Essay

Scale Dependency of Rarity, Extinction Risk, and Conservation Priority

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Abstract: *In developing red data books of threatened species, the World Conservation Union uses measures of rarity, rates of decline, and population fragmentation to categorize species according to their risk of extinction. However, most quantitative measures of these three concepts are sensitive to the scale at which they are made. In particular, definitions of rarity based on an area-of-occupancy threshold can nearly always be met if area of occupancy is calculated from a sufficiently fine-scale (high-resolution) grid. Recommendations for dealing with scale dependency include (1) choosing a standard scale of measurement, (2) using multiple scales of measurement, and (3) developing indices that combine information from multiple scales. As an example of the second and third approach, the construction of a species' scale-area curve represents a unifying method for quantifying all three indicators of extinction risk—rarity, rate of decline, and population fragmentation—as functions of area of occupancy and measurement scale. A multiscale analysis is also of practical importance because measurements made at different scales are relevant to different extinction processes. Coarse-scale measures of rarity are most appropriate when threat is assessed on the basis of spatially autocorrelated events of a large extent, such as global climate change, whereas fine-scale measures may best predict extinction risk due to local processes such as demographic stochasticity. We illustrate our arguments with a case study of the British distributions of two related plant species that show a 200-fold reversal in their relative rarity when measured at different scales.*

Dependencia de la Escala de la Rareza, Riesgo de Extinción y Prioridad de Conservación

Resumen: *Al desarrollar los libros rojos de especies amenazadas, la Unión para la Conservación Mundial utiliza medidas de rareza, tasas de declinación y fragmentación de la población para categorizar especies según su riesgo de extinción. Sin embargo, la mayoría de las medidas cuantitativas de estos tres conceptos son sensibles a la escala en la que son hechas. En particular, las definiciones de rareza basadas en un umbral de área de ocupación casi siempre pueden ser satisfechas si el área de ocupación es calculada en una rejilla de escala lo suficientemente fina (alta resolución). Las recomendaciones para tratar con la dependencia de la escala incluyen (1) selección de una escala estándar de medida, (2) utilización de múltiples escalas de medición y (3) desarrollo de índices que combinan información de múltiples escalas. Como ejemplo del segundo y tercer método, la construcción de una curva escala-área de una especie representa un método unificador para cuantificar los tres indicadores del riesgo de extinción (rareza, tasa de declinación y fragmentación de la población) como funciones del área de ocupación y escala de medición. Un análisis multiescala también tiene importancia práctica porque las medidas tomadas a diferente escala son relevantes para diferentes procesos de extinción. Medidas de grano grueso de la rareza son más apropiadas cuando se evalúa la amenaza de eventos espacialmente autocorrelacionados de gran extensión, tal como el cambio climático global, mientras que las medidas de grano fino pueden predecir mejor el riesgo de extinción debido a procesos locales como la estocacidad demográfica. Ejemplificamos nuestros argumentos con un estudio de caso de la distribución británica de dos especies de plantas relacionadas que muestran una reversión de 200 veces en su rareza relativa cuando se miden en escalas diferentes.*

Introduction

In an effort to conserve biodiversity, resources are often directed toward protecting rare species in the belief that these are the species most at risk of extinction (Gaston 1994). Few would argue with this general premise, but its successful implementation as policy demands an explicit definition of rarity and the way in which rarity relates to extinction risk. This highly important, yet almost unattainable, goal of defining a species' relative extinction risk has been confronted by the World Conservation Union (IUCN) in its development of rules for assigning species to various IUCN Red Data Book categories (World Conservation Union 1994, 2001). In the absence of detailed population viability analyses, some of the main indicators used for the assessment of extinction risk are rarity, rates of decline, and degree of population fragmentation. Although the revised IUCN criteria (World Conservation Union 1994, 2001) are based on more quantitative measures and decision rules than had been used previously, issues of spatial scale have still not been adequately resolved. Here, we focus on three widely used indicators of extinction risk—rarity, decline, and fragmentation—and demonstrate how each is sensitive to the scale at which it is measured. We then consider several approaches that have been taken to respond to such scale dependence. These include the use of standard scales of analysis, collection of data at multiple scales, and various methods for combining multiple-scale information into an aggregate index. Finally, we suggest how an explicit consideration of scale could provide much-needed focus and cohesion to the challenge of relating indicators of risk to the actual processes leading to extinction.

Case Studies

To illustrate various concepts developed in this essay, we refer throughout to the distributions of two plant species from the family Caryophyllaceae: *Dianthus armeria* L. (Deptford pink) and *Silene otites* (L.) Wibel (Spanish catchfly). Both species are distributed across continental Europe and beyond, but we restrict our attention to Britain because this is the area for which we have the most detailed and comprehensive data. For the sake of argument, we ask the reader to imagine that these distributions represent the total extent of the species' global ranges (the general methods and arguments would apply equally well had we used the true global-scale data). British distributional data for these two species are of high quality, compiled from the field records of a large number of dedicated amateur and professional botanists and collated by the Botanical Society of the British Isles and the Biological Records Centre at the Centre for Ecology and Hydrology, Monks Wood (U.K.) (Stewart et al. 1998; Wigginton 1999). We supplemented the national distri-

bution data (assumed to be comprehensive at a 1-km resolution) with finer-scale field surveys of a subsample of occupied square kilometers (Hartley et al. 2003).

Rarity

Single-Scale Measures

Most people have their own intuitive idea of what constitutes a rare species. However, finding a universally acceptable definition and measure of rarity is not straightforward. Some of the many possible measures that have been used include the breadth of geographic range size, degree of habitat specificity, local frequency, endemism, ephemerality, relative abundance, area of occurrence, and absolute population numbers (e.g., Harper 1981; Rabinowitz 1981; Gaston 1994; Quinn et al. 1996). Three of the most commonly applied and easily quantified measures (as used by the IUCN and others) are extent of occurrence (EOO), area of occupancy (AOO), and numbers of individuals. These three measures can be arranged on an axis of increasing spatial resolution (Fig. 1). At the coarsest scale, EOO is a measure of geographical range size. It is conveniently defined by the area of the minimum convex polygon (MCP) that encompasses all known records of the species. As an index of rarity, EOO reveals nothing about the distribution of a species' population within its range; indeed, its value can be highly influenced by the presence of a single outlying population or individual (Gaston 1994; World Conservation Union 2001). At the other extreme, population counts require the enumeration of all individuals, data which are usually very difficult and expensive to obtain.

Between (and even beyond) these two extremes, measures of AOO can be made across a wide range of spatial scales. Typically, AOO is measured by dividing the study area into a number of contiguous sample units and summing the area of the occupied units. Ideally, the sampling units will be of equal size (e.g., grid squares), although in practice the spatial referencing of records may be based on geopolitical units of unequal sizes (e.g., counties or countries). Relatively large sample units produce high

Population Count	Area of Occupancy	Extent of Occurrence
(Individuals)		(Range size)

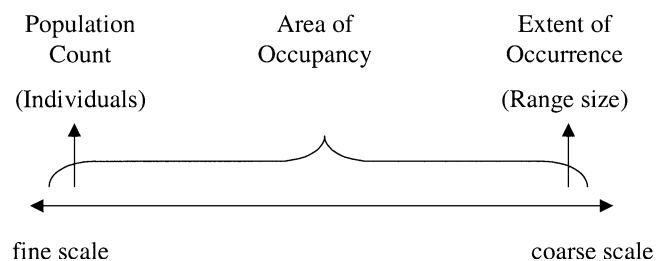fine scale   coarse scale

Figure 1. Three quantitative measures of "rarity" arranged on an axis of spatial resolution. In principle, area of occupancy may be measured at any scale.

values for AOO (World Conservation Union 1994, 2001; Palmer et al. 1997; Keith 1998; Keith et al. 2000), which may approximate or even exceed the EOO-defined range size. Conversely, the use of relatively small units produces lower values for AOO that correlate well with population counts (He & Gaston 2000a). If sessile organisms are being measured at a very fine scale, then individuals may be deemed to occupy multiple grid cells and AOO approaches a measure of ground cover (Kunin 1998; Kunin et al. 2000).

The IUCN criteria for categorizing extinction risk consider all three of the measures mentioned above. With respect to "area of occurrence," species are considered critically endangered if they occupy <10 km^2, endangered if they occupy <500 km^2, and vulnerable if they occupy <20,000 km^2 (Table 1, criterion B2). Because data sources are varied, and because some species cannot be mapped sensibly at very fine resolutions (e.g., highly mobile species), the criteria allow for flexibility in the scale of mapping. The AOO thresholds in criterion B remain fixed, however, which has the unfortunate effect of making those species mapped at high resolution appear the rarest, with low AOO values, whereas species for which only coarse-scale information is available will appear less rare, with large AOO values (Keith 1998; Cowley et al. 1999; Keith et al. 2000). Thus, contrary to the precautionary principle, those species about which we have the least information are more likely to receive a lower extinction-risk rating.

In Britain, species distributions are often summarized as presences and absences recorded on a regular grid of 100-km^2 square cells, these cells being used as the sample unit with which to calculate AOO (e.g., Stewart et al. 1998; Wigginton 1999). Nationally "rare" plant species are defined as those that occupy 15 or fewer grid squares (AOO $\leq$ 15,000 km^2), and nationally "scarce" plants are those that occupy between 16 and 100 squares (AOO $\leq$ 100,000 km^2). This is a well-defined and standardized measure, although concern exists that the rankings might be substantially altered if a different resolution grid were to be used (Pearman 1997). Under this system, no extant British plant species, however rare, can achieve an "area of occurrence" of <100 km^2 because this is the size of a single grid cell. Therefore, in the absence of higher-resolution information, no British species could qualify as critically endangered by the IUCN criterion B. In most countries, the resolution of distributional information is much poorer than in Britain, thus raising concerns about the general applicability of the existing AOO criteria.

Figure 2 illustrates the MCP and AOO (measured at two different scales) for the British distributions of *Dianthus armeria* and *Silene otites*. As the resolution of mapping increases, the area occupied by each species declines markedly because fine-scale mapping inevitably uncovers unoccupied space within "occupied" coarse cells (Erickson 1945; Kunin 1998). The rate of change across

Table 1. Summary of some of the World Conservation Union (IUCN) criteria applied to determine a species risk category.[a]

| Risk category[b] | Rarity | | | Rate of decline | Fragmentation or population structure | | | Probability of extinction[j] |
	population size[c] (individuals)	AOO[d] (km²)	EOO[e] (km²)	percentage decline in 10 yrs[f]	no. of locations[g]	even distribution of individuals[h]	uneven distribution[i]	
CR	>50 or >250	>10	>100	≤90 or ≤80 or ≤25[k]	1	all subpopulations ≤50 individuals	1 subpopulation with ≥90% individuals	≥50% in 10 years
EN	>250 or >2,500	>500	>5,000	≤70 or ≤50 or ≤20[l]	≤5	all subpopulations ≤250 individuals	1 subpopulation with ≥95% individuals	≥20% in 20 years
VU	>1000 or >10,000	>2,000	>20,000	≤50 or ≤30 or ≤10	≤10	all subpopulations ≤1000 individuals	1 subpopulations with 100% individuals	≥10% in 100 years

[a]To be included in a particular risk category; species must meet one main criterion or a specified combination of subcriteria. For further details refer to World Conservation Union (2001).
[b]CR, critically endangered; EN, endangered; VU, vulnerable.
[c]Criterion D or subcriterion of C.
[d]Area of occupancy; subcriterion B2.
[e]Extent of occurrence, subcriterion B1.
[f]Subcriterion A1 or A2-4 or C1, applied to population size.
[g]Subcriterion B1a.
[h]Subcriterion B2a.
[i]Subcriterion C2a(i,ii).
[j]Criterion E, as determined from a quantitative analysis.
[k]CR subcriterion C1 calculated over 3 years.
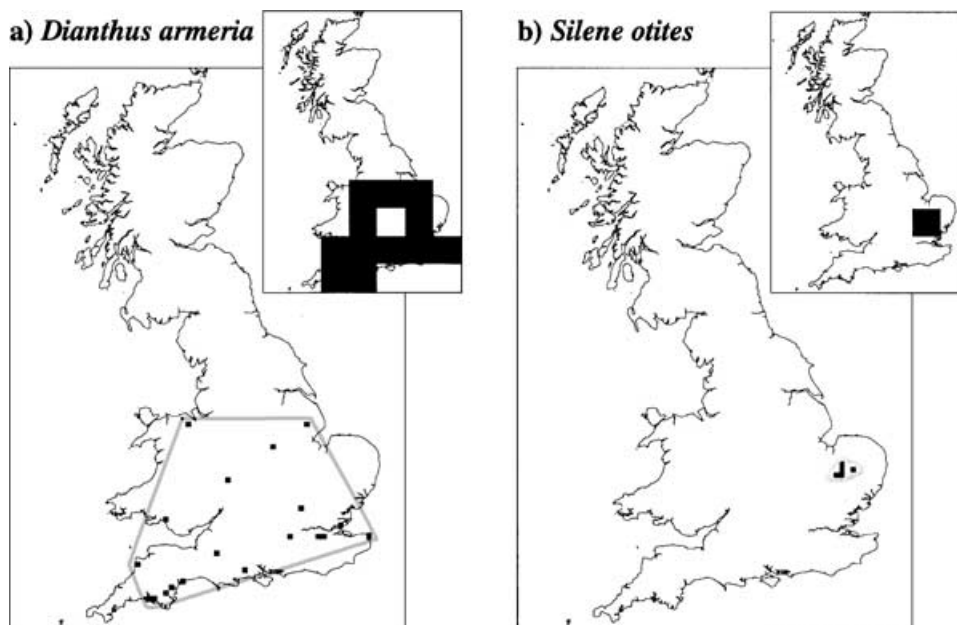[l]EN subcriterion C1 calculated over 5 years.

Figure 2. Minimum convex polygon (MCP, gray line) and the area of occupancy (AOO, black squares) for the British ranges of two plants. In (a) MCP ≈ 100,000 km²; AOO at 100-km² resolution = 1900 km²; inset AOO at 10,000-km² resolution = 120,000 km². In (b) MCP ≈ 1500 km²; AOO at 100-km² resolution = 500 km²; inset AOO at 10,000-km² resolution = 10,000 km².

scales of area occupied differs dramatically between *D. armeria* and *S. otites* because of the different spatial patterns of the two species' populations.

It might appear that the finer the resolution of the grid used to calculate AOO, the more accurately it would reflect the relative rarity or commonness of a species. However, the concept of rarity, and in particular the manner in which it relates to extinction risk, is a multiscale phenomenon, and when a single index is under consideration it is not clear whether finer-resolution scales return an a priori "better" measure of rarity than coarser ones. Just as a measurement of range size reveals nothing about the density or distribution of the population within the range, so a population count, by itself, reveals nothing of the spatial distribution of those individuals and their collective vulnerability.

Dual-Scale Measures

Whatever the scale at which one chooses to enumerate AOO, information from other scales will be overlooked. In an attempt to combine range-size descriptions with measures of local abundance, naturalists have developed a suite of terms to describe species distributions. For example, "common throughout," "widespread but infrequent," "restricted but locally abundant," and "restricted and rare" represent the four possible combinations of regional and local ubiquity.

At a more quantitative level, the *British Red Data Book for Vascular Plants* (Wigginton 1999) lists the number of 100-km² squares and 1-km² squares occupied by each species. The two figures are combined into a single frequency ratio (no. of 1-km² squares/no. of 100-km² squares), which is used to indicate which species have a high local abundance. For example, *Dianthus armeria*

has a ratio of 1 (19/19) and *Silene otites* a ratio of 4.4 (22/4). Thus, the ratio can also be thought of as a geometric (as opposed to functional) measure of population fragmentation.

A Tri-Scale Approach

Over 20 years ago, Rabinowitz (1981) introduced a typology of rarity based on three aspects of a species' distribution that relate broadly to three different scales of analysis: geographic range size, habitat specificity, and local density. By rating a species as either "rare" or "common" at each of these scales, eight possible combinations were produced, seven of which Rabinowitz considered to be different forms of rarity. Using this classification, she found that certain types of rarity were less common than others. In particular, she could think of no convincing examples in which a species had a limited geographical range and occupied a wide variety of habitats within a region but was locally rare wherever it did occur (i.e., rare-common-rare; Rabinowitz et al. 1986). She also commented that species that are geographically widespread, but regionally and locally rare (i.e., common-rare-rare), are often overlooked in lists of "rare" species. In her opinion, this suggests that too much emphasis is placed on range size and coarse-scale measurements of area of occupancy when overall levels of rarity are characterized.

Rates of Decline

In principle, any of the measures of rarity—extent of occurrence, area of occupancy, or population counts—can be measured at two or more points in time and a rate of decline can be calculated (criterion B2b [World

Conservation Union 2001] and Table 1). Depending on the way individuals and subpopulations are lost, however, it is quite possible for each measure to show a very different rate of decline for any particular time period. Schoenewald-Cox and Buechner (1991) consider four possible trajectories to extinction that are characterized by the relative decline of the range size versus the change in number of individuals. Put briefly, a decline could affect all occupied sites equally, resulting in no change in range size but a substantial drop in the number of individuals, or, conversely, a range could contract substantially with the loss of a few small but far-flung populations, with only a slight reduction in the total number of individuals present. Thomas and Abery (1995) considered the case in which rates of decline are calculated from measures of AOO. They demonstrated that rates of decline calculated from coarse-scale AOO measurements are usually much lower than those calculated from fine-scale measures, although in theory the reverse situation is also possible. Thus, just as rarity is a scale-dependent property, so too is rate of decline.

Fragmentation and Population Structure

As well as rarity and rates of decline, the IUCN criteria also consider population fragmentation (or more accurately, population structure with respect to dispersal potential) as an indicator of extinction risk. However, the relationship between degree of fragmentation and extinction risk is not straightforward, because both severe fragmentation (many small, isolated subpopulations) and lack of sufficient fragmentation (individuals concentrated into one or a few subpopulations) are considered indicative of an increased risk (Table 1, criteria B1, C2a, and C2b).

A large number of pattern measures exist in the ecological literature, most of which are typically applied to maps of individuals within a population (e.g., Grieg-Smith 1983; Dale 1999). Hanski and Ovaskainen's (2000) metapopulation capacity index is an interesting metric in which the distribution of suitable habitat is important. When the fragmentation of occupied range is considered, however, two measures have been used: the frequency ratio (FR) (Wigginton 1999) and the box-counting fractal dimension (*D*) (Maurer & Heywood 1993; Lennon et al. 2002). Both measures can be derived from a knowledge of AOO at two or more scales, and, because AOO itself is extremely scale-dependent, it is not surprising that the degree of fragmentation observed may also vary with the scales used to make the measurement.

We calculated frequency ratios based on our case-study field data collected at four different resolutions (Table 2). To obtain these estimates of occupancy, we chose four separate square kilometers from the range of each species at random and surveyed each for 4 person-days to determine presence and absence on a hectare-by-hectare basis

Table 2. Average frequency ratios (of occupancy) of two plant species measured at four different pairs of resolutions.[a]

	Frequency ratio (no. field samples)			
Species	$0.01\text{-}km^2/$ $1\text{-}km^2$	$100\text{-}m^2/$ $0.01\text{-}km^2$	$1\text{-}m^2/$ $100\text{-}m^2$	$0.01\text{-}m^2/$ $1\text{-}m^2$
S. otites	4.00 (4)	11.50 (6)	12.90 (10)	5.64 (129)
D. armeria	1.25 (4)	2.00 (5)	4.00 (7)	2.00 (28)

[a]*In each case, the larger square was divided into a 10 × 10 grid of smaller squares. Numbers in parentheses refer to the number of separate 1-km², 0.01-km², 100-m², and 1-m² squares surveyed in the field. To ensure a degree of independence between samples, no more than two 0.01-km² squares from the same 1-km² square were surveyed at a 100-m² resolution, and no more than two 100-m² squares from the same 0.01-km² square were surveyed at 1-m² resolution. All the squares identified as occupied in the 1-m² resolution surveys were resurveyed at a 0.01-m² resolution. Includes data from Hartley and Kunin (2000).*

(i.e., at a 0.01-km² resolution). Two occupied hectares at each site were then surveyed at 100-m² resolution (unless, of course, only 1 ha was occupied). Finally, two occupied 100-m² squares in each hectare were surveyed at 1-m² resolution (where possible), and the position of individuals within occupied 1-m² cells was mapped to the nearest centimeter. Both species displayed an approximately three-fold variation in frequency ratio, depending on the pair of scales considered, and both species showed the greatest degree of fragmentation (i.e., lowest frequency ratios) at the 1-ha resolution. At any given scale, however, the frequency ratios of *D. armeria* were consistently 2.5–6 times lower than those of *S. otites*.

Dealing with Scale Dependence

Because rarity, rates of decline, and fragmentation are all sensitive to the scale(s) at which they are measured, conservation decision-makers must explicitly consider scale in interpreting them. Three possible courses of action present themselves. The first is to adopt a single-scale approach by ensuring that a standard scale is always used when comparing species. This is the approach applied in Britain through the use of a fixed 100-km² resolution national grid in categorizing rare and scarce species. The use of a standardized scale of analysis has the advantage of allowing straightforward comparisons between species, but at the cost of disregarding potentially valuable information at other scales. As we shall see, the relative ubiquity of species may shift dramatically between scales (Fig. 3), suggesting that different conservation priorities might have been chosen had a different arbitrary scale been chosen as standard (Pearman 1997).

A second approach to dealing with the scale dependence of risk indices is to measure each index across as wide a range of scales as possible. This, in essence, was

(a)

(b)
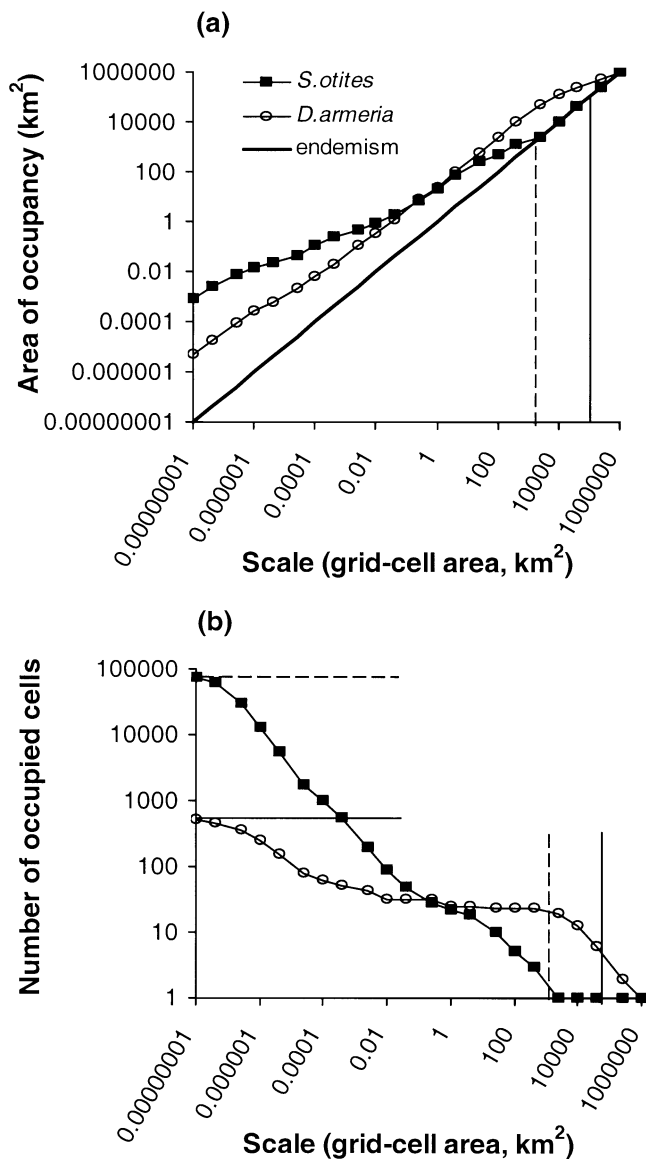
Figure 3. (a) Scale-area curves for the British distributions of Silene otites *and* Dianthus armeria. *Vertical lines projected onto the x-axis represent the minimum convex polygon values for extent of occurrence as estimated in Fig. 2. (b) Number of grid cells occupied by each species as a function of scale. Horizontal lines projected onto the y-axis represent the estimated population size; vertical lines represent minimum convex polygons as in (a). As suggested in Fig. 1, measures of grid-cell occupancy can approximate a range of other rarity measures from population numbers to geographic range size.*

Rabinowitz's approach, considering each species' rarity at three different scales. This approach has the advantage of overcoming the arbitrariness of a single standardized scale, but it presents a different risk: information overload. The typology of rarity will increase exponentially with each additional scale being considered. Fur-

thermore, there may be as many different sets of conservation priorities as there are scales under consideration, leaving decision-makers with no clear guidance.

A third approach to the scale specificity of rarity and extinction risk is to combine information from multiple scales in a simple, unified, and quantitative manner. Because AOO provides a common currency for calculating rarity, rates of decline, and fragmentation, we argue that plotting AOO against scale of measurement, a so-called scale-area curve (sensu Kunin 1998) or range-area relationship (Ostling et al. 2003), will convey information on the three main indicators of risk and will greatly facilitate comparison between disparate data sets. Later, we develop the link between the patterns underlying scale-area curves and the processes leading to extinction.

A Multiscale Measure of Rarity

Area of occupancy can be measured at any scale equal to or coarser than the original census data and, if desired, estimates for finer scales can be generated from sample field data (as in this paper) or extrapolation (e.g., Kunin 1998; He & Gaston 2000b; Kunin et al. 2000). In the case of *D. armeria* and *S. otites*, we used national distribution maps available at 1-km^2 resolution and blocked these up to obtain additional measures of AOO at 16 coarser scales. The national 1-km^2 resolution data were then combined with representative field-survey results (Table 1) to plot scale-area curves for each species spanning resolutions from 100 cm^2 to 10^6 km^2 (Fig. 3). According to the British criterion of the number of 100-km^2 squares occupied, *Silene otites* was much less common than *Dianthus armeria*, and this was reflected in their different British classifications as "rare" and "scarce," respectively. From inspection of the scale-area plots, however, it was clear that when AOO was calculated with 1-km^2 squares the two species were very similar in abundance. Continuing this comparison to the level of 100-cm^2 squares, we witnessed a dramatic reversal in the relative "rarity" of the two species: the estimated national AOO for *D. armeria* became just 5 m^2, whereas that for *S. otites* was over 730 m^2. Thus, at this scale, *D. armeria* was over two orders of magnitude rarer than *S. otites*.

When occupancy is measured across a set of predetermined grid cells (such as the National Grid in Britain), the precise number of occupied cells depends to some extent on the arbitrary location of the grid boundaries relative to the recorded points of the species' distribution. This effect is relatively unimportant for species (and scales) with a large number of occupied cells, but for rare species (and even for common species at very coarse scales) the precise grid registration can prove critical. To minimize the possibility of recording atypical values, two modifications to the measurement procedure are possible: (1)

find the grid registration that, for each scale, minimizes the number of cells required to encompass all the record points or (2) calculate an average AOO for each scale by using a large number of different grid registrations. With the second method, the y-axis can also be interpreted as "the probability of recording the species present using a quadrat of scale *x*"—in essence, a rarefied species-area curve involving only one species (Lennon et al. 2002).

Range Size and the Scale of Endemism

Range size can be estimated from a scale-area curve by observing the scale at which only one mapping unit is occupied (a logical limit that constrains all scale-area curves to the upper-left half of a log-log plot). This scale may also be thought of as the species' own "scale of endemism" (cf. Harte & Kinzig 1997). Within Britain, *S. otites* was an "endemic" at the scale of 2500 km^2 and above, whereas *D. armeria* did not attain this status until the entire British map was covered by a single cell of 1×10^6 km^2 (Figs. 2 & 3).

Range size estimated in this way will always be greater than the MCP measure because ranges rarely have square boundaries, and even small MCPs may straddle two or more mapping units. Therefore, for many purposes the MCP may remain a better measure of overall range size. Nevertheless, as grid resolutions approach the species-specific "scale of endemism," AOO becomes a measure of range size similar to MCP.

Population Size and the Scale-Area Intercept

At the opposite extreme of the scale spectrum, one could, in theory, use a scale-area curve to reflect or even estimate population size by plotting or extrapolating the curve down to a sufficiently fine scale so that each occupied cell contains, on average, only a single individual. Our 100-cm^2-resolution field surveys came close to this individual-scale AOO measure for *D. armeria* and *S. otites* (Fig. 3b). In practice, it is difficult to estimate a priori what this minimum scale should be; it depends on the size of an individual, its mobility, and the degree of aggregation between individuals. Thus, in practice, more direct measures of population size are preferable (He & Gaston 2000*b*; Kunin et al. 2000).

Multiscale Rates of Decline

The scale-dependency of "rate of decline" can be simply illustrated by plotting scale-area curves for a species' distribution observed at two different times. The scale at which the lines show the greatest vertical separation (on logarithmic axes) will be the scale at which percentage decline is the greatest. In the case of *Dianthus armeria,* the 30-year decline calculated from AOO measurements made at a 100-km^2 resolution was 57%, whereas at a 10,000-km^2 resolution it was only 24%, and when viewed at the very

coarse scale of 100,000-km^2 there was no apparent decline (Fig. 4; Wilson 1999). This mirrors Thomas and Abery's (1995) finding for British butterflies that apparently stable coarse-scale distributions could mask rapid fine-scale declines.

Monitoring for declines is important because decline is the first step toward the perilous state of small population sizes. Moreover, conservation management will often be more effective if it is targeted against the cause(s) of the decline rather than trying to deal with the stochastic problems associated with maintaining small populations (Caughley 1994). A multiscale measurement of decline will not only detect declines earlier, but it may also provide important information on the spatial characteristics of the decline that might help identify the causative process.

Multiscale Fragmentation

If AOO is measured at two or more scales, then a scale-specific measure of fragmentation can be derived. The frequency ratio (FR) and the box-counting fractal dimension (*D*) can both be derived from the slope (*b*) of a scale-area curve (Eq. 1). When distributions are diffuse and highly fragmented, $b \approx 1$, $D \approx 0$, and FR ≈ 1 (typically, one occupied fine-scale cell in each occupied coarse-scale cell). When distributions are continuous, $b \approx 0$, $D \approx 2$, and FR $\approx$ (no. of fine-scale cells in each coarse-scale cell). In general, the use of a fractal dimension implies a constant slope over multiple scales, whereas the frequency ratio is defined by AOO at just two particular scales.

$$b = 1 - \left(\frac{D}{2}\right) = 1 - \left(\frac{\log_x \text{FR}}{2}\right), \qquad (1)$$

where $x = $ (area of a coarse-scale cell/area of a fine-scale cell)$^{\frac{1}{2}}$.

Changes in the local slope measured along different sections of a scale-area curve reflect changes in the degree of fragmentation of the distribution at different scales of analysis. In addition, if one succeeded in calculating occupancy at the scale of individuals, then the ratio of the number of cells occupied at the individual scale to the number of cells occupied at some slightly coarser scale becomes a measure of local density (i.e., the average number of individuals per occupied unit area).

Summarizing Information across Scales

Although scale-area curves successfully reflect species distributions across a wide range of scales, they are nonetheless information-rich graphics. Is there some way to digest the information into a simpler form? To the extent that scale-area curves are approximately linear, a species' distribution might be specified by the use of two parameters: one indicating AOO at some arbitrarily fine scale (e.g., the y-"intercept" of a scale-area curve) and a second describing how AOO changes with scale (e.g., the
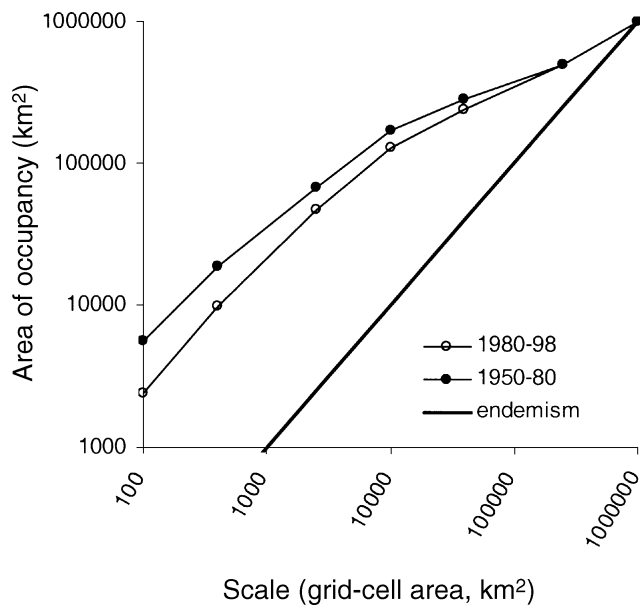
Figure 4. Scale-area curves for the British distribution of Dianthus armeria *as recorded over two different time periods.*
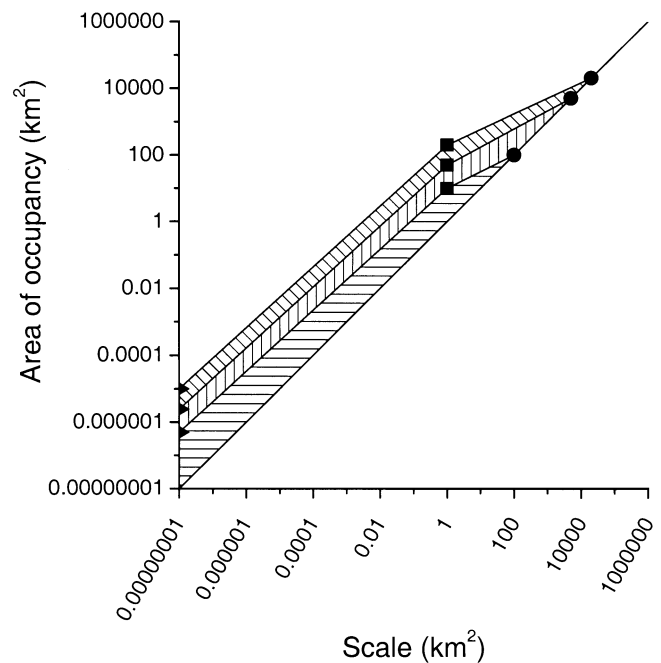

Figure 5. A scale-area plot defining four hypothetical zones of extinction risk: horizontal hatching, critically endangered; vertical hatching, endangered; diagonal hatching, vulnerable; and top-left no hatching, least risk. All distributions are constrained to lie on or above the 45° line of endemism. Triangles mark "individual-scale" thresholds (criterion C), assuming each individual occupies a separate 100-cm² grid cell. Squares mark area-of-occupancy thresholds (subcriterion B2) measured at a 1-km² resolution. Circles mark extent-of-occurrence thresholds (subcriterion B1) located on the line of endemism. See Table 1 for specific values of criteria.

slope of the scale-area curve). As increasing numbers of scale-area curves are prepared, however, there is growing evidence that most are not strictly linear (Kunin 1998; He & Gaston 2000b; Kunin et al. 2000; Hartley et al. 2003). Nonetheless, predictable nonlinearity suggests that interspecific differences could still be captured by an appropriately curved scaling relationship described by relatively few parameters (e.g., He & Gaston 2000b). More high-quality empirical data across wide ranges of scales and taxa are needed before we can make firm recommendations on this issue.

Scale-Dependent Thresholds for Red-List Categories

Many of the problems associated with using AOO thresholds to define red-list categories stem from the dramatic scale dependence of AOO measurements. This suggests that AOO thresholds should always relate to a particular scale of measurement and that different thresholds might be set at different scales (Keith et al. 2000). To avoid a proliferation of thresholds, however, a more general approach might be to specify different zones on a scale-area plot that relate to the various extinction-risk categories (see Fig. 5 for a hypothetical example). Similarly, it is not clear whether a given rate of decline or fragmentation carries with it the same degree of risk, regardless of the scale at which it is measured; thus, one might wish to define different thresholds for these indicators as well, depending on the scale(s) of analysis. The rationale for doing this depends on how one translates a distributional pattern (or the change of one) into an extinction risk.

Linking Pattern and Process

Extinction Processes

The logic for developing red-list categories based on criteria of rarity, rates of decline, and fragmentation is that these are measurable properties that correlate well with extinction risk. However, just as there are many ways of viewing and measuring these properties, there are many processes that contribute to a species' risk of extinction, such as demographic stochasticity, inbreeding and loss of genetic diversity, metapopulation dynamics, habitat loss, diseases and parasites, novel predators, novel competitors, hybridization, environmental catastrophe, and climate change (Mace & Lande 1991; Caughley 1994; Shafer 2001 and references therein).

For any particular extinction process, the different measures will vary in their usefulness for predicting the risk of extinction. For example, when the effects of demographic stochasticity and inbreeding are considered, local

population counts of the number of individuals present will be the key parameter of interest. At the other extreme, when the impacts of large-scale environmental catastrophes are considered, range size may be the crucial factor determining extinction risk. Thus, many of the different extinction-risk factors can be thought of as operating in particular regions of the scale-area curve. Moreover, some risk factors are primarily influenced by the height of the curve (corresponding to the abundance of the species at that scale), whereas others are most sensitive to the slope of the curve (corresponding to the degree of aggregation or fragmentation of occupied cells at that scale). In building a logical link between rarity and overall extinction risk, a single-scale measure of rarity cannot suffice.

Given a fixed number of individuals, distributions that minimize the risk from one factor may increase the risk from another. Thus, fragmentation may be considered a "bad thing" for metapopulation dynamics, yet it can also be a "good thing" as insurance against the spread of disease. The two processes may operate at different scales, however, such that a species' distribution could be well-connected with respect to metapopulation dynamics but fragmented at the scale relevant to disease transmission.

Even single processes can act at multiple scales. Disturbances such as wind throw can topple a single tree or vast tracts of forests, depending on intensity and extent. This raises the interesting possibility that at least part of a species' extinction risk could be estimated by the interaction between its own spatial distribution and the size-frequency distribution of disturbances that have deleterious impacts. However, the impact of other processes, such as introduced predators or competitors, will be much more difficult to incorporate into such a framework.

Assessing the relative importance of each process at any particular scale is a difficult problem that, to date, has not been satisfactorily modeled, let alone empirically measured. Indeed, few attempts have been made to combine more than one or two of these processes into a single model (Mace & Lande 1991, but see Burgman et al. 2001). Nonetheless, IUCN categories are ostensibly based on quantitative, fully integrated probabilities of extinction within a specified time frame. In the absence of the information necessary to calculate such probabilities, we have attempted a qualitative risk assessment based on the rarity and fragmentation information depicted in the scale-area plots of Fig. 3. The results indicate how the risk factors deemed relevant to each species differ dramatically, simply as a result of their different spatial distribution patterns (Table 3).

Incorporating Details of Species Biology

A given spatial distribution will not carry with it the same risk for all species. This is because there are many fea-

Table 3. Extinction processes, their characteristic scale of operation, and the consequent national risk assessment for two British plant species, based on the distributional information in Fig. 3.

		Relevant measure from scale-area curve[a]	*Qualitative risk assessment*	
Extinction process	*Scale of process*		D. armeria	S. otites
Demographic stochasticity	fine	height	high	low
Inbreeding and loss of genetic diversity	fine	slope	high	low[b]
Habitat loss and degradation	moderate	height	high	medium
Metapopulation extinctions > recolonizations	moderate	slope[c]	high	low
Environmental catastrophe and climate change	coarse	height	low	high
Disease, parasites, invasions and competitors	coarse	slope	low	high

[a]*Height represents the number of cells occupied (at that scale), and slope indicates the degree of spatial aggregation of occupied cells (at that scale).*
[b]*This assessment may be altered because of the rarity of male flowers, which will greatly reduce the effective genetic population size relative to the demographic population size.*
[c]*Some models show that both the amount and fragmentation of available habitat are important to metapopulation persistence (Ritchie 1997; With & King 1999).*

tures of a species' biology that will modify its vulnerability to each threat. An obvious example relates to how the pattern of fragmentation translates into "functional isolation" between subpopulations, because this depends on a species' dispersal ability and its behavioral responses to landscape features (Ricketts 2001). Similarly, the reproductive implications of small or low-density local populations in plants will depend critically on the species' pollination mode and breeding system (Kunin 1997; Larson & Barrett 2000). In making the leap from a pattern-based measure of rarity and fragmentation to the processes of extinction, such details are likely to be of crucial importance.

Scaling Social, Economic, and Political Considerations

Social, political, and economic considerations also have a spatial component that can influence the interplay between distribution patterns and extinction risks. For example, given a particular range, it is probably safer to occupy two (or more) different countries rather than one, as a bet-hedging strategy against adverse changes in national land-use policy or conservation management. Economic pressures that favor particular land uses can also be scale dependent. In an intriguing analysis, Kremen et al. (2000) illustrate how the economic incentives for and against the sustainable use of tropical forest can be dramatically different depending on whether one takes a local-, national- or global-scale account of costs and benefits. In the

situation they analyzed, although the local and global optimum was to maintain natural forest cover, the national-scale benefit arising from the sale of logging concessions dominated because most influential decision-making occurred at a national level.

The various noneconomic motivations for species conservation (moral, aesthetic) also scale differently, and from certain perspectives a "regional extinction" will be regarded with as much concern as a global extinction (Begon et al. 1990:601–602), thus fuelling the demand for the development of regional red data books. Although the scientific basis for such assessments is essentially the same as that used in compiling global red lists, the way in which the subsequent regional categorizations are used to inform the setting of conservation priorities may be substantially different (Gärdenfors et al. 2001).

Implications

Survey and Monitoring

The construction of scale-area curves demands presence-absence information on the distribution of a species collected over a wide range of scales. Because fine-scale data (if collected over a large extent) can always be amalgamated to provide coarse-scale data (but not the reverse), one would assume that the best possible source of data would be a comprehensive and spatially explicit survey, conducted at an extremely fine scale. But how fine a scale is fine enough? The ideal survey would be conducted at a scale so fine that each occupied cell would contain only a single individual, allowing the whole range of abundance scales to be examined. In practice, however, it will generally prove prohibitively expensive and time-consuming to conduct such surveys for any but the very rarest of species.

There are many possible places to stop short of this ideal. One might survey the presence-absence of species down to some moderate spatial scale and then estimate population sizes within these cells (or a subset of them). This would provide a fine-scale measure of rarity in the form of a population count, while retaining sufficient spatial information to generate AOO measures of rarity across a significant range of scales. If this level of survey is still too expensive, the best solution might be to conduct a hierarchical sampling scheme, with presence-absence mapping occurring at several nested scales, possibly culminating in counts of individuals collected at the finest scale. This is the approach we have adopted in our own field work.

Menges and Gordon (1996) suggest three levels of monitoring intensity, with presence-absence mapping being the first level, population counts being the second, and the following of tagged individuals (longitudinal studies) as the third and most intensive form of monitoring. Where feasible, longitudinal monitoring has much

to recommend it because it has the potential to reveal details about the proximate causes of individual deaths and population-level declines. Realistically though, this level of survey and monitoring may have to be reserved for those species that have already been identified as belonging to the critically endangered or endangered risk categories.

At the opposite extreme, many mapping programs are conducted with little project-specific field work, simply mapping the known records of a species onto a superimposed grid. Here too there are questions about the appropriate scale to use. Too fine a scale will result in unreliable data, with an unacceptably high level of "false negatives"—apparent absences due to lack of information. On the other hand, too coarse a scale will result in a loss of information content, at the extreme simply indicating the species to be present in the study region as a whole. There should be an optimal level of resolution in between, at which the amount of accurate information is maximized, but how one might best choose this scale remains an open question for future research (e.g., Costanza & Maxwell 1994).

Conservation and Management

In many ways, this essay has been a rephrasing of the SLOSS debate about whether it is better to have one single large or several small reserves, to maximize the conservation of biodiversity (e.g., Diamond 1976; Simberloff & Abele 1976; Lahti & Ranta 1986; Murphy & Wilcox 1986). In this case we ask, "Does a species minimize its risk of extinction by having a single large or several small populations?" (Ovaskainen 2002). We have argued that the answer depends critically on the scale of the processes that could lead to future decline. No single measure of rarity is sufficient to assess the threats from every process, and different rankings could be achieved using different measures.

It is often argued that rare species suffer a double jeopardy because they tend to have both low local population sizes and restricted ranges (Lawton 1993; Johnson 1998). This is undoubtedly true, but if we are to improve our assessment of species' extinction risks and provide sensible advice to conservation managers, we must develop a better (quantitative) understanding of the relative merits of high local abundance versus regional ubiquity. Conservation managers will need to know whether they should direct their efforts primarily toward reserve acquisition, to preserve additional populations and facilitate (re)introductions (natural or artificial), or whether they should be concentrating on increasing population numbers at existing reserve localities.

Shafer (2001) suggests that, in the past, too much emphasis has been put on the benefits of locating reserves close together, whereas if most major threats to modern-day species persistence are from large-scale, spatially

autocorrelated processes, such as climate change and habitat loss, then the best strategy for species conservation is to locate populations in several reserves that are widely separated. Clearly, the debate is not settled.

Conclusions

The range of potential processes that may lead a species to extinction is often wide and complex, so it is only natural that a number of different indicators, such as rarity, rates of decline, and population fragmentation are required to assess overall extinction risk. Here we have demonstrated how these three indicators can all be quantified by means of measurements of area of occupancy. Furthermore, area of occupancy can be measured at resolutions that vary from the scale of individuals to the scale of entire geographic biomes. By plotting the value of AOO as a function of scale, one can calculate the value of each indicator at any scale. This is a useful outcome because different indicators and different scales of analysis are relevant to different extinction processes. However, it also means that different threshold values will have to be applied at each scale. By encouraging a multiscale view of both species distributions and the extinction processes that threaten them, we can make greater progress in understanding the functional link between the two. Ultimately this will lead not only to more accurate risk assessments, but also to better informed conservation strategies to reduce these risks.

Acknowledgments

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