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Downscaling species occupancy from coarse spatial scales

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Abstract. The measurement and prediction of species' populations at different spatial scales is crucial to spatial ecology as well as conservation biology. An efficient yet challenging goal to achieve such population estimates consists of recording empirical species' presence and absence at a specific regional scale and then trying to predict occupancies at finer scales. So far the majority of the methods have been based on particular species' distributional features deemed to be crucial for downscaling occupancy. However, only a minority of them have dealt explicitly with specific spatial features. Here we employ a wide class of spatial point processes, the shot noise Cox processes (SNCP), to model species occupancies at different spatial scales and show that species' spatial aggregation is crucial for predicting population estimates at fine scales starting from coarser ones. These models are formulated in continuous space and locate points regardless of the arbitrary resolution that one employs to study the spatial pattern. We compare the performances of nine models, calibrated at regional scales and demonstrate that a very simple class of SNCP, the Thomas process, is able to outperform other published models in predicting occupancies down to areas four orders of magnitude smaller than the ones employed for the parameterization. We conclude by explaining the ability of the approach to infer spatially explicit information from spatially implicit measures, the potential of the framework to combine niche and spatial models, and the possibility of reversing the method to allow upscaling.

Key words: *downscaling; Neyman-Scott process; occupancy–area curve; Poisson cluster process; shot noise Cox processes; spatial point processes; species aggregation; species occupancy; Thomas process.*

INTRODUCTION

In recent years the issue of species occupancy at different spatial scales has been of growing interest in spatial ecology (Kunin 1998, He and Gaston 2000, Kunin et al. 2000, Tosh et al. 2004, Hui et al. 2009). Species occupancy, or the fraction of area occupied by a given species, is obtained by dividing the study area into an artificial regular grid of cells of (ideally) equal size and then calculating the fraction of such cells occupied by a focal species. In this study, the word “resolution” refers to the spatial size of any unit cell of the regular grid superimposed on the entire study region, whose extent is always held constant. Thus, resolution refers to the unit cell size of the tool being used. On the other hand, the word “scale” refers to the underlying characteristic length of the pattern itself. Thus, increasing the resolution allows one to study patterns possessing relatively smaller length scales and vice versa. Any empirical spatial pattern can be studied by using arbitrary cell sizes according to different resolutions, thus unveiling different characteristics of the underlying pattern.

If we fix an arbitrary resolution to study species occupancies, we obtain a measure that provides an index

of a species' range size (“area of occupancy” in Gaston 1994), regional ubiquity, or local abundance, depending on the resolution employed (Hartley and Kunin 2003). Such issues may be of interest in comparing the commonness or rarity of different species. However, because analyses conducted at different resolutions reflect different aspects of species' distributions, a far richer description can be developed by using multiple resolutions. To do so, one varies the cell size unit from near zero to the whole of the study area, thus obtaining different occupancy values at each resolution, generating an occupancy–area curve, also called “scale area curve” (Kunin 1998) or “range–area relationship” (Harte and Kinzig 1997, Harte et al. 1999). Such a curve captures important features of a species' patchiness at different spatial resolutions, thus addressing one of the crucial topics in spatial ecology. Moreover, such curves readily can be converted to probabilities of occupancy (by dividing them by the total area or the number of cells available at each resolution), and the sum of such probability curves across species creates the well-known species–area relationship (Arrhenius 1921, Rosenzweig 1995), one of the cornerstones of spatial ecological research.

At relatively coarse resolutions, species occupancy is easy to document because it only relies on occurrences. However, large cell sizes may mask very different spatial patterns that can be revealed only at finer resolutions: species occupying the same proportion of area at coarse

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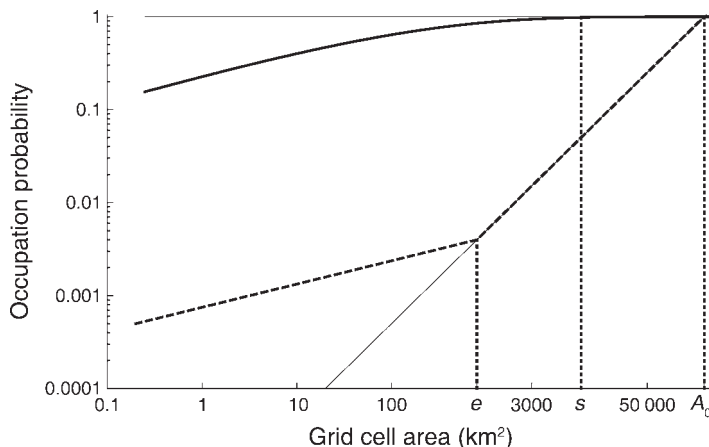


FIG. 1. Occupancy–area curves. The thick solid curve represents the typical behavior of the occupancy–area curve for widespread species. These species generally have occupancy curves that saturate, i.e., reach occupancy 1, at resolutions smaller than the study region (here indicated by A_0). The “scale of saturation” (indicated by s in the figure) is defined as the smallest grid cell for which the occupation probability is 1. In contrast, the thick dashed curve represents the typical behavior of the occupancy–area curve for species with distributions restricted to only a portion of the study region. These species reach a “scale of endemism” (indicated by e in the figure) beyond which all of the individuals belonging to such species are contained in a single grid cell. The scale of endemism corresponds to the smallest cell unit encompassing the entire population of a species. For cell sizes larger than the endemic scale, such species have an occupancy probability equal to A/A_0 (indicated by the thin solid line), where A is the area of a grid cell. Because areas coarser than the scale of saturation (s) or endemism (e) are useless for downscaling purposes, we fitted the models to the three coarsest unsaturated or non-endemic areas.

resolutions could dramatically differ in their spatial patterns at a finer mapping. This is simply because the rate of occupancy change across resolutions strongly depends on the spatial distribution of species’ populations. As the cell size decreases, we are able to delve into finer and finer details by uncovering unoccupied units within occupied coarser grid cells. Continuing to increase the resolution, when the unit area is sufficiently fine that only one individual, on average, occupies a cell, we could in principle even estimate the population abundance of a species (although in practice there may be limits to the extent of downscaling possible). This underscores the importance of achieving reliable downscaling models, because conducting surveys at high levels of spatial resolution over large study areas may be prohibitively resource-demanding and time-consuming.

Widespread species relative to the region of study will generally have occupancy curves that saturate at scales smaller than the study area. By saturation we mean that a species is present within every grid cell of a given area so that the probability, p , that a given cell is occupied is 1 (see Fig. 1). In contrast, species that are only located within a portion of the study region can reach a “scale (or area) of endemism” above which all the individuals belonging to such species are contained in a single grid cell; at all coarser resolutions, such a species will have an occupancy probability equal to A/A_0 , where A is the area of a grid cell (equal to or coarser than the scale of endemism) and A_0 is the area of the whole region (see Fig. 1). The saturation and endemism curves constitute upper and lower geometrical bounds between which all species occupancies are constrained.

Such occupancy curves provide efficient descriptions of species’ distributions across multiple resolutions, but they may have an additional use, as alluded to previously: if we understand the shape of an occupancy curve, we ought to be able to extrapolate it to provide information about distributions at resolutions other than those measured. Extrapolating to coarser resolutions (“upscaling”) in this context is not difficult, as a fine-resolution map already contains coarser resolution information; however it is a more challenging task to use relatively coarse resolution information to draw inferences about fine-scale patterns (“downscaling”). Since this prospect was first raised (Kunin 1998), a number of methods have been developed to attempt this task.

In the *Methods* section we review some occupancy–scale models that have been used for distributional downscaling and related tasks in the literature. Their performances will be compared and discussed in *Results* and *Discussion*. Most of these models do not accommodate spatial features in an explicit manner and the derivation of the species occupancy curve is quite empirical (for example, see He and Condit in Storch et al. [2007:32]). In contrast, we suggest a wide class of stochastic point processes that explicitly incorporate space and aggregation, are analytically tractable, and allow the occupancy–area curve to be derived straightforwardly along with useful summary statistics. These models are formulated in continuous space and locate each point regardless of any resolution employed to analyze a pattern, and thus they enable us to study how the underlying point pattern will translate into occupancy patterns at different resolutions. Thus, when

superimposing a grid with a varying unit cell size on the study region, one can see how a fixed pattern of spatial locations of individuals looks under different resolutions. For the spatial point processes that we suggest, the fraction of occupied cells (regardless of the spatial location of the cells) can be calculated analytically and therefore we know exactly how the species' occupancies vary by changing the unit cell size of the superimposed grid. This calculation allows us to link directly the parameters of the spatial point process to the distribution of occupancies. This latter, additionally, can be employed to estimate the parameters from empirical data by using standard techniques of model inference. It is worth pointing out that this protocol allows one to infer several spatially explicit properties of species' distribution from the occupancy–area curve, which, in contrast, carries no information about the spatial location of individuals. For instance, we can estimate the spatial autocorrelation function and clarify the main characteristics of species' spatial aggregation.

More specifically, we will focus on a family of Cox processes (Cressie 1993, Illian 2008): the shot noise Cox processes, SNCs (Møller 2003). This class is rich enough to include a wide subfamily of Neyman-Scott processes (Thomas 1949, Neyman and Scott 1958), Poisson/Gamma processes (Wolpert and Ickstadt 1998), and shot noise G Cox processes (Brix 1999). A particular case of SNC is the Thomas model (Thomas 1949), which has been successfully used to model natural vegetation patterns (see, e.g., Plotkin et al. 2000, Morlon et al. 2008), but it has not been applied previously to downscaling. In this study we show that the SNCs (specifically, the Thomas model) can be used as a powerful tool to scale species' occupancy down to areas several orders of magnitude smaller than those used to train the model itself. In addition, the framework is able to provide information about the spatial autocorrelation function even though one knows only the proportion of occupied area by any species.

METHODS

Review of the models

The purpose of this section is to outline different models that have been used in the ecological literature to downscale species occupancy and that we will examine and compare. Although some of them were originally devised as occupancy–abundance models, they can easily be turned into occupancy–area models because the number of individuals of any species is usually proportional to area (Preston 1962).

The simplest is the Poisson model (Wright 1991). It assumes that all of the inter- and intraspecific interactions are negligible and the study region is homogeneous. Under such circumstances, individuals occur independently from each other and are distributed according to a binomial distribution across a finite area: this is at the core of the random placement model proposed by Coleman (1981). For large enough areas

and populations, a binomial distribution is well approximated by a Poisson one that yields

$$P_{\text{rand}}(A) = 1 - e^{-\gamma A} \quad (1)$$

as the probability of finding a species within a cell unit of size A , if it has constant density γ . Eq. 1 shows a theoretical drawback common to all models that are intrinsically based on infinite landscapes: $P_{\text{rand}}(A)$ is exactly 1 only when A goes to infinity. For any finite study region, or population, these models do not yield saturation. Thus, infinite-landscape models can describe reality under limited conditions and are meant as approximations of more accurate, but usually less tractable, approaches that are explicitly able to deal with finite populations. For instance, despite saturating at infinitely large areas, the Poisson occupancy approaches 1 as $\gamma A \gg 1$, the error being exponentially small. Thus, it can be meaningfully used for all species' densities much greater than $(A_0)^{-1}$, where A_0 is the area of the whole study region. This assumption usually holds for common or scarce species, but brings about theoretical issues for rare or very rare species, which will typically have densities less than $(A_0)^{-1}$. Interestingly, this consideration shows that infinite-landscape models may describe occupancy of at most a subset of species present within a very large study area.

The finiteness of a focal landscape is not the only issue that the Poisson model is not able to deal with. There is growing evidence from a wide range of systems that conspecific individuals are generally spatially aggregated (see also Plotkin et al. 2002). Clustering of conspecifics leads to spatially autocorrelated landscapes that, ultimately, are responsible for the nonindependence of individuals' locations and make Poisson sampling inadequate in most cases. Thus the introduction of spatial clustering into statistical approaches may be expected to improve model performance. Whether we should focus on a particular type of aggregation consistently emerging from empirical patterns remains a matter of debate, and the absence of consensus on this point has resulted in a plethora of models trying to deal with aggregation. Rather than attempting to develop spatially explicit approaches to clumping or spatial autocorrelation, some authors prefer to model overdispersion, which is implied by clumping, and which can be modeled without any explicit spatial reference. This approach led He and Gaston (2000) to suggest the negative binomial distribution (NB) as a good candidate for species occupancy. In this case the probability of occurrence is

$$P_{\text{NB}}(A) = 1 - \left(1 + \frac{\gamma A}{k}\right)^{-k} \quad (2)$$

where γ is a density as in the Poisson model and k is a parameter measuring the degree of overdispersion. Small positive values of k indicate spatial aggregation, whereas $P_{\text{nb}}(A)$ approaches $P_{\text{rand}}(A)$ for very large k

values, thereby including independent sampling as a special case.

Recently, this model has been corrected to accommodate the finiteness of landscapes or populations, which should be important when the model is applied to focal regions of relatively small size. Zillio and He (2010) have derived a finite negative binomial distribution that predicts the following occupancy–area curve:

$$P_{\text{fng}}(A) = 1 - \frac{\Gamma\left(N + \frac{A_0k}{A} - k\right)\Gamma\left(\frac{A_0k}{A}\right)}{\Gamma\left(N + \frac{A_0k}{A}\right)\Gamma\left(\frac{A_0k}{A} - k\right)} \quad (3)$$

where Γ is the gamma function, N is the total number of individuals in the study area A_0 , and k has the same meaning as in Eq. 2.

Typically, aggregation is different for different species but, more challenging, a given species may vary in its degree of aggregation (Plotkin and Muller-Landau 2002), even with scaling discontinuities (Hartley et al. 2004). At relatively coarse resolutions, species’ distributions tend to be less clumped than they are at finer resolutions. If clumping intensity varies with resolution, then overdispersion will no longer be constant and the clumping parameter k will be scale dependent. To overcome such difficulties, He and Gaston (2003) generalized their model by introducing into the NB distribution a scale-dependent variance with the form of Taylor’s power law (Taylor 1961), i.e., $\sigma^2(A) = c(\gamma A)^b$, thereby making k a function of area, i.e., $k(A) = \gamma A / (c(\gamma A)^{b-1} - 1)$. The improved negative binomial (INB) distribution gives the following probability of occurrence:

$$P_{\text{INB}}(A) = 1 - \left[c(\gamma A)^{b-1} \right]^{\frac{\gamma A}{1 - c(\gamma A)^{b-1}}} \quad (4)$$

where c and b are now constant parameters that account for the spatial aggregation of species (the majority of estimates of b range between 1 and 2, whereas c strongly depends on the study case). Clearly, one can estimate the clumping intensity by using different functions for k . For instance, Plotkin and Muller-Landau (2002) suggest a phenomenological curve, $k(A) = cA^z + d$, which best describes empirical data in a tropical forest but has no theoretical explanation. In the following, we will stick with Eq. 4.

A completely different approach focuses attention most sharply on the scaling pattern of occupancy. Put it another way, instead of modeling overdispersion, one can delve into occupancy change across resolutions and put forward a reasonable function to downscale the pattern at finer resolutions. Assuming a fractal spatial distribution of species, Kunin (1998) suggested a power-law (PL) relationship between occupancy and area:

$$P_{\text{PL}}(A) = cA^z. \quad (5)$$

Obviously, such a model cannot be realistic across all

resolutions, simply because it exceeds unity for large areas. However, it makes reasonably good predictions at relatively sparsely occupied spatial scales for a set of rare British plant species, although it generally overestimates occupancy (Kunin 1998).

The power-law model can be improved and generalized in several ways. Although originally devised for different purposes, the Nachman model (Nachman 1981) can be considered a generalization of Kunin’s. It naturally bends down the power-law function at saturating scales where the fractal model fails. The improved occupancy–area curve reads

$$P_{\text{nach}}(A) = 1 - e^{-cA^z}. \quad (6)$$

This curve is not noticeably different from Eq. 5 for $cA^z \ll 1$ and saturates at 1 if $cA^z \gg 1$.

An alternative model was put forward by Hanski and Gyllenberg (1997) under a metapopulation framework. According to a standard approach in metapopulation dynamics, they were able to calculate a species occupancy curve that turned out to be a logistic relationship:

$$P_{\text{logis}}(A) = \frac{cA^z}{1 + cA^z}. \quad (7)$$

The power-law model is easily brought into the same framework as this logistic curve, because Eq. 7 reduces to Eq. 5 when $cA^z \ll 1$, although the convergence is less rapid than in the Nachman’s case. Indeed, all the distributions defined in Eqs. 1, 2, 5, 6, and 7 can be summarized with only one formula (He et al. 2002):

$$P_{\text{czk}}(A) = 1 - \left(1 + \frac{cA^z}{k} \right)^{-k}. \quad (8)$$

Although it does not have a compelling theoretical explanation, Eq. 8 merges different curves and usefully discriminates toward which model empirical occupancies are skewed. For instance, $P_{\text{czk}}(A)$ with $k = -1$ is equivalent to Eq. 5; with $k = +1$, it is equivalent to Eq. 7; whereas for large values of k , one obtains the Nachman and Poisson (with $c = \gamma$ and $z = 1$) models. Finally we recover the NB occupancy for any finite k as $c = \gamma$ and $z = 1$.

Recently, an alternative model has been proposed for downscaling purposes (Hui et al. 2006). It has many merits (Hui et al. 2009), but would have been difficult to apply in the present case. In fact, at each resolution it needs spatially explicit occupancy information that is not available in many data sets as well as in the empirical data we considered in this study.

The models we have been discussing so far deal with space only implicitly (except the one suggested by Hui et al. (2006), which can be considered spatially explicit). At a deeper level of description, however, the explicit introduction of space arguably has the potential ability to broaden the spectrum of possible clumping features and intensities. Along these lines, spatial point processes

(SPPs) constitute a promising pursuit because of their flexibility as well as analytical tractability (Diggle 1983, Cressie 1993, Illian 2008). The simplest SPP, the Poisson point process, plays a fundamental role as reference process for the absence of interactions or complete spatial randomness but, as discussed earlier, is too simplistic to reproduce empirical patterns of species' distribution. Nonetheless, it can be exploited to obtain more realistic models that explicitly allow for aggregation. Cox processes represent such a convenient and wide class of models: they form a natural and elegant extension of a Poisson point process, while being always overdispersed relative to it (Lawson and Denison 2002:37). If \vec{x} represents a spatial location, the inhomogeneous Poisson process is characterized by an intensity function $z(\vec{x})$ that generally varies across space, and $\int_A z(\vec{x})d\vec{x}$ measures the average number of points found within area A (Stoyan and Stoyan 1994). In this case the intensity function is deterministic; nevertheless, one can substitute it with a space-dependent random variable called random field or random intensity surface $Z(\vec{x})$. The Cox process is obtained when the intensity function of an inhomogeneous Poisson process is a realization (or replicate) of $Z(\vec{x})$ (Cressie 1993, Lawson and Denison 2002, Møller and Waagepetersen 2007, Illian 2008). For a more rigorous definition we refer to the Appendix. Let us take a simple example and assume for a moment that Z is a constant positive random variable. If Z is gamma distributed as well, then the number of individuals within area A follows a negative binomial distribution (Lawson and Denison 2002), which predicts the species occupancy in Eq. 2. The most interesting situation, evidently, arises when Z is a location-dependent random field. In this case, one of the most mathematically tractable family of Cox processes, the shot noise Cox processes (SNCPs; Møller 2003, Møller and Waagepetersen 2007), is defined by the following random intensity surface:

$$Z(\vec{x}) = \sum_{(\mu, \vec{c}) \in P} \mu k(\vec{c}, \vec{x}). \tag{9}$$

Here $k(\vec{c}, \vec{x})$ is a probability density function such that $\int k(\vec{c}, \vec{x})d\vec{x} = 1$ for any spatial location \vec{c} , $\mu > 0$ and \vec{c} are randomly distributed according to a Poisson process P with intensity function $\rho(\mu, \vec{c})$ (see the Appendix for a mathematically more rigorous definition). Eq. 9 suggests that SNCPs are distributed as a superposition or union of independent Poisson processes with intensity functions $\mu k(\vec{c}, \dots)$. Each of the latter can be interpreted as a cluster with center \vec{c} , mean number of points μ , and dispersal probability distribution $k(\vec{c}, \dots)$. Therefore, according to the SNCP scenario, species are spread out in independent clusters of individuals dispersing around each center \vec{c} and falling at the point \vec{x} with probability density $k(\vec{c}, \vec{x})$. The recipe of the model is not grounded upon any specific biological ingredient; it simply offers a statistical and phenomenological framework apt to

incorporate clumping patterns. SNCPs are formulated in continuous space with given sets of parameters. Thus, once we infer from data what the parameters are, we can predict whatever pattern or summary statistics, including the occupancy curve. Note that the resolution at which occupancy patterns are measured is superimposed on top of the point pattern, and it is not a property of the SNCP process itself. As we will explain later on, we will choose some suitable empirical occupancies to calculate the numerical value of the parameters. It is worth noting that what we are modeling here is the aggregation of conspecific individuals, implicitly assuming that interspecific interactions are relatively less important for species' clumping. However, it may be useful to point out that the assumption of independence among species within a taxon is not so unrealistic: recent empirical and theoretical studies have provided some support for this hypothesis (Hoagland and Collins 1997, Veech 2006, Houlahan et al. 2007, Azaele et al. 2010).

Despite the fact that these processes do not specifically model any of the myriad actual mechanisms that drive aggregation across ranges of spatial resolutions, as we shall see later on, the framework is able to capture some of the essential features at the core of the spatial distribution structure of species. In addition, without losing the analytical tractability, it easily integrates aggregation caused by habitat heterogeneities (Waagepetersen 2007). This may potentially bridge the gap between purely environmentally driven models and more mechanistic approaches that usually harness much less information but cannot easily be applied to heterogeneous habitats.

From the intensity surface in Eq. 9 one can readily derive the SNCP intensity function

$$\alpha(\vec{x}) = E[Z(\vec{x})] = \int \mu k(\vec{c}, \vec{x}) \rho(\mu, \vec{c}) d\mu d\vec{c} \tag{10}$$

where we used the intensity function, $\rho(\mu, \vec{c})$, of the Poisson process to calculate the expectation as in Møller (2003). Intuitively, $\alpha(\vec{x})d\vec{x}$ is the probability that a point falls within the area $d\vec{x}$ centered in \vec{x} . This interpretation can be generalized to all product moments of the form $E(Z(\vec{x}_1)Z(\vec{x}_2)\dots Z(\vec{x}_n))$, so that $E[Z(\vec{x})Z(\vec{y})]d\vec{x}d\vec{y}$ is the joint probability that a pair of points falls within the areas $d\vec{x}$ and $d\vec{y}$ centered in \vec{x} and \vec{y} , respectively. Explicit expressions can also be obtained for the pair correlation function, i.e., $g(\vec{x}, \vec{y}) = E[Z(\vec{x})Z(\vec{y})]/\alpha(\vec{x})\alpha(\vec{y})$. It is given (Møller 2003) as follows:

$$g(\vec{x}, \vec{y}) = 1 + \frac{\int \mu^2 k(\vec{c}, \vec{x})k(\vec{c}, \vec{y})\rho(\mu, \vec{c})d\mu d\vec{c}}{\alpha(\vec{x})\alpha(\vec{y})}. \tag{11}$$

The formula explicitly shows that $g(\vec{x}, \vec{y}) \geq 1$, because k and ρ are always positive, and it directly underscores that SNCPs spawn more aggregated points relative to corresponding Poisson processes, being completely uncorrelated only when $g(\vec{x}, \vec{y}) = 1$. The generating functional (see Appendix) of these models, however, is more closely tied up with species occupancies: it is not

only a useful mathematical tool that completely characterizes the process at hand, but also provides the probability of finding n individuals within a given area, which is crucial to many spatial issues. In the Appendix we calculate the probability generating function for $N(A)$, i.e., $G_A(t) = E(t^{N(A)})$, where $N(A)$ is the number of points of a SCNP falling within area A . The final result is

$$G_A(t) = \exp \left\{ - \int \left[1 - \exp \left(-(1-t)\mu \int_A k(\vec{c}, \vec{x}) d\vec{x} \right) \right] \times \rho(\mu, \vec{c}) d\mu d\vec{c} \right\}. \tag{12}$$

From this function one can obtain the probability of finding n individuals within a given area A , i.e., $p(n|A)$, by repeated differentiation, i.e.,

$$p(n|A) = \frac{1}{n!} \left. \frac{d^n G_A(t)}{dt^n} \right|_{t=0}$$

for $n = 0, 1, 2, \dots$. We calculated only $p(0|A)$ because $1 - p(0|A)$ provides the species occupancy we are interested in: this is simply $G_A(0)$. In the following we will be making a series of further assumptions to handle formulas more easily. For instance, we will be considering only translation- and rotation-invariant processes: they are stationary and isotropic with a simpler pair correlation function, $g(\vec{x}, \vec{y}) = g(\|\vec{x} - \vec{y}\|)$. Additionally, because we are not interested in the specific locations of points but only in counting individuals within varying areas, for simplicity the integrals were calculated on squared regions.

For parsimony of parameters and to facilitate the comparison between models, in the following we focus on SNCPs in which the mean number of individuals per cluster is constant, so that μ in Eq. 9 is no longer a random variable but simply a constant. This process is equivalent to the (modified) Thomas model (Cressie 1993, Lawson and Denison 2002, Illian 2008) for which we derived the following species occupancy with the aid of Eq. 12:

$$P_{th}(A) = 1 - \exp \left\{ -\rho \int \left[1 - \exp \left(-\mu \int_A k(\|\vec{c} - \vec{x}\|) d\vec{x} \right) \right] d\vec{c} \right\} \tag{13}$$

where $k(\|\vec{x}\|)$ is an isotropic bivariate Gaussian distribution with variance σ^2 . The intensity of the process is $\alpha = \rho\mu$ and

$$g(r) = 1 + \frac{\exp\left(-\frac{r^2}{4\sigma^2}\right)}{4\pi\rho\sigma^2}.$$

Interestingly, the parameters of the model have an

intuitive meaning: cluster centers are scattered around with a characteristic pair distance $1/\sqrt{\rho}$; each cluster hosts μ individuals, on average, which form a fuzzy cloud of points whose characteristic size is σ .

Data

We analyzed an empirical data set of 16 British plant species using nested survey data spanning a spectrum of several orders of magnitude in unit cell sizes: from 40 000 km² to 10⁻⁶ km². These intensively surveyed vascular plant species were chosen from the set of British “rare” (those occupying 15 or fewer 10 × 10 km cells; (Wigginton 1999)) or “scarce” species (those occupying 16–100 such cells; (Stewart et al. 1994)), as such species often have exceptionally well-documented national distributions. Species were selected in order to provide a variety of different levels of aggregation at a national scale: paired species were selected sharing a common family but with one species in each pair showing an unusually clumped national distribution, while the other had an unusually sparsely scattered distribution. Intensive field studies were carried out on stratified random samples of these species’ British distributions (we refer to Hartley et al. [2004] for detailed protocols, sampling locations, map of the study region, and general considerations about the data), allowing species occupancies to be determined at 17 spatial resolutions: 40 000, 10 000, 2500, 400, 100, 25, 4, 1, 0.25, 0.04, 0.01, 0.0025, 0.0004, 0.0001, 0.000025, 0.000004, and 0.000001 km². However, for our model comparisons we only used the coarsest nine resolutions (down to 0.25 km²) because of the relatively coherent behavior of the cross-scale species’ aggregation over this range. Hartley et al. (2004) pinpointed an empirical discontinuity in the clumping intensity of species at ~0.25 km², which splits species occupancies into two domains in which different processes are deemed to be acting.

Model fitting and assessment

For each species we used maps at the three coarsest spatial resolutions (40 000, 10 000, and 2500 km² if these resolutions were neither saturated nor endemic; see also Fig. 1) to predict the occupancy through all of the finer resolutions down to areas four orders of magnitude smaller than the original ones (400, 100, 25, 4, 1, and 0.25 km²). As we have defined in the *Introduction*, the scale of saturation for a given species is the smallest grid cell for which the occupation probability is 1, whereas the scale of endemism corresponds to the smallest cell unit encompassing the entire population of a species (see Fig. 1). Thus, because saturated or endemic areas are useless for downscaling purposes, we fitted the models only to the coarsest unsaturated and non-endemic areas. As a result, models have to face two major challenges: the lack of information intrinsic to the coarse resolution and the curvature of the occupancy curve at large resolutions.

TABLE 1. For every species occupancy–area model tested, this table presents the value of $\Delta = \sum_k \Delta_k / S$ (where S is the total number of species and Δ_k is defined in Eq. 14) and the number of free parameters (np).

Model	Δ	np
Thomas (Eq. 13)	0.4815	3
Improved negative binomial (Eq. 4)	0.7089	3
CZK (Eq. 8)	0.9428	3
Finite negative binomial (Eq. 3)	1.0212	2
Nachman (Eq. 6)	1.0304	2
Negative binomial (Eq. 6)	1.0612	2
Power law (Eq. 5)	1.1892	2
Logistic (Eq. 7)	1.5482	2
Poisson (Eq. 1)	1.2487	1

Although spatially explicit occupancy data can always be deduced from similar data at relatively finer resolutions, we cannot do this if we only know the fraction of cells that are occupied (without knowing their explicit spatial location). Nevertheless, occupancy data at different resolutions cannot be considered statistically independent. This complicates the statistics of model-fitting, preventing a simple and direct estimation of the parameters by optimizing the log-likelihood function of the corresponding model. We therefore cannot express the log-likelihood function as a simple expansion at several resolutions, but instead chose to use an intuitive and easy-to-interpret approach that minimizes the mean of the squared log-errors for each species, i.e.,

$$\Delta_k^2 = \frac{1}{n} \sum_{i=1}^n (\log p_{i,k}^{\text{obs}} - \log p_{i,k}^{\text{pred}})^2 \quad (14)$$

where $p_{i,k}^{\text{obs}}$ and $p_{i,k}^{\text{pred}}$ are the observed and predicted occupancies at resolution i for species k , respectively, and n is the total number of resolutions used to train the model, in our case $n = 3$. The observed occupancy is calculated by choosing the species k , superimposing a regular grid of unit cells with area A ($i = 1, 2, \dots$ from the coarsest to the finest resolution), and finally taking the ratio of the occupied number of cells over the total number of cells. The predicted occupancies are those given by the models according to the equations defined in the previous section. Because Eq. 13 requires several numerical integrations to minimize Eq. 14, in order to achieve as robust a set of parameters as possible, we utilized a stochastic global optimization algorithm, specifically, simulated annealing (Bolker 2008), in the minimization protocol. This minimization with simulated annealing and all other numerical calculations were carried out using Mathematica 8 (Wolfram Research 2010).

When the parameters had been obtained, we used the models to predict occupancy at the six finer resolutions for which we had empirical data. Several diagnostic tools were used to assess model performances; specifically, $\Delta = \sum_k \Delta_k / S$ was used as an indicator of the global

performance across resolutions of each model in the log-transformed occupancies (S is the total number of species). We calculated the frequencies of $(\log p_{i,k}^{\text{obs}} - \log p_{i,k}^{\text{pred}})$ along with the standard deviation and skewness across resolutions and species; the tails of the distribution inform us about how many cases were given grossly inaccurate predictions. Finally, we compared the empirical and predicted log-transformed occupancies in order to assess the propagation of errors as the resolution increases.

RESULTS

The means of the squared log-transformed errors averaged across species for the different models are listed in Table 1. This measure allows one to examine the model performances across resolutions and species. As expected, models with more free parameters generally perform better than the others, the only exception being the (two-parameter) logistic model, which performed more poorly than the (one-parameter) Poisson model. The Thomas model performed substantially better on this aggregate measure than did any of the other models tested.

A finer description of model performances across resolutions and species is provided by the distributions of log errors, i.e., $(\log p_{i,k}^{\text{obs}} - \log p_{i,k}^{\text{pred}})$, which are plotted in Fig. 2. The Thomas model has the highest peak at zero with the smallest standard deviation; thus, when approaching the saturating region, it is able to extract enough information to generate the best downscaled predictions, on average. As shown by the negative skewness within the insets, the model tends globally to underestimate occupancies. The second-best model, the improved negative binomial, has a broader peak and, on average, its underestimation is more severe.

The increase of dispersion in predictions at increasing grid resolution is shown in Fig. 3, which illustrates the log-predicted vs. log-observed values for the models. The angle of dispersion is the smallest for the Thomas model, although for very fine resolutions there is a systematic underestimation of occupancies, which is common to all the other models except the power-law one (which tends to overestimate occupancy instead).

DISCUSSION

Stochastic processes that explicitly account for spatial features in general have the potential to improve the performances of models that assume well-mixed populations. The class of shot noise Cox processes (SNCP) is rich enough to encompass a wide suite of different spatial patterns. In the present study we have considered a very specific and simple case of SNCP, the Thomas model, and the results show that even this simplified model can produce substantially more precise estimates of fine-resolution species occupancy than can previously published approaches, over a spectrum of four orders of magnitude in spatial resolution.

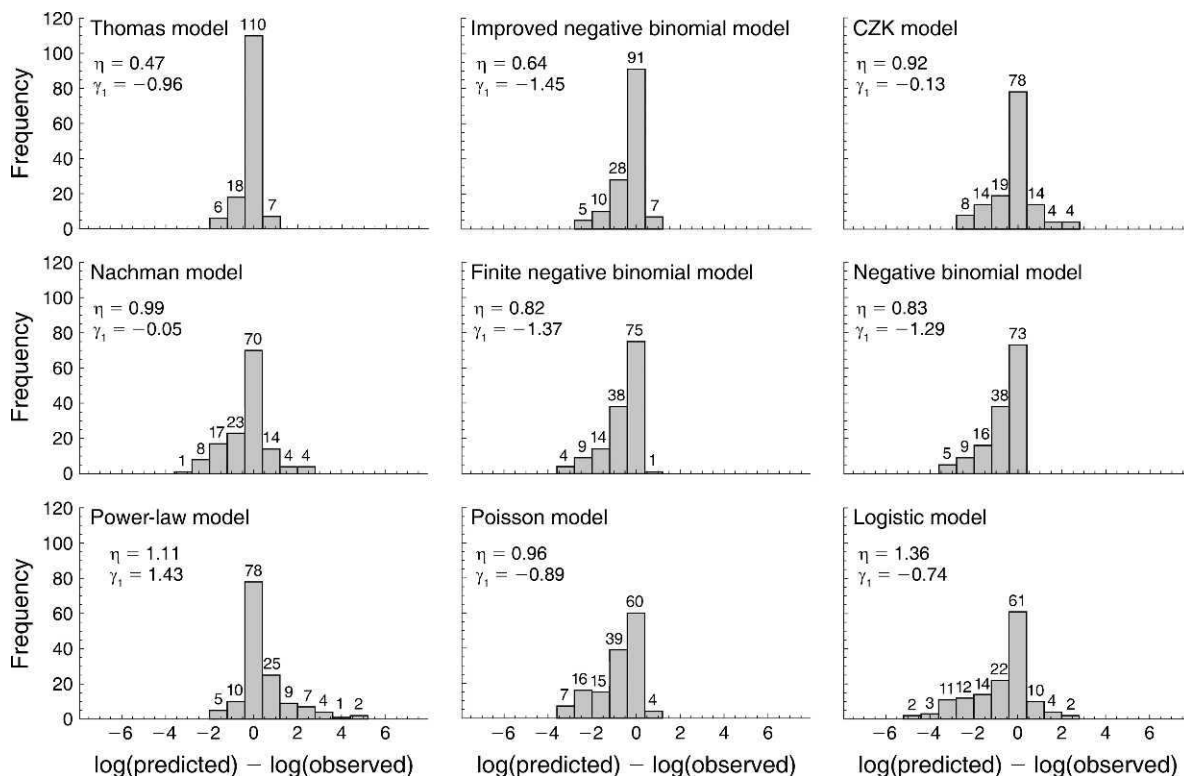


FIG. 2. Histograms representing the frequencies of $(\log p_{i,k}^{obs} - \log p_{i,k}^{pred})$ for every model (see Table 1 for the corresponding equations). The variables $p_{i,k}^{obs}$ and $p_{i,k}^{pred}$ are the observed and predicted occupancies at resolution i for species k , respectively, as defined in *Methods: Model fitting and assessment*. The insets have the standard deviation, η , and the skewness, γ_1 , for the corresponding model. The bin size is 0.8, and the number of predictions falling within each bin is written above every bin.

However, a general comment is in order. One should be cautious about trying to infer the relative superiority of a model from a specific test. In our analyses, we fit models to the three coarsest resolutions at which distributions had not yet saturated, but this condition of parameterization works variously across the models that we considered. Models, in fact, cope very differently with the lack of information close to the saturated region and this inevitably rebounds on downscaled occupancies. Fine-resolution predictions with strong biased estimates (i.e., with a substantial over- or underestimation of species' occupancies; see the skewness γ_1 in Fig. 2) or unbiased but imprecise values (see the standard deviation η in Fig. 2), therefore, cannot conclusively imply that we should get rid of poorly performing models. Had substantially finer resolutions been chosen to train the models, different predictions might have been obtained, thereby shuffling part of the list in Table 1. Rather, we can more soundly conclude that our test unveils which models cannot safely be applied when finite size effects are at stake and which other models, instead, are prone to be misled by relatively scarce or biased information.

In this respect, the Thomas model is able to provide satisfactory performances under conditions (presence of finite size effects within the training region, biased

information, species with very different spatial distributions, large downscaling, ...) that turn out to be prohibitive for other models, impairing their respective predictions. This is even more striking when highlighting the gross simplifications that we assumed in the model: translational and rotational invariance that are generally violated in natural populations; smoothed geometry of the study region; temporal stationarity; and a simple form for the pair correlation function. Had we employed more general, yet realistic, functions (e.g., see Azaele et al. 2009) for this latter, we would likely have obtained even more satisfactory results.

Fig. 2 highlights that overall the peak at zero is less informative than the elongation and asymmetry of the tails. For instance, the power-law model has a relatively high peak at zero, but a wild dispersion that includes predictions that are up to two orders of magnitude larger than the actual values. This proves that this model can be fruitfully applied only far from the saturating region. Besides, although the finite negative binomial model is theoretically more satisfactory, it improves upon the negative binomial model only slightly and the skewness toward underestimated occupancies is still systematic, presumably because the national scale analyses considered here are unlikely to be much affected by the finite size of species' populations. Fig.

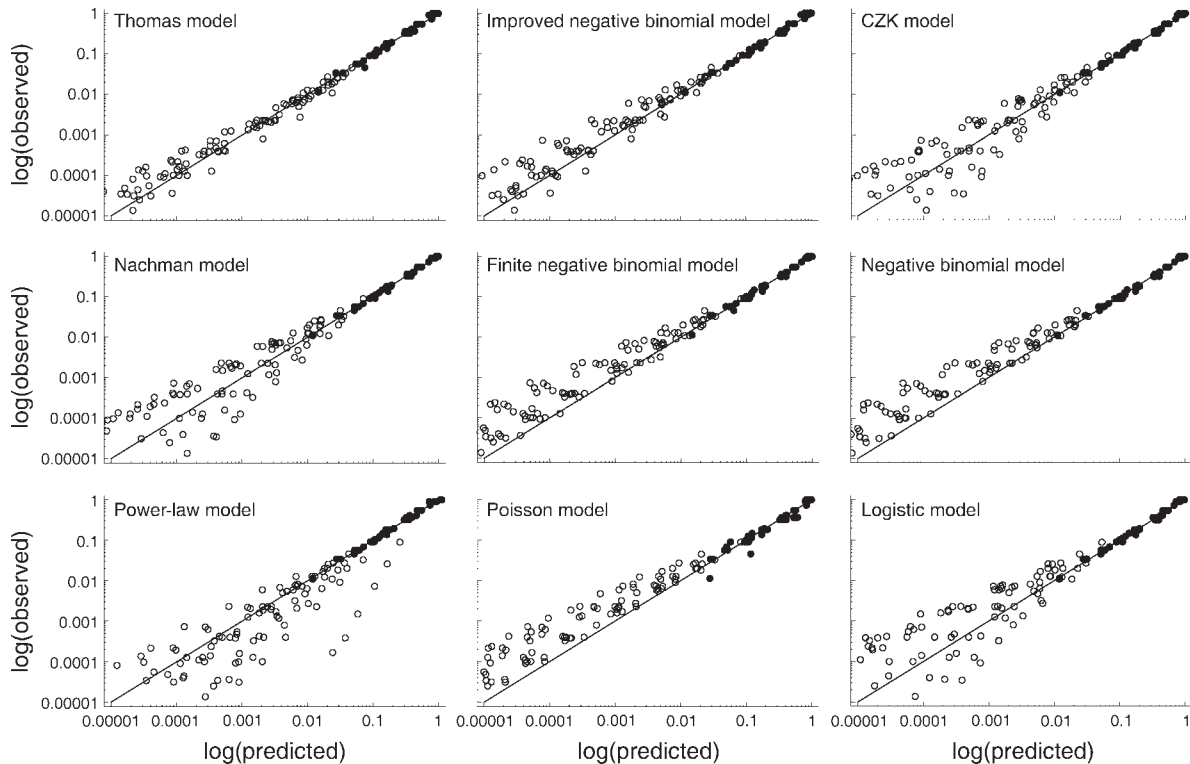


FIG. 3. Log-log plots of model-predicted vs. observed occupancies (see Table 1 for corresponding equations). Black circles represent the occupancy values that were used to parameterize the models; open circles are the actual predictions.

3 confirms that the improved negative binomial, finite negative binomial, negative binomial, and Poisson models on average underestimate occupancies at every resolution, whereas the power-law model is the only one that regularly overestimates, propagating errors within regions of completely unrealistic predictions. The power-law model is tantamount to a linear extrapolation (in log-log space) of the occupancy curve at the resolutions over which it is parameterized. As such it is very prone to being fooled by the sort of coarse resolution curvature alluded to previously.

Although the Thomas model produces the most precise downscaling estimates in our tests, it is worth noting that it is negatively biased in its predictions, a feature shared by almost all of the models tested. In contrast, other models, like Nachman's or CZK's, are nearly unbiased, but at the expense of substantially greater errors (approximately twice those of the Thomas model in the logarithmic scale), thus impairing the precision in the estimates. For these less biased, but less precise, models, it is likely that the performances would have been better under different (and probably less stringent) conditions in the parameterization of the models. On the other hand, more sophisticated SNCPs could have chosen to decrease the bias of the simple and naïve Thomas model. A further source of skewness toward an underestimation of occupancies may also come from a discontinuity present in species' distribu-

tions. We argue this because the area of the finest cell grid that we considered (0.25 km^2) is comparable to the characteristic scale of human land use in Britain, being the squared median size of an entire farm $\sim 0.24 \text{ km}^2$ (Hartley et al. 2004). If human activity disrupts natural ecological processes at such scales, one can plausibly expect a corresponding discontinuity in spatial distribution patterns that reverberates in empirical species occupancies as well. This is corroborated by the very different behaviors of these latter above and below the threshold of 0.25 km^2 , as documented by Hartley et al. (2004). Because of this discontinuity, we downscaled occupancies only to the resolutions of local populations; consequently, each point of the model can be thought of as representing a local population that may contain hundreds or thousands of individual plants. In more "natural" landscapes than the UK, it may be possible to downscale to even finer resolutions, potentially to individual counts.

In general we expect that models are more similar in their respective performances when used to downscale occupancies over only one or two orders of magnitude with respect to larger downscaling predictions. Nonetheless, spatial point processes naturally offer the advantage to infer properties of spatial patterns from measures where space is only implicit. With SNCPs, for instance, we can draw information about the spatial pair correlation function simply by using the occupancy

curve calculated for the model (see Eqs. 12 and 13). For the Thomas model, the pair correlation function is an isotropic bivariate Gaussian distribution with standard deviation σ , which provides a typical length for clusters as well. The present data set has no information regarding spatial correlation, but the parameters that we have obtained for the Thomas model suggest that species' correlation lengths approximately range from 3 to 30 km, and cluster-center pair distances range roughly from 70 to 640 km.

The Thomas model explains satisfactorily why species appear less aggregated at large resolutions than at small ones. On coarsening the resolution, the inner structure of clusters becomes progressively less important compared to the location of clusters, which are by construction Poisson distributed in space, and thereby genuinely unclustered. Interestingly, the model is amenable to further extensions that can explicitly deal with environmental heterogeneity. For instance, Waagepetersen (2007) introduces a vector of regression parameters in order to account for species' habitat preferences such as altitude or slopes. This supports the notion that niche models (which generally ignore spatial structure; Bahn and McGill 2007, Beale et al. 2008) and spatial scaling models (which generally ignore environment) can fruitfully be combined within the framework of SNCP.

Finally, the SNCP could be used to reverse the protocol and allow upscaling. One could parameterize the model by fitting the theoretical spatial correlation to the empirical one. Once it is calibrated at fine resolutions across multiple species, one could then predict the number of total species present inside the entire study region. Many different models have been proposed to upscale species richness from fine to coarse areas (see e.g., Ulrich and Ollik 2005, Shen and He 2008, Conlisk et al. 2009). This approach provides an alternative method, defined within a unified and coherent framework, that may complement such predictions.

The management of rare species (or conversely, of pest species), the monitoring of invasive aliens, as well as the design of appropriate conservation programs all need careful estimates of species' populations across space. However, it is often prohibitively expensive or logistically impractical to collect such data in a sufficiently intensive and extensive manner for reliable estimates over substantial areas. However, the relative ease of collecting species presence/absence data sets has resulted in increasing availability of such distributional data sets, over national or even continental extents. Downscaling techniques have the potential to form a link between easy-to-collect occupancy distributions and the population estimates necessary for management (e.g., Tosh et al. 2004, Sara 2008, Figueiredo and Grelle 2009, Veldtman et al. 2010). To do so will require models more accurate and reliable than those hitherto available. The model that we have studied provides several improvements over previous published approaches used for population downscaling, and thus

represents a substantial step toward realizing that ambition. It can be used to extract information about the spatial autocorrelation function of species, it is sufficiently flexible to accommodate spatial heterogeneities, and we have shown it to make more accurate downscaling predictions than other methods currently in use. However, extensive testing in other species sets and other regions would be needed before the predictions of this or any other model could be applied with confidence.

The advantage in using the SNCPs also rests on their ability to accommodate frameworks with nested complexity, so that simple models are special cases of more complex ones. This nested structure could turn out to be a valuable indicator of what is crucial to several predictions when varying the resolution, a further finding that could potentially prove useful in devising conservation strategies and reserve design.

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SUPPLEMENTAL MATERIAL

Appendix

Mathematical definitions and calculations showing how one can derive the generating functional (Eq. 12) of SNCPs (*Ecological Archives* A022-057-A1).