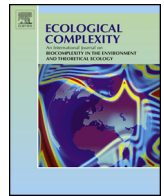




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Short note

Colonization rules and spatial distributions in ecology

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ABSTRACT

Because they are intuitive and mathematically straight-forward, colonization rules are often used to model spatial patterns in ecology. Colonization rules assign individuals to categories according to the locations of previous colonists. In this note, a compact introduction to colonization rules in ecology is presented with implications for autocorrelation and spatial distributions. I use the colonization rule approach to unify a diverse set of spatial and species diversity analyses, exploring future extensions to incorporate greater realism.

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1. Introduction

Compact models of species abundances, such as Coleman's (1981) random placement model or Hubbell's (2001) neutral theory, provide important benchmarks in ecology. Many theoretical models exist to describe plant and animal communities (Brännström et al., 2012), where important “colonization rules” describe how plant or animals distribute over categories. Rules assign individuals to categories according to assignment probabilities which depend on the locations of previous colonists. Once the colonization rule is stated, its implications are often easily worked out using mathematics and simulation. Through examples from the literature, I suggest that colonization rules provide a very helpful way of investigating ecological issues. The approach unifies a broad set of existing models and suggests new models.

2. Random placement models

Consider a species distributing over a uniform spatial grid. Let the cells be indexed $k = 1, 2, \dots, K$; and let n_1, n_2, \dots, n_K denote the numbers of individuals in the cells. A simple colonization rule is

$$\Pr \left(\begin{array}{c} \text{next colonist} \\ \text{allocated to cell } k \end{array} \middle| \begin{array}{c} \text{current abundances} \\ n_1, n_2, \dots, n_K \end{array} \right) = a_k, \quad (1)$$

where the probabilities a_k are constant parameters summing to one. Rule (1) is applied, one individual at a time (although Hubbell, 2001), describes accommodating multiple individuals at once, until some given total number J of individuals have been spatially allocated. J might be the overall carrying capacity of the area (where Etienne et al., 2007 describes accommodating changing carrying capacities through time). Differences in a_k might represent cross-cell differences in habitat quality, such as rainfall, quality of soil, abundance of prey, and so on. In that case, the allocation probabilities a_k may be viewed, for example, as relative habitability measures. Under rule (1), the cell abundances n_1, n_2, \dots, n_K will have a multinomial distribution. The marginal distribution for a particular n_k will be binomial with mean $a_k J$. As J is made larger, the marginal distributions tend toward a normal bell shape. The special case when the allocation probabilities are equal ($a_k = 1/K$) is the classic random placement model of Coleman (1981); then the histogram of the abundance vector n_1, n_2, \dots, n_K will also tend toward a normal bell shape.

However, empirical studies of spatial grids (e.g., Krebs 1989; Plotkin et al., 2000; He and Gaston 2000; Holt et al., 2002) find that histograms of n_1, n_2, \dots, n_K are typically shaped more like a negative binomial distribution than a normal distribution. To bring rule (1) into agreement with such findings, it may be generalized to:

$$\Pr \left(\begin{array}{c} \text{next colonist} \\ \text{allocated to cell } k \end{array} \middle| \begin{array}{c} \text{current abundances} \\ n_1, n_2, \dots, n_K \end{array} \right) = \frac{a_k + b n_k}{1 + b \sum_j n_j}. \quad (2)$$

Here b is a nonnegative parameter, and the a_k are again assumed nonnegative with sum equal to one. The denominator on the right

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of (2) merely assures that the allocation probabilities sum to one. Hence attention focuses on the numerator. The change between rule (1) and rule (2) is the added term bn_k , where b can be thought of as a parameter describing density-dependent facilitation (such as an Allee effect).

Rule (2) allows a particular cell k to attract colonists in two ways. The first is the exogenous attractive force of the cell's given a_k . The second is the endogenous attractive force of bn_k , through which a cell with greater success early in colonization will tend to have greater success later in colonization also. This second, endogenous mechanism can generate a "clustered" or "aggregated" pattern even if the a_k are all set equal to $1/K$. The force of the bn_k terms might be viewed as a reproductive effect; more parents within a cell might generate more offspring within the cell. For rule (2), as for rule (1), colonization continues until the given total abundance J is reached. Rule (1) is, of course, the $b=0$ special case of rule (2).

Rule (2) implies a multivariate Polya-Eggenberger distribution for n_1, n_2, \dots, n_K (e.g., see Zillio and He, 2010 or Conlisk et al., 2007; Theorem 1.5), which has a close connection to a negative binomial distribution. Suppose, instead of rule (2), the cell abundances n_1, n_2, \dots, n_K were generated as K independent draws from a given negative binomial distribution. The sum of these draws n_1, n_2, \dots, n_K would be a random variable, not a constant. However, if the multivariate distribution of n_1, n_2, \dots, n_K from these draws was conditioned to have the given total abundance J , that conditional multivariate distribution would be Polya-Eggenberger (e.g., see Conlisk et al., 2007; Theorem 1.5). Thus, the empirical finding that the histogram of a grid sample n_1, n_2, \dots, n_K of given total abundance J tends to have a negative binomial shape is expected under the colonization rule (2).

3. Local abundance distribution of Hubbell's neutral theory

The most famous ecological model following rule (2) is the local abundance distribution of Hubbell's neutral theory (Hubbell, 2001). Hubbell's context requires that the categories be reinterpreted as species rather than spatial grid cells. Consider an "island" on which K species may live. Let $k = 1, 2, \dots, K$ index the species, and let n_1, n_2, \dots, n_K denote the numbers of individuals of the K species on the island. Assume the island has J spots in total for colonists to occupy, so $\sum_j n_j \leq J$.

Near the island is a large and stable "mainland" on which the K species live in unchanging proportions a_1, a_2, \dots, a_K . An island colonist may be either an immigrant from the mainland or an offspring of an existing island individual. Assume that the probability of immigrant status is $1/(1+b\sum_j n_j)$, which equals one, as it should, when the island is empty (when $\sum_j n_j = 0$), and which declines as the island populates. The probability of island offspring status is the complementary probability $b\sum_j n_j / (1+b\sum_j n_j)$. If the colonist is an immigrant, it will be of species k with probability equal to the mainland frequency of species k , namely a_k . If the colonist is an island offspring, the individual will be of species k with probability equal to the island frequency of species k , namely $n_k / (\sum_j n_j)$. Under these assumptions, colonization rule (2) applies, which generates a Polya-Eggenberger distribution for the island abundances n_1, n_2, \dots, n_K when the island is fully colonized ($\sum_j n_j = J$) or at any colonization step along the way. Thus, Hubbell's local abundance distribution for the island is a Polya-Eggenberger distribution.

Hubbell used a Markov chain approach in his analysis, not a colonization rule approach. Later McKane et al. (2004) and Etienne et al. (2007) used a differential equation approach; Etienne and Alonso (2005) used a statistical sampling approach; and Conlisk et al. (2010) proposed the colonization rule approach of (2).

4. Extinction, speciation, and the species abundance distribution (SAD)

For a given community of species, such as the trees in a forest, a "species abundance distribution" is a histogram listing the number of species at the abundance values 1, 2, 3, . . . If $SAD(n)$ denotes the species abundance distribution, then $SAD(1)$ is the number of species with $n=1$ individuals in the community; $SAD(2)$ is the number of species with $n=2$ individuals in the community; and $SAD(n)$ is the number of species with n individuals in the community. The function $SAD(n)$ describes a salient property of the community, often presented in field study reports.

A SAD typically has a hollow shape—downward sloping and concave from above. In their broad review of SAD's, McGill et al. (2007, p. 995) call the hollow shape "one of ecology's oldest and most universal laws." Although they list a "proliferation of models" (p. 998) explaining the shape, they nonetheless call the hollow shape "surprising" and "counterintuitive" (p. 997). In this section, I present a simple colonization rule model of a SAD, and its hollow shape, as a consequence of extinction and speciation. The model is in the spirit of Hubbell's analysis (2001, Chapter 5), but simpler.

Over the relatively short time spans of the local island model in the preceding section, the mainland species proportions a_1, a_2, \dots, a_K were treated as constants. However, over the very long time spans relevant to extinction and speciation, the a_k are variables. Moving to these long time spans for an isolated community, let n_1, n_2, \dots, n_K be the abundances of the K species. The number of species K is now a variable since it will change as extinctions and speciations occur. Consider a colonization rule approach.

At each step in a sequence of colonization events, assume a single individual is selected purely at random from the entire population across all species in the isolated community. For a given individual, this selection probability is $1/\sum_k n_k$. Assume the selected individual experiences one of three exclusive and exhaustive events according to given probabilities: (i) The individual generates one offspring with probability β . (ii) The individual dies with probability δ , with $\delta \leq \beta$ assumed. (iii) The individual mutates into a new species with probability $1 - \beta - \delta$. The colonization rule is thus:

$$\Pr\left(\begin{array}{l} \text{next event is} \\ \text{a species } k \text{ birth} \end{array} \middle| \begin{array}{l} \text{current abundances} \\ n_1, n_2, \dots, n_K \end{array}\right) = \frac{n_k}{\sum_j n_j} \beta. \quad (3)$$

$$\Pr\left(\begin{array}{l} \text{next event is} \\ \text{a species } k \text{ death} \end{array} \middle| \begin{array}{l} \text{current abundances} \\ n_1, n_2, \dots, n_K \end{array}\right) = \frac{n_k}{\sum_j n_j} \delta. \quad (4)$$

$$\Pr\left(\begin{array}{l} \text{next event is} \\ \text{a species } k \text{ mutation} \end{array} \middle| \begin{array}{l} \text{current abundances} \\ n_1, n_2, \dots, n_K \end{array}\right) = \frac{n_k}{\sum_j n_j} (1 - \beta - \delta). \quad (5)$$

These three probabilities sum to one over the species index k . The total number of species K may change. Suppose the selected individual is not the only one of its species. Then, if the event is a birth or a death, K will not change; but, if the event is a mutation, K will increase by one. Alternatively, suppose the selected individual is the only one of its species. Then, if the event is a birth, K will not change; if the event is a death, K will decrease by one; and, if the event is a mutation, K will increase by one.

Finally, assume there is a fixed total number of slots in the community, denoted J , beyond which the total $\sum_k n_k$ may not go. That is, J is a carrying capacity. Thus, a birth event drawn via probability (3) is assumed to be a still birth if $\sum_k n_k = J$. To start the model, parameter values and initial values of n_1, n_2, \dots, n_K are needed.

Since deaths are possible, any species may go extinct, and in principle global extinction must ultimately occur, though, for

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