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Species' geographic ranges and distributional limits: pattern analysis and statistical issues

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With the increasing concern about species conservation, a need exists for quantitative characterization of species' geographic range and their borders. In this paper, we survey tools appropriate for the quantification of static spatial patterns related to geographical ranges and their borders. We then build on these static methods to consider the problem of changes in geographic range through time. Methods discussed are illustrated using lark sparrow data from the North American Breeding Bird Survey. While there is no such thing as the ''best'' or ''only'' method to analyze species geographical range and border, we show that a series of methods can be used in sequence to provide complementary and useful quantitative information for species occupancy of range. Indeed, the location of species' borders estimated at different times can be compared to identify locations where species expand or go locally extinct. The ability to delineate accurately species' ranges will be useful to conservation biologists, managers and ecologists.

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There are a number of theoretical and practical reasons to quantify spatial pattern in species' ranges and their borders (Hoffmann and Blows 1994, Gaston 2003). With increasing concern about species conservation, it is important to obtain quantitative descriptions of species' range structure and extent of geographical ranges of species to provide accurate information for management purposes (Lawton 1993). Specific questions related to the quantitative characterization of species' ranges and their borders that need to be addressed include: (i) how large are geographic ranges?; (ii) how can geographic range boundaries be identified?; (iii) are range boundaries gradual or sharp transitions?; (iv) are the shapes of species' boundaries jagged or smooth?; (v) how much variation in the use of the landscape is found within range boundaries?; (vi) are there internal boundaries?; and (vii) is the range fragmented? Once some of these questions have been answered, other questions naturally arise, such as: with what attributes of the landscape (both abiotic and biotic) are the various structures of a species' range associated? How does the structure of a species' range vary through time?

To answer these questions, maps that accurately delineate the geographical range of a species are needed. The characterization of species' ranges is, however, complicated by their spatial and temporal dynamics. For many species, ranges may expand in some geographical regions while contracting in others (Hengeveld 1990).

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Hence, descriptions of species range boundaries require not only that borders are determined accurately at any given point in time, but also that these limits can be characterized in terms of their shape and width (Maurer 1994, 1999, Curnutt et al. 1996, Maurer and Nott 1998, Gaston 2003). Furthermore, it is important to identify the internal distribution of abundance within range boundaries. Indeed, large variations in abundance result in gaps within a species' range that can create internal borders (Brown et al. 1996). Hence the quantification of spatial pattern of the outer species' border limit, as well as within-species range boundaries, may help to resolve outstanding questions in spatial ecology such as the importance of source and sink demography (Pulliam 1988).

The exercise of producing species' range maps is not new (Rapoport 1982) and in fact is common in biogeography (Hengeveld 1990, Maurer 1994, Gaston 2003). Similarly, the delineation of ecological boundaries to better understand the relationship between boundary structures and their functions is an active research area in ecology (Cadenasso et al. 2003, Fagan et al. 2003, Strayer et al. 2003). Here, we want to present recent approaches that can be used to better characterize the location of geographic range borders as well as changes in these locations (Gaston 2003). Specifically, we present an overview of the different quantitative methods specific to: (1) the delineation of species' distributional limits; (2) the characterization of the spatial pattern of the border itself (e.g. shape, width); (3) the quantification of spatial variation of species abundance within the range; and (4) the detection of changes in geographic range structure through time.

Lark sparrow (*Chondestes grammacus*) distribution data from the North American Breeding Bird Survey (BBS, Robbins et al. 1989) will be used to illustrate these methods and facilitate the comparison among them in terms of their abilities to describe and quantify species ranges and their borders. (Further examples may also be found in Gaston 2003.)

Case study data: lark sparrow

This sparrow is distributed throughout the Great Plains of North America (Fig. 1) and prefers open woodlands and savannah habitats throughout its range. Its breeding range extends from northern Mexico to southern Canada and as far east as West Virginia (where it is rare). By far, it is most common in the southern Great Plains, particularly from northern Texas to southeastern Colorado.

Historically, lark sparrows were limited to the west, but expanded their range with forest clearing in the eastern North America (Rising 1996). With extensive forest regrowth, however, eastern populations have declined. The species is migratory, wintering throughout the southern United States and Mexico, so that in south western North America breeding and wintering ranges overlap.

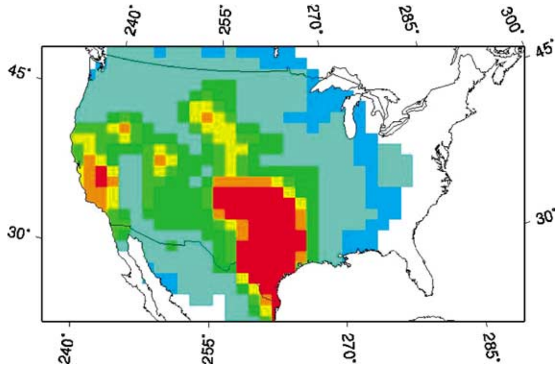

Fig. 1. Relative abundance distribution map of lark sparrow, from 1966 to 1995, computed by resampling the presence-absence data of BBS routes using 2° × 2°quadrats.

Issues related to data

Our ability to detect and characterize both species' range and border is limited by the quality and types of data available. Typically, ranges are delimited using sample data and these may be either local abundance or simply presence and absence (Maurer 1990, 1994). The accuracy of sample data is strongly influenced by the spatial (grain and extent) and temporal (duration and frequency) resolution at which data are collected and interpreted. Furthermore, field data have inevitably some degree of uncertainty due to measurement errors resulting either from species misidentification, incorrect abundance counts, or lack of accurate location information. Hence, inferences regarding range structure are limited by the spatial resolution of data. In some cases, resolution can have only a minor effect on analytical outcomes and consequent conclusions (Hawkins and Porter 2003, Blackburn et al. 2004). Most of the time however, sample sites are generally quite local compared to the scale of species' ranges such that interpolation or aggregation of data is necessary to characterize species' ranges. This process can generate sampling error even if none is present at the level of sample sites. For instance, sampling error may be introduced when one assumes that a species is absent from a region because it is absent from all sites sampled within the region. The species may be found within the region at localities not in the sampling design.

With mobile species, other considerations need to be taken into account. These include decision rules to determine when to stop sampling the outer species' border and when a species is locally extinct at a given site based on occurrences through time (Green and Young 1993, Reed 1996). Thompson (1992) proposed several types of adaptive spatial designs to sample mobile species such as using a given sampling step, or distance between sampling sites, until at least one individual is encounter and then exhaustively counting individuals in the immediate neighbourhood. This approach can be appropriate in the centre of the species' range but not at the border. At the border, other approaches should be used such as the one suggested by Green and Young (1993) where the sampling effort necessary to detect rare species is calculated assuming either a Poisson or negative binomial distribution of abundances (McArdle 1990).

Besides measurement error, other sources of variability (e.g. demographic, environmental, dispersal) affect our ability to locate species' borders accurately. Unlike plant species that are sessile, animal species are mobile so their abundance within their range fluctuates from year to year (Guo et al. in press). The magnitude of these fluctuations varies according to both demographic and environmental variability. The ability of species to disperse as a function of landscape fragmentation also can limit species expansion (Holt and Keitt 2000).

Species' range maps based on only one year of data are less accurate, sometimes drastically so (Gibbons et al. 1993), than those based on multiple years of records. Indeed, given inherent species demographic variation, species' range maps based on spatial time series data longer than the species generation time are more likely to be reliable as they integrate population fluctuations. The analysis of long space–time series needs to be subtler than simple aggregation. Indeed, the major drawback of aggregating temporally in long time series is the risk of missing expansion or extinction events. Species' range borders are probabilistic entities, and the challenging task is to characterize this probability profile in space, and how it shifts in time. When accurate species' range maps are available, combining several years of data could indicate the maximum extent of the range.

Species' border analysis

Approaches to delimit species' range boundaries (Fig. 2) are similar to those used to detect ecotone and ecological boundaries (Jacquez et al. 2000, Fagan et al. 2003) and those used to characterize species home range (Worton 1995a). With presence–absence data, a home range boundary can be determined by linking all the point locations such that no angle between points exceeds 180° using the minimum convex polygon algorithm or the α-hull algorithm, as recommended by Burgman and Fox (2003). This procedure minimizes the effect of extreme points that might enlarge a species' range artificially. Presence and absence data can also be aggregated at a coarser spatial resolution such that relative abundance data (e.g. Fig. 1 where presence–absence data from the BBS routes were resampled using 2° × 2° quadrats to obtain relative abundance data) and other edge detector methods can be used.

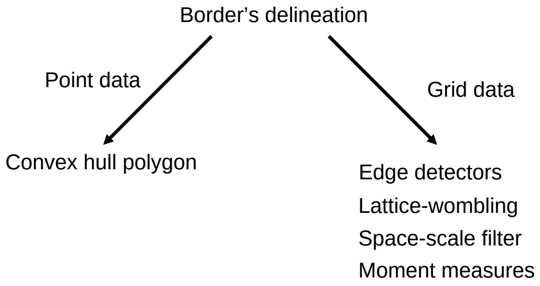

Fig. 2. Methods to delineate boundaries according to data type.

The method used to detect boundaries depends on the spatial structure of the sampling protocol (regularly versus irregularly spaced samples; abundance versus presence–absence; Jacquez et al. 2000). In remote sensing, detection of boundaries is achieved by measuring gradients (i.e. rate of change) among locally neighbouring pixels using edge detection kernels known as edge filters (Fagan et al. 2003). There are several algorithms, called operators or image enhancement filters, which are available in most GIS and remote sensing software packages. Such kernel operators use moving windows of four, nine, or even more pixels. Gradients computed from 3 × 3 windows are smoother than those computed from 2 × 2 windows (such as lattice-wombling; Jacquez et al. 2000), and hence reduce more of the noise. These operators are sensitive to noise, making it necessary to smooth the data first. Smoothing the data can be achieved either by aggregating adjacent cells obtaining fewer larger cells or by using a Gaussian filter that preserves the same number of cells. Efficient filters are those that both reduce the noise and enhance boundaries, such as the Canny adaptive filter or the scale–space techniques (Fig. 3) using the Laplacian of Gaussian algorithm (Faghih and Smith 2002, Hay et al. 2002). The scale–space techniques perform a series of smoothing using a Gaussian kernel of increasing size, allowing the detection of boundaries persistence across scales (Csillag et al. 2001). The size of the window is critical, as is the quadrat size in field data, in the trade-off between noise reduction and the ability to accurately localize boundaries as well as detecting boundary zones. Finally, given the inherent degree of uncertainty attributed to field data, fuzzy logic has recently been used to detect boundary zones (Lowell 1994, Wang and Hall 1996, Jacquez et al. 2000).

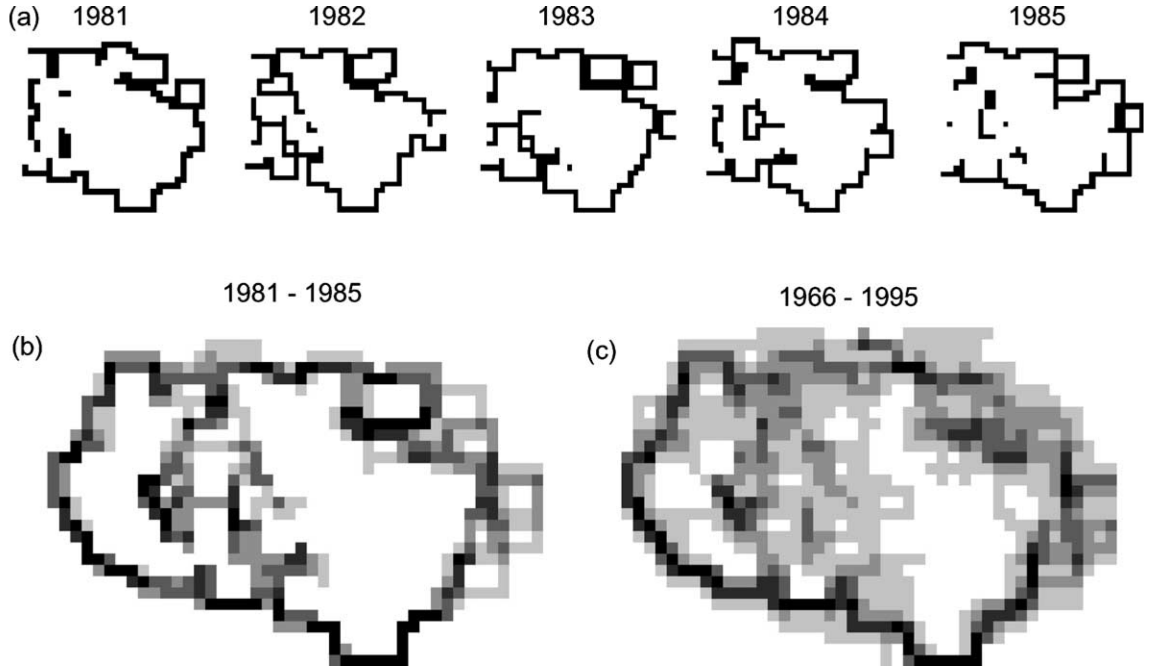

Fig. 3. Species' border based on scale-space filter using 2° × 2° quadrats of lark sparrow. (a) yearly boundary for 1981 to 1985. (b) number of yearly delineated boundary per quadrat from 1981 to 1985 [grey shade 1 = 1, grey shade 2 = 2, grey shade 3 = 3, grey shade 4 = 4, and black = 5]. (c) number of yearly delineated boundary per quadrat from 1966 to 1995 [grey shade 1 = 1 to 5, grey shade 2 = 6 to 10, grey shade 3 = 11 to 15, grey shade 4 = 15 to 20, and black = 20 to 30].

Moments measures

When the distribution of a species has been quantified in terms of presence–absence data over a uniform sampling grid, as is often the case in regional distribution atlases (Gibbons et al. 1993), these presences and absences can be used to produce an estimate of the position of any location occupied by the species with respect to the range edge. One such measure is simply the average distance (D_0) of that site from all other occupied sampling locations (Blackburn et al. 1999). This average distance will be small when the location in question is centrally positioned relative to other occupied locations on the sampling grid, and will increase the closer the site is to the periphery of the species' distribution. No attempt is made to quantify exactly where the edge of the species distribution lies. This may be advantageous in circumstances where a range edge is diffuse, or where a measure of the distance to the range edge does not well represent how peripheral a particular location is. For example, the two shaded occupied grid squares in Fig. 4a are both close to the range edge, but the one on the right is more peripheral in terms of the overall distribution of the species. This difference is embodied in the average distances of these sites from all other occupied grid squares, values of which for every occupied grid square are shown in Fig. 4b. Clearly, this measure requires taking into account some level of spatial autocorrelation if variation in the magnitude of a variable (e.g. local abundance) is studied using data on that variable from a high proportion of all occupied squares. The maximum value of D_0 also varies with range size, and so requires standardization for comparisons of ranges over time, populations, or species.

Boundary shape and width

Since more than one process can interact in the creation and maintenance of boundaries (environmental conditions and species interaction), boundary shape and width may vary widely along the periphery of a species' range. To detect different boundary shape behaviours, different landscape metrics (Gustafson 1998, Fortin et al. 2003) and others (Maurer 1994) can be computed for subsections and the values compared (Fig. 5). Similarly, these landscape metrics might be useful in describing the species' range.

For ranges here a finite "boundary" has been determined, but for which there is only one dimension (i.e. a line). Fractal dimension can be computed to characterize boundary level of spatial complexity (Mandelbrot 1982). With respect to species' borders, multifractal analysis (Feder 1988, Milne 1992) allows one to study spatial variation in the dimension of the range boundary and therefore can be used to infer changes in

Fig. 4. (a) Lark sparrow distribution represented by presence (1) and absences (empty squares) across a sampling grid of 2° × 2° of the presence/absence data of BBS routes from 1966 to 1995. (b) The average distance of each of the occupied grid squares in (a) from all other occupied squares, D_0, which equals

$$\sum_{1}^{n-1} \frac{\sqrt{((|x - x_i|)^2 + (|y - y_i|)^2)}}{n-1}$$

where x and y are the co-ordinates of the focal square, x_i and y_i are the co-ordinates of the ith occupied square, and n is the total number of occupied squares (rounded down to the nearest integer).

processes limiting a species' distribution in different geographical regions.

Species' boundaries are rarely lines, but should instead be represented as gradients, boundary zones in abundance. These boundary zones may vary in intensity and width along the entire species' border. To investigate that the boundary width is not an artefact of the sampling design, species' border persistence can be assessed in delineating boundary using different spatial unit resolutions (Csillag et al. 2001), and by then computing the minimum and maximum boundary zone widths as the minimum and maximum distances between the two edges of the boundary zone (McIntire 2003). Note that population variability along the border can only be detected when abundance data are available.

Comparing boundary shape

Once the border is delineated, it could be of interest to detect differences in boundary shape and changes in location (Fig. 6). Kaufman (1998) developed two metrics, the perimeter/area measurement (following Rapoport 1982) and the edge-consistency index (ECI) to compare boundary shape for subsections of the range. The perimeter/area allows a fractal-type analysis of the range boundary, where data quality or other conditions make multifractal analysis inappropriate (Maurer 1994). This method requires the delineation of a range boundary, but is evaluated at the level of grid squares. The ECI allows for the comparison of range edges based on presence–absence data from grid squares. Often, data

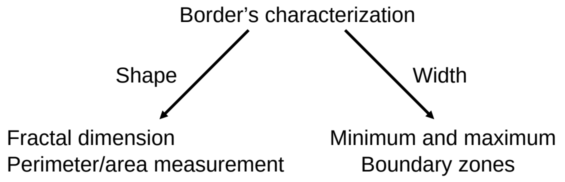

Fig. 5. Methods to characterize boundary's shape and width.

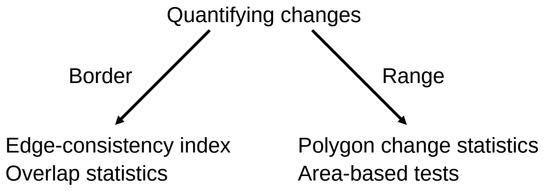

Fig. 6. Methods to analyse borders and ranges changes.

are too coarse to allow for an accurate delineation of a range edge, and this method makes those data available for analysis. Both metrics can be applied to questions where there are a priori predictions about differences in variability of the range edge between subsections of the range for a group of individuals, species, or taxa. For example, one could compare northern and southern edges for a group of species and test for inequality of directional differences based on hypothetical predictions. The perimeter/area measures boundary geometry and, in the subsection of range examined, compares the number of grid squares through which the boundary passes to those where the species is present. The ECI measures the consistency of the edge relative to the coordinate system (e.g. latitude). These metrics permit the evaluation and comparison of subsections of the range edge, while being sensitive to the limits of the data (Kaufman 1998).

These calculations are made to utilize presence–absence of a species across the grid system and to compare the shape and placement of the boundaries for selected subsections (such as northern and southern range boundaries). For these metrics, the range needs to be contiguous relative to quadrats (see Kaufman 1998 for criteria making ranges amenable to analysis via these metrics); therefore, the metrics are here computed for the lark sparrow using 3° lat/long quadrats. The ECI requires only presence–absence data and tests for the level of correspondence to, in this example, latitude. The perimeter/area requires the delineation of a boundary (here, based on a minimum convex polygon) and tests for the geometric complexity of that boundary. Both indices range from low values (always >0) up to 100. An ECI of 100 means that the range edge corresponds perfectly to a row of latitude, whereas low values mean that a weaker relationship exists with latitude. For the example of lark sparrow, the ECI value is 66.7 for the northern boundary and 42.7 for the southern boundary. A perimeter/area of 100 means a high level of complexity or that the range boundary passes through every quadrat where the species is present in the tested section, whereas low values mean more "linear" or simple geometries. For our avian example, the perimeter/area value is 68.2 for the northern boundary and 80.9 for the southern boundary. That means, for the lark sparrow that the northern edge has a tighter correspondence to a single latitude than does the southern edge, and that the northern edge is more linear or regular than the southern edge.

In some circumstances, it may be of interest to compare the ranges' border of different species, or the border of a single species estimated by different methods or at different times. Further, one may wish to compare empirically identified species limits with those predicted by theories or models (Holt and Keitt 2000). Comparisons between empirical borders estimated at different times can be useful to stress areas of potential species extinction and expansion, while comparisons between empirical and theoretical borders can highlight some ecological or evolutionary processes not included in the theoretical models. Comparisons between empirical and theoretical boundaries also provide the opportunity to test the predictions of theory. For example, Kaufman (1995) proposed that species tend to be limited by different factors at high latitudes than at low ones–that abiotic factors are most limiting at high latitudes and decrease in importance toward the tropics, while biotic interactions are most limiting in the tropics and decrease in importance as abiotic factors become limiting. Kaufman (1998) further developed this idea for the high-and low-latitude boundaries of individual ranges and predicted, for example, that species distributed across that temperate zone would tend to have ranges where the high-latitude edge would more closely parallel latitude and be more geometrically simple or "linear" than the low-latitude edge. This prediction was based on the idea that, because abiotic factors (e.g. temperature) are relatively well correlated with latitude and because biotic interactions (e.g. competition) would tend to exclude, by chunks, the potential parts of the species' range, abiotically produced range edges would be more highly related to latitude and geometrically simple than biotically limited range edges. For mammals in the temperate zones of the New World, the data were consistent with these predictions and high latitude edges paralleled latitude more closely and were more linear in geometry than low latitude edges (as was also true for our example of the lark sparrow).

While several methods exist to delineate boundaries and to characterize boundary shape, not that many statistics exist to quantify their movements. Fortin et al. (1996) proposed a series of overlap statistics to test whether boundaries from different sources overlap spatially or not. These overlap statistics compute the minimum spatial distance between boundaries based from different data sets and their significance is assessed using randomization tests. They can allow us to discriminate between boundaries that completely coincide spatially for one part of the species' range (O_D: direct overlap statistic) from those parts where boundaries are not overlapping (O_M: minimum spatial distance statistics). Here, we investigate whether or not lark sparrow boundary location fluctuates through time, we computed these two overlap statistics on boundaries delineated using three different time periods (5, 10, and 15 years) based on the lattice-wombling edge detector algorithm (Jacquez et al. 2000). The results of the direct overlap statistic O_D (Table 1) inform us that the species border locations (i.e. pixels that are forming the boundaries) overlapped more within one another in the earlier part of the time series (1966 to 1985) having values around 94 (94, and 96) than in the later part (1986–1995) where the values decreased to 90 and 85. This was true of boundaries delineated using both 5-year and 10-

Table 1. Overlap statistics between boundaries based on lattice-wombling for lark sparrow over different period of time. (ex.: 1966–1970: 5 years presence–absence summed to produce a species' range boundary). All the values are significant at $\alpha = 0.05$.

Years	O_D	O_M (distance in °)
1966–1970 compare to 1971–1975	94	0.512
1971–1975 compare to 1976–1980	94	0.457
1976–1980 compare to 1981–1985	96	0.336
1981–1985 compare to 1986–1990	90	0.359
1986–1990 compare to 1991–1995	85	0.312
1966–1975 compare to 1976–1985	93	0.429
1976–1985 compare to 1986–1995	85	0.483
1966–1980 compare to 1981–1995	88	0.435

year periods; when the 15-year period was used the overlap was of 88 locations. The results of the minimum spatial distance statistic O_M (Table 1) are providing information about the degree of movement (distance) between the two compared boundaries. When comparing the results of the two overlap statistics, we detect that while there are more boundary locations at the same location earlier (as indicated by the O_D), there is also the most distance between the boundaries at other locations (as illustrated in Fig. 3). These overlap statistics are therefore informative about the spatial dynamics of the boundaries and whether or not these movements are significant.

Species' range pattern analysis

As species occupancy varies over its geographical range, the characterization and quantification of the species spatial abundance can provide valuable insights about this response to environmental changes and habitat alterations. Here we present two families of techniques to perform such spatial pattern quantification (Fig. 7).

Kernel density methods

The problem of identifying a species' range is comparable to identifying an individual's or group's home range, although at a higher level of organization. Simply drawing a line around some estimate of the range is a less than optimal solution. As mentioned above, the localities utilized by individuals, packs or species varies with time. Furthermore, the utilized localities may not be visited with equal frequency. It is therefore more useful to represent a species' range with a density surface portraying the probability that a species can be detected in a locality (Fig. 8).

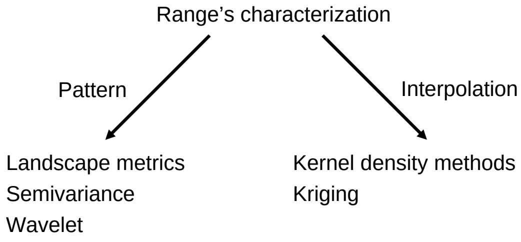

Fig. 7. Methods to analyse the spatial pattern of ranges and to map them.

This change in thinking helps the researcher to realize that the concept of the species' range as some fixed area within which all individuals of a species will be found is at best an idealization, and at worst, specious. Nonetheless, species' ranges can still be characterized and compared. The species' range can be operationally defined as the area where the probability of finding an individual of the species is greater than some defined value. Alternatively, the range could be defined as the area containing some arbitrary proportion (such as 0.95 or 0.99) of the total species' population. This concept has been utilized successfully in the study of home ranges (Worton 1989a, b, 1995a, b, Seaman and Powell 1996).

A number of methods are available for the estimation of probability densities (Izenman 1991). One of the most widely used approaches is kernel density estimation. The kernel density estimate has a number of very attractive statistical properties. It is a true probability density function, and furthermore, it is very easy to bootstrap from the kernel density estimate (Worton 1995a, b). This means that the kernel density estimate is more than just a heuristic graphical representation, but can be used as a probability density function in statistical analyses. Bootstrapping can also be used to construct confidence intervals for range estimates (Kern et al. 2003). Simulations have shown that kernel density estimation based estimates of home range perform well compared to other methods (Worton 1995a, b, Seaman and Powell, 1996, Kenward et al. 2001, Kernohan et al. 2001, Girard et al. 2002, Matthiopoulos 2003). Silverman (1986) and Scott (1992) provide very readable

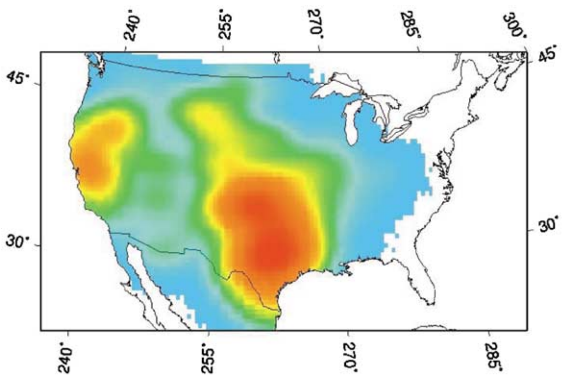

Fig. 8. Kernel density map of lark sparrow relative abundance, from 1966 to 1995, computed by resampling the presence–absence data of BBS routes using 2° × 2° quadrats. Bandwidth selected by jackknife crossvalidation.

introductions to the theory and application of kernel density estimation.

Geostatistics

Ecological and evolutionary processes that set species' range boundaries may influence not only the shape of the range border, but also local variation in abundance across the species' range (Maurer 1999). Spatial pattern across the entire species' range can be quantified using global spatial statistics and geostatistics (Legendre and Fortin 1989, Cressie 1991, Maurer 1994). The basic process assumed by global spatial statistics, to range border estimation, is that the abundance of a species is determined by geographical scale variation in ecological conditions (Villard and Maurer 1996). These spatial statistics quantify, therefore, the intensity and scale of spatial pattern by estimating the degree of spatial autocorrelation using either variogram function or spatial autocorrelation coefficients (Legendre and Fortin 1989). These global spatial statistics assume however that the spatial process is stationary such that it can be parameterized with the same values for the entire extent of the study area. Spatial stationarity implies that the statistical moments describing variation in abundance do not change over space. Lack of stationary occurs in the presence of trend or local variability in variance across the entire study area. Many geographic ranges probably do not meet this requirement since there is a definite pattern in abundance across geographic ranges (Brown et al. 1996, Maurer 1999). If there is a spatial trend in the data, then a geostatistical model can still be used if large-scale variation in abundance can be attributed to changes in environmental conditions across geographic space (below). When species abundances are influenced by several different processes over the entire range, the assumption of stationarity of the global spatial statistics are not fulfilled and spatial characterization should be performed using local spatial statistics (Boots 2002) or wavelets analysis (Bradshaw and Spies 1992, Dale and Mah 1998) which are less sensitive to departure from stationarity and could be used to quantify species' range spatial structure.

Geostatistical methods of estimating the within-range variation in abundance use data obtained for a collection of grid cells (pixels) within a species' geographic range (Maurer 1994, Villard and Maurer 1996). The goal of the spatial analysis using geostatistics is to first estimate the spatial variation in abundance from these sampled sites using the semivariance function and then to use this information about the spatial autocorrelation to interpolate values, called kriging, at unsampled locations (Fig. 9; Legendre and Fortin 1989, Cressie 1991, Maurer 1994).

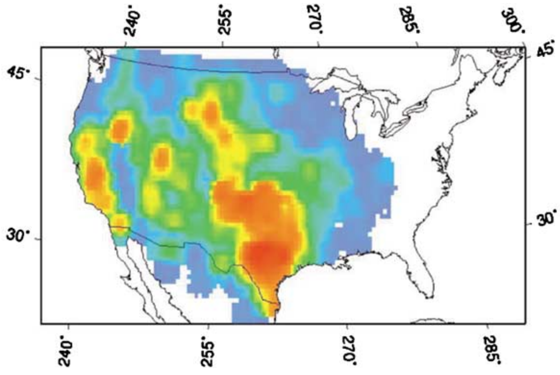

Fig. 9. Kriged map of the lark sparrow lark sparrow relative abundance, from 1966 to 1995, computed by resampling the presence–absence data of BBS routes using 2° × 2° quadrats.

Several modifications of the basic semivariogram and kriging procedures can be used when the available data depart from the basic assumptions requires for estimation of spatial variation in abundance. When abundance data are available and it is suspected that the data show a spatial trend, the assumption of stationarity cannot be made. Universal kriging can be used, however to quantify the spatial trend and estimate spatial autocorrelation of the residuals (Cressie 1991). When the spatial pattern shows non-linearity that cannot be fitted by a polynomial function, nonlinear kriging can be used (Goovaerts 1997). When presence–absence data are used, kriging is based on the indicator variogram. An indicator variogram that quantifies the spatial structure of binary data, or of quantitative data that are converted to binary data by using an arbitrary threshold, can be used to map the spatial pattern. Finally, species may respond to different types of habitats within their geographical range. In such circumstances, stratified kriging offers a way to interpolate over regions that have different spatial variances due to some change in strata types. For example, in fragmented landscapes, it is inappropriate to krige deciduous forest and agricultural lands using the same semivariance function. Instead, the spatial dependence should be determined separately for each habitat type and then spatial pattern should be interpolated using stratified kriging (Wallerman et al. 2002).

Range changes

Changes in species' ranges (Fig. 6), defined as polygons, can be characterized using Sadahiro and Umemura (2002) polygon changes analysis which describe polygon dynamics in terms of their spatial (geometric) dynamics using six primitive events: (1) generation: appearance of a polygon, (2) disappearance: loss of a polygon, (3) expansion: increase in area, (4) shrinkage: loss of area, (5) union: two polygons merging, and (6) division: a polygon splitting into two. Also, in the same spirit as the overlap statistics for comparing boundary locations, Maruca and Jacquez (2002) proposed to test difference in polygon locations using area-based tests comparing the amount of area overlapping between polygons.

Species' range prediction

Species spatial distribution is linked to the specific habitat requirements. The amount and spatial configuration of habitats are however also spatially dynamic. Hence, species geographical range extent and spatial pattern is linked to the availability and arrangement of habitats. Spatial and quantitative data about habitats can be extremely useful in the estimation of species' boundaries. Indeed, knowledge of species habitat and climate requirements can be used to obtain a probabilistic map of species occurrence based on logistic regression and predictive models (Davis et al. 1998, Pearce and Ferrier 2000, Guisan and Hofer 2003, Sutherst 2003, Loiselle et al. 2003). Such probabilistic maps can be used to locate a potential species' border. Habitat information can also be combined with kernel density information to improve boundary predictions (Matthiopoulos 2003). Spatially explicit population dynamics can be useful for delineating source portions of a species' range in data rich situations (Lele et al. 1998). Predictions based on habitat covariates can be very important in regions where the biota has not been exhaustively surveyed, allowing range analysis to be extended beyond limited observations.

Conclusion

There is no such thing as the best method to delineate border and characterize range. In fact, the choice of the most appropriate methods is guided the combination of data type, data quality, and research questions. Here our goal was to stress how the combination of existing and novel quantitative and spatial statistics could be used in a complementary way to better describe species' geographical range. This wealth of statistical methods comes, however, with a suite of technical challenges related to the spatial and temporal resolution of the data: too fine a resolution would portray highly fragmented species occupancy patterns and range edges that seem exceedingly variable, while too coarse a resolution would not pick up species responses to environmental changes and changing land use pressures. Taxonomic accuracy is also a fundamental problem as species taxonomy is a moving target: speciation events do occur and the novel abilities that separate species into sub-species may become more and more apparent with intensive study.

Having these concerns in mind, the spatial statistics presented here can still be used to produce reliable species' range maps, which are needed for conservation purposes. By doing so, important questions regarding the identification of the locations where species expand or go locally extinct can be investigated by comparing the locations of species' borders estimated at different times. Caution should be taken when comparing historic geographic ranges, which presumably reflect thousands of years of species dispersal, occupancy and speciation, with recent estimates of geographic ranges which are based on a few decades of data in highly changing landscapes. Hence, a comparison of historic and current geographic ranges based solely on their physical properties (size, limits and pattern) may be misleading, akin to comparing apples to oranges.

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