-abundance analyses, especially when sampling intensity is low or is carried out at small spatial scales. However, the generality of distribution-abundance relationships cannot be ascribed only to the effect of sampling bias; positive relationships are also found in studies where the species inventory in each site is almost complete (e.g., Figure 3).

Gaston and Lawton (1997) also suggested that distribution-abundance relationships among related species may be biased by phylogeny, as a result of the phylogenetic nonindependence of ecological traits (Harvey and Pagel 1991). However, this postulate has received no empirical support (see Paivinen et al. 2005), and there is no *a priori* reason to assume that phylogeny itself should lead to the inference of spurious distribution–abundance relationships.

DIRECTION OF CAUSALITY

Correlation between two variables indicates the existence of an unresolved causal relationship (Shipley 2004). This correlation may indicate that one of the variables causes the other, that both cause the other over time, that both are caused by some external latent (unmeasured) factor, or that the two variables are merely measures of the same entity (see Figure 6).

Studies of distribution-abundance patterns have plotted both distribution and abundance on the *x* axis. The low consistency with regard to plotting this relationship probably reflects a generally assumed consensus that causality between the two variables is likely to be bidirectional (e.g., Bock 1987; Gregory 1998). However, there is no clear empirical evidence supporting this as-

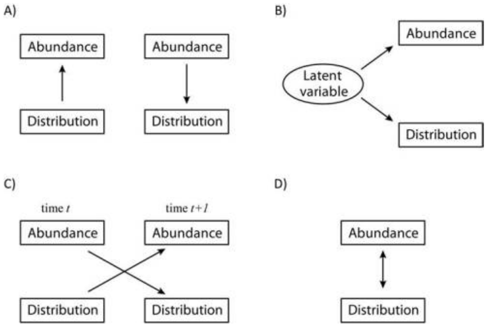

FIGURE 6. POSSIBLE CAUSAL PATHWAYS FOR DISTRIBUTION-ABUNDANCE RELATIONSHIPS

A correlation between two variables may indicate A) that one variable causes the other; B) that both are controlled by another (unmeasured) variable; C) that both variables affect each other (i.e., as causality cannot be completely mutual, they can only affect each other at a future time [Shipley 2004]); and D) that there is no causality as such between the variables, as they are just different manifestations of an underlying entity.

sumption, and the mechanistic hypotheses are based on different assumptions of the causal pattern underlying the distribution-abundance correlation (as shown in Table 1).

Clarifying the causal direction of distribution-abundance relationships has important implications within the context of conservation biology. Arguably, the most serious threat against the world's plants and animal species is habitat destruction (Balmford and Bond 2005; Jetz et al. 2007). If there is a strong effect of distribution on the abundance that a species can attain within the distributional range, species experiencing habitat destruction or range retraction as a result of climatic change may actually face a "double jeopardy" from the combined effects of small distribution and low population numbers (Gaston 1998; Johnson 1998). Similarly, species whose population numbers are dwindling as a consequence of human harvesting may experience double jeopardy if the influence of local abundance on distribution causes the ranges of these species to collapse (Gaston 1999).

Types of Distribution-Abundance Relationships

There are at least three types of relationships between distribution and abundance (Figure 1): interspecific, intraspecific temporal, and intraspecific spatial relationships. Interspecific relationships, which are the most empirically well-supported, refer to a positive correlation in a plot where each data point represents the distribution and abundance of one species (or other taxonomic level, such as genus or family [e.g., Harcourt et al. 2005]). The distribution of data points usually comprises all of the species belonging to an ecological community or taxonomic group within the study area (Gaston 1994). Interspecific relationships between local abundance and distribution have been reported to reveal both linear (e.g., Falster et al. 2001) and triangular (e.g., Gaston et al. 1998c) shapes on log-log plots ("triangular," in this sense, means that all the points of a scatter plot are located within a triangular region in one corner of the graph [Brown and Maurer 1987]). In logit distribution-log local abundance plots, interspecific relationships are generally linear (Figure 3) (Hanski and Gyllenberg 1997; Frost et al. 2004).

Intraspecific temporal relationships describe a positive correlation between the distribution and abundance of a single species where each data point is a point in time—for instance, a census done each year over a longer period of time (e.g., Gaston et al. 1999a). Intraspecific temporal relationships are far less prevalent than interspecific ones, and positive, negative, and nonsignificant intraspecific temporal relationships have all been reported (Gaston et al. 1999a; Borregaard and Rahbek 2006). In fact, the question of whether positive intraspecific temporal relationships are a general phenomenon is still not settled (Gaston et al. 1998a), although recent evidence indicates that they are exhibited by most species of an assemblage over longer time scales (10 years) (Borregaard and Rahbek 2006; Zuckerberg et al. 2009).

Somewhat misleadingly, most researchers refer to temporal relationships merely as "intraspecific relationships" (but see Venier and Fahrig 1998 and Guo et al. 2000 for exceptions). However, intraspecific spatial distribution-abundance relationships also appear in the literature. These refer to a positive relationship between the density of occupied sites and the local abundance across different parts of a species' range, with the greatest abundance and occupancy usually occurring near the central parts of the range (Whittaker 1965; Brown 1984). Although this pattern is generally assumed to exist, only few empirical analyses actually demonstrate it (but see Venier and Fahrig 1998), and there are also theoretical grounds upon which to assume an opposing, negative relationship. If the relative lack of dispersers near the range edges leads to extinction of patches with low abundance, then only a few high-abundance patches will persist here, thus leading to a pattern of larger local abundances together with lower occupancy near range edges (Hanski 1999; Paivinen et al. 2005).

Structural and Dynamic Modes of Causality

Although the three types of distribution-abundance relationships may be perceived as different patterns, they are not causally inde-

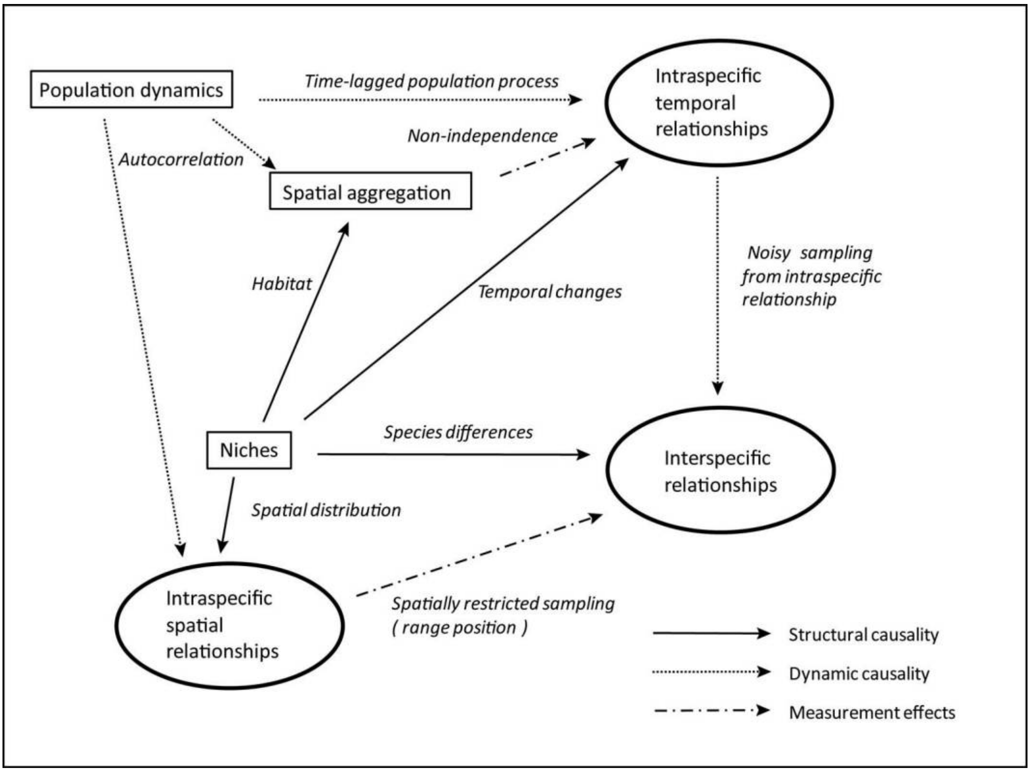

FIGURE 7. CAUSALITY OF DISTRIBUTION-ABUNDANCE RELATIONSHIPS
The flow diagram illustrates the interlinks between the types of distribution-abundance relationships and the different types of causality. The solid line denominates structural causality, the uniform dashed line represents dynamic causality, and the slashed dotted line indicates measurement effects. (See the text for details.)

pendent and can all be generated, indirectly, by the same set of processes; however, the causal pathways leading from the processes to each type of relationship are different (see Figure 7). There are two main causal pathways for distribution-abundance relationships, and each generates the three types of relationships in different manners. We refer to these as "structural" and "dynamic" causality.

To illustrate this point, consider the causality of interspecific relationships. These relationships may arise because of differences between the species of an assemblage, as some species have ecological characteristics that enable them to attain a greater distribution and a larger local abundance than others. This is an example of "structural" causality; the distribution-abundance relationship is a result of the attributes of the studied system, and is not likely to be very dynamic over time. On the other hand, interspecific relationships may arise because we are comparing species that each undergoes some dynamic process linking distribution and abundance, and, in this case, a positive relationship will occur even in the absence of any species differences. This is an example of "dynamic" causality. The distinction is conceptually similar to that between neutral and niche-based models of community assembly, but it does not represent two competing models, as the two modes of causality act together in most cases to generate the relationship.

Structurally causal models follow the type of causality illustrated in Figure 6B. A relationship between distribution and abundance is created because both are affected by some latent variable, such as the range of resources employed by a species. A consequence of this is that distribution and abundance are not directly causally linked (i.e., there are no arrows leading from one to the other in Figure 6B). Therefore, if the distribution of a species were suddenly halved by habitat destruction, these models would not necessarily predict any abundance changes in the remaining habitat.

Even though they are not dynamic *per se*, structural mechanisms will lead to temporal intraspecific relationships if the latent variable (e.g., the niche of a species) changes over time (Gaston and Lawton 1997). Such temporal changes are predicted to move the species along the regression line of the interspecific relationship in distribution-abundance scatter plots—a pattern which has not been found in empirical studies (Webb et al. 2007). However, this is probably not a very common cause of temporal relationships.

Dynamic causality works through a direct mechanistic linkage between distribution and abundance—the type of causality illustrated in Figure 6C. This implies that if one of the variables changes, it will be reflected by changes in the other; hence, distribution and abundance will track each other dynamically over time, although there may be a time lag in the response of one variable to the other (Gaston et al. 1999b; Conrad et al. 2001). Because the distribution and abundance of the same species are linked, the direct effect of dynamic causality is to create intraspecific temporal distribution-abundance relationships. As described above, dynamic causality will also generate interspecific relationships, although differences in the biology of species (e.g., dispersal ability) will generate "noise" and may lead to triangular relationships (Hartley 1998; Harte and Ostling 2001).

It should be noted that the division into dynamic and structural mechanisms is not clear-cut. Metapopulation dynamics, for instance, have both dynamic and structural components. The basic model has dynamic causality, as it provides a mechanistic linkage between the distribution and abundance of one species: both distribution and abundance contribute to the number of dispersers in the system, and both are again affected by the number of dispersers. But interspecific differences in dispersal propensity, for example, which may affect both distribution and abundance (Figure 6B), will contribute to interspecific relationships in a structural manner (this was discussed, though using different terms, in Hanski et al. 1993).

Figure 7 shows the causal linkage between intraspecific temporal and interspecific relationships. In addition, intraspecific spatial relationships may lead to local interspecific distribution-abundance relationships; this occurs if the study area overlaps the central part of the range of some species, and the edges of the ranges of others (Brown 1984). This has been termed the "range position" hypothesis (Gaston and Gregory 1997) (see Table 1), but it is not a first order biological mechanism in itself.

The higher empirical prevalence of interspecific relationships (Gaston et al. 1999a) seems to indicate that structural mechanisms play a role in the causality of distribution-abundance relationships; however, as temporal relationships are regularly observed (e.g., Borregaard and Rahbek 2006), there is also evidence for dynamic mechanisms. A number of factors may make intraspecific relationships appear weaker than they are. For instance, the time lag of intraspecific causality tends to increase the statistical noise in representations of the intraspecific distribution-abundance relationship, and may pose a major problem for the detection of patterns (Conrad et al. 2001). Furthermore, it has been argued that temporal changes in the distribution and abundance of a single species are generally of a significantly smaller magnitude than the range of values across the entire assemblage, which may in itself make it more difficult to detect intraspecific relationships (Gaston et al. 1999a).

A last group of mechanisms can be said to operate within a third mode of "causality," where distribution and abundance are not separate entities, but merely two representations of the same pattern (as argued by Gregory 1998) (see Type D in Figure 6). For example, an interpretation of self-similarity theory is that distribution and abundance are just manifestations, at different scales, of a scale-invariant clustering tendency of species distributions, measured by the fractal dimension (Kunin et al. 2000). This is not a causal relationship, but occurs because distribution and local abundance are both measures of the spatial configuration of individuals (see above) and, hence, are not necessarily independent. Such nonindependence between measurement of distribution and measurement of abundance may cause the observed relationship between distribution and abundance to be tightly dynamic. A change in one of the measured variables is immediately mirrored in the measurement of the other variable. Although the consideration of nonindependence is conceptually important, self-similarity in itself must still have a cause. Thus, some other mechanism-based factor must link the distributional patterns of species across different spatial scales, following a straightforward Type B causality (Figure 6).

A Fresh Look at the Mechanisms: What are Distribution-Abundance Relationships, and How Are They Created?

Hypotheses proposed to explain distribution-abundance relationships can be divided into groups based on their type of causality. These groups represent views describing complementary components of the process that determines the distribution and abundance of species, and an integrated approach incorporating these viewpoints is needed to give a full picture of ecological causality.

The hypotheses are formulated broadly, emphasizing general ecological structures and dynamics while ignoring potential differences between organisms. This is clearly an oversimplification. As previously noted, each hypothesis pertains to a certain range of scales and to certain measures of distribution and abundance, and each also reflects the biology of the organism. For instance, metapopulation dynamics are expected to occur at very different time scales for a population of fruit flies than for forest trees. Studies should consider the explicit causality implied in relation to the temporal and spatial scale of the study, as well as how distribution and abundance were measured, and the way in which the organism at the focus of the study may perceive scale (Wiens 1989; Rahbek 2005).

STRUCTURAL HYPOTHESES

Structural hypotheses have tended to deal with the amount of resources available to organisms. As originally formulated, the "resource use" hypothesis is based on the breadth of resource usage (Brown 1984): a species that can exploit a wider range of different resources is expected to be able to exist over larger areas, and is also expected to attain a higher density where it does occur, as a greater range of resources would be available to the organism at any specific site. A problematic implication of this argument is that there should be no advantage to habitat specialization, which can be expressed as a trade-off between high distribution and high local abundance. Since a specialist may be more efficient than a generalist at exploiting the same resource, it may be able to attain a high abundance locally, at the cost of a wide distribution. This implication seems unrealistic in many cases, and there is some empirical evidence that a high degree of resource specialization may counteract the resource use mechanism and lead to negative distribution-abundance relationships (see Paivinen et al. 2005 for an example among butterflies in Finland). In spite of this, many authors, somewhat misleadingly, refer to the hypothesis as the specialist-generalist hypothesis (e.g., Kotze et al. 2003).

Despite the intuitive appeal of the resource hypothesis, the central assumption that high resource breadth should result in the attainment of higher local abundance has not always been empirically supported (e.g., Gregory and Gaston 2000; Köckemann et al. 2009), although several empirical studies have supported this and all other key assumptions of the hypothesis (Barger and Esch 2002; Kotze et al. 2003; Heino 2005). Breadth of resource use practically always correlates well with distribution (e.g., Harcourt et al. 2005), and so claims that the resource use hypothesis can be discarded on the basis of empirical evidence (e.g., Paivinen et al. 2005) seem premature.

Alternatively, a species may have more resources available to it if it is specialized with respect to a very plentiful resource. This "resource availability" hypothesis argues that some species will be more widespread and abundant if the resources that they use are themselves both widespread and abundant (Hanski et al. 1993). As the mechanism depends on a correlation between the distribution and abundance of the resource, it has been argued that this explanation merely moves the question of causality to a lower trophic level (Hanski et al. 1993) and, therefore, is a secondary-level mechanism (i.e., the distribution and abundance of the resource still remains to be explained).

Since the distribution of resources is autocorrelated in the environment, the resource-based hypotheses are predicted to lead to intraspecific spatial distribution-abundance relationships. The amount of suitable resources and habitat is predicted to be highest in an area close to the center of the range of the species, and to diminish away from this point. As the amount of resource available controls both distribution and abundance, a similar pattern is expected to appear for these two variables, creating a spatially unimodal relationship (Brown 1984; Brown et al. 1995).

The resource use of an organism has been interpreted as its "niche," so that resource breadth is measured by niche width, and resource availability by niche position (Gaston and Lawton 1997).This is convenient, since niche width and niche position can be quantified by using ordination analysis (Gregory and Gaston 2000; e.g., Tales et al. 2004), for example, or co-occurrence data (Fridley et al. 2007). However, care must be taken when using niche measures to evaluate resource-based hypotheses, as the niche encompasses both biotic resources as well as abiotic conditions (Hutchinson 1957). Investigations of the impact of niche factors on distribution-abundance relationships should therefore consider the causality implied, and not merely invoke the theory of resource availability. The link between niche and distribution size is straightforward (Grinnell 1917), whereas the influence of niche on abundance is far less clear and depends on how the niche is defined. While the idea that more resources will allow a species to become more abundant is not a matter of contention, there is no obvious link between the commonality of a habitat—or any set of abiotic conditions—and abundance.

Several studies have reported strong correlations between niche position and both distribution and local abundance (Gregory and Gaston 2000; Tales et al. 2004; Heino 2005). However, in these studies, niche position was based on habitat conditions at the site where the species was found. This means that the resource availability mechanism, as described here, cannot explain the distribution-abundance correlations in these studies. Instead, studies quantifying the niche from habitat variables may in fact be comparing occupancy at two scales. When the grain size of a study is coarser than the scale of habitat turnover, the species associated with the most sparsely distributed habitat will appear to have lesser abundance than the species that are evenly distributed over the landscape, even though the abundance within the species' habitats may be the same.

In a paper entitled "Back to basics," Holt et al. (1997) generalized the structurally causal mechanism and integrated it with a population ecological perspective. Framing a theory of distribution-abundance relationships in terms of a simple population model, they described the limiting case in which no spatial dispersal connects the occupied sites, effectively enabling the model to ignore dynamic processes directly linking distribution and abundance. In such a system, the relative growth rate r of a population is determined by the rates of birth and death—the "vital rates" of the population. High r leads to higher local abundances, and, since all sites with $r > 0$ are predicted to be occupied, a correlation of abundance and distribution is expected (Figure 6B with r as the latent variable), assuming that the r of populations of the same species are correlated (e.g., because death rates are identical).

The idea is conceptually similar to Brown's resource use hypothesis, which can be thought of as a special case of vital rates dynamics—the case in which the variation in r between species is determined by the resource usage of the species. Additionally, the vital rates model makes explicit the required assumption that the strength of density-dependence is similar among species (Holt et al. 1997). Since the vital rates model is cast explicitly in terms of demographic parameters, it should, at least in theory, be more amenable to empirical testing. However, very few empirical tests of this model have been conducted, probably because of the inherent difficulty in measuring population-level birth and death rates.

One prediction of the vital rates model is that interspecific distribution-abundance relationships should be shaped by the distribution of habitat suitability on the landscape and its effect on the birth rates of populations. This prediction was recently tested by Freckleton et al. (2006), in a study that provided support for several of the predictions of the vital rates model.

DYNAMIC MECHANISMS

For a species to be present in an area, the presence or availability of suitable habitat and environment is not sufficient. The species also has to be able to reach the area and must be sufficiently numerous (in terms of individuals) for viable population dynamics to occur (Hanski 1999). Whereas resource-based mechanisms determine the distribution and size of areas that are potentially habitable by a species, population dynamic mechanisms determine how large a proportion of these habitable sites will be occupied by the species at any given time (see Figure 8 for an example).

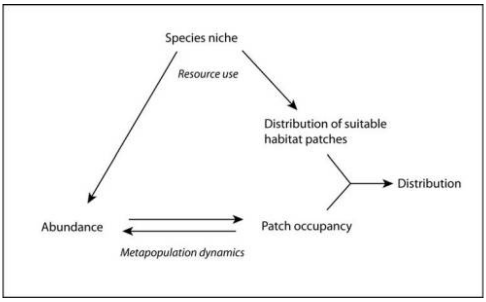

FIGURE 8. THE RELATIONSHIP BETWEEN STRUCTURAL AND DYNAMIC CAUSAL PATHWAYS

Different mechanisms affect different aspects of the distribution of species, and may work together to create observed patterns. Here the interaction is demonstrated for the most commonly quoted hypotheses: the resource use hypothesis and meta-population dynamics.

According to the metapopulation theory for distribution-abundance relationships, a positive correlation between site occupancy and local population arises due to dispersal between patches of suitable habitat (Hanski 1991a,b). The causality works in both directions, and is based on the number of dispersing individuals in the metapopulation. This number is assumed to be a function of the number of occupied patches, as well as the abundance at each patch. A larger number of dispersers will act to increase patch occupancy by increasing the number of colonization events, and may also serve to prevent small subpopulations from undergoing extinction (the "rescue effect") (Hanski and Gyllenberg 1993). If the level of dispersal is sufficiently high compared to local population growth, immigrants may increase the local abundance of subpopulations by facilitating a more rapid attainment of carrying capacity (Hanski et al. 1993).

The metapopulation hypothesis has received some empirical support. Gonzalez et al. (1998) found that distribution-abundance relationships in a system of moss patches on rocks disappeared when dispersal between patches was prevented, and Riis and Jensen (2002) demonstrated that aquatic plant species with better dispersal ability exhibited stronger relationships between site occupancy and local abundance. However, some authors have questioned whether most species exhibit metapopulation dynamics at the relevant temporal and spatial scales (e.g., Lawton 1996; Newton 1997; Cowley et al. 2001).

Dynamic causality is not confined to population dynamic mechanisms. A hypothesis based on resources was proposed by O'Connor (1987), who argued that individuals in populations existing at high densities could be forced to colonize lower quality habitats, which is effectively equivalent to increasing the width of the realized niche. This "density-dependent habitat selection" is expected to lead to distribution-abundance correlations at very local scales, although it is unlikely to result in the linear relationships shown in Figure 3. Since density is expected to be lower in the low-quality habitat, this mechanism might even lead to a negative correlation between occupancy and average local density (Paivinen et al.

2005). Nevertheless, this mechanism has been demonstrated to play an important role for some organisms, such as cod in the North Atlantic (Blanchard et al. 2005).

A hypothesis aimed at integrating these views was proposed by Venier and Fahrig (1996, 1998), who suggested that a synthesis between habitat availability and dispersal dynamics would not have to make metapopulation assumptions in order to generate distribution-abundance relationships: If a species can establish and breed in a larger proportion of the available landscape, a larger proportion of dispersal propagules will be successful and will elevate both local abundance and site occupancy at a landscape scale.

INTERSPECIES INTERACTIONS

At inspection, all of the proposed mechanisms are found to fall within a noninteracting community paradigm, in which species act out their population processes independently of the other species within the community. However, species interactions are a fact of ecological reality and are repeatedly found in local as well as individual-based studies (e.g., Brown et al. 2001; Suttle et al. 2007). In addition, the long-lasting debate concerning whether species interactions play an important role in structuring community-level patterns now seems to indicate that this is in fact the case (Gotelli and McCabe 2002). Processes such as interspecific competition could certainly play an important role in structuring interspecific distribution-abundance relationships (Holt et al. 2002b). By way of example, competitively dominant species have been hypothesized to expropriate portions of the potential niche space of other species, enabling the dominants to attain higher species densities and greater geographical distributions (McNaughton and Wolf 1970). The mechanism driving this process is basically an extension of the resource use hypothesis to incorporate interactions between the niches of species in the community. This "competitive dominance" hypothesis is also amenable to the critique that the efficiency of a species at exploiting a resource may be related to niche breadth (as noted above for specialists vs. generalists); i.e., the competitive dominant may have a smaller niche, and hence attain a smaller spatial distribution (the "included niche" phenomenon) (Chase 1996).

Although the dispute over the influence of interspecific interactions on community patterns has persisted for more than 30 years (Diamond 1975; Connor and Simberloff 1979; Gotelli and McCabe 2002), their potential importance for distribution-abundance relationships has been addressed by few studies. In studies of microcosms, Holt et al. (2002b) demonstrated that communities where several species were allowed to interact did, in fact, generate stronger distribution-abundance relationships than noninteracting communities. While these results are promising, microcosms are different from natural systems (Ricklefs 2004), and we have yet to see any field studies demonstrating the role of interspecific interactions.

DISTRIBUTION-ABUNDANCE RELATIONSHIPS AS SPATIAL AGGREGATION

Based on an argument by Wright (1991), a different school of thought maintains that distribution-abundance relationships are merely the result of the clumped nature of the spatial distribution of organisms (Hartley 1998; Holt et al. 2002a). To understand this, one can consider two extreme cases for a species increasing its population size: (1) if new individuals never occupy the same site as existing individuals, the number of occupied sites will increase linearly with population size, and (2) if new individuals always settle in already occupied sites, the local abundance will increase linearly with population size. For any case between those two extremes, both the number of occupied sites and the local abundance will increase when population size increases (Figure 6B).

Accordingly, even if the individuals of a species are randomly distributed, a positive distribution-abundance relationship can be expected (Wright 1991). This suggests that a Poisson distribution is a more correct null hypothesis for testing distribution-abundance relationships than the flat baseline assumption of no relationship that is used in most studies (Hartley 1998; for a discussion of null models, see Gotelli and Graves 1996). However, the use of a Poisson-based baseline has not, somewhat surprisingly, been generally implemented (but see Falster et al. 2001; Conlisk et al 2009).

Regressions of observed values of local abundance on distribution size are steeper than those predicted by the Poisson distribution (Wright 1991). However, the distribution of most organisms is not random but rather exhibits some degree of spatial aggregation, which may be modeled as a negative binomial (or similar) distribution (Hartley 1998; He et al. 2002). Using realistic values for the aggregation parameter in these distributions renders a good fit with observed distribution-abundance relationships (Hartley 1998).

Modeling aggregation patterns of individuals usually assumes rather small spatial extents (e.g. Hartley 1998) in which the habitat is relatively homogenous; however, there is no reason why aggregation at higher levels could not also be described by models of individual aggregation (hence the dotted line in Figure 4).

A different way of expressing aggregation in species' distributions is described by the self-similarity theory. Whereas the individual aggregation theory models the structure of species distributions at larger scales from very local-scale, individual locations, the self-similarity theory takes a top-down approach and uses large-scale distribution patterns to model aggregation at smaller scales (Kunin et al. 2000). The basis for this model is an observation that many natural patterns have a similar structure regardless of spatial scale; i.e., they have fractal properties (Halley et al. 2004). The distribution of the individuals of a species is one measure that has been shown to be self-similar over a certain range of scales (Ostling et al. 2000). Models incorporating this species-level self-similarity consistently generate a positive relationship between occupancy and local abundance (Harte and Ostling 2001).

Since self-similarity theory makes explicit mathematical predictions about the relationship between distribution and abundance, a number of studies have attempted to use it to estimate abundance directly based on the density of occupied sites at larger scales. The studies carried out so far have yielded some promising results (Hui and McGeoch 2007; Conlisk et al 2009), with potential application for conservation-orientated monitoring programs (Kunin 1998; He and Gaston 2000a; Figueiredo and Grelle 2009).

The main theoretical difficulty associated with the application of the self-similarity hypothesis to distribution-abundance relationships is that it is not clear whether the self-similarity condition should be assumed to apply to the distribution of individuals of one species (species-level self-similarity), or to the distribution of the species within a community (community-level self-similarity) (Harte et al. 1999; Ostling et al. 2000). These two types of self-similarity are mutually exclusive unless the fractal dimensions of all species are identical (Green et al. 2003), and only species-level similarity is expected to lead to realistic distribution-abundance relationships (Harte and Ostling 2001). However, it has been suggested that the homogenizing effect of factors such as geometric constraints and the distribution of habitat on the fractal dimension of species could reconcile these theories (Sizling and Storch 2004).

Recently, Storch and colleagues implemented the general concept of aggregation as a determinant of most macroecological patterns in a framework based on the idea of "general fractals" (Storch et al. 2008). By subdividing patches into random sub-patches at consecutive, discrete levels of spatial scale in a simulation model, they were able to generate several empirically established macroecological patterns, including species-area relationships and realistic abundance frequency distributions. They also suggested that the distribution-abundance relationship might be explained by this framework. This work further strengthens the argument for an aggregation-based causality for distribution-abundance relationships.

It has been repeatedly argued that the concept of spatial aggregation is merely a way of rephrasing distribution-abundance relationships in terms of a different pattern and is, thus, of limited value (Gaston et al. 1998b; Paivinen et al. 2005; Blackburn et al. 2006). However, synonymizing separate patterns and combining the theory surrounding them is in itself a worthwhile goal of theoretical science (Lakatos 1978). Furthermore, it should not be overlooked that if distribution-abundance relationships are merely another expression of aggregation across spatial scales, this will significantly increase the number of potential mechanisms and change our view of their causality. Any behavioral or ecological process that acts to increase aggregation (e.g., limitations on juvenile dispersal, flocking behavior, and habitat requirements) will then play a role in generating distribution-abundance relationships.

This accounts for the appearance of distribution-abundance relationships in the neutral model of biodiversity (Hubbell 2001). In neutral models, distribution-abundance relationships appear as a result of the spatial structure of colonization and dispersal on the community grid (Bell 2000, 2001). These factors act to produce positive relationships through their combined effect on the spatial aggregation of individuals, as dispersers originate from a few colonized spots and move only a limited distance before settling (Bell 2001).

Not only does spatial aggregation underlie the distribution-abundance relationships generated by these "unifying theories" of macroecology (Harte et al. 1999; Bell 2001; McGill and Collins 2003; Storch et al. 2008), but, as described in the section on structural mechanisms, it may also be the factor driving the effect of niche characteristics on relationships between distribution and abundance, as habitat specificity creates aggregation.

A Tentative Synthesis

Have all the pieces of the puzzle regarding the causality of distribution-abundance relationships fallen into place? Not quite yet. But the scale-specific causal framework outlined in this paper indicates how the complete picture may appear.

Distribution-abundance relationships occur as a complex interplay of ecosystem structural factors and the dynamics of individual populations (Figure 7). The different habitat and resource requirements of organisms mean that each species perceives the landscape in a specific manner. Species with abundantly available resources have dense distributions and attain greater local abundances, resulting in positive interspecific distribution-abundance relationships. Within that context, population dynamics link the occupancy of habitat patches with local abundances of each species dynamically, creating consistent relationships across time (temporal intraspecific relationships). These two pathways are not sharply delimited, and they affect each other mutually. Since interspecific relationships are comparisons of species that each experience population dynamics, these relationships are also affected by dispersal-based mechanisms, although the effect may be obscured by species differences. Similarly, since the resource basis for species varies in time and space, both temporal and local spatial relationships of the distribution and abundance of individual species will be created by the structural causal pathway.

This entire system describes a series of processes that causally link distribution and abundance as though they were two separate measures. However, it is questionable whether they can be treated like completely independent entities. The spatial clustering will affect measures of both distribution and abundance for each species, further contributing to linking the two variables. This noncausal link has very different properties from the mechanistic hypotheses, as it is primarily an effect of how distribution and abundance are measured and defined. Importantly, this view of distribution-abundance relationships allows for a much wider range of potential ecological explanations. However, the degree to which distribution and abundance are mechanistically linked or merely linked through aggregation remains a largely unresolved question that should be a priority for future investigations. This can only be investigated, most likely, through controlled experiments specifically targeted at the individual hypotheses. The few experimental studies that have been conducted thus far seem to indicate that a mechanistic causality plays at least some role in generating the various forms of distribution-abundance relationships (e.g., Gonzalez et al. 1998).

ACKNOWLEDGMENTS

The authors thank the Danish National Research Foundation for its support of the Center for Macroecology, Evolution and Climate. We also thank Dr. Robert Holt and an anonymous reviewer for insightful comments and constructive criticism of the manuscript, which significantly improved the final version.

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Associate Editor: Monica G. Turner