



Species distributions and area relationships



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HIGHLIGHTS

- Show a new, concise, derivation of Yule's equilibrium distribution.
- Derive the species–area relationship based on the evolution of species through mutations.
- Calculate the exponent of the species–area relationship for four different data sets.
- Confirm that the exponent term, based on mutation rates, agrees with previously observed values.

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ABSTRACT

The well-known species–area relationship is one of many scaling laws, or allometries, in ecology and biology that have received much attention over the years. We present a new derivation of this relationship based on Yule's theory of evolution of species. Using definitions of mutation rates, our analysis yields species–area exponents that are in close agreement with previously observed values.

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1. Introduction

The species–area relationship (SAR)

$$S = cA^z, \quad (1)$$

dates back to at least 1921 when Arrhenius (1921) proposed Eq. (1) as an empirical formula for the number of species S of a given taxonomic group (or genus) found in a region of area A . Alternative SARs and their derivations, which are often based on assumed underlying species-abundance distributions (SADs), have been considered and debated over the years (May, 1975; May and Stumpf, 2000; McGuinness, 1984; Chisholm, 2007). While there has been no general consensus on the range of validity of particular SARs (for varying A), recent empirical and theoretical studies by Harte et al. (2009), O'Dwyer and Green (2010) and Storch et al. (2012) strongly suggest that Eq. (1) is not valid for 'small A ', but that in certain situations, may be valid asymptotically

for larger values of A . Our purpose here is not to discuss or comment on the large body of work that has been published on this problem (see May, 1975; May and Stumpf, 2000; McGuinness, 1984; Chisholm, 2007; Harte et al., 2009; O'Dwyer and Green, 2010; Storch et al., 2012 and references quoted therein), but rather to present a new derivation of Eq. (1) which is valid asymptotically for large A .

Our derivation of Eq. (1) is based on ideas published over ninety years ago by Yule (1925) on the evolution of species through specific and generic mutations within and between genera of species. In the following section we present a stochastic dynamical systems model based on Yule's original ideas. In Section 3 we show that the species–area relation (1) follows from the asymptotic form of Yule's equilibrium distribution for a large number of species in a genus. Moreover, our asymptotic derivation of (1) provides an explicit expression for the exponent z in Eq. (1) in terms of Yule's species and generic mutation rates. In Section 4 we present some case studies as examples, showing close agreement between our formulae for z and the previous empirical studies based on Eq. (1). Our results are summarised and discussed in the final section.

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2. The Yule distribution

In his original work Yule (1925) proposed evolution of species and genera through two kinds of mutations which he described as follows:

- Within any species, in any time interval, a ‘specific mutation’ can occur yielding a new species, but within the same genus as the parent.
- Within any genus, in any time interval, a ‘generic mutation’ can occur yielding a new species so different from the parent that it is placed in a new genus.

We assume (with Yule) that the rate s of specific mutations is a constant, and the same for all species within a genus; and that the rate g of generic mutations is a constant and same for all genera. Notice that at any time, the number of a species within a genera increases due to both s and the number of species within the genera. That is, the rich get richer (also known as ‘preferential attachment’).

Yule (1925) was at pains to point out that these assumptions are simplistic and were designed solely to elicit quantitative comparisons with well-known facts. He provides the following example to demonstrate the last of his simplifying assumptions: if A , B , C , and D are the existing genera, and one of them throws a generic mutation, it is assumed that this will represent a new genus E . That is, the possibility that the new species may be classed under an existing genera is ignored. Combine this with the absence of a death process, and it becomes clear that the number of genera with few species could easily be overestimated. This overestimation has recently been addressed by the Birth–Death–Mutation (BDM) Process (Maruvka et al., 2011).

Despite these assumptions, we will see in Section 4 that Yule’s comparisons with Willis’ data proved to be successful. Not surprisingly, Yule’s analysis (in the early 1920s) was long and complicated. Our main purpose in this section is to present a simple dynamical systems model for

$P_n(t)$ = the probability that the genus has n species at time t . (2)

and to show that Yule’s (equilibrium) distribution is a steady state solution of this system.

Consider first the case $n=1$. In continuous time it follows from Yule’s assumptions that

$$\frac{dP_1(t)}{dt} = g - (s+g)P_1(t), \quad (3)$$

where the first (input) term on the right-hand side of (3) represents a generic mutation from another genus, and the second term represents losses from the single species in the (new) genus through specific and generic mutations.

Similarly, for an established genus with at least two species, it follows from Yule’s assumptions that

$$\frac{dP_n(t)}{dt} = (n-1)sP_{n-1}(t) - (ns+g)P_n(t), \quad n = 2, 3, \dots \quad (4)$$

In Eq. (4) the first term arises from the $n-1$ possible specific mutations from $n-1$ species in the genus, and the second term represents losses from n species in the genus due to n specific mutations, and a constant loss rate g due to generic mutations.

There are of course many possible dynamical models for $P_n(t)$. We again note that Yule’s scheme ignores death, and therefore extinction. As a consequence, and as mentioned by Yule (1925, p.38), ‘on our assumptions, the mean size of a genus after infinite time must itself be infinite’. Extinction could of course be included in our system, by adding appropriate $P_{n+1}(t)$ terms to the right-hand side of (4) for example. We will return to these issues in the

final section. The important point to stress here is that Eqs. (3) and (4) although simplistic are biologically reasonable and logically consistent in the sense that on summation of Eqs. (3) and (4) we deduce that

$$\frac{d}{dt} \left(\sum_{n=1}^{\infty} P_n(t) \right) = g \left(1 - \sum_{n=1}^{\infty} P_n(t) \right), \quad (5)$$

as required by conservation of probabilities, i.e., the initial condition

$$\sum_{n=1}^{\infty} P_n(0) = 1 \quad \text{implies} \quad \sum_{n=1}^{\infty} P_n(t) = 1,$$

for all $t > 0$.

In the Appendix we present an exact solution of Eqs. (3) and (4) and show that in the limit $t \rightarrow \infty$ $P_n(t)$ approaches a globally stable equilibrium given by steady-state solution P_n^* obtained by setting the left hand sides of (3) and (4) to zero, i.e.,

$$P_1^* = \frac{g}{s+g} = (1+\sigma)^{-1}, \quad (6)$$

and

$$(n\sigma+1)P_n^* = (n-1)\sigma P_{n-1}^*, \quad n = 2, 3, \dots \quad (7)$$

where

$$\sigma = \frac{s}{g} \quad (8)$$

is the ratio of the specific and generic mutation rates which we assume henceforth (with Yule) to be larger than unity.

Iterating Eq. (7) we deduce (as shown in the Appendix) that

$$P_n^* = \frac{\Gamma(n)\Gamma(1+1/\sigma)}{\sigma\Gamma(n+1+1/\sigma)}, \quad n = 1, 2, \dots, \quad (9)$$

where $\Gamma(k)$ is the gamma function. Using Stirling’s formula for $\Gamma(k)$ when k is large, we arrive at the asymptotic form (as shown in the Appendix)

$$P_n^* \sim \frac{1}{\sigma} \Gamma\left(1+\frac{1}{\sigma}\right) n^{-(1+1/\sigma)} \quad \text{as } n \rightarrow \infty. \quad (10)$$

The distribution P_n^* equation (9) was obtained by Yule in a rather lengthy and complicated derivation. This is not surprising since his work predated developments in stochastic processes and dynamical systems theory. His notion of equilibrium was also at odds with modern interpretations in terms of steady states. These shortcomings were in fact pointed out by Simon (1955) some thirty years after Yule’s paper. Simon re-derived Yule’s results, and Eqs. (9) and (10) in particular, in a more general and contemporary setting with interesting applications to word frequencies, city sizes, income distributions and frequencies of scientific publications. Simon (1955) correctly referred to (9) as the (equilibrium) Yule distribution, although that citation has been largely forgotten in recent times.

We note in passing that although the P_n^* , from Eqs. (6) and (7), sum to unity as required, there is no reason for the asymptotic form values (10) to do likewise (see the Appendix). Nevertheless, the Yule distribution has some unusual and even ‘paradoxical’ properties (as stated by Yule, 1925, p. 38). In particular it follows from (9) and (10) that the (equilibrium) mean number of species in a genus, obtained by multiplying P_n^* , Eq. (9), by n and summing on n from 1 to ∞ , diverges when $\sigma > 1$ by virtue of the asymptotic form (10) for the tail distribution P_n^* .

In the following section we show that the asymptotic form of Yule’s distribution (10) can be used to derive the species–area relationship (1) (for large A) with an explicit expression for the exponent z in terms of Yule’s parameter σ defined in (8).

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