Estimating extinction from species–area relationships: why the numbers do not add up

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Abstract. Researchers commonly use species–area relationships (SAR) to estimate extinction rates caused by habitat loss by reversing the SAR, extrapolating backward from area to calculate expected species loss. We have previously shown that the backward SAR method considerably overestimates extinction rates due to a previously unrecognized sampling artifact. Jacob Bock Axelsen, Uri Roll, Lewi Stone, and Andrew Solow recently argued that the backward SAR method is correct and the method does not overestimate extinction rates. In this paper, we further elaborate and clarify our previous results. We show that the backward SAR method gives the correct extinction rate only under a strict complementary-area sampling design, which is not used in practice because it requires knowing which species are endemic to the area of destroyed habitat, or the number of species in the complementary area. Because of this problem, researchers substitute a power-law model for the SAR in the backward SAR equation. However, this substitution violates the backward SAR method's requirement for complementary sampling. With this model substitution, the backward SAR equation is no longer correct, except in the special case of randomly distributed species. For the complementary sampling or random distribution of species, the first individual of a species to be encountered and the last individual to be encountered to lose the species are exchangeable (or the same individual). But this is not the case for other sampling designs or if species are not randomly distributed and explains why the backward SAR method fails to correctly estimate extinction rates. Our proofs and results are general and explain the widely recognized overestimation of extinction by the backward SAR method. We suggest future directions for developing general theory for estimating species extinction from species–area relationships. Until then, however, the backward SAR method should not be used to estimate species extinction in practice.

Key words: *conservation biology; endemics–area relationship; extinction; Pasoh Nature Reserve, Malaysia; power-law model; species–area relationships (SAR).*

INTRODUCTION

No other macroecological patterns have played a more important role in describing and understanding species distributions in space than species–area relationships (SAR). Because of its spatial character, the SAR is widely used as a tool for assessing the impact of disturbances and landscape fragmentation on biological communities (Lawrey 1991, Cannon et al. 1998, Brown and Gurevitch 2004, Tittensor et al. 2007, Powell et al. 2013) and for estimating the loss of species caused by habitat destruction and changes in climate and land use (Simberloff 1992, Pimm et al. 1995, Thomas et al. 2004, Pereira et al. 2010). Underlying these applications are two forms of biotic relaxation derived from the SAR.

One is "weak" relaxation, in which landscape disturbance and fragmentation change the slope of species–area relationships, often making the SAR slope steeper than before disturbance. In this case, the change in slope does not necessarily suggest a loss of species. If the spatial distributions of species become more localized after disturbance, or the relative species–abundance distribution becomes more skewed, the slope of SAR will become steeper (Bazzaz 1975, He and Legendre 2002). This weaker form of biotic relaxation is generated by reassembling the species (i.e., reorganization of spatial and abundance patterns) when a formerly intact landscape becomes fragmented as it approaches a new equilibrium.

The literature usually refers to "strong" biotic relaxation, i.e., the decline in the number of species over time when a formerly intact landscape becomes fragmented or disturbed and approaches a new equilibrium. However, we have recently shown that the
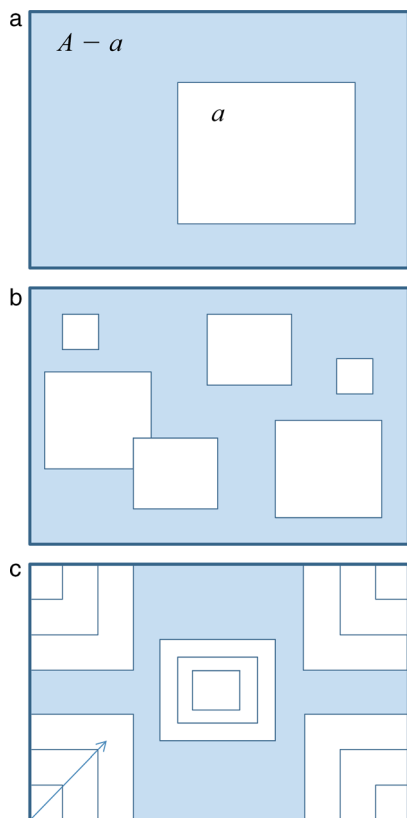
Fig. 1. Three sampling designs for constructing species–area relationships. A is the area of the region, and a is the subarea within A. (a) The complementary sampling to which Eq. 1 applies. In this case, the species–area relationship constructed from the complementary area $A - a$ can be used to predict the endemics–area relationship in panel (a). (b) The non-nested sampling design that produces the species–area relationship by taking samples throughout the region. The sampling areas may or may not be overlapping. In this study, for a given size of a sampling quadrat, 100–3500 quadrats were sampled depending on the size of the quadrats. (c) The nested sampling design that accumulates species by progressively increasing the nested sampling areas. In this study, we considered nested sampling from the four corners and the center and used the average of these five nested samples to represent the species–area and endemics–area relationships for the whole area, but other nested designs could be used.

dynamics of strong biotic relaxation has nothing to do with, and cannot be properly estimated from, species–area relationships. One can use the species–area relationship to estimate the immediate loss of species at the time of habitat destruction, not the future equilibrium number of species (He and Hubbell 2011). The method for estimating immediate species extinction caused by habitat loss is based on the following general formula (He and Hubbell 2011, 2012; see Fig. 1a):

$$EAR(a) = S - SAR(A - a) \qquad (1)$$

where $EAR(a)$ is the number of species endemic to subarea a that is located within the regional area A, S is

the total number of species in the region, $SAR(A - a)$ is the number of species in the complementary area $A - a$. Because of this complementarity, this method is commonly called the backward SAR method. It is obvious that Eq. 1 is a method for estimating imminent extinction (i.e., the loss of endemic species), not the "extinction debt" of species that are committed to extinction as the disturbed system approaches a new equilibrium.

Ideally, it would be best to estimate imminent extinction directly by using the endemics–area relationship, $EAR(a)$. However, this can seldom be done because the construction of the $EAR(a)$ requires data on the global distribution of species, and such data are rarely available. Instead, researchers typically use the complementary species–area relationship, $SAR(A - a)$, to estimate imminent extinction. But again, because the global distribution of species in the complementary area is also not known, researchers then take a crucial step and insert a *model* of $SAR(A - a)$ into Eq. 1. Almost universally, the inserted model is the power-law model. However, we have shown that species extinction is overestimated when using this backward method, i.e., $S - SAR(A - a) \geq EAR(a)$ when the power-law SAR model (or other models) is substituted for $SAR(A - a)$. The equal sign holds only when all species are randomly distributed (He and Hubbell 2011). This result is apparently not consistent with the prediction of Eq. 1 that, by definition, must be true. Axelsen et al. (2013) argue that Eq. 1 must be true regardless of the spatial distribution of species, and thus species–area relationships can be used to estimate extinction rates. We don't disagree that Eq. 1 is true by definition. We make that point in the appendix of He and Hubbell (2011) and He and Hubbell (2012). The reason the problem with the backward SAR method has been so elusive and controversial is that most people have not realized that the forward species–area relationship $SAR(a)$ and the backward $SAR(A - a)$ are not consistent in real-world applications. The quantities $SAR(a)$ and $SAR(A - a)$ do not measure the SAR of the same spatial distributions of species once a specific SAR model (e.g., the power-law SAR or any other SAR model) is substituted into the generic Eq. 1. The substitution in Eq. 1, by inverting the forward SAR of a specific model, destroys the equality in the original equation except under the very special case of randomly distributed species. The unappreciated effect of this functional substitution is why the numbers in Eq. 1 do not add up in real-world applications. Conservation biologists need to understand this problem fully to appreciate the overestimation problem and to find correct methods for estimating imminent extinction due to habitat loss.

It is easy to demonstrate, from simulated or empirical data, that the number of endemic species in a ($EAR(a)$ in Eq. 1) is correctly predicted from the complementary species–area relationship, $SAR(A - a)$ (see *Results*). But, this is only true if $EAR(a)$ is calculated from the species–

area relationship constructed exclusively from the complementary area $A - a$, or the other way around (i.e., to predict the endemic species in area $A - a$ from the SAR constructed exclusively from area a). In practice, however, this complementary-area sampling design is a very specific and extremely difficult sampling design to implement. Note that as the relative sizes of areas $A - a$ and a change, this method requires essentially as much information about species' distributions as a complete global map of the ranges of every species. Presumably this is why this method has never been used to estimate extinction rates in practice. Researchers invariably substitute the power-law SAR model into Eq. 1 for SAR($A - a$), and herein lies the problem that we addressed in He and Hubbell (2011). This is not a problem with Eq. 1, but with the use of the power-law SAR (or any empirical SAR models) substitution in Eq. 1 to estimate the number of endemic species in area a (i.e., those species immediately lost when habitat a is destroyed).

In real-world applications, the power-law SAR (Connor and McCoy 1979, Palmer and White 1994, Crawley and Harral 2001, Drakare et al. 2006, Storch et al. 2012) is used to estimate species extinction in *any* area within the landscape from which the SAR is constructed. The sampling designs typically used (either nested or not) violate the requirement that sampling areas are complementary, as implied by Eq. 1. The backward power-law SAR method using sampling schemes other than the complementary sampling overestimates species extinction and the overestimation becomes worse with increasing spatial aggregation of the distributions of individual species (He and Hubbell 2011). This is so because the sampling procedure for encountering a species is different from that of losing a species. As we prove in He and Hubbell (2011), the expected area needed to encounter the first individual of a species (a^1) is much smaller than the expected area to encounter the last individual of the species (a^N), and for aggregated species their sum is smaller than the total area of the region ($a^1 + a^N < A$). Only for randomly distributed species is it true that $a^1 + a^N = A$. In this random case, EAR(a) and SAR($A - a$) form a mirror image relationship and Eq. 1 is valid regardless of sampling design. It is important to note the equality $a^1 + a^N = A$ universally holds for the complementary sampling design because in such sampling the first individual in forward sampling becomes the last individual in backward sampling. In other words, the first individual and the last individual are exchangeable (i.e., the same individual) in the complementary sampling, but this is not true for any non-complementary sampling designs. For example, in the nested sampling, after the first individual being encountered, we will expand the sampling area to continue to search for the last individual of the species. The first and last individuals are not the same individual. This difference in sampling design is crucial for understanding why the backward

method in Eq. 1 overestimates extinction in real-world applications. Our results are general and correctly explain the widely recognized overestimation of extinction by the backward SAR method. Here, we implement simulations to further illustrate the generality of our results. Such a test was not presented in He and Hubbell (2011) but could facilitate greater understanding of our theoretical analysis.

METHODS

For the simulation, we used the data from the 50-ha (1000×500 m) stem-mapped plot of a lowland tropical rainforest in the Pasoh Nature Reserve of Malaysia (see the Supplement for the simulation program and the abundance data). The Pasoh plot has 814 tree species and 323 262 stems (He and Hubbell 2011). The most abundant species has 8671 individuals and there are 27 singleton species. In our simulation, we held the abundance of each species at its observed value but varied the degree of spatial aggregation of each species from random to moderately aggregated to highly aggregated. We generated the spatial distributions by the Thomas process using function rThomas in R package spatstat (Baddeley and Turner 2005). rThomas has three parameters: kappa, mu, and sigma. The first two parameters define the number of clusters and the expected number of trees in each cluster, respectively, while sigma is the standard deviation of the dispersal kernel around a cluster center and controls the spatial aggregation of species. We simulated the distribution of 814 Pasoh tree species for three values of sigma: 300 m (random distribution), 50 m (moderately aggregated), and 25 m (highly aggregated). Fig. 2 shows three distributions of a representative species.

We constructed species–area relationships using two sampling designs (nested and non-nested; see Fig. 1b and c) for each of the three simulated "Pasoh" forests (random, moderately aggregated, and highly aggregated). We fitted the power-law model to the species–area data and then used the backward SAR method to predict the endemics–area relationship. The power-law species–area model and endemics–area model are, respectively,

$$\mathrm{SAR}(a) = ca^z \tag{2}$$

$$\mathrm{EAR}(a) = S\left[1 - \left(1 - \frac{a}{A}\right)^z\right] \tag{3}$$

where a is sampling area, c and z are two parameters, and S is the total number of species in the region A.

The fitting of models 2 and 3 to the real data obtained from the Pasoh forest and the simulated "Pasoh" forests (Fig. 2) for the three sampling designs (Fig. 1) was implemented by the nonlinear least function nls of R package (R Core Development Team 2013). The steps were:

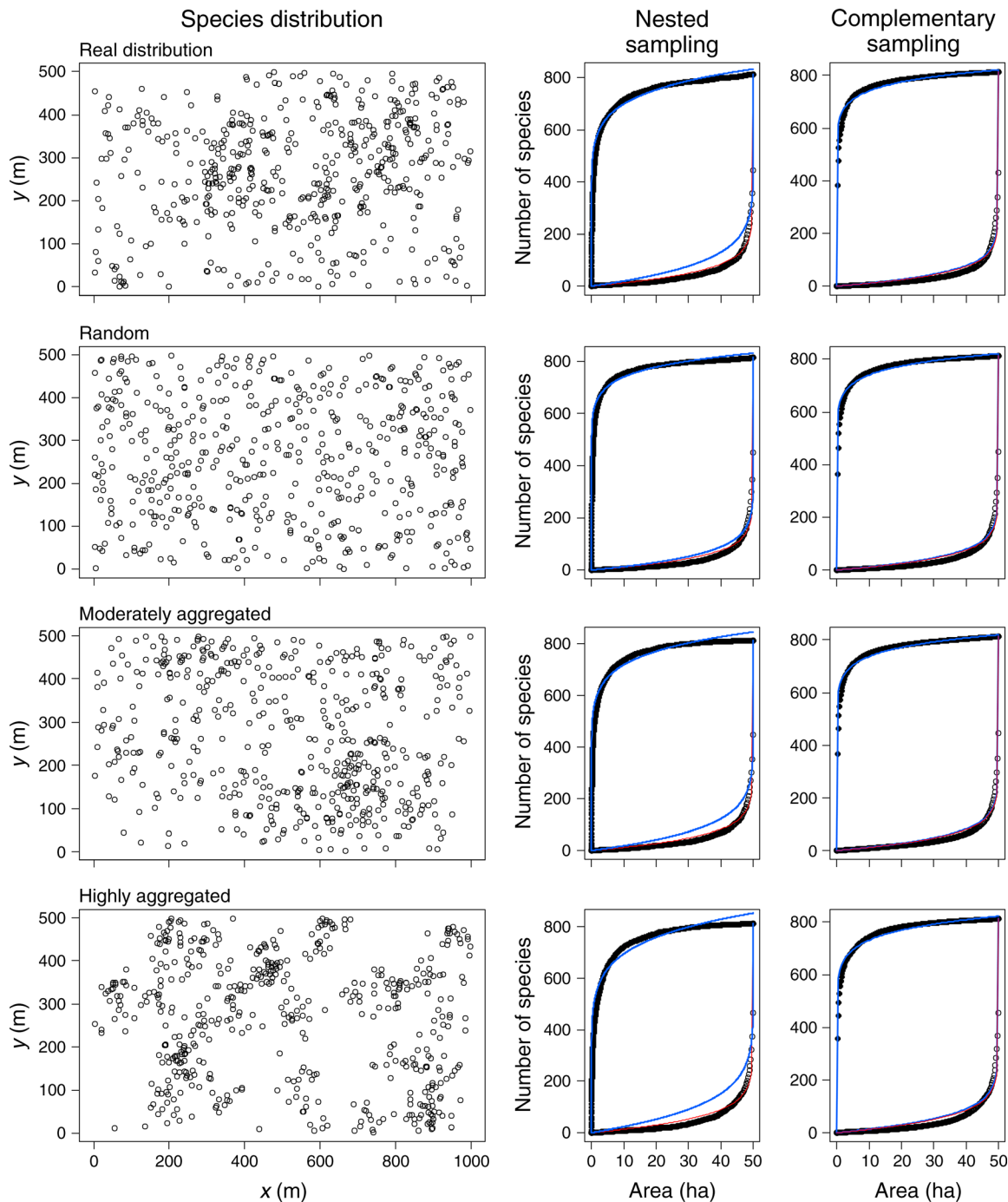1) Fit model 2 to the species–area data for complementary, non-nested, and nested sampling designs,

FIG. 2. Distribution of a species (*Symplocos crassipes*, abundance = 510) and the simulated distributions of different aggregation (values of sigma). Species–area relationships (SAR) and endemics–area relationships (EAR) for non-nested sampling are not shown because they look almost the same as the nested sampling design. The blue curves are the fitted SAR and its complementary EAR, while the red curve is the direct fit of EAR. Only the species–area data and endemics–area data for area ≥1 ha were used to fit the power-law SAR model 2 and EAR model 3, although it is worth noting that the area cutoff has little effect on the EAR model. It is obvious that the backward complementary SARs estimate EAR very well, but not the SAR for other sampling designs.

TABLE 1. Fitted slopes of species–area relationships (z_{SAR}) and the endemics–area relationships (z_{EAR}) for three sampling designs as shown in Fig. 1.

Distribution	Non-nested sampling		Nested sampling		Complementary sampling	
	z_{SAR}	z_{EAR}	z_{SAR}	z_{EAR}	z_{SAR}	z_{EAR}
Pasoh forest	0.105 (0.00105)	0.0599 (0.00100)	0.109 (0.00107)	0.0689 (0.000979)	0.0567 (0.000944)	0.0599 (0.00100)
Random	0.0706 (0.00888)	0.0612 (0.00104)	0.0723 (0.00880)	0.0612 (0.00105)	0.0580 (0.000951)	0.0612 (0.00104)
Moderately aggregated	0.0997 (0.00129)	0.0644 (0.000962)	0.102 (0.00130)	0.0667 (0.000964)	0.0601 (0.000897)	0.0644 (0.000962)
Highly aggregated	0.125 (0.00168)	0.0687 (0.00110)	0.128 (0.00178)	0.0724 (0.00108)	0.0667 (0.00105)	0.0687 (0.00110)

Notes: Only the species–area data and endemics–area data for area ≥1 ha were used to fit the power-law SAR model 2 and EAR model 3. Including smaller areas will make the difference between z_{SAR} and z_{EAR} in the non-nested and nested samplings bigger but has little effect on the complementary sampling. The values in the parentheses are standard errors of the slopes.

respectively. Denote the slope of the fitted model 2 as z_{SAR}.

2) Substitute the estimated z_{SAR} into model 3 to predict the number of endemic species.

3) Use model 3 directly to fit endemics–area data. Denote the resultant slope as z_{EAR}.

4) Compare the difference between the slopes of complementary, non-nested, and nested SAR slopes z_{SAR} against the EAR slope z_{EAR}.

We further used the backward SAR derived from the logarithmic SAR model, $EAR(a) = z \log(A/[A − a])$, to estimate the number of extinctions (i.e., the number of endemic species). This model was derived from the widely used logarithmic SAR that has the form (Gleason 1922): $SAR(a) = z \log(a) + c$, where z and c are two parameters, following Eq. 1. The addition of this analysis reinforces our argument that the power-law model is not the reason for the overestimation, but the sampling design involving in species–area relationships is as we have shown in He and Hubbell (2011).

Results

As expected, for the complementary sampling design, Eq. 1 accurately predicts the number of endemic species (Fig. 2, right-hand column). The estimates of the complementary SAR slope, z_{SAR}, and the EAR slope, z_{EAR}, are very close (Table 1). However, for the non-complementary sampling designs, both non-nested and nested backward SAR methods overestimate the en-demics–area relationship, and the overestimation be-comes greater with an increase in degree of spatial aggregation (Fig. 2). The overestimation can be further documented by comparing the SAR slope, z_{SAR}, and the EAR slope, z_{EAR} (Table 1). It is worth noting that the overestimation is not a goodness-of-fit issue: it persists even if we improve the goodness-of-fit of the power-law model to the species–area data for the non-nested and nested samplings (He and Hubbell 2011) and even other SAR models (e.g., the logarithmic model) are used in replacing the power-law model (Table 2). The real issue is that the SAR for the complementary sampling and the SARs fitted to data from other sampling designs are very different (Fig. 3). Only for randomly distributed species does the backward SAR method predict the endemics–area relationship well (Fig. 3, the second panel). The fact that all the complementary SAR slopes, z_{SAR}, are very close (around 0.06; see Table 1) indicates that the complementary SAR is very robust to variation in the spatial distribution of species. Indeed, if we combine the four panels in Fig. 3 into one, it is easy to see that the complementary SAR curves collapse into a single curve that is no different from the random placement SAR model (the second panel of Fig. 3). This is easy to understand if we remember that the first individual and the last individual of a species are exchangeable (in this case, the same tree) in complementary sampling. For the 814 species of the Pasoh forest there are 814 such individuals and their distributions over the 50 ha plot are no different from a random distribution (Fig. 4).

TABLE 2. The estimated numbers of extinctions by assuming that half of the 50-ha "Pasoh" plot is destroyed.

Distribution	Non-nested sampling			Nested sampling			Complementary sampling		
	Observed extinctions	Power-law SAR	Log series SAR	Observed extinctions	Power-law SAR	Log series SAR	Observed extinctions	Power-law SAR	Log series SAR
Pasoh forest	21.1	58.2	51.8	25.2	60.5	53.5	21.1	31.6	30.5
Random	19.5	39.6	36.7	20.3	40.6	37.5	19.5	32.3	31.1
Moderately aggregated	24.7	56.5	50.9	25.0	51.7	40.7	24.7	33.4	32.1
Highly aggregated	21.6	70.8	62.1	21.4	72.5	63.5	21.6	37.1	35.5

Notes: The estimation was done by both the power-law backward SAR model (Eq. 3) and the new backward logarithmic SAR model (see *Methods*). The observed extinctions are the number of endemic species that would be lost if a 25-ha area were destroyed. The real Pasoh forest and the three simulated "Pasoh forests" are the same as in Table 1. It is clear that the overestimation increases from random to highly aggregated forests for both the non-nested and nested sampling designs, while the overestimation is much smaller and less varied for the complementary design.
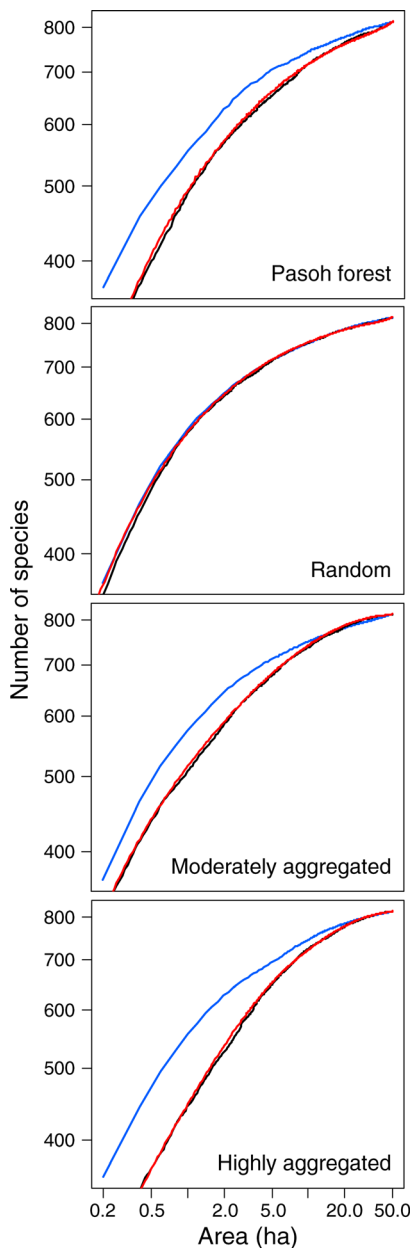
FIG. 3. The species–area relationships for the three sampling designs for the Pasoh forest and for random, moderately aggregated, and highly aggregated "Pasoh" forests (see Fig. 2). Blue lines are for complementary SAR, black lines for nested SAR, and red lines for non-nested SAR.

The proof of this last result is given in the appendix of He and Hubbell (2011).

DISCUSSION

If a theory does not predict data, what should we believe: the theory, the data, neither, or both? In estimating species extinction from species–area relationships, both the theory (Eq. 1) and the data (Fig. 2 and

Table 1) are correct. However, the conditions for the theory to hold are not met when non-complementary sampling methods are used to obtain the data. The deviation between the theory and the data arises because Eq. 1 is only applicable to a strictly complementary sampling design. Researchers never use this design in constructing species–area relationships because it requires knowing which species are endemic to the destroyed habitat, or the number of species in the complementary area as the relative size of areas $A - a$ and a change, which is no improvement over not knowing the species endemic to subarea a in the first place. We agree with Axelsen et al. (2013) that Eq. 1 is correct (see He and Hubbell 2011, 2012). However, the sampling methods people use to estimate species extinction by substituting $c(A - a)^z$ for $SAR(A - a)$ in Eq. 1 do not enforce complementary sampling and therefore are not the same as the sampling methods required and defined by Eq. 1. Only when species are randomly distributed in landscapes is Eq. 1 valid because of the complementarity $a^1 + a^N = A$. This complementarity is universally true if the complementary sampling design is implemented because, in this case, the first individual to be encountered of a species and the last individual to be encountered to lose the species are the same individual. This complementarity breaks down for general sampling designs whenever species are clumped in distribution. He and Hubbell (2011) discuss the general case to which our proofs and empirical tests apply. One can easily confirm these results by repeating these analyses on any mapped community of species whose distributions are clumped, by following the same steps we list above. Note that Axelsen et al. (2013) show the SAR for the finite negative binomial model of Zillio and He (2010) is true for the complementary sampling design because the aggregation parameter k changes proportionally with a and $A - a$. He and Hubbell (2011) used this finite negative binomial model to derive the expected areas of encountering first individual (a^1) and
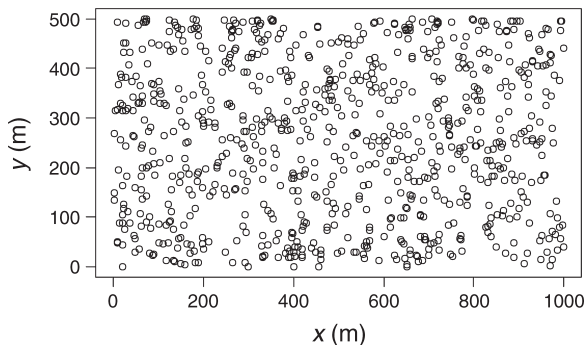

FIG. 4. The distributions of the first nearest neighbor of each of the 814 Pasoh species to a randomly located point in the 50-ha plot. For the complementary sampling design, the first individual to encounter a species is also the last individual to lose the species.

the last individual (a^N) of a species, and the derivation was based on nearest neighbor distances in which k is kept constant. In other words, Axelsen et al.'s (2013) calculation is not the same as ours, and so does not apply to nor invalidate our calculation.

The problem with the use of the backward SAR method to estimate extinction is subtle and elusive because most researchers have not realized that substituting the power-law model SAR into Eq. 1 breaks the equality of the relationship. Clearly, one should never expect that any arbitrary mathematical function of area substituted for $SAR(A - a)$ would satisfy the equality in Eq. 1 (e.g., see Table 2). Many people have not realized that and have inadvertently broken the requirement for complementary sampling in Eq. 1 when substituting $c(A - a)^z$ for $SAR(A - a)$.

To put the issue finally to rest, ecologists need to develop a general theory for estimating species extinction from species–area relationships. Such theory is not yet available, although He and Hubbell (2011) is a first step in that direction. Here, we identify two directions for future research. First, there is an urgent need to develop a consistent theory that applies to general sampling designs of species–area relationships. This new theory should generalize Eq. 1 and include it as a special case. Central to this theory is the development of models linking species–area relationships and endemics–area species relationships (Kinzig and Harte 2000, Storch et al. 2012). Before such theory is established, however, there should be no further use of the backward SAR method to estimate species extinction in practice. Second, while "extinction debt" is a valid and important concept in conservation biology, the backward SAR method is not the correct model for measuring the debt. To model such a debt, a dynamic species–area model is needed to describe the process of biotic relaxation as a disturbed system approaches a new equilibrium. The recent work of Wearn et al. (2012) and a subsequent discussion (Halley et al. 2013) is an important step. The dynamic theory should not only predict the strong form of biotic relaxation (loss of species) but also the weak form of biotic relaxation (not loss of species but shifts in patterns of the abundance and distribution of species).

Conservation biology is a field that has broad public and policy implications. Great care and thoughtfulness are needed when scrutinizing the conditions in which conservation theory may or may not be applied. We should do our utmost to avoid conceptual and empirical errors in estimating species extinctions, whether they be an overestimation or underestimation. We may not live another 40 years to witness whether a predicted 20–30% loss in species by 2050 due to climate and land use change actually comes to pass, but history will tell. However, if err we must, we should err on the side of caution. The cautionary principle exhorts us to take the current extinction crisis extremely seriously.

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Supplemental Material

Supplement

The R codes that were used for simulating random, moderately aggregated, and highly aggregated distributions of tree species shown in Fig. 2 (*Ecological Archives* E094-173-S1).

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