Occupancy-abundance relationships and sampling scales

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The area of occupancy of a species and its abundance are dependent on the spatial scale at which they are measured. However, it is less obvious how the scale of sampling affects their correlation. This study investigated and modeled the effects of sampling unit size and areal extent on the interspecific occupancy-abundance relationships for a tropical tree species assemblage at a local scale and a temperate bird species assemblage at a regional scale. The results showed that both sampling unit size and study extent had profound quantitative effects on the occupancy-abundance relationship, although it remained positive. Several properties of the occupancy-abundance relationship can result from the effects of scale: 1) the linearity of the relationship decreases with the increase of sampling unit size; 2) for a given abundance, the area of occupancy increases with sampling unit size; and 3) variation in the area of occupancy increases with the increase of both sampling unit size and extent, and if the extent is large enough may be sufficient that no occupancy-abundance relationship is observed. Although the occupancy-abundance relationship can be satisfactorily modeled, the parameters depend on the scale used. This suggests that a model derived from one scale cannot be applied to another. In other words, to estimate the rarity or commonness of species using such a model, the estimation must be strictly done using the same sampling scale for all the species.

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One of the most general patterns in macroecology is the positive interspecific correlation between occupancy and abundance (Gaston and Blackburn 1999); locally abundant species tend to be widely distributed, whilst locally rare ones tend to be of restricted occurrence. Attempts to understand the determinants of this relationship have, however, met with only limited success (Gaston et al. 1997). There may be at least two reasons. First, the different ecological mechanisms that have been proposed to explain the pattern are not always readily distinguished, more than one may be operating at any one time, some may simply constitute different levels of explanation, and the formulation of strict null hypotheses for the pattern has proven difficult (Wright 1991, Hanski et al. 1993, Gaston 1996, Gaston et al. 1997, 1998, Hartley 1998).

Second, the form of the interspecific occupancy-abundance relationship may depend not only on the underlying ecological mechanisms, but also on how occupancy and abundance are measured (Brown 1984, Hanski et al. 1993, Gaston 1994a, b, 1996, 1998). Different measures tend to be employed by researchers conducting studies at different temporal and spatial scales, and it remains unclear how this affects the qualitative, and more particularly the quantitative, pattern observed, and perhaps also its ecological interpretation. Although in some species assemblages the qualitative positive correlation between abundance and occupancy is invariant to changes in the spatial scales at which the two variables are measured (Bock 1987), in other cases this correlation can change from being positive, to being absent, and even to being negative (Gaston and Lawton 1990).

The distribution of a species can be measured either as its extent of occurrence (the area within the outermost limits to its geographic extent) or as its area of occupancy (the area within this extent which it actually occupies; Gaston 1991, 1994a, b). The former is pertinent to analysis of the entire geographic ranges of species, while the latter is more appropriate when studying local populations and is used more widely in the literature. The area of occupancy of a species is obviously determined by three elements: the abundance of the species, its spatial distribution, and the size of the sampling scale (He and Gaston in press). The measurement of species abundance is relatively straightforward, and usually it is determined as the total number of organisms of a species in a defined area or the mean density of individuals averaged across all sampling sites or only over the sites where the species actually occurs. The quantification of spatial distribution is more obscure, and is generally described in terms of clustering, random or regular patterns using various statistical models (e.g., the Poisson, the negative binomial or the Neyman's type A distributions).

Although the effects of the spatial extent of studies on occupancy-abundance relationships have been discussed in the literature (Gaston 1996), the effects of the size of the sampling unit (called grain size in landscape ecology, and minimum mapping unit or modifiable areal unit in geography; see Openshaw 1984, Turner et al. 1989, Haining 1990, Jelinski and Wu 1996) have not received much attention, despite the fact that seldom do two studies employ sampling units of the same (or comparable) size; indeed the possible effects of sampling unit size and sampling extent have not been well distinguished in studies of effects of spatial scale on occupancy-abundance relationships (Bock 1987). Differences in the spatial extents of studies will not only change the ecological patterns and processes that are observed, but also the models best describing them (Turner et al. 1989, Gaston and Blackburn 1996, He and Legendre 1996, Jelinski and Wu 1996, Maurer 1999). Likewise, ignoring the effects of sampling unit size can, at best, reduce the accuracy of interpretation; various studies have demonstrated that changes in sampling unit size changes the quantities (estimate and variability) of ecological parameters, their spatial patterns and model sensitivity (Turner et al. 1989, Haining 1990, Stoms 1994, He et al. 1994, Jelinski and Wu 1996, Gaston et al. 1999).

In estimating species abundance from binary maps, He and Gaston (in press) recently proposed an "area-area" model to quantify the relationships amongst the occupancy, abundance, spatial distribution pattern and sampling scale of a species. This is a generalization of several other models of species occupancy (Nachman 1981, Maurer 1990, Wright 1991, Hanski and Gyllenberg 1997). Its advantage is that spatial scale and spatial pattern are explicitly expressed, which makes it useful in evaluating their consequences for occupancy-abundance relationships.

The objective of this study is to investigate the effects of spatial scale and the distribution pattern of species on occupancy-abundance relationships. First, we will introduce He and Gaston's (in press) area-area model and two others to show how an intraspecific occupancy-abundance relationship described by these models depends on spatial scale as well as on the spatial distribution of a species. Second, two data sets will be used to provide empirical evaluations of the effect of scale on interspecific occupancy-abundance relationships by changing the size of the sampling unit and the spatial extent of the study area. In this section, an emphasis will be given to modeling the interspecific occupancy-abundance relationships of the two data sets to demonstrate the adequacy of the intraspecific occupancy models to describe interspecific relationships. Third, an attempt will be made to evaluate the effect of spatial pattern of species on occupancy-abundance relationships using He and Gaston's model.

Area-area models

In the context of estimating species abundance, a binary map (i.e., of presence/absence) is usually divided into a grid with the size of a cell being the minimum mapping unit (MMU) that defines the resolution. He and Gaston (in press) use a binomial distribution to model the number of occupied MMUs, m, out of the total number of (i.e., occupied + unoccupied) MMUs, M, of the map:

$$b(M, m; p) = \binom{M}{m} p^m (1 - p)^{M - m}, \tag{1}$$

with the probability of occurrence defined to be

$$p = 1 - \left(1 + \frac{Na}{Ak}\right)^{-k}, \tag{2}$$

where A is the total area of the map, N is the total number of individuals (abundance) of a species occurring in A, k is a parameter describing spatial pattern of the species, and a is the sampling unit size (i.e., MMU).

Using the above notation, it is obvious that the map area (A) is the product of the total number of MMUs (M) and MMU size (a), while the total area of occupancy (A_a) of the species is m × a. From eqs 1 and 2, an area-area model (area of occupancy A_a vs sampling unit area a) can easily be derived by the maximum likelihood method, such that:

$$A_a = A \left[1 - \left(1 + \frac{Na}{Ak} \right)^{-k} \right].$$ (3)

This model shows that the area of occupancy (A_a) of a species depends not only on its abundance (N) but also on sampling unit size (a), the extent of the study area (A) and spatial pattern (k).

To further understand the property of spatial parameter k, we substitute the term Na/A in eq. 2 with the mean density (μ) of the species in an MMU a. It now becomes clear that when k > 0 eq. 2 is the probability of occurrence derived from the negative binomial distribution (i.e., the sum of non-zero terms of the distribution); a smaller value of k represents stronger aggregation of species, and vice versa (Wright 1991). It is straightforward to show that when $k < -\mu$, eq. 2 is the probability of occurrence derived from a binomial distribution which describes a regular distribution of a species (Greig-Smith 1983). When $k \to \pm \infty$, the spatial distributions converge to random from different directions: regular to random, and aggregated to random. Therefore, eq. 2 describes an entire spectrum of spatial patterns, from regular to random to aggregated (He and Gaston in press).

Another two models used to describe the intraspecific relationship between the occupancy of a species and its density are those proposed by Nachman (1981) and Hanski and Gyllenberg (1997), respectively:

Nachman: $p = 1 - \exp(-\alpha\mu^\beta),$ (4)

Hanski-Gyllenberg: $p = \dfrac{1}{1 + \alpha\mu^{-\beta}},$ (5)

where $p = A_a/A$, the proportion of occupied samples (i.e., occupied MMUs), and α and β are two positive parameters. If $p = A_a/A$ and $\mu = Na/A$ are substituted into eqs 4 and 5, they become area-area type models and are comparable with eq. 3 in format. He and Gaston (in press) showed that eqs 4 and 5 are empirical extensions of eq. 3.

These three area-area models will be used to model interspecific occupancy-abundance relationships for two sets of data. Although intraspecific relationships are adequately described by these models, there is no guarantee that this will also be true for interspecific relationships as the abundances and the areas of occupancy of different species are highly variable (Gaston 1994a).

The data sets

The data sets concern, respectively, tree species from a tropical rain forest plot at a local scale, and passerine bird species from a temperate area at a regional scale.

Tree species in Malaysia

This is a stand mapping data set of tree species in a lowland tropical rain forest in the Pasoh Forest Reserve of Malaysia (Manokaran et al. 1999; thereafter called Pasoh data). The study area is a 500 × 1000 m rectangular plot (50 ha). The plot was initially set up and surveyed in 1987. The census was repeated in 1990 and 1995. The data from the 1995 census are used in this study. In each survey, all free-standing trees and shrubs with diameter at breast height ≥ 1 cm were located by geographical coordinates on a reference map, and identified to species. In the 1995 survey, there were a total of 378 224 trees belonging to 824 species. The most abundant species had 10 470 individuals. The spatial patterns of the species surveyed in 1990 were analyzed by He et al. (1997). The results showed that ca 80% of the species were aggregated, 20% had random distributions and only one displayed a regular distribution. These census data allow us to experiment with the scale effect on the occupancy-abundance relationship using various sampling scales by changing MMU and the extent of the study.

Passerine bird species in Bedfordshire

This is a data set derived from the most recent atlas of the distributions of breeding birds of Bedfordshire, U.K. (Dazley and Trodd 1994; thereafter called Bedfordshire data). Bedfordshire is one of the smallest counties in England, with an area of ca 1230 km². The presence of 61 breeding passerine species was mapped at the scale of the tetrad (2 × 2 km), between the years 1988 and 1992. The survey was performed such that if any part of the county fell within the bounds of a tetrad, all of that tetrad was surveyed; in practice this results in a buffer strip round the edge of Bedfordshire being surveyed even though it is beyond the boundary line. In extreme cases where a tiny proportion of the relevant tetrad's area falls within Bedfordshire, the whole of the tetrad was surveyed. Possible, probable and confirmed breeding records were distinguished, but the aggregate of all three is used here. The atlas also provides estimates of the population sizes of the species for the same period, based on patterns of change in occurrence from a previous atlas, patterns of observer effort, and analysis of county bird reports. For each species a range of values is given (in pairs, but converted for present purposes to individuals), in which the authors express "a fair degree of confidence". Here we use the average of these values, which for the most abundant species is 120 000 individuals.

Table 1. Fitting of eqs 3 (He-Gaston), 4 (Nachman) and 5 (Hanski-Gyllenberg) to the occupancy-abundance data of the Pasoh plot at seven sampling scales (minimum mapping units). R^2 represents the variance explained by the models. RSE is the residual standard error, associated with 822 (eq. 3) and 823 degrees of freedom (eqs 4 and 5).

Scale (m)	He-Gaston	Nachman	Hanski-Gyllenberg
5 × 5	k = 0.6701	α = 0.7588, β = 0.9331	α = 1.0727, β = 0.9940
	R^2 = 0.981	R^2 = 0.981	R^2 = 0.981
	RSE = 2534.3	RSE = 2520.1	RSE = 2483.4
10 × 10	k = 0.7794	α = 0.6684, β = 0.8687	α = 1.0665, β = 1.0101
	R^2 = 0.957	R^2 = 0.954	R^2 = 0.958
	RSE = 10176.8	RSE = 10460.5	RSE = 9984.5
12.5 × 12.5	k = 0.8150	α = 0.6565, β = 0.8541	α = 1.0599, β = 1.0214
	R^2 = 0.949	R^2 = 0.947	R^2 = 0.951
	RSE = 14313.0	RSE = 14689.7	RSE = 14017.4
20 × 20	k = 0.8600	α = 0.6357, β = 0.8410	α = 1.0688, β = 1.0532
	R^2 = 0.929	R^2 = 0.930	R^2 = 0.933
	RSE = 26607.2	RSE = 26522.8	RSE = 25884.1
25 × 25	k = 0.8964	α = 0.6281, β = 8240	α = 1.0682, β = 1.0604
	R^2 = 0.919	R^2 = 0.921	R^2 = 0.923
	RSE = 33629.9	RSE = 33414.7	RSE = 32903.7
50 × 50	k = 0.9428	α = 0.6070, β = 0.7592	α = 1.0925, β = 1.0781
	R^2 = 0.893	R^2 = 0.892	R^2 = 0.896
	RSE = 53396.0	RSE = 53879.5	RSE = 52673.1
100 × 100	k = 1.0192	α = 0.5966, β = 0.7549	α = 1.1245, β = 1.1348
	R^2 = 0.879	R^2 = 0.879	R^2 = 0.883
	RSE = 60328.1	RSE = 60293.1	RSE = 59276.9

Sampling unit effect

To investigate the effect of the size of the sampling unit on the interspecific occupancy-abundance relationship,

for the Pasoh data seven different MMUs were used to divide the entire 500 × 1000 m plot into different grid systems (the numbers in parentheses are the number of cells for each grid): 5 × 5 (20000), 10 × 10 (5000), 12.5 × 12.5 (3200), 20 × 20 (1250), 25 × 25 (800), 50 × 50 (200) and 100 × 100 (50) m. For each grid system, the number of cells in which a species was present was counted. The total occupied area of that species is the product of the number of occupied cells and the MMU applied. This procedure was iterated for all the 824 species in the plot to calculate their areas of occupancy, and was repeated for each different MMU. The occupancy-abundance relationships at each resolution were modeled using the three intraspecific models described in the previous section (eqs 3, 4 and 5).

All three models adequately described the interspecific occupancy-abundance relationships (Table 1). Although the Hanski-Gyllenberg logistic model appears to give a slightly better fit, the superiority is in no sense significant. For clarity of presentation, occupancy-abundance relationships are shown in Fig. 1 for four of the seven sizes of sampling unit. Three properties are immediately apparent from the results in Table 1 and Fig. 1: 1) the linearity of the relationship decreases with the increase of MMU size, or the curvature of the relationship increases with MMU size, 2) for a given abundance, the area of occupancy increases with MMU size, and 3) the variation in the area of occupancy increases as the MMU size increases and goodness-of-fit of the model consistently decreases with the increase of MMU size, as shown by the R^2 and RSE (residual standard error) in Table 1.

The same procedure as used for the Pasoh tree data was also applied to test the effect of sampling unit size on the interspecific occupancy-abundance relationship
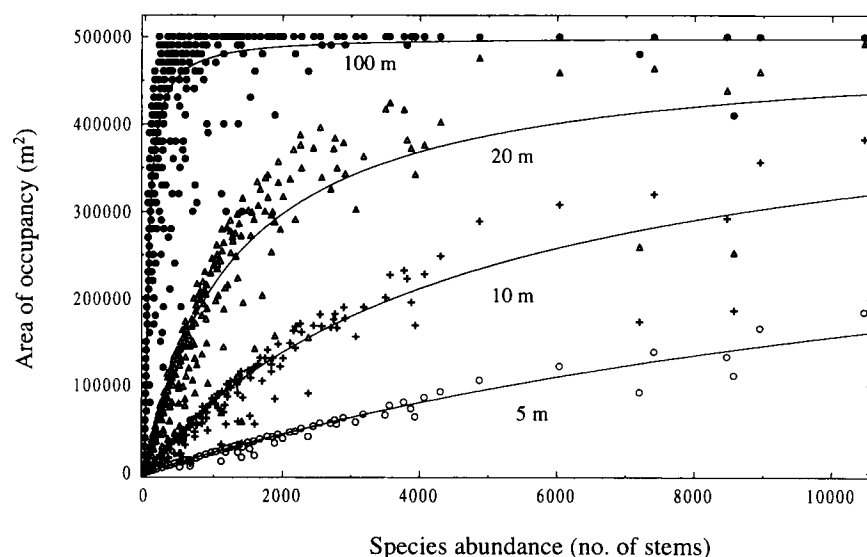

Fig. 1. Occupancy-abundance relationships for the Pasoh data at four sampling scales (minimum mapping units). The smooth curves are those fitted using eq. 3. The curves for the other two models (eqs 4 and 5) are very similar to eq. 3.

Table 2. Fitting of eqs 3 (He-Gaston), 4 (Nachman) and 5 (Hanski-Gyllenberg) to the occupancy-abundance of the Bedfordshire study at two sampling scales (minimum mapping units). The extents for the two samples are 1512 and 1728 km², respectively. R² represents the variance explained by the models. RSE is the residual standard error, associated with 59 (eq. 3) and 60 degrees of freedom (eqs 4 and 5).

Scale (km)	He-Gaston	Nachman	Hanski-Gyllenberg
2×2	$k = 0.3227$	$\alpha = 0.1645$, $\beta = 0.6834$	$\alpha = 9.9037$, $\beta = 1.1210$
	$R^2 = 0.792$	$R^2 = 0.900$	$R^2 = 0.899$
	$RSE = 1989.4$	$RSE = 1375.6$	$RSE = 1381.6$
4×4	$k = 0.3947$	$\alpha = 0.3423$, $\beta = 0.4438$	$\alpha = 2.6804$, $\beta = 0.6949$
	$R^2 = 0.802$	$R^2 = 0.862$	$R^2 = 0.835$
	$RSE = 2015.8$	$RSE = 1685.3$	$RSE = 1839.6$

for the Bedfordshire bird data. Two different MMUs were used: 2×2 and 4×4 km. Because of the irregular shape of the county there are not records of occurrence of species in some of the 2×2 km cells comprising 4×4 km cells on the borders. Consequently, whilst a total of 378 tetrads were surveyed (extent area A = 1512 km²), there were records for all or part of a total of 108 4×4 km cells (extent area A = 1728 km²). This results in a moderate increase in sampling extent from the smaller sample unit size to the larger.

Overall, the three models were adequate in modeling the Bedfordshire data (Table 2). However, unlike the Pasoh data, the Nachman's model was apparently superior to the other two (Table 2, Fig. 2), and the models of Hanski-Gyllenberg and He-Gaston underestimated the area of occupancy (He-Gaston's model performed worst). In addition, some of the properties of occupancy-abundance relationships found in the Pasoh data

were also evident in the Bedfordshire data, e.g., the area of occupancy increases with MMU, and the variation increases and goodness-of-fit decreases with MMU. However, unlike the Pasoh data, the effect of scaling on the linearity of the relationships is not obvious simply because there are only two sampling scales (combined with the discrepancy in sampling extent) in the Bedfordshire data. Nevertheless, the area-area models were robust to the variation in sampling scales, i.e., they are adequate in describing all the data.

Sampling extent effect

To determine the effect of sampling extent on the interspecific occupancy-abundance relationship, the Pasoh plot was sampled using five extents: 100×200, 200×400, 300×600, 400×800, and 500×1000 m (the entire plot). Each sample extent was centered on the midpoint of the plot, and was then divided into a grid system using a sampling unit (MMU) of 10×10 m. Based on the grid, the occupied areas for those species occurring within the sample extent were calculated, as were the abundances of the species. Equation 3 was fitted to the resultant interspecific occupancy-abundance data. (Equations 4 and 5 gave very similar results, thus not reported here.) The results show that sample extent has a substantial effect on the quantitative relationship between area of occupancy and abundance, although the general shape of the relationship remains similar. In other words, the validity of the He-Gaston occupancy-abundance model is invariant to the change in study extent, whereas the model parameter (k) is dependent on the extent used. This is evident from the variance explained (R^2) by the model and the different k values for the five extents (Fig. 3).
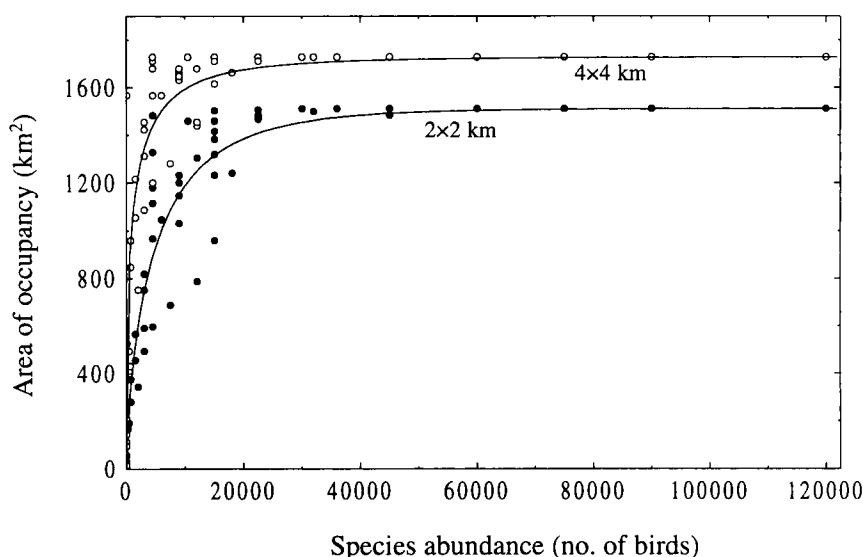

Fig. 2. Occupancy-abundance relationships for the Bedfordshire data at two sampling scales (minimum mapping units): 2×2 and 4×4 km. The two samples have different extent size: 1512 and 1728 km², respectively. The smooth curves are those fitted using eq. 4. The curves (not shown) for the other two models (eqs 3 and 5) underestimated the area of occupancy to a certain degree.
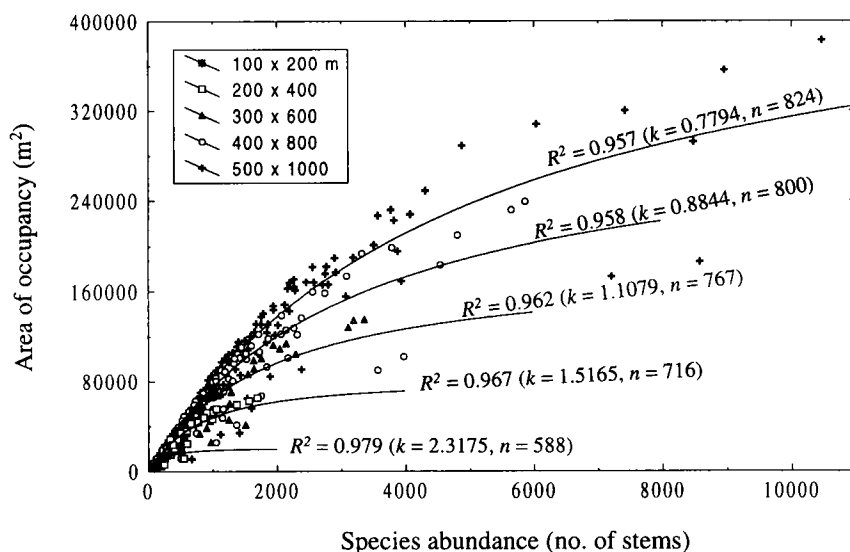
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Fig. 3. Occupancy-abundance relationships for the Pasoh data at five different area extents. Each of the extent areas was centered on the Pasoh plot and was divided into a grid of 10 × 10 m MMU. The area of occupancy for each species was calculated on the basis of the 10 × 10 m grid, whereas abundance was the total number of individuals of the species occurring within each area extent. The smooth curves are the fitted lines of eq. 3 to the observed data for each extent, R^2 is the variance explained by the model, k is the parameter in eq. 3 and n is the number of species that occurred in each extent.

Regardless of other parameters, eq. 3 suggests that area of occupancy (A_a) also changes directly with the extent of study (A). Although it is not possible to model the $A_a - A$ relationship with the data using eq. 3, because both N and k cannot be determined for multiple species, it is clear from Fig. 4 that both mean and variation in the area of occupancy increase with the extent of the sample area.

Spatial pattern effect (k)

It is not feasible to experiment with the effect of spatial distributions of multiple species on the interspecific occupancy-abundance relationship. For aggregated populations, it has been demonstrated that a positive occupancy-abundance relationship is expected regardless of the variation in spatial aggregation of the species involved (Wright 1991, Hartley 1998). We know that eq. 3 describes the entire spectrum of spatial distributions of a species, from regular to random to aggregated (He and Gaston in press). When $k > 0$, the occupancy-abundance relationship is the same as that of Wright (1991) and Hartley (1998), which is described on the right-hand side of Fig. 5 for five populations with different abundance. The area of occupancy decreases with the intensity of aggregation (i.e., when $k \rightarrow 0^+$). When k is negative (left-hand side of Fig. 5) the area of occupancy increases with the degree of regularity (i.e., when $k \rightarrow -\mu^-$; note that k will never fall in the interval $(-\mu, 0)$), the more regular the distribution of the species the higher the area of occupancy. When k approaches either large positive or negative values from left- or right-hand sides of Fig. 5 (i.e., $k \rightarrow \pm \infty$), the area of occupancy for a given species will converge to $A(1 - e^{-\mu})$, which is expected if

the species has a random distribution (i.e., the Poisson). It is obvious from either side of Fig. 5 that given a k value the area of occupancy monotonically increases with species abundance, i.e., a positive occupancy-abundance relationship is expected regardless of how species are distributed.

Discussion

Ecological systems can be considered as hierarchical patch dynamic complexes (Wu and Louks 1995). One consequence of this viewpoint is that, with few exceptions, the perception of ecological phenomena is subject to the spatial and temporal scales at which the phenomena are observed. In other words, understanding of an ecological pattern or process is conditional on the scales of investigation. The results of this study unambiguously demonstrate this conditioning. Indeed, the effects of the scale of sampling on the observed area of occupancy for a population are so profound that they change observed interspecific occupancy-abundance relationships and impact on other related issues.

The effects of sampling scale on occupancy-abundance relationships

Although the results from this study showed that the qualitative positive interspecific relationship between occupancy and abundance is invariant to changes in the scale of sampling (Bock 1987), the quantitative relationship is substantially contingent on the scales used. The dependence of the area of occupancy of a species on sample unit size (MMU), for a given extent of sampling, is intuitive. The finer the resolution, the smaller

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the occupied area (Gaston 1991, 1994a). If the MMU is so small that each sample contains only one individual of the species, then the area of occupancy is virtually equivalent to the abundance. If the MMU is the entire study area, all species have an equal area of occupancy (= the study area) regardless of their abundance. At intermediate MMUs, occupancy-abundance relationships are expected to be nonlinear. Indeed, for the data sets examined here, the larger the MMU, the more rapidly area of occupancy increases with increasing species abundance, the further the relationship between area of occupancy and abundance departs from linearity, and the more variance there is about the relationship between the two (Fig. 1).

This discussion warns that when documenting an occupancy-abundance relationship for multiple species one must avoid combining data that derive from sampling units of different areas (say, for different species), even though these units may seem superficially to vary in a "comparable" fashion. Such relationships are likely to be misleading. No or a negative correlation between occupancy and abundance may result if an abundant species happened to be sampled using a slightly smaller sampling unit while a less abundant species was sampled using a relatively large sampling unit.

The effects of sampling extent on the interspecific occupancy-abundance relationship are perhaps rather less intuitive than are those of sampling unit size. However, for a given MMU, the shape of the relationship remains broadly similar with increasing sampling extent, although inevitably the magnitude of both area of occupancy and abundance increase (Fig. 3). There is also an increase in variation about the occupancy-abundance relationship with increasing sampling extent, which suggests that the relationship should become relatively weak when extents are very large (e.g., at landscape and regional extents). This tends to be what occurs, with interspecific occupancy-abundance relationships at continental scales being particularly poor (Gaston 1994a). It has often proven difficult to distinguish between increasing sampling extent and increasing taxonomic diversity (which tends also to accompany large sampling extents, and is likely to increase the breadth of spatial population dynamic behaviours of the species) as causes of this effect, but it is clear that the former is sufficient. Ultimately, of course, variation about the occupancy-abundance relationship may become such that at large spatial extents it swamps any trend.

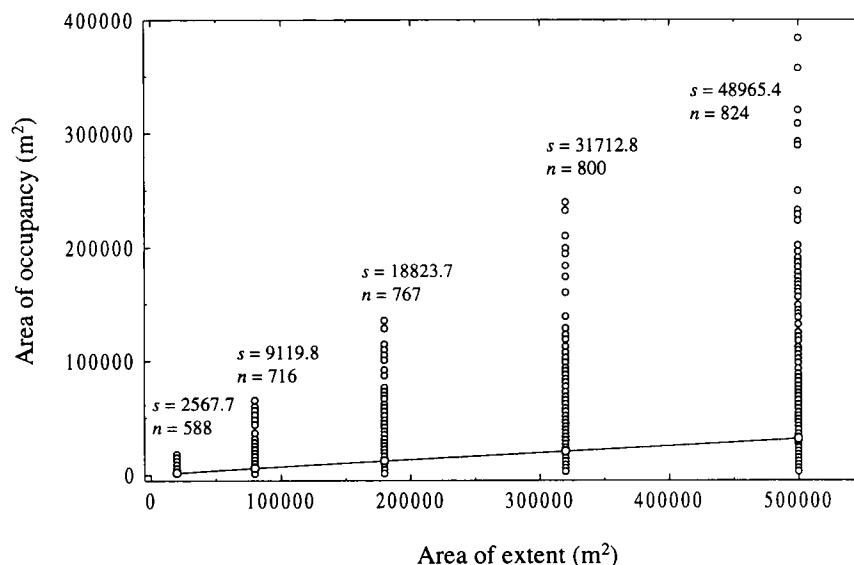## Estimation of species abundance from occupancy

An important potential application of occupancy-abundance relationships is to estimate the abundance of a species from its more readily measured area of occupancy in order to determine its commonness or rarity for management and conservation purposes (Gaston 1999 and references therein). Our results showed that all three models (eqs 3, 4 and 5) are suitable for estimating species abundance; for this the models are rewritten as follows:

He-Gaston: $\mu = k(p^{-1/k} - 1)$,

Nachman: $\mu = \left(-\dfrac{\ln(1-p)}{\alpha} \right)^{1/\beta}$,

Hanski-Gyllenberg: $\mu = \left(-\dfrac{1/p - 1}{\alpha} \right)^{-1/\beta}$,

Fig. 4. The relationship between area of occupancy and extent of the study area for the Pasoh data. The five extents were the same as used in Fig. 3. Each circle represents one species. The line links the mean of the area of occupancy at each extent. s is the standard deviation for the area of occupancy. n is the number of species occurring in each extent.
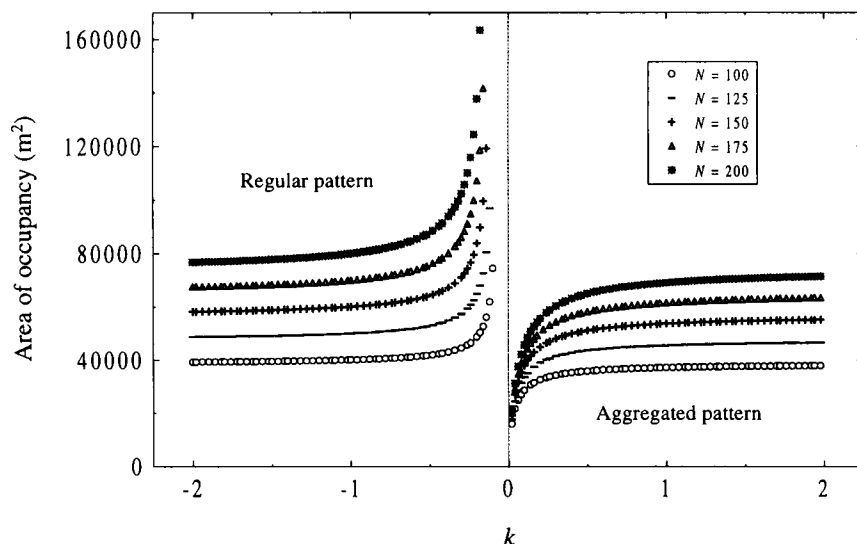
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where μ is the density of a population across the sampling extent, p is the proportion of area occupied, and the other parameters are defined as in eqs 3, 4 and 5.

The relationship between abundance and area of occupancy has become of particular practical significance in the context of the World Conservation Union (IUCN) Red List criteria for identifying species at high risk of extinction in the near future (Anon. 1994). The paucity of information on population sizes for most species has forced heavy reliance on measurements of geographic range size (both extent of occurrence and area of occupancy), in conjunction with other variables, as indicators of extinction risk. However, in calculating area of occupancy it is difficult to be highly prescriptive about the sampling scale which should be employed if sufficient flexibility is to be retained to enable use of the diverse kinds and qualities of distribution data available for different groups of organisms (e.g., some groups have been mapped at much finer resolutions than have others, the distributions of some groups have been mapped as point data and others as grid cell occupancy). Thus, whilst acknowledging the problem of sampling scale in calculating area of occupancy, the Red List criteria make no specific recommendations in this regard (Anon. 1994). The results of the present analyses showed that an occupancy-abundance relationship derived from one sampling scale (either sampling unit size or extent) cannot be used to predict or infer the relationship for another scale. For example, it is obvious from Fig. 3 that we cannot use the occupancy-abundance relationship for a sampling extent of 100 × 200 m to predict the area of occupancy of a species with abundance = 2000 but sampled using an extent of 400 × 800 m. This is also true for the inverse issue: estimating species abundance from area of occupancy. Therefore, the rarity or commonness for a spe-

cies derived from different scales of sampling is not comparable. This will make difficult the use of range size as a proxy for abundance if the desired degree of flexibility in sampling scales is to be retained, although given the pressing need for conservation prioritisation the options are limited.

For the Pasoh tree data, all three of the models examined performed well in describing occupancy-abundance relationships, whereas the Nachman model worked best for the Bedfordshire bird data. In the latter case, both the models of He-Gaston and Hanski-Gyllenberg underestimated the area of occupancy to a certain degree. In contrast, the apparent underestimation in Fig. 1 for the Pasoh data largely results from two strongly aggregated abundant species (with abundance ≈ 7200 and 8600, respectively) that had exceptionally small areas of occupancy.

Compared with the models of Nachman and Hanski-Gyllenberg, the He-Gaston model has two advantages: it is a one-parameter model, and its derivation has a theoretical basis (He and Gaston in press). In the situation where we want to determine abundance from occupancy for a single species, the He-Gaston model is probably the only one suitable for the task because it is not possible to derive more than one parameter for the models of Nachman and Hanski-Gyllenberg for a single species (He and Gaston in press).

Occupancy-abundance relationships and species-area curves

A widely accepted generalization in community ecology is that, as well as more individuals of any given species, more species will be encountered as the extent of sampling is increased. There have been several attempts to determine the link between the occupancy-abundance

relationship and the species-area relationship (Hanski and Gyllenberg 1997, Leitner and Rosenzweig 1997, Ney-Nifle and Mangel 1999). Two approaches have been employed. First, Hanski and Gyllenberg (1997) modeled the probability of occurrence of a species from the theory of metapopulation dynamics, empirically defining the occurrence to have logistic form. Second, the probability of occurrence of a species in a sampling area (window) has been defined as conditional on the distributional range or occupancy of the species (Leitner and Rosenzweig 1997, Ney-Nifle and Mangel 1999).

The findings from the current study suggest that the probability of occurrence of a species, and hence the results of either method, are subject to the scale of sampling used (Figs 1, 2 and 3). Ney-Nifle and Mangel (1999) have demonstrated the effect of study extent on the slope of a species-area curve. To make the results conclusive, it is also necessary to investigate the effects of sampling unit size on the parameters of species-area curves in this context (Palmer and White 1994). Scale effects on occupancy-abundance relationships make it difficult simply to assemble sets of parameter values for occupancy-abundance relationships and use these to test theories of species-area relationships without some cognizance being taken of the relevant scales in a study.

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