On the Distribution and Abundance of Species

Harte *et al*. (*1*) assumed the probability rule: if a species occurs in an area A_0, then the probability that it occurs in half of that area is a constant, a, independent of area A_0, satisfying $0.5 \le a \le 1$. From this rule, Harte *et al*. (*1*) give a mathematical proof of the power law form of the species-area curve: if S is the number of species in A, then $S = cA^z$, where $(0.5)^z = a$, $0 \le z \le 1$, and c is constant.

Harte *et al*. (*1*) do not justify the last step in their proof. Their final equation, $S_i = cA_i^z$, is equivalent to $S_i = (2^{-i})^z S_0$. To complete their proof, it would be necessary to prove, for example, that the number of species occurring in an area $(0.75)A_0$ is $(0.75)^z S_0$.

The distribution of a given species in a habitat can be thought of as a random point distribution over that habitat. Harte *et al*. (*1*) need to provide at least one nontrivial example of such a distribution that satisfies their probability rule. As far as we can see, no random point distribution satisfies the rule unless $a = 0.5$, in which case the only example known to us is the uniform distribution of a single, randomly chosen, point.

We shall demonstrate from the probability rule of Harte *et al*. (*1*) that $a = 1$ or $a = 0.5$ or $c = 0$. The power law happens to hold for these values, but in all other cases the rule and the power-law are in conflict.

Let $\mathrm{x|o}$ mean "species occurs only in right half,"

$\mathrm{o|x}$: species occurs only in left half

$\frac{\mathrm{o}}{\mathrm{x}}$: species occurs only in upper half

$\mathrm{o|o}$: species occurs in right and left half

$\frac{\mathrm{o}}{\mathrm{o}}\Big|\mathrm{x}$: species in upper left quarter, in lower left quarter, but not in right half

$\frac{\mathrm{o}}{\mathrm{o|x}}$: species occurs in upper half, in lower left quarter, but not in lower right quarter

$\frac{\mathrm{o|o}}{\mathrm{o|x}}$: species occurs in all quarters except the lower right quarter.

The probability rule of Harte *et al*. (*1*) yields

1. $P(\mathrm{o|x}) = 1 - a$,
2. $P(\mathrm{x|o}) = 1 - a$,
3. $P(\mathrm{o|o}) = 2a - 1$,
4. $P\left(\frac{\mathrm{o}}{\mathrm{x}}\right) = 1 - a$,
5. $P\left(\frac{\mathrm{x}}{\mathrm{o}}\right) = 1 - a$,
6. $P\left(\frac{\mathrm{o}}{\mathrm{o}}\right) = 2a - 1$.

Applying 6. to 1. and 1. to 6. gives

$$P\left(\frac{\mathrm{o}}{\mathrm{o}}\Big|\mathrm{x}\right) = (1-a)(2a-1) = P\left(\frac{\mathrm{o}}{\mathrm{o|x}}\right),$$

The first equality is derived in (*2*). Notice that

$$P\left(\frac{\mathrm{o}}{\mathrm{o|x}}\right) = P\left(\frac{\mathrm{x|o}}{\mathrm{o|x}}\right) + P\left(\frac{\mathrm{o|o}}{\mathrm{o|x}}\right) + P\left(\frac{\mathrm{o}}{\mathrm{o}}\Big|\mathrm{x}\right).$$

Cancelling equal probabilities, we are left with

$$P\left(\frac{\mathrm{x|o}}{\mathrm{o|x}}\right) = 0 = P\left(\frac{\mathrm{o|o}}{\mathrm{o|x}}\right).$$

The probability rule also yields

$$P\left(\frac{\mathrm{x|o}}{\mathrm{o|x}}\right) = (2a-1)(1-a)(1-a)$$

and

$$P\left(\frac{\mathrm{o|o}}{\mathrm{o|x}}\right) = (2a-1)(2a-1)(1-a),$$

hence, $a = 1$ or $a = 0.5$.

Another way of arriving at this conclusion is to apply the probability rule and the power law to an area consisting of three of the quarters created by subdividing the habitat into four quarters. E_2 is the number of species found only in one of the quarters. The rule implies, by Eq. 7. of Harte *et al*. (*1*), $E_2 = (1 - a)^2 S_0$. Therefore, the number of species in the remaining three quarters is

$$S_0 - E_2 = S_0(1 - (1-a)^2) = S_0(2\mathrm{a} - \mathrm{a}^2) = (2^{1-z} - 2^{-2z})S_0.$$

By the power law,

$$S_0 - E_2 = (0.75)^z S_0 = 3^z 2^{-2z} S_0.$$

Therefore,

$$(2^{1-z} - 2^{-2z})S_0 = 3^z 2^{-2z} S_0,$$

which holds if $S_0 = 0 = c$. If $S_0 \ne 0$, multiplying both sides by $2^{2z}/S_0$ produces

$$2^{z+1} - 1 = 3^z,$$

which implies $z = 0$ or $z = 1$, hence, a is either 0.5 or 1.

The rule proposed by Harte *et al*. (*1*) implies that species are distributed in one of three trivial ways. In general, the equivalence of the probability rule with the power law is invalid, as are all conclusions that rely upon it, such as the "endemics-area relationship" (*1, 2*).

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References

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2. J. Harte and A. Kinzig, *Oikos* **80**, 417 (1997).

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Response: In our derivation of the familiar species-area relationship (SAR), of a new endemics-area relationship, and of a new abundance distribution from self-similarity, we explicitly made use of successive shape-preserving bisections of a biome that is taken initially to be a golden rectangle with length-to-width ratio of $\sqrt{2}$ (*1*). We also stated in our report that species richness per unit area is dependent on patch shape. Odd-shaped patches of habitat will contain a different number of species than do squares or golden rectangles of the same area, and thus the SAR only holds across scales when applied to "well-shaped" patches (golden rectangles or squares). Maddux and Athreya seem not to have noted this relationship, examine species richness in an odd shaped patch (the L-shaped patch that is left when they go immediately from the whole biome to a quadrant), and conclude that the fundamental self-similarity parameter in our theory, ***a***, can take on only particular values. There is plenty of evidence cited in our report that shape does matter, and that the specific prediction made by our self-similarity theory about the dependence of species richness on patch shape is reasonable.

Maddux and Athreya also refer to the example of a random placement model, in which the parameter a is indeed restricted to the value 1/2. In our theory, the fraction of the species in a rectangle that is also found in a particular half of that rectangle is not given by random placement but rather is governed by the parameter, a, which is independent of scale and not restricted to 1/2. Whereas the assumption of independence is necessary to our findings, our statement that there averages 1 species per unit square was unnecessary and overly restrictive; if S_m differs from 1, the distribution plotted on a ln(n)

scale is displaced horizontally but its shape is unchanged.

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