

REPORT

The 'abundant centre' distribution: to what extent is it a biogeographical rule?

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Abstract

Several ecological and evolutionary hypotheses are based on the assumption that species reach their highest abundance in the centre of their range and decline in abundance toward the range edges. We reviewed empirical tests of this assumption, which we call the 'abundant centre' hypothesis. We found that of 145 separate tests conducted as part of 22 direct empirical studies, only 56 (39%) support the abundant centre hypothesis. More problematic than the percentage of studies that support the hypothesis is the finding that most studies inadequately sampled the species' ranges. Only two of the studies analysed data that were collected throughout the species' range. The remaining studies relied on data from a small number of points in their analysis, meaning that the range edges were severely under-sampled. Patterns of abundance across the entire range must be known to draw testable hypotheses about the consequences of species' geographical abundance distributions. Indirect tests of the abundant centre hypothesis, in which ecological or evolutionary expectations of abundant centre distributions were examined, did not support or reject the abundant centre hypothesis overall. We conclude that more exploration of species' abundance distributions is necessary and we suggest methods to use in future studies.

Keywords

Biogeography, distribution of abundance, range edge, central and marginal populations.

Ecology Letters (2002) 5: 137–147

INTRODUCTION

A widely held belief in biogeographical ecology is that a species' abundance is typically greatest at the centre of its geographical range and uniformly low toward the edges. Many biogeography texts have described this 'abundant centre' distribution (Wulff 1950; Andrewartha & Birch 1954; Udvardy 1969; Naumov 1972; Kendeigh 1974; Whittaker 1975; Rapoport 1982; Brown & Gibson 1983; Cox & Moore 1985; Hengeveld 1990; Maurer 1994; but see Gaston 1994) and it has even been called a 'general rule' or 'rule of thumb' of biogeography (Hengeveld & Haeck 1982; Cotgreave 1993; Hochberg & Ives 1999).

A number of different mechanisms have been proposed that could theoretically support an abundant centre distribution. In Grinnell's (1922) formulation, populations of dispersive animals (i.e. birds) were likened to molecules of gas, dispersing from a central 'metropolis' of high abundance. Another early and now widespread formulation of the abundant centre hypothesis proposes that species

abundance distributions are coupled to environmental gradients (Shelford 1911; Andrewartha & Birch 1954; Kendeigh 1974; Cox & Moore 1985). At some point along this gradient (e.g. a temperature or moisture gradient), conditions are optimal for the species. This is where it reaches its highest population density. As distance from the optimal point increases in any direction, the species experiences less favourable conditions, and its population declines. Ultimately, the environment becomes too extreme for the species' survival. Brown (1984) argued that local abundance is a reflection of how well a particular site meets the needs of a species along many niche axes. These axes include the physiological characteristics of the species (e.g. temperature tolerance) as well as ecological characteristics (e.g. response to competitors or predators). Brown assumed that these parameters are spatially autocorrelated, so that sites close to one another should be similar in their capabilities for meeting the multidimensional needs of the species. Increasing the distance from an optimal site decreases the probability of a site meeting the multidimen-

sional needs of a species and thus, population size declines. Hengeveld (1993) emphasized the need to consider dynamic aspects of abundance distributions and described how abundant centre patterns would arise in response to 'risk surfaces' that identify threats to individual survival among and between generations in different parts of the range.

The abundant centre distribution has widely been used as the basis for hypotheses about ecological and evolutionary processes (Table 1). These hypotheses directly address many fundamental issues in ecology and evolution, such as how genes flow between populations, as well as applied ecological issues, such as how populations will respond to climate change and what populations should be the focus of limited conservation resources.

The persistence of the abundant centre concept in the literature, including its inclusion in many introductory textbooks and its ubiquity in ecological and evolutionary theories, suggests that the pattern should be widespread in natural populations. Nonetheless, there has been no systematic examination of empirical evidence for the pattern. We review here the recent literature of direct and indirect empirical examinations of the distribution of species' abundances. Our initial review simply quantifies the percentage of studies that support the abundant centre hypothesis based on the original authors' data and interpretations. We then discuss the quality of the data and appropriateness of the analyses used with emphasis on the difficulty of adequately quantifying species'

Table 1 Hypotheses based on the assumption that species are most abundant in the centre of the range and decline in abundance toward the range edges.

Hypothesis	Source
Edge population dynamics more variable	1, 7, 11, 13, 18, 30, 32, 34, 38, 39, 42, 50
Central populations are sources, edge populations are sinks	1, 7, 11, 18, 30, 32, 34, 38, 39
Extinction more likely at edges	9, 10, 19, 28, 29, 36, 37, 52
Central populations inhabit a greater variety of habitats	17
Competition less important at range edges	41
Competition more important at range edges	17
Competitors/parasites may limit species near edges	21
Gene flow from centre will swamp edges	2, 8, 12, 14, 16, 23, 24, 49
Edge populations less likely to be swamped by central populations	22
Edge populations genetically distinct	27, 44, 45
Edge populations less genetically variable	3, 33, 42, 46
Speciation likely to occur at edges	5, 40, 54
Vicariant event at edge will have greater impact than at centre	14, 27, 42
Siting of reserves/monitoring (protect edges)	27, 37, 42, 45
Siting of reserves/monitoring (protect centres)	6, 25, 26, 27, 35, 47
Pest outbreaks more likely from central populations	4, 20, 41
Reintroduced species will do better in historical range centre	26, 53
Site near range edge will see gradual population changes as climate change shifts species' ranges	18, 34, 43
Edge populations more resistant to climate change	42
Central part of range is centre of origin	35
Abundant centre pattern leads to observation of bimodal distribution of site occupancy and abundance	15, 31, 48, 52
Abundant centre pattern leads to latitudinal gradients in diversity	51

Sources: 1. Andrewartha & Birch (1954). 2. Antonovics (1976). 3. Aronson *et al.* (1990). 4. Birch (1957). 5. Brown (1984). 6. Brown *et al.* (1995). 7. Brussard (1984). 8. Case & Taper (2000). 9. Channell & Lomolino (2000a). 10. Channell & Lomolino (2000b). 11. Curnutt *et al.* (1996). 12. Emlen *et al.* (1986). 13. Enquist *et al.* (1995). 14. Garcia-Ramos & Kirkpatrick (1997). 15. Gotelli & Simberloff (1987). 16. Haldane (1956). 17. Hall *et al.* (1992). 18. Hengeveld (1990). 19. Hengeveld (1994). 20. Hengeveld & Haeck (1982). 21. Hochberg & Ives (1999). 22. Hoffman & Blows (1994). 23. Holt (1983). 24. Kirkpatrick & Barton (1997). 25. Lawton (1993). 26. Lawton *et al.* (1994). 27. Lesica & Allendorf (1995). 28. Linder *et al.* (2000). 29. Lomolino & Channell (1995). 30. Maurer & Brown (1989). 31. Maurer (1990). 32. Maurer (1994). 33. McClenaghan & Gaines (1981). 34. Mehlman (1997). 35. Murray *et al.* (1999). 36. Nantel & Gagnon (1999). 37. Nathan *et al.* (1996). 38. Ratcliffe (1968). 39. Richards & Southwood (1968). 40. Ridley (1996). 41. Rogers & Randolph (1986). 42. Safriel *et al.* (1994). 43. Sagarin *et al.* (1999). 44. Shreeve *et al.* (1996). 45. Smith & Theberge (1986). 46. Soule (1973). 47. Turpie *et al.* (2000). 48. Vetger *et al.* (1988). 49. Virgos & Telleria (1998). 50. Whittaker (1971). 51. Whittaker (1999). 52. Williams (1988). 53. Wolf *et al.* (1996). 54. Wulff (1950).

geographical abundance distributions. Where possible, we use examples from the literature to examine how investigators have tried to circumvent or overcome this difficulty.

METHODS

We reviewed the literature of studies that empirically examined the abundant centre hypothesis—that species should be most abundant in the centre of their range and decline in abundance toward the range edge. Searches were conducted as follows. (1) For the most recent literature we searched BIOSIS with Los Alamos National Laboratories' (LANL) interface for 'Title/Abstract/Keywords' fields containing the words 'distribution', 'abundance', and 'range' between 1998 and the present. Of these 685 citations, we examined those with title or abstracts that suggested species were sampled over a large part of their ranges, or those that mentioned species ranges or biogeographical patterns explicitly. (2) Using the Science Citation Index (SciSearch at LANL) we examined citations that had cited either Brown (1984) or Hengeveld & Haeck (1982), which are the studies most commonly cited as evidence of abundant centre distributions. (3) We examined studies cited in the papers found above and in biogeography textbooks. (4) We included results from our own abundance surveys of 12 species of North-eastern Pacific intertidal invertebrates (R.D. Sagarin and S.D. Gaines, unpublished data), because they represent one of the few studies that analysed data collected throughout all or most of the species ranges. Both our literature search method and the nature of macroecological literature (i.e. positive results are more likely to be reported, see Gaston & Blackburn 1999) may bias our study towards finding evidence of abundant centre patterns, although there is no way to quantify this bias.

We limited our analysis of empirical studies to those that focused on intraspecific variation over the species' geographical distribution and thus we did not include studies of variation over altitudinal gradients or local environmental clines. We did not include studies that featured data on geographical distributions of species' abundance in formats (such as contour maps of species density) that could only be analysed visually. Drawing conclusions from these data is rather subjective and has resulted in occasionally conflicting conclusions about the same data (Wiens 1989). For the same reason, we did not include abundance distribution maps generated by large bird censuses which have been variously cited as showing or not showing abundant centre distributions. Several papers that have used bird survey data as examples in more rigorous analyses (Brown 1984; Brown *et al.* 1995; Curnutt *et al.* 1996) were included in our analysis.

We divided our analyses into two categories: (1) studies that directly examined the abundant centre hypothesis, and

(2) studies that indirectly examined the abundant centre hypothesis by testing hypotheses derived from one or more assumptions of an abundant centre distribution.

In analysing the direct empirical studies of the abundant centre hypothesis each study was classified by the study system, number of sites, area of coverage, method of analysis used by the original authors, number of species studied, and the number of individual tests of the abundant centre hypothesis that could be performed on the data. Number of sites is reported directly or as 'multiple' if data came from large surveys that typically incorporate hundreds to thousands of sites. Coverage area was defined as 'whole' if sites were sampled throughout the range (this does not account for the variability in survey intensity often found in large, multiple observer data sets, such as the Breeding Bird Survey), and as 'partial' if survey sites were not evenly spread across the range. Analysis methods included: running transects to record density along a path cutting through either 'whole' or 'partial' data sets, measuring correlation coefficients between abundance and distance from the range edge or centre, or comparing densities found among varying numbers of 'range classes' that are defined by their distance from the centre or edge. In all of these cases, the assumption is that sites sampled nearer the range centre will show higher abundance than sites nearer the range edge.

We calculated the number of tests within each study that validated the abundant centre hypothesis in order to obtain an overall percentage of tests that support the hypothesis. In some cases, multiple tests were performed on a single species (e.g. if the patterns of abundance distribution relative to southern and northern boundaries were considered separately). Alternatively, a single test could represent an analysis of the entire distribution of a single species, or the overall pattern of a group of species combined. In determining the number of tests that validated the abundant centre hypothesis, we assumed that the type of data collected and the type of test conducted were appropriate for the hypothesis. For example, if a study sampled populations of several species at points near and far from the range edge and presented correlation coefficients for the relationship between abundance and distance from the edge for each species, we considered all significant, positive correlations to be tests that validated the abundant centre hypothesis. This is a vote-counting approach that avoids over-interpreting original data, but does not account for the quality of the data or the appropriateness of the data analysis for addressing questions about the geographical distribution of abundance.

The same level of detail was not possible with most of the indirect empirical studies. These studies are classified by study system, number of sites and species, as with the direct studies. However, these studies were scored as simply

supporting, not supporting, or inconclusive with regard to the abundant centre hypothesis. This score was based in most cases on the original authors' conclusions. Indirect studies that did provide enough detail to analyse individual species separately were considered inconclusive if the percentage of species showing the expected pattern was not significantly different from 50% (Chi-square test, $P > 0.05$).

RESULTS

Surprisingly few studies were found that directly tested the abundant centre hypothesis (Table 2). Even using fairly liberal criteria for finding support for the abundant centre hypothesis, only 39% of the individual tests supported the hypothesis. The majority of species had abundance distributions that differed from the expectation of an abundant centre. The low percentage of species showing abundant centre distributions is not corrected for the quality of the data or the merits of the study design, two factors that are critical to interpreting distributions of species' abundance (see Discussion). Thus, the overall percentage of tests supporting the hypothesis should be viewed as a starting point for discussion, rather than a measure of how frequently the abundant centre distribution occurs in nature.

In addition to the relatively low fraction of studies supporting the abundant centre hypothesis, several limitations of the studies can be observed directly in Table 2. First, the spatial coverage of the studies was limited. Spatial coverage is a function of the number of sites sampled and their geographical coverage. Most studies relied on transect or point sampling that covered a small number of sites spread over a restricted area of the range. Only eight studies included data collected throughout the entire range of the species. Moreover, among these geographically comprehensive studies, only two actually used data from throughout the range for statistical analysis (e.g. by examining abundance as a function of range classes of varying distances from the range edges).

Second, the geographical, ecological and taxonomic extent of the studies was limited. Twenty-one of the 23 studies were conducted in Europe (primarily in Britain) or North America (primarily in the United States). Only two studies featured marine species, and only one featured freshwater species. Only two studies featured non-avian vertebrates.

Finally, most studies tested the abundant centre hypothesis indirectly rather than directly (Table 3). Compared with the direct studies, more species, locations, habitats and taxa were represented in indirect tests, yet few examined the entire range of the species. There was no significant difference in the number of studies that supported (46%), did not support (25%) or were inconclusive (29%) compared to the null expectation of even numbers of studies in these three categories (Chi-square test, $P > 0.32$).

DISCUSSION

Intuitively, the abundant centre theory makes sense. Examples of biological responses to environmental gradients that yield approximately normal distributions are common (Whittaker 1967; Cox & Moore 1985), and the distribution of individuals across space might be expected to follow a similar pattern (Hengeveld 1993). The abundant centre distribution, if present, also simplifies many hypotheses about population dynamics, conservation biology, and factors that set species' ranges. Accordingly, a wide variety of ecological and evolutionary theories and models based on the assumption that species are most abundant in the geographical centres of their range appear in the literature. This theoretical work relates to some of the most fundamental and practical issues in ecology, including questions of where to situate nature reserves, where pest outbreaks are expected, how species will respond to climate change, and the genetic structure of populations. Empirically, however, our review suggests that calling the abundant centre pattern a general rule in ecology is at best premature. The majority of studies we surveyed support some alternative pattern of distribution of abundance.

In order to test the abundant centre pattern rigorously, the complete distribution of species' abundance must be known. However, it is difficult to collect and interpret data gathered over large, two-dimensional ranges. This problem is both logistical and geometrical. As the area of two-dimensional polygonal species ranges increases with distance from the centre, the edge of the range requires greater sampling than the centre to adequately characterize the patterns of abundance. Moreover, hypotheses based on abundant centre distributions cannot be rigorously tested without data on the complete distribution of abundance. This applies to all of the hypotheses in Table 1. For example, theory and models based on the idea that populations in depauperate areas will be swamped by gene flow from populous areas requires explicit information on where these populations are located in relation to one another. Likewise, density-dependent theories about pest outbreaks or population stability in relation to range location require spatially explicit data gathered from the entire range. This can be appreciated by considering alternative distribution patterns. For example, if species are most abundant at the edge of their range, genes and individuals may flow from the edges to the centre, leading to the opposite conclusions of abundant centre-based hypotheses. Alternatively, if species were most abundant at only one edge of the range (e.g. species became gradually more abundant toward the south edge of the range), the direction and magnitude of gene swamping or population outbreaks could not be predicted without identifying specific study locations.

Nonetheless, most studies have under-sampled the edges of species' ranges, suggesting that the actual fraction of tests

Table 2 Direct empirical studies of the abundant centre hypothesis.

Source (<i>n</i> = 22)	System	Sites	Coverage	Method of analysis	<i>n</i> species	<i>n</i> tests	<i>n</i> supporting
Bart & Klosiewski (1989)*	North American birds	Multiple	Partial	Transects from centre	3	3	1
Blackburn <i>et al.</i> (1999)	European birds	Multiple	Partial (northern)	Abundance/distance to edge correlation	32	64	15
Brown (1984)†	North American birds	Multiple	Whole	4 transects from centre	2	2	2
Brown <i>et al.</i> (1995)†	North American birds	Multiple	Whole	4 range classes	4	4	3
Carey <i>et al.</i> (1995)*	European grass	4 sites	Partial (northern)	Transect	1	1	1
Carter & Prince (1985)*	British prickly lettuce	36 sites	Partial (northern)	Surveys	1	1	0
Caughley <i>et al.</i> (1988)	Australian kangaroos	Multiple	Whole (1 sp.)/ partial (1 sp.)	Transect	2	2	2
Chiang (1961)*	North American corn borer	Multiple	Northern edge	2 transects	1	1	0
Curnutt <i>et al.</i> (1996)	North American sparrows	Multiple	Whole	5–8 range classes	6	6	4
Emlen <i>et al.</i> (1986)	North American birds	12 sites	Partial	Transect	18	18	8
Graves (1997)	North American bird	23 sites	Whole	Transect	1	1	0
Hengeveld (1994)*	European moth	Multiple	Partial	4 range classes	1	1	1
Massuti <i>et al.</i> (2001)*	European fish	816 trawls	Partial (northern)	Transect	1	1	1
McClure & Price (1976)‡	North American leafhoppers	37 sites	Partial	8 range classes	8	8	4
Norman & Brown (1988)	Australian bird	Multiple	Whole	Abundance/distance to edge correlation	1	1	0
Perez-Tris <i>et al.</i> (2000)	European bird	72 sites	Partial (southern)	3 range classes	1	1	0
Prince <i>et al.</i> (1985)*	British prickly lettuce	500 sites	Whole	Transect	1	1	0
Sagarin & Gaines, unpublished	North-eastern Pacific intertidal invertebrates	42 sites	Whole	42 range classes	12	12	2
Svensson (1992)	Northern European beetles	1100 sites	Partial	7 range classes	3	6	4
Telleria & Santos (1993)	European birds	58 sites	Partial (southern)	Abundance/distance to edge correlation	6	6	5
Williams (1988)	British bumble bees	2 areas	Partial (edge and centre)	Density comparison	15	1	1
Woodson (1964)§	North American butterflyweed	303 sites	Partial	4 Lat/long transects from centre	1	4	2
				Total	121	145	56

Notes: Because of obscurities in data reporting '*n* sites' may be approximate. Multiple site studies taken from surveys may indicate several 100 to > 1000 sites.

*Support based on original authors' conclusions—no statistical test was reported.

†Example species were selected by original author from a larger data set.

‡Hypothesis supported if peaks of abundance occurred in four range classes closest to centre of range.

§Support based on linear regression analysis (abundance vs. range class) by R.D. Sagarin on original data.

Table 3 Empirical studies testing indirect hypotheses that assume abundant centre distributions.

Hypothesis	Source (<i>n</i> = 28)	System	<i>n</i> species	<i>n</i> sites	Coverage	Support? ² *
Edge population dynamics more variable	Curnutt <i>et al.</i> (1996)	North American birds	6	multiple	Whole	I
Edge population dynamics more variable	Enquist <i>et al.</i> (1995)	Fossil North American molluscs	16	1	Point	Yes
Edge population dynamics more variable	Henderson & Seaby (1999)	North Atlantic fish	1	multiple	Southern edge	No
Edge population dynamics more variable	Mehlman (1997)	North American birds	3	multiple	Whole	Yes
Edge population dynamics more variable	Nantel & Gagnon (1999)	North American plants	2	2	Edge and centre	Yes
Edge population dynamics more variable	Whittaker (1971)	British insect	1	2	Point	Yes
Edge population dynamics more variable	Woodson (1964)	North American butterflyweed	1	multiple	Partial	I
Edge populations more fragmented	Blackburn <i>et al.</i> (1999)	British birds	32	multiple	Northern edge	No
Edge populations more fragmented	Linder <i>et al.</i> (2000)	North American birds	258	multiple	Whole	I
Edge populations more fragmented	Rapoport (1982)	South American tree	1	multiple	Edge and centre	Yes
Recruitment varies in relation to edge	Leggett & Frank (1997)	North Atlantic flatfish	3	multiple	Whole	No
Recruitment varies in relation to edge	Phillipart <i>et al.</i> (1998)	European fish	4	12	Whole	I
Extinction more likely at edges	Channell & Lomolino (2000b)	Worldwide, multiple taxa	309	multiple	Whole	No
Extinction more likely at edges	Channell & Lomolino (2000a)	Worldwide, multiple taxa	245	multiple	Whole	No
Extinction more likely at edges	Gotelli & Taylor (1999)	North American stream fish	41	10	Edge and centre	Yes
Extinction more likely at edges	Haeck & Hengeveld (1981)	European plants	1310	1	Point	Yes
Extinction more likely at edges	Lomolino & Channell (1995)	Worldwide, mammals	31	multiple	Whole	No
Extinction more likely at edges	Nathan <i>et al.</i> (1996)	Israeli birds	185	multiple	edge	Yes
Extinction more likely at edges	Villard & Maurer (1996)	North American birds	2	multiple	Whole	I
Extinction more likely at edges	Wilcove & Terborgh (1984)	North American birds	4	multiple	Partial	I
Translocations more successful in centre of range	Griffith <i>et al.</i> (1989)	Worldwide, birds and mammals	187	multiple	Point	Yes
Translocations more successful in centre of range	Wolf <i>et al.</i> (1996)	Worldwide, birds and mammals	182	multiple	Point	Yes
Niche breadth greater in centre	Svensson (1992)	European beetles	3	multiple	Partial	I
Edge populations more genetically variable	Lesica & Allendorf (1995)	Worldwide plants	18	multiple	Edge and centre	I
Edge populations less genetically variable	McClenaghan & Gaines (1981)	North American rat	1	16	Edge and centre	Yes
Members of an assemblage near their own range edge will have low abundance	Enquist <i>et al.</i> (1995)	Fossil North American molluscs	67	1	Partial	Yes

Table 3 (continued)

Hypothesis	Source ($n = 28$)	System	n species	n sites	Coverage	Support?*
Members of an assemblage near their own range edge will have low abundance	Griggs (1914)	North American plants	106	1	Edge	No
Members of an assemblage near their own range edge will have low abundance	Hengeveld & Haeck (1982)	European beetles, birds, plants	1590	1	Point	Yes
					Total (%)	7 (25)
					No	
					Total (%)	13 (46)
					Yes	
					Total (%)	8 (29)
					Inconclusive	

*Support: 'yes' indicates that the conclusions of the indirect test are suggestive of an abundant centre distribution. 'I' indicates that the study was inconclusive.

that adequately support the abundant centre hypothesis is even smaller than that calculated in Tables 2 and 3. Studies that featured data from multiple sites, but only examined one part of the species overall range (marked 'partial' in Table 2) cannot conclude that species' abundances are generally higher in the range centre compared to the range edges. For instance, a study that examines half of the range and finds lower abundances at the range edge than at the centre would misrepresent a distribution where abundances continue to increase on the other side of the range centre. In fact, some species' abundances have been shown to decline continually from one edge of the range to the other (Graves 1997; Ferguson & McLoughlin 2000). In studies we conducted of the entire ranges of 12 species, five had distributions that declined uniformly from peak abundances at one range edge to lowest abundances at the other (R.D. Sagarin and S.D. Gaines, unpublished data).

Some studies used linear regression analysis on abundance data collected from sites near the centre and edges, and concluded that a negative slope from centre to edge was evidence of an abundant centre distribution (Emlen *et al.* 1986; Curnutt *et al.* 1996). There are problems with the use of linear regression when comparing abundance to a continuous variable such as latitude or range position when sampling is not completely uniform across the range (Pacheco & Henderson 1996; Scharf *et al.* 1998). In the studies we reviewed, a conclusion that a species has an abundant centre distribution based on linear regression analysis sometimes masked the existence of high abundance sites near the edge of the range (e.g. Emlen *et al.* 1986, fig. 3, and Curnutt *et al.* 1996, fig. 7). This is especially problematic when only a small number of sites near the range edge were sampled, as there is no way to determine if abundant edge sites are anomalies that should not detract from the

conclusion of the regression analysis, or representative of abundance at the edge in general.

Even studies that utilized data collected from the entire range (marked 'whole' in Table 2) often under-sampled the range edges by analysing only data taken from transects running through parts of the range (Brown 1984; Prince *et al.* 1985; Caughley *et al.* 1988; Graves 1997). As a result, areas of high abundance at the range edge are likely to be missed or under-represented. In cases where data are available from the entire range, it would be more appropriate to use geostatistics to analyse the spatial distribution of the data. Brian Maurer and colleagues have used fractal dimensions of the semivariance function (which is related to measures of spatial autocorrelation among sites) (Maurer & Heywood 1993; Maurer & Villard 1994; Villard & Maurer 1996) and measures of the volume dimension (Maurer 1994; Linder *et al.* 2000) on density maps of BBS data to examine spatial patterns of population fragmentation across species ranges. Although these measures tell us something about the overall three-dimensional texture of the abundance distribution, and have been argued in some cases to show evidence of abundant centre distributions (Villard & Maurer 1996), they do not pinpoint the location of areas of high or low abundance. Rossi (1992), however, showed how these geostatistical measures can be made with respect to direction away from the range centre, to provide spatially explicit information about features of the data such as abundance peaks. Although Rossi applied these methods to local scale data (e.g. beetle abundances from fields), they are equally applicable to geographical scale data such as bird density maps.

The indirect studies of the abundant centre hypothesis did not avoid the problems encountered in the direct tests. Spatial coverage in the indirect tests was often incomplete

(Table 3). Moreover, hypotheses to explain geographical scale patterns are based in a wide range of theoretical frameworks and thus may propose multiple explanations for the same pattern or may contradict one another (Gaston & Blackburn 1999, also see Table 1). For example, abundant centre patterns are alternatively expected to lead to genetic differentiation of edge populations (due to genetic bottlenecks and drift) (Lesica & Allendorf 1995) or swamping of genetic diversity at the edges (due to immigration from abundant central populations) (Haldane 1956; Holt 1983). Since these opposing predictions are tested in the indirect studies, the studies' conclusions are ambiguous in relation to the abundant centre hypothesis. As Griggs (1914, p. 42) commented of his own indirect study: "...it cannot be generalized nor can it serve as a guide to the optimum habitats of plants whose preferences are unknown. Like much *a priori* reasoning it presents a conclusion which may be true rather than one that must be true. Moreover, another line of *a priori* reasoning might in this case lead us to diametrically opposite conclusions." Additionally, there are likely to be alternative explanations for observed patterns that do not rely on abundant centre distributions. For example, although Channell & Lomolino (2000b) did not find that ranges collapsed from the edges to the centre as expected under the abundant centre assumption, they concluded that human pressure, rather than alternative underlying abundance distributions, led to the observed patterns. Although potentially valuable for examination of some ecological and evolutionary questions on smaller scales, the indirect tests are a poor substitute for direct survey-based studies when considering the abundant centre hypothesis.

Given the inherent empirical challenge of sampling distributions over broad geographical scales, we need new approaches that simplify the logistical tasks or enhance the analytical rigor. One simplification of this problem is to examine species with ranges that are essentially one-dimensional. Intertidal species, for example, occupy a narrow strip of shoreline along coastlines that may be thousands of kilometres long. Sampling one-dimensional ranges greatly simplifies questions related to defining species borders (there are only two endpoints to define rather than an infinite number of points around a polygonal range). Moreover, the problem of increasing range area as a function of distance from the range centre disappears, which greatly facilitates the problem of adequately sampling the entire range. Most species ranges, however, cannot be approximated as one-dimensional, making this method limited in its applicability.

Understanding geographical patterns in species abundance may provide insight into fundamental ecological and evolutionary questions such as how genes flow between populations, how species' ranges shift under changing

climatic conditions, and what determines the boundaries of species' ranges. Moreover, it may suggest shortcuts for notoriously difficult problems in applied ecology, such as situating reserves and identifying species that are threatened by human activities. At present, we do not have an adequate understanding of geographical abundance patterns for most species and environments on Earth. It is thus premature to generalize about these patterns, let alone to use generalizations with little empirical support to guide resource conservation strategies.

But beyond simply testing the abundant centre hypothesis, we should consider how distributions of abundance can be used to refine ecological and evolutionary hypotheses. In this regard, the lack of convincing evidence in support of abundant centre distributions can be seen as an opportunity. Our studies on intertidal species, for example, showed a diversity of abundance distributions, including those where abundance was highest right at the range edges (R.D. Sagarin and S.D. Gaines, unpublished data). These distributions would seem to suggest radically different underlying mechanisms and consequences for gene flow, range limits, population dynamics, etc., than the hypotheses listed in Table 1. Ideally, however, we must combine geographical distributions of abundance with similarly scaled data on relevant factors such as physiological condition and population recruitment rates. Overlaying these data may provide a filter by which to rule out multiple alternative hypotheses and move macroecology beyond pattern recognition.

ACKNOWLEDGEMENTS

The Hopkins Marine Station Librarian, Joe Wible, was instrumental in acquiring many of the sources cited. Fiorenza Micheli made useful suggestions to improve an earlier manuscript. R.D.S. acknowledges the support of the Switzer Environmental Fellowship, NASA Earth Systems Science Fellowship (grant no. NGT 30339), and National Science Foundation graduate student fellowships (RTG grant no. BIR94-13141 and GRT grant no. GER 93-54870), and Fiorenza Micheli. R.D.S. and S.D.G. acknowledge the support of the A. W. Mellon Foundation and the National Science Foundation (grant no. OCE 98-13983). This is contribution number 62 from PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans: A Long-term Ecological Consortium funded by the David and Lucile Packard Foundation.

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Editor, P. Marquet

Received 26 September 2001

First decision made 6 November 2001

Manuscript accepted 15 November 2001