NEUTRAL MODELS FOR THE SPATIAL DISTRIBUTION OF ORGANISMS: IMPLICATIONS FOR PALEOENVIRONMENTAL INTERPRETATION

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A fundamental assumption of paleoecology is that spatial variability in species distributions and associations reflect underlying spatial variability in physical environmental parameters. For example, gradients in species composition are usually interpreted as relating to gradients in variables such as water depth, temperature, or soil moisture. Numerous examples support the idea that when an environmental gradient is known to exist, there is a corresponding non-random community gradient. We suggest, however, that the reverse may not necessarily be true; i.e., a community gradient may exist even in the absence of an underlying physical gradient.

We have developed a series of models for the spatial distribution of organisms on landscapes (spatially heterogenous areas ranging in size from hectares to many square kilometers). In these models, a landscape is represented by a two-dimensional lattice, where each node of the lattice is a habitat site. Each habitat site is randomly assigned to one of a set of multiple habitat types (generally 3-6). A map of the lattice would thus show a random distribution of habitat types.

Habitat sites are competed for by sessile organisms that complete their life cycle in one time step (e.g., annual plants). "Seeds" are spread to a site from its eight next nearest neighbors. Each species' seeds successfully germinate on only a subset of the available habitat types (its "niche"), with one or more types being optimal (highest probability of germination). These subsets can overlap, so that different species can potentially occupy the same site. The probability of a given species taking over a site depends on the number of neighboring sites it occupies and whether the site is optimal. A site can be taken over by a suboptimal species if it locally more abundant.

Each organism's niche directly controls its ability to spread ("percolate") through the landscape. Under the next-nearest neighbor rule, a species must be able to live on >40% of all possible sites in order to spread. Competition, by reducing the number of available sites, may prevent a species from reaching all habitable sites, even those that are optimal.

In one model, five habitat types are randomly distributed on a 201 x 201 matrix. Five species, each of which has an optimal habitat corresponding to one of the five habitats but can live on two additional habitats, are randomly introduced at one edge of the map and are allowed to spread. When the resulting distribution maps are examined, preferred species associations and gradients are observed, although there is no underlying habitat gradient. Instead, the observed patterns result from a combination of biotic interactions and historical contingencies, such as founder effects.

This and related models show how random processes can produce biotic patterns in the absence of environmental patterns. They provide appropriate neutral models for the interpretation of paleoenvironmental patterns based solely on species distributions.

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