

RESEARCH ARTICLE

Fast evaluation of study designs for spatially explicit capture–recapture

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Abstract

1. Spatially explicit capture–recapture methods use data from the detection of marked animals at known points in space to estimate animal population density without bias from edge effects. Detection is by means of stationary devices such as traps, automatic cameras or DNA hair snags. Data collection is often expensive, and it is not obvious how to optimize the frequency of sampling and the spatial layout of detectors. Results from a pilot study may be extrapolated by simulation to predict the effectiveness of different configurations of multiple detectors, but simulation is slow and requires technical expertise.
2. Another approach for evaluating novel designs is to compute intermediate variables such as the expected number of detected individuals $E(n)$ and expected number of recapture events $E(r)$, and to seek relationships between these variables and quantities of interest such as precision and power.
3. We present formulae for the expected counts and power. For many scenarios the relative standard error (RSE) of estimated density is close to $1/\sqrt{\min\{E(n), E(r)\}}$, and for maximum precision $E(n) \approx E(r)$. We compare the approximation for $RSE(\hat{D})$ with more rigorous results from simulation.
4. Computation of $E(n)$ and $E(r)$ is deterministic and much faster than simulation, so it is readily included in interactive software for designing studies with enough power to answer ecological questions. The related approximation for $RSE(\hat{D})$ is adequate for many purposes.

KEYWORDS

capture–recapture, density estimation, power analysis, precision, SCR, SECR, study design, trap spacing

1 | INTRODUCTION

Spatially explicit capture–recapture (SECR or SCR) is a set of methods for estimating animal population density with data from an array of passive detectors (Borchers & Efford, 2008; Efford, 2004; Efford, Borchers, & Byrom, 2009; Royle, Chandler, Sollmann, & Gardner, 2014). Unbiased estimates of population density may be obtained with a rich variety of detector configurations – putting aside

potential bias with linear configurations (Efford, 2019a) – and the method has been applied *post hoc* to many different datasets. The robustness of SECR shifts the focus of study design from avoiding bias to maximizing precision (Efford, Warburton, Coleman, & Barker, 2005). Many applications have yielded estimates with inadequate precision, and it is time to consider how this can be avoided.

A dataset for SECR comprises a set of detection histories, one for each detected individual, and the known locations of the detectors.

A detection history records the number of detections of an individual at each detector on each sampling occasion, and possibly other information associated with each detection. Procedures for the analysis of such data by maximum likelihood or Bayesian approaches are now well established (Borchers & Efford, 2008; Borchers & Fewster, 2016; Efford et al., 2009; Royle et al., 2014; Royle & Young, 2008). We use maximum likelihood in our simulations, but the same design considerations apply when Bayesian analyses are used. Our focus is on demographically closed populations and the estimation of population density; other considerations come into play for the estimation of survival, recruitment and movement in models for open populations.

The relative efficiency of detector configurations for SECR has been assessed by simulation for black bear *Ursus americanus* (Clark, 2019; Sollmann, Gardner, & Belant, 2012; Sun, Fuller, & Royle, 2014) and a few other species (Kristensen & Kovach, 2018; Tobler & Powell, 2013). Datasets are generated stochastically from the parameterized probability models for spatial distribution and the detection process, and estimates are obtained from each dataset by the chosen analysis method. Precision is measured by the average over replicates of the estimated relative standard error $\widehat{RSE}(\hat{D}) = \widehat{SE}(\hat{D})/\hat{D}$, sometimes denoted $CV(\hat{D})$. Simulation is feasible because the detection model in SECR is modular and scalable: the model describes the probability of detecting a particular individual in a particular detector, and data for populations and arbitrary detector arrays are extrapolated from the individual-based model.

Simulation can be laborious because model fitting is computer-intensive and inference requires multiple replicates. Formal analysis of the SECR model for the prediction of precision has not been attempted and may be intractable. However, we show in this paper that important properties of a spatial capture–recapture design, the expected numbers of unique individuals and recaptures, may be computed deterministically from pilot estimates of the parameters, without recourse to simulation. We demonstrate that the expected numbers are in turn highly predictive of the precision of SECR estimates. This approach enables fast comparison of candidate study designs in freely available software (Efford, 2019b, 2019c).

2 | MATERIALS AND METHODS

SECR combines a model for the spatial distribution of individuals (the population model) and a model for the spatial detection process (primarily a radial decline in detection probability with distance). Each submodel contributes to the sampling variance of density estimates.

2.1 | Population model

The population is conceived as a spatial point process; each animal is represented by a unique and persistent point, nominally its ‘activity centre’. The intensity of the point process is the density of the population. The intensity may vary over space, leading to an inhomogeneous model for the expected density $D(\mathbf{x})$ where \mathbf{x} represents a point in two dimensions.

A random uniform distribution of animals corresponds to a Poisson spatial point process. In the pure Poisson model, the population extends indefinitely in all directions. Only animals near the detectors are likely to be detected and, for well-behaved detection functions that decline rapidly towards zero, the number of detected animals n is a Poisson random variable.

Descriptions of SECR commonly focus on a fixed number of individuals N distributed uniformly in a region A (i.e. a binomial spatial point process). Fixing the number of individuals in A is equivalent to considering one realization of the Poisson model (e.g. Efford & Fewster, 2013). For fixed N the number of detected animals is a binomial random variable with size N , which is convenient for Bayesian analyses using data augmentation (Royle et al., 2014). The choice between the binomial and Poisson spatial point processes (and hence between binomial and Poisson n) otherwise depends on the sampling context and is not addressed here. Density estimates are identical or nearly so under the two models, but the binomial model has lower sampling variance. The difference in RSE^2 is shown in Appendix S1 to depend only on $E(N) = DA$ for uniform density D . Thus, given a value for precision under the Poisson model $RSE_P \equiv \sqrt{\text{var}_P(\hat{D})/\hat{D}}$, the binomial-model precision is $RSE_B = \sqrt{RSE_P^2 - 1/(DA)}$.

2.2 | Detection model

We assume detections have been made at K detectors on S occasions (sampling intervals), and that the hazard of detection in detector k for an animal centred at \mathbf{x} depends on the distance $d_k(\mathbf{x})$. The form of the relationship is not critical – a half-normal relationship is commonly assumed i.e. $\lambda(d_k(\mathbf{x})) = \lambda_0 \exp[-d_k(\mathbf{x})^2/(2\sigma^2)]$ where λ_0 and σ are parameters. It is convenient to formulate the detection process in terms of hazard $\lambda(d)$ rather than probability $g(d)$, but the two are interchangeable ($g(d_k(\mathbf{x})) = 1 - \exp[-\lambda(d_k(\mathbf{x}))]$).

SECR models accommodate variation in detection probability with respect to individual (i), time (j) or detector (k), but we suppress these for notational simplicity, and hence $\lambda_0(ijk) = \lambda_0$ and $\sigma(ijk) = \sigma$ for all i, j, k . Detector arrays may be of almost any shape and the spacing between detectors need not be uniform.

2.3 | Detector types

We distinguish four detector types that use a sampling device at a point. Each type implies a different process of interaction among animals and detectors, and hence different possible detection histories (Efford et al., 2009; Table 1). We use ‘trap’ specifically for a device that detains an animal once caught; an animal therefore may be detected only once on any occasion. Traps may be either exclusive (‘single-catch’) or allow the simultaneous capture of multiple animals (‘multi-catch’). Modelling of data from multi-catch traps uses a competing risk model (Borchers & Efford, 2008). Probability modelling of single-catch trap arrays is intractable. It is usually adequate to treat data from single-catch traps as if they came from multi-catch traps. Proximity detectors do not detain the animals they detect, so any animal may be detected at multiple detectors on one occasion. Repeated visits of an

TABLE 1 Point detector types for SECR

Detector type	secr	Royle	Data
Single-catch trap	single	—	Binary animal \times occasion, exclusive
Multi-catch trap	multi	Multinomial	Binary animal \times occasion
Binary proximity	proximity	Bernoulli	Binary animal \times occasion \times detector
Count proximity	count	Poisson	Integer animal \times occasion \times detector

Notes: 'secr' is the name used for the detector type in the software **secr** (Efford, 2019b). 'Royle' is the corresponding model of Royle et al. (2014: Chap. 9). Single-catch traps are 'exclusive' in the sense that capture of an animal by one trap excludes the possibility of capture in other traps on the same occasion; there is no simple probability model for such data (—).

animal to a single detector within an occasion may be indistinguishable or treated as such, to give a single binary observation, or they may be recorded and modelled as an integer count. Counts are typically treated as Poisson-distributed.

3 | EXPECTED SAMPLE SIZE

This section introduces quantities derived from the parameterized SECR model that are used later. We define the quantity $\Lambda_s(\mathbf{x}) \equiv \sum_k \lambda(d_k(\mathbf{x}))$ for the cumulative hazard of detection on occasion s of an individual centered at \mathbf{x} . Aggregating over occasions gives $\Lambda(\mathbf{x}) = \sum_s \Lambda_s(\mathbf{x})$. If all potential detections are recorded then $\Lambda_s(\mathbf{x})$ is the expected total number of detections on one occasion for an animal centred at \mathbf{x} . Only Poisson 'count' detectors are assumed to act like this. Nevertheless, $\Lambda_s(\mathbf{x})$ is useful for predicting the outcome for binary detector types as we show next. Formulae for the expected number of movements (spatial recaptures) are in Appendix S2. Single-catch traps are a special case for which there are not closed-form expressions for $E(n)$ and $E(r)$.

3.1 | Expected number of individuals detected

The probability an individual is detected at least once follows directly as one minus the zero term of a Poisson distribution with parameter equal to the hazard aggregated across all times and detectors. This quantity depends on location \mathbf{x} and, in general, so does density $D(\mathbf{x})$; their product represents the contribution of \mathbf{x} to the expected number of individuals. We obtain the expected number of individuals detected at least once by integrating the product across \mathbf{x} :

$$E(n) = \int [1 - \exp\{-\Lambda(\mathbf{x})\}] \times D(\mathbf{x}) d\mathbf{x}.$$

Integration is over all locations in the plane from which an individual might be detected. The expected number is the same for all detector types in which individuals are detected independently of each other (multi-catch traps and binary or count proximity detectors).

3.2 | Expected number of recaptures

The total number of detections C depends on the detector type, as follows. For the simplest case of Poisson counts, logic similar to that in the preceding section gives

$$E(C) = \int \Lambda(\mathbf{x}) \times D(\mathbf{x}) d\mathbf{x}.$$

Data from multi-catch traps are binary at the level of each animal \times occasion, with Bernoulli probability $p_s = 1 - \exp\{-\Lambda_s(\mathbf{x})\}$. This leads to the overall number of detections:

$$E(C) = \int \sum_s p_s(\mathbf{x}) \times D(\mathbf{x}) d\mathbf{x}.$$

Data from binary proximity detectors are binary at the level of each animal \times detector \times occasion, with Bernoulli probability $p_{ks}(\mathbf{x}) = 1 - \exp\{-\lambda(d_k(\mathbf{x}))\}$. This leads to the overall number of detections

$$E(C) = \int \sum_s \sum_k p_{ks}(\mathbf{x}) \times D(\mathbf{x}) d\mathbf{x}.$$

We define a recapture as any detection other than the first. For all detector types the expected number of recaptures is simply $E(r) = E(C) - E(n)$.

4 | SAMPLING VARIANCE

The sampling variance of maximum likelihood estimates (MLE) of density is routinely estimated from the curvature of the likelihood surface evaluated numerically on the log scale at the MLE (Borchers & Efford, 2008). Technically, this uses the inverse of the information matrix and is theoretically exact for large samples. Sampling variance V on the log scale is related to $RSE(\hat{D})$ on the natural scale by $\widehat{RSE}(\hat{D}) = \sqrt{\exp(\hat{V}) - 1}$. V is the more fundamental quantity, but it is more intuitive to work with RSE on the natural scale.

4.1 | Required $RSE(\hat{D})$

It is critical that a sampling design should yield enough data to answer the question being asked, i.e. that it will have sufficient statistical power. We focus on the ratio of population densities in two independent surveys. This is an important general case for which knowledge of $RSE(\hat{D})$ is sufficient to determine power (power estimates for trend across multiple samples must also allow for stochastic variation in the population process).

The power is a function of the effect size (D_2/D_1) and the precision of the estimates, expressed as RSE , assuming log-normal errors in both the initial and final surveys. Formulae for power ($1 - \text{probability of Type II error}$) are given in Appendix S3. We relate power to the precision of the initial estimate $RSE(\hat{D}_1)$. If sampling effort is constant and density changes then the expected sample size will also change. Specifically, if the population declines then fewer animals will probably be detected in the final survey and the relative precision of the estimate will be reduced, lowering the power of any comparison. Although this is outside the control of the researcher, it is a direct function of the effect size and may be allowed for in the power calculation by routinely adjusting RSE for the final survey by the factor $\sqrt{D_1/D_2}$ that predicts the change in $E(n)$ and $E(r)$. This is the only part of our power analysis that is specific to SECR. Power is plotted against effect size for two levels of $RSE(\hat{D})$ in Figure 1.

4.2 | Prediction of $RSE(\hat{D})$ for novel sampling regimes

Monte Carlo simulation that obtains the MLE for each generated dataset is the gold standard for predicting $RSE(\hat{D})$. An alternative is to numerically estimate the information matrix for each simulated dataset at the known parameter values, rather than at their MLE; this is substantially faster, but still requires multiple evaluations of the likelihood. We suggest a much faster two-part approximation for $RSE_p(\hat{D})$. Firstly, Poisson variation in n sets a floor to $RSE_p(\hat{D})$ of $1/\sqrt{n}$ (the CV of a Poisson distribution). Secondly, the precision of capture–recapture estimates conditional on n varies with the number of recaptures. That relationship is direct for the modified Lincoln–Petersen closed population estimate: $RSE(\hat{N}) \approx 1/\sqrt{E(r)}$ (Seber, 1982, p. 60). For Poisson-distributed n our proposed approximation is

$$rse_p(\hat{D}) = 1/\sqrt{\min\{E(n), E(r)\}}. \quad (1)$$

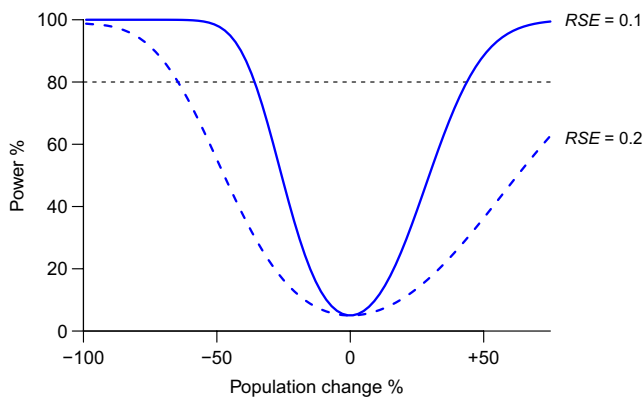


FIGURE 1 Power of a two-sided test ($\alpha = 0.05$) to detect a change in density between two surveys as a function of effect size ($(D_2/D_1 - 1) \times 100$ on the x axis) for two levels of precision in the initial survey, $RSE(\hat{D}_1)$. Precision of the final estimate is scaled for the expected change in sample size $RSE(\hat{D}_2) = RSE(\hat{D}_1)\sqrt{D_1/D_2}$. See Appendix S3 for calculation

The corresponding approximation for binomial n in area A is $rse_B = \sqrt{rse_p^2 - 1/(DA)}$. The approximation is compared to simulated values for some spacing scenarios in Figure 2. Appendix S4 gives details of these simulations. The approximation was broadly unbiased for square grids of binary proximity detectors (Figure 2). Discrepancies were greatest in scenarios with inadequate grid size that would in any case be rejected for excessive bias, and in scenarios with simulated $RSE_p(\hat{D}) > 20\%$. The approximation showed a nearly linear convex-up relationship with detector spacing for large spacings ($E(r) > E(n)$), whereas simulated $RSE_p(\hat{D})$ was concave-up over this range (Figure 2, Appendix S4, Figure S3a). The approximation underestimated $RSE_p(\hat{D})$ by about 25% when the detector array was linear (Appendix S4). Computation of the approximation was more than 200 times faster than efficient simulation using the information matrix at known parameter values and only 20 replicates (Appendix S4).

5 | SOFTWARE

Software has been developed in R (R Core Team, 2019) to perform the preceding calculations and simulation for detectors of common SECR types in many configurations (R package ‘SECRDESIGN’; Efford, 2019b). The R functions may be run interactively in the web-based application ‘SECRDESIGNAPP’ (Efford, 2019c). The web-based application also enables one-click simulation to check the approximation and estimate an optional correction factor; graphical outputs include the spatial distribution of detection probability and interactive plots of statistical power as described in Appendix S3.

6 | DISCUSSION

The great majority of published SECR analyses have enough statistical power to detect only gross population differences. The commonly cited target of $RSE(\hat{D}) < 20\%$ provides an 80% probability of rejecting the hypothesis of no difference at $p < 0.05$ only for decline of $>64\%$ and increase of $>96\%$ in a 2-sided test (Figure 1, Appendix S3). The tools provided here should encourage greater ambition.

Some designs are categorically inappropriate because they are poorly matched to the spatial behaviour of the target species and result in biased estimates even when the fitted model corresponds to the model used to generate the data. We label these designs ‘pathological’. Pathology is due primarily to inadequate extent of the detector array (significantly less than one home range; Efford, 2011; Sollmann et al., 2012; Tobler & Powell, 2013) or extreme detector spacing (leading to few or no spatial recaptures). Non-pathological designs give unbiased estimates, but within the set of non-pathological designs the precision achieved for a given sampling effort varies widely. The precision of density estimates from a particular sampling design may be predicted from the expected sample sizes, which are a deterministic outcome of the design and a parameterized model.

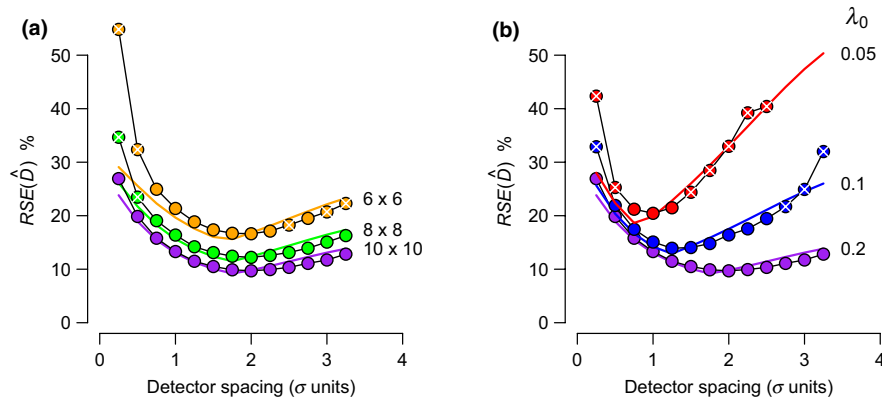


FIGURE 2 Approximation for precision of SECR density estimates $RSE(\hat{D})$ (solid lines) compared to simulated precision (points) for square grids over a range of detector spacings expressed in units of the half-normal scale of detection, σ . (a) varying grid size, constant sampling intensity $\lambda_0 = 0.2$, (b) constant grid size 10×10 , varying λ_0 . Simulated scenarios with relative bias of density estimate $> 5\%$ marked with white \times . Density $0.4\sigma^{-2}$, 5 sampling occasions. See Appendix S4 for further details and numerical results. The approximation is reliable for a broad range of spacings around the optimum

There is no merit in pathological designs, which invariably also yield poor precision. It is therefore desirable, if not strictly necessary, to remove obviously pathological designs from the set under consideration. If this is merely a step towards optimizing for precision then the criteria need not be precise. The bias criterion used in our definition is unwieldy because it requires simulation, so we suggest using ad hoc criteria. Inadequate extent is likely to cause bias when the area or diameter of the array is less than the matching metric of the average home range (references above). Extreme detector spacing may be diagnosed from the expected number of spatial recaptures (Appendix S2); we suggest rejecting designs for which that number is 5 or less (this may also eliminate some designs with adequate spacing but inadequate duration or detection rate).

6.1 | Approximation for $RSE_p(\hat{D})$

The approximation appears reliable for two-dimensional designs such as grids of binary proximity detectors when $RSE_p(\hat{D}) < 20\%$ (Figure 2). The approximate RSE is compared in Appendix S5 to simulated values from the numerous and varied scenarios of Kristensen and Kovach (2018) and Clark (2019). Discrepancies were small except in scenarios for which inadequate sample size led to convergence problems (Kristensen & Kovach, 2018) or inadequate cluster size caused bias (Clark, 2019). SECR methods should not be used with such data.

The approximation is an underestimate when the design is linear (Appendix S4, Figure S4) and shows a moderate bias for greater-than-optimum grid spacings, especially with multi-catch traps (Appendix S4). Future investigation of these and other systematic deviations between the simulated and approximate RSE may lead to an approximation that improves on Equation (1). Models with additional detection parameters may sometimes be needed to avoid bias due to learned responses, individual heterogeneity etc.; some loss of precision is to be expected, especially when such models are averaged, with correct accounting for model uncertainty.

Our results are for a population of animals distributed uniformly and independently of each other. Clustering of activity centres or unmodelled spatial variation in density will result in overdispersion; the sampling variance from a uniform Poisson model then underestimates the true sampling variance, with flow-on effects on $RSE(\hat{D})$ and confidence interval coverage. The effect can be severe in highly clustered populations, as we illustrate by simulation in Appendix S4. Our approximation takes no account of overdispersion and will underestimate true $RSE(\hat{D})$, while matching estimates from the incorrect, uniform model. If overdispersion is expected at the design stage then a more conservative (lower) target should be set for $RSE(\hat{D})$. The potential effect of overdispersion on $RSE(\hat{D})$ may be assessed by simulating clustered distributions. Adjustment for overdispersion in SECR models is an important topic for future research.

Expected sample sizes (n , r) scale directly with density when detections are independent ('multi', 'proximity' and 'count' detectors), and rse_p consequently scales with $1/\sqrt{D}$ for these detector types. This does not apply exactly for single-catch traps as trap saturation at high density suppresses capture probability and sample size.

6.2 | Optimum detector spacing

One component of Equation (1) is an increasing function of detector spacing ($E(n)$), while the other is a decreasing function ($E(r)$). This is a quantitative description of phenomena that have been well understood at a qualitative level: wide spacing results in few recaptures (and especially few movement recaptures), while a fixed number of detectors placed close together detects few individuals (e.g. Sollmann et al., 2012).

The minimum of rse_p occurs when the curves intersect at $E(n) = E(r)$ and the 'average' animal is detected twice. It is thus easy to determine an optimum spacing numerically, assuming that the approximation is reliable and ignoring external factors such as travel costs. Switching to a binomial model for n does not change the optimum spacing, nor does any adjustment by a constant factor.

The optimal spacing is commonly in the range 1–3 σ for a half-normal detection function with scale parameter σ , as found by previous authors (e.g. Clark, 2019; Royle et al., 2017; Sun et al., 2014). However, when the sampling intensity is low (low g_0 or λ_0 , few sampling occasions, or linear configuration) the optimal spacing may be less than σ (Figure 2b) as also noted by Kristensen and Kovach (2018). Some authors (e.g. Otis, Burnham, White, & Anderson, 1978) have suggested aiming for a certain number of detectors per home range, but this ignores the effect of sampling intensity on optimal spacing.

6.3 | Clustered detectors

Modular sampling with small clusters of detectors is an effective option for representative sampling of a large region (Clark, 2019; Efford & Fewster, 2013; Efford et al., 2005; Sun et al., 2014). The optimum within-cluster spacing for a collection of similar clusters is the same as for one cluster as long as clusters are independent (widely spaced). As a result, (a) $E(n)$ and $E(r)$ both scale with the number of clusters, (b) the within-cluster spacing at which $E(n) = E(r)$ does not change, and (c) rse_p scales with $1/\sqrt{c}$ where c is the number of clusters. For a given cluster size with cluster-level precision $RSE_p(\hat{D}_1)$, the precision for an estimate of density D in a specified region with area A is $RSE_B(\hat{D}) \approx \sqrt{RSE_p(\hat{D}_1)^2/c - 1/(DA)}$, allowing c to be chosen to yield the required precision. Each cluster should be large enough to span a home range to avoid the risk of bias. Once that criterion is met, the optimum cluster size for a specified total effort is subject to trade-offs. Many small clusters maximizes $E(n)$ while fewer large clusters maximizes $E(r)$; the optimum allocation depends on which is most limiting for precision, itself a function of density and detection parameters, and on travel costs. These factors are study-specific. The impact of cluster number and cluster size on precision and cost may be explored in software (Efford, 2019b, 2019c) using the approximation in Equation (1) to narrow the set of candidate designs, followed by simulation for confirmation. We emphasize the need for rigorous spatial sampling, such as a random systematic sample of cluster locations.

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AUTHORS' CONTRIBUTIONS

M.G.E. and J.B. conceived the work. M.G.E. performed the simulations. M.G.E. and J.B. wrote the paper.

DATA AVAILABILITY STATEMENT

R code and simulation output are available at Zenodo <https://doi.org/10.5281/zenodo.3239532>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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