Notes and Comments

Estimating Species Abundance from Occurrence

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The number of individuals, or the abundance, of a species in an area is a fundamental ecological parameter and a critical consideration when making management and conservation decisions (Andrewartha and Birch 1954; Krebs 1978; Gaston 1994; Caughley and Gunn 1996). However, unless the scale is very fine or localized (e.g., in a measurable habitat or a forest stand), abundance is not readily determined. At coarse or regional scales for many species, information on commonness and rarity is, at best, limited to a map of their presence or absence from recording units in a specified time frame. Various species data at large scales are increasingly documented in this presence/absence format (e.g., Perring and Walters 1962; Little 1971; Arnold 1993, 1995; Mitchell-Jones et al. 1999).

The pattern of spatial occurrence of a species on a map is largely determined by three elements: the abundance of the species, its spatial distribution, and the size of the minimum mapping unit (MMU) or sampling scale. Because different species exhibit different distribution patterns, two having the same total area of occupancy can have different abundances. The estimation of the abundance of a species from its occupancy is thus a challenging, as well as being a significant, problem. Answers touch at the heart of the relationship between the abundance and the occupancy of species, which is presently attracting much attention in the context of macroecology (Brown 1984, 1995; Hanski et at. 1993; Lawton 1993; Gaston 1994, 1996; Gaston et al. 1997). Indeed, the formalization in mathematical terms of relationships between abundance and occupancy has largely been prevented because of the lack of knowledge about the levels of abundance associated with a given occurrence map. If abundance can generally be inferred from occupancy, the procedure itself formalizes the relationship.

An attempt to solve the problem of predicting levels of commonness and rarity from occurrence maps has recently been pursued by Kunin (1998). He suggested that, for a given species, the total area occupied (i.e., the sum of the occupied MMUs) might increase with the size of the MMU according to a fractal power relationship (see also Williamson and Lawton 1991; Gaston 1994); we shall term this an "area-area curve" (occupied area vs. sampling unit area). He used this relationship to estimate the total area occupied on a fine-scale map, based on the equation

$$A_a = A_{a2}\left(\frac{a}{a2}\right)^{\frac{\ln A_{a2} - \ln A_{a1}}{\ln a2 - \ln a1}},$$ (1)

where A_a is the total occupied area at fine-scale a, and A_{a1} and A_{a2} are the total areas occupied on two given coarse-scale maps with MMU $= a1$ and $a2$, respectively.

Kunin (1998) applied equation (1) to 73 rare British plant species to estimate the total area occupied at fine scales but found that the predicted values consistently overestimated those observed. This suggests that equation (1) may not be a good model of the area-area relationship; its statistical properties are also unknown, giving no confidence intervals on the estimates that result. Although a further empirical correction to equation (1) markedly improved the estimation of the occupied area of a species at a fine scale (Kunin 1998), it seems difficult to use the method to estimate species abundance itself because the MMU that should be used for such an estimation is unknown.

Here, unlike Kunin's method (1998), whose emphasis

was to estimate the area occupied by a species, our objective is to predict the abundance of a species from its occupancy, although the method can equally be used to estimate area of occupancy. From first principles of sampling theory, we begin by deriving an area-area curve for a null situation in which all the individuals of a species are distributed randomly in a given area. A similar approach is then used to derive an area-area curve for species that are aggregated in their distribution. The latter model is evaluated using data for the abundances of tropical tree species in a tract of Malaysian forest. Finally, the generality of the area-area curve is discussed by comparing it with several other relationships between abundance and occupancy.

Randomly Distributed Individuals

Assume a species with N individuals is distributed randomly in an area A. The probability of obtaining a particular individual in a sampling area a is a/A. Therefore, the number of individuals, n, in a follows a binomial distribution,

$$b(N, n; p) = \binom{N}{n}(a/A)^n(1 - a/A)^{N-n},$$

where $n = 0, 1, 2, \ldots, N$. The presence or absence of the species in a is a Bernoulli trial ($x = 1$, present with $p = 1 - [1 - a/A]^N$; $x = 0$, absent with $q = [1 - a/A]^N$). Then the total area occupied (A_a) by the species in the entire area A is the sum of independent and identical Bernoulli trials: $A_a = \Sigma ax$. An area-area curve can be derived:

$$A_a = A[1 - (1 - a/A)^N], \tag{2}$$

with a variance $V(A_a) = aA_a(1 - a/A)^N$. An abundance estimate can then be obtained by rearranging equation (2), which gives an abundance-occupancy curve. It is a maximum likelihood estimate of a binomial distribution, $b(M, m; p)$, where $M = A/a$ (the total number of MMUs), $m = A_a/a$ (the number of occupied MMUs, a random variable), and $p = 1 - (1 - a/A)^N$:

$$\hat{N} = \frac{\ln(1 - A_a/A)}{\ln(1 - a/A)} \tag{3}$$

with an asymptotic normal variance

$$V(\hat{N}) = \frac{a}{A} \frac{1 - (1 - a/A)^N}{(1 - a/A)^N \ln^2(1 - a/A)}.$$

Equation (3), verified using simulated random point maps, estimates the abundances of the randomly distributed "species" extremely well.

Aggregated Individuals

In nature, except at very low abundances, individuals of most species are typically aggregated (Pielou 1977; Taylor et al. 1978; Greig-Smith 1983; McArdle et al. 1990). Although a variety of probabilistic models have been used to describe spatial distributions of biological populations, the most frequently applied is the negative binomial distribution (NBD; Boswell and Patil 1970; Perry and Taylor 1985; Krebs 1989). By the NBD, the probability of the presence of a species in sampling area a is $1 - [1 + (\mu/k)]^{-k}$, where k is a "clumping" parameter and μ is the mean abundance across sampling unit a. For a given area A, $\mu = Na/A$. Following the same procedure as used for equation (2), we can derive an area-area curve for the NBD, such that

$$A_a = A\left[1 - \left(1 + \frac{Na}{Ak}\right)^{-k}\right], \tag{4}$$

with a variance $V(A_a) = aA_a[1 - (Na/Ak)]^{-k}$. A maximum likelihood estimate of abundance for a binomial distribution $b(M, m; p)$ with $p = 1 - [1 + (Na/Ak)]^{-k}$ is

$$\hat{N} = \frac{Ak}{a}\left[\left(1 - \frac{A_a}{A}\right)^{-1/k} - 1\right], \tag{5}$$

with an asymptotic normal variance $V(\hat{N}) = (A/a)[1 + (Na/Ak)]^2\{[1 + (Na/Ak)]^k - 1\}$.

The population density of a species can be calculated by averaging across all samples or only across those in which the species actually occurs. The abundance-occupancy relationship of equation (5) can be rewritten to describe these differences. If the former situation is of interest, this can be rewritten as $\mu = k\{[1 - (A_a/A)]^{-1/k} - 1\}$, while for the latter situation this is $\mu' = (Ak/A_a)\{[1 - (A_a/A)]^{-1/k} - 1\}$, where μ' is the density for the occupied samples only.

Unlike equation (3), in which only N is unknown for a given map, equation (5) has two unknown parameters (N and k). Because there is only one sample (i.e., one map) available in our problem, we need two maps with different MMUs to obtain these parameters for a given species. As recognized by Kunin (1998), a second map (with MMU = $a2$ and the total occupied area = A_{a2}) can be generated by aggregation of the units of recording (with MMU = $a1$ and the total occupied area = A_{a1}). Then N and k can be solved numerically, by substituting $a1$, A_{a1} and $a2$, A_{a2} into equation (4) or (5).

Empirical Evaluation

To evaluate equation (5), we used a stand-mapping data set of tree species in a tropical rain forest in the Pasoh Forest Reserve of Malaysia (He et al. 1997). The study area is a 500 × 1,000–m rectangular plot (50 ha; fig. 1). 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 with diameter at breast height ≥ 0.01 m were located in the plot by x and y coordinates, accurate to 0.1 m, meaning that the smallest possible MMU for locating a tree (or a point) is 0.01 m^2 (i.e., this MMU can accommodate either one tree point only or no points). 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, based on the 1990 survey data, were variously aggregated, random or even, with the majority being aggregated (He et al. 1997).

Species abundance can be estimated based on any two maps with different MMUs. To illustrate, we first divided the Pasoh plot into 12.5 × 12.5–m MMUs and generated a presence/absence map for each species, then we aggregated each map into 25 × 25–m MMUs. Equation (5) was evaluated numerically using the Newton-Raphson method (Press et al. 1989) and performed well. There was a close fit between the observed and predicted abundances (fig. 2*A*). There was a small degree of underestimation of observed abundances. This may occur for two reasons. First, the underlying spatial distribution of a species may deviate from the NBD. Second, an occurrence map is necessarily insensitive to some patterns of variation in abundance. For example, it cannot differentiate between a species that occurs in only a single grid cell at the finer of the MMUs used and has only a single individual in that cell and another species that also occurs in only a single cell but has more individuals there. Likewise, once all grid cells are occupied at the finer of the MMUs, numbers of individuals can continue to increase without any change in grid cell occupancy.

Equation (1) was initially proposed as a method for extrapolating to the area occupied by a species at a finer scale from coarser scales. It might be used to estimate abundance if the distribution of a species is truly fractal and if we know what MMU should be used. For the Pasoh data, we estimated the abundances of the 824 species by extrapolating from two coarse-scale maps (12.5 × 12.5 and 25 × 25 m) to a grid cell size of 0.1 × 0.1 m (the smallest MMU) and found that equation (1) gave an unrealistic overestimation (similar to the results in Kunin 1998). This suggests that the distributions of the Pasoh species are not fractal (indeed, it is hard to believe that
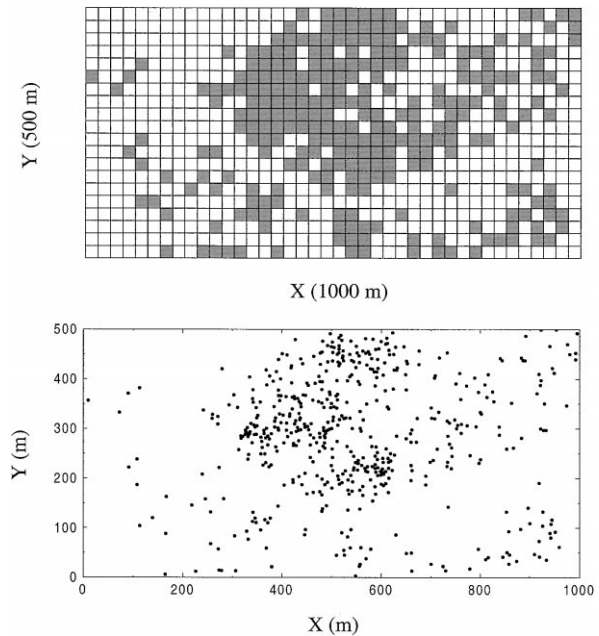

Figure 1: Occurrence map of the population of *Dacryodes rubiginosa* (MMU = 25 × 25 m) and its actual distribution of 591 individuals in a 50-ha forest plot in the Pasoh Forest, Malaysia.

they are), or that the MMU used (0.1 × 0.1 m) is inappropriate, or both. A direct comparison can be made between equations (1) and (4), although we still have to decide what MMU should be used for such a comparison. There is no easy basis for choosing the MMU; however, the size of the average area occupied per tree (i.e., the total number of trees divided by the size of the Pasoh plot, resulting in 1.32 m^2) may provide a first approximation (W. E. Kunin, personal communication). The results show that equation (1) gives a very marked overestimation of predicted area occupied (A_a) at the finer scale (1.32 m^2) compared to the prediction given by equation (4) (fig. 2*B*); the occupied area predicted for *Dacryodes rubiginosa* (fig. 1) at MMU = 1.32 m^2 was 2,785.34 m^2 by equation (1) and 724.11 m^2 by equation (4), compared with an observed figure of 774.12 m^2. These numbers and figure 2*B* can be approximately translated into species abundance by dividing by 1.32. Kunin (1998) was more successful in using equation (1) to predict the occupancy of his rare plant species at a 25-fold finer scale than the maps he used. Our results suggest, perhaps unsurprisingly, that predictions using equation (1) become progressively poorer with increasing disparity between the coarse-scale maps and the scales of prediction because of the influence of any departures from fractal distributions.

Because the apparent distribution of a species is dependent, at least in part, on the scale of observation, dif-

ferent pairs of MMU maps will give different results for both equations (1) and (5). As evaluated in terms of the square root of the sum of squared differences between the estimated and the observed abundance, the estimation by equation (5) is fairly robust to this effect (table 1). The estimation for those species of rare to intermediate abundance is particularly accurate and reliable. Unsurprisingly, the accuracy of prediction declines as the MMU maps become coarser (table 2). Although k in equation (5) changes with scale, the change is also limited (table 2).

Generality and Limits

Although the derivation of equation (4) (or equivalently eq. [5]) was based on the NBD, the k computed is not necessarily the same as that of the true NBD, where it is defined to be positive (Boswell and Patil 1970; Krebs 1989). Indeed, k in equation (4) can vary in two intervals: $(-\infty, -\mu)$ and $(0, +\infty)$. When $k \in (0, +\infty)$, the probability of presence, $p = 1 - [1 + (\mu/k)]^{-k}$, is derived from the negative binomial distribution (i.e., the sum of nonzero terms of NBD); a smaller value of k represents stronger aggregation of species and vice versa. When $k \in (-\infty, -\mu)$, the probability of presence is derived from a binomial distribution that describes regular distributions of species (Greig-Smith 1983). Figure 3 clearly shows that the probability of presence describes an entire spectrum of spatial patterns, from regular to random to aggregated. Therefore,

Table 1: Square roots of the sum of squared differences between the estimated and the observed abundance for 824 species in the Pasoh Forest of Malaysia

MMU	12.5 × 12.5	20 × 20	25 × 25	50 × 50
10 × 10	5,898.3	5,961.1	6,423.2	8,518.2
	(1,414.3)	(1,311.8)	(1,598.4)	(1,722.0)
12.5 × 12.5	...	8,082.3	9,160.2	12,338.8
	...	(1,108.4)	(1,074.1)	(1,178.0)
20 × 20	...	...	14,203.5	19,970.7
	...	...	(1,746.9)	(1,735.8)
25 × 25	...	...	...	24,415.5
	...	...	...	(1,865.1)

Note: Estimated abundance was calculated using equation (5) based on map pairs of different MMUs (e.g., 10 × 10 and 20 × 20 m, which has square root = 5,961.1). The values in parentheses are the square roots for the 725 species whose abundance are ≤1,000 individuals.

we can simply define the binomial distribution $b(M, m; p)$ with $p = 1 - [1 + (Na/Ak)]^{-k}$, ignoring its roots in the NBD. This broadens the generality of equation (4) to many other types of spatial distributions. In the Pasoh Forest, k values varied between -38.973 and 54.149. Some very rare species had $k = -N$, and the NBD actually became a binomial distribution and equation (4) equals equation (2). When $k \to 0$, equation (4) describes a logarithmic series distribution of individuals of a species in space (Quenouille 1949). When $k = 1$, equation (4) describes a geometric distribution. When $k \to \pm\infty$, the spatial
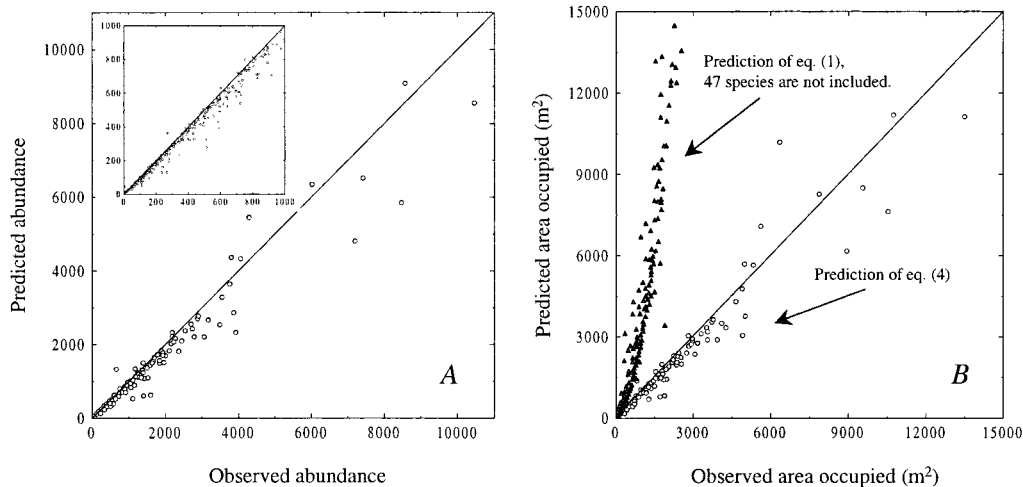

Figure 2: *A*, Predicted and observed abundance for 824 species in the Pasoh Forest in Malaysia. The predicted values were calculated using equation (5) from two occurrence maps with MMU = 12.5 × 12.5 and 25 × 25 m, respectively. The diagonal line is for prediction = observation. The insert shows the 725 species whose abundance ≤1,000 individuals. One species is not included here because the predicted number of individuals of 15,565 (actual abundance is 8,954) is beyond the bounds of the figure. *B*, Predicted and observed area occupied (A_a) for each of the 824 species in the Pasoh plot. The predicted values were calculated using equations (1) and (4), respectively, based on the same two occurrence maps used in *A* for a grid size $a = 1.32$ m². Because the occupied areas of 47 species predicted from equation (1) are too high (ranging from 15,293 up to 271,670 m²), these species are not shown in the figure.

distributions converge to random (the Poisson) from different directions: regular to random on the left and aggregated to random on the right (fig. 3) with

$$p = 1 - e^{-\mu}, \tag{6}$$

where $p = (A_a/A)$ is the proportion of occupied samples or a probability of presence.

The flexibility of equation (4) means that the area-area curve is closely related to several other abundance-occupancy models. One that is used widely to describe the relationship between population density and spatial distribution, particularly in agricultural entomology, is that of Nachman (1981, 1984; see also Kuno 1986, 1991; Ward et al. 1986; Ekbom 1987; Perry 1987; Yamamura 1990; Hepworth and MacFarlane 1992; Feng et al. 1993). This takes the form $q = e^{-\alpha\mu\beta}$, where $q = 1 - p$ is the proportion of unoccupied samples (i.e., unoccupied MMUs). This model is actually an empirical extension of equation (6) that adds two positive parameters, α and β, which are determined through regression on a case by case basis. A fitted curve of the Nachman model may be equally well described by equation (4) by adjusting k.

A second abundance-occupancy model that has close relations to equation (4) is the logistic model proposed by Hanski and Gyllenberg (1997). This takes the form $p = [1/(1 + \alpha\mu^{-\beta})]$, where, as with the Nachman model, α and β are two positive empirical parameters to be determined by regression. This is an empirical extension of equation (4) at $k = -1$ and therefore describes a geometric distribution of the individuals of a species. The resulting density-occupancy model is $p = [1/(1 + \mu^{-1})]$. For both the Nachman and the logistic models, the determination of α and β requires actual density (or abun-
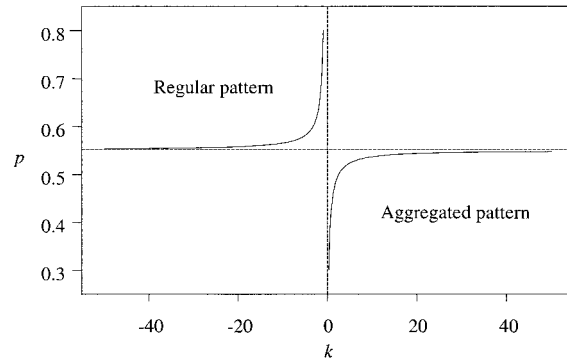

Figure 3: Probability of presence, $p = 1 - [1 + (Na/A)]^{-k}$ for a species in a given area. The plot illustrates how p changes with k for $\mu(= Na/Ak) = 0.8$. When a species is aggregated, the probability of presence is less than for a random distribution, while it is larger if the species is regularly distributed. When $k \to \pm\infty$ in opposite directions (from aggregated on the positive side of the abscissa or from regular on the negative side), the spatial distributions of the species converge to random (i.e., Poisson distribution) in which the expected probability of presence is $1 - e^{-\mu}$, resulting in $p = 0.55$ for $\mu = 0.8$.

dance) observations; it is unlikely that they could be estimated solely from occurrence data such as that of figure 1.

Another model of the relationship between abundance and occupancy that has frequently been cited (e.g., Lawton et al. 1994) is that derived by Maurer (1990, his eq. [4]). However, it is not difficult to show that this model is exactly the same as our equation (2), which in turn is a special case of our equation (4) at $k = -N$, as mentioned above.

Wright (1991) drew attention to the fact that a rela-

Table 2: Estimated abundance for *Dacryodes rubiginosa* in figure 1

MMU	12.5 × 12.5	20 × 20	25 × 25	50 × 50
10 × 10:				
N	581.0 ± 62.8	567.1 ± 86.9	562.5 ± 103.8	543.6 ± 201.5
k	.463	.415	.443	.627
12.5 × 12.5:				
N	...	555.1 ± 83.7	549.8 ± 99.7	524.3 ± 190.3
k	...	.437	.463	.649
20 × 20:				
N	...	...	528.7 ± 93.1	478.6 ± 164.4
k	...	...	.500	.714
25 × 25:				
N	...	...	...	448.8 ± 148.1
k	...	...	...	.768

Note: The N and k in equation (5) were evaluated using the Newton-Raphson method, based on map pairs of different MMUs (e.g., at 10 × 10 and 20 × 20 m, the numerical solutions for N and k are 567.1 and 0.415, respectively). An approximate 95% confidence interval is also given, based on an asymptotic normal variance of N. The actual number of individuals is 591.

tionship between abundance and occupancy is implicit in the NBD, and since then this has been used widely as a conceptual model to explain the relationship (for discussion, see Hanski et al. 1993; Gaston et al. 1997, 1998; Hartley 1998). Indeed, it has been argued that the observed interspecific positive relationship between abundance and occupancy is nothing more than a reflection of the fact that the abundances of organisms exhibit an NBD (Hartley 1998; but see Gaston et al. 1998). Here, we have demonstrated that the NBD is just one of a broad spectrum of models that may yield abundance-occupancy relationships, although it is one that is frequently documented in nature.

Aside from the constraints on the accuracy of predictions of abundances already noted, the most obvious circumstance in which equation (4) seems likely to be problematic is that in which a high proportion of the overall sampling area cannot be occupied (as opposed simply to being unoccupied) by the species of concern, for example, for reasons of environmental unsuitability. If unoccupiable and occupiable areas cannot be sufficiently differentiated, then the extent of the sampling universe will tend to be overestimated.

In addition, the derivation of equations (2) and (4) was based on the sum of independent and identical Bernoulli trials of presence and absence, which results in a binomial distribution. A problem may arise for equation (4) because of the potential spatial autocorrelation of occurrence of a species in MMUs that violates the independent assumption of Bernoulli trials. A solution to this problem can be complicated to obtain and will likely be strictly empirical. We have explored several direct modifications to equation (4) to address the issue but have failed to obtain better predictions to obtain better predictions of abundance. We have also used other models of occupancy distribution (Johnson et al. 1993) that do not necessitate the assumption that occurrences are independent, but again they do not perform as well as equation (4).

In sum, the generality of equation (4) suggests that the area-area curve can provide a useful tool for estimating the abundances of species in circumstances where these estimates are difficult or expensive to obtain by more direct means. It also serves to unify what have previously been seen as a disparate set of models of abundance-occupancy relationships. The explicit inclusion of sampling scale in the area-area curve of equation (4) makes it possible to evaluate the effects of spatial scales on these relationships. The study example of the Pasoh data demonstrated that the method proposed in this note was fairly satisfactory; however, the accuracy and usefulness of the method for large-scale (e.g., geographical) estimation remain to be tested.

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