

Comparison of spatial statistics for identifying underlying process in forest ecology

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Abstract: A number of different mechanisms have been suggested to explain species coexistence in diverse communities such as tropical rainforests. Spatial statistics appear to hold great potential for distinguishing the effects of these in empirical data, and a wide range of measures intended to describe spatial structure have been proposed. Using patterns generated by stochastic individual-based models, we examine the relative sensitivity of several of these measures to processes thought to be occurring in tropical rainforests, and so assess the potential for identifying specific coexistence mechanisms from empirical data. We then apply the measures to spatially explicit census data from a number of large-scale tropical rainforest plots in order to investigate the manifestation of ecological processes in forest spatial structure.

Keywords: spatial structure, coexistence mechanisms, tropical rainforest

1. Introduction

Statistics that summarise spatial pattern are of great interest in ecology, where a large number of processes influence, and are influenced by, spatial structure (Watt 1947; Bolker & Pacala 1997; Law *et al.* 2009). Spatial analysis is used for a wide range of purposes in plant ecology: for example to illuminate the relationship between environmental conditions and community structure (e.g. Kharuk *et al.* 2010; Obertegger *et al.* 2010); to study interactions between species (Hurlbert 1971; Wiegand 2007); and to isolate the signals of environmental and interactive effects and so assess their relative importance in producing observed community structure (Tuomisto *et al.* 2003; Kraan *et al.* 2010). This is particularly important to attempts to investigate the processes that support the coexistence of species in diverse communities such as tropical rainforests (Brown *et al.* 2011). These processes may include niche differentiation, lottery dynamics, the Janzen-Connell effect, heteromyopia, or neutral drift.

The diversity of processes of interest has meant that a very large number of spatial summary statistics have been developed, even in place of those that have previously proved successful. These statistics tend to fall into discrete groups. Some of the most

established and widely-used deal with β -diversity (Whittaker 1972), summarising some aspect of the turnover in species composition with site. Measures of neighbourhood structure developed from spatial point process theory, however, represent the bulk of currently used spatial statistics (Wiegand & Moloney 2004; Illian *et al.* 2008).

While these measures have been useful both in descriptive and inferential studies of community ecology, their relative merits in detecting specific processes have been reviewed only infrequently (e.g. Koleff *et al.* 2003). In fact, many such measures share information used in their construction, and can be broken down into the individual counts or measurements which comprise them (Table 1). Furthermore, these can be considered in a multi-dimensional framework describing the level at which they operate. Information can be divided in this way between conspecific and heterospecific levels, scale-independent and scale-dependent, and individual, species or community level. The ‘lowest’ level information can therefore be seen as scale-independent descriptions of behaviour within species at the individual level; the ‘highest’ as scale-dependent multi-species community-level data. Measures of spatial structure use information from several different levels, often in combination, and can be formulated at higher levels by averaging some or all of the information they contain.

Here, we compare a limited number of popular measures of spatial structure on the basis of their ability to distinguish the spatial effects of models of species coexistence. Our aim is to determine which of the individual pieces of information which comprise these measures contain the most useful and robust signals. This allows for more accurate consideration of which information, and in what form, may best be used for the study of particular processes.

2. Materials and Methods

We consider a limited but representative number of measures of spatial structure that exemplify particular techniques for summarising spatial data. These measures can be divided between three broad groups – of β -diversity, within-species structure, and between-species structure. We consider three measures describing the spatial structure within species: the degree of aggregation; the measure of interspecific segregation; and the proportion of conspecific neighbours. All are intended to operate at the species or community level, although it is possible to calculate the proportion of conspecific neighbours at the individual level. Five measures describe spatial structure between species: the individual species-area relationship (ISAR); the mingling index; the spatial Simpson index; the degree of association; and the cross-pair overlap distribution (xPOD). Several measures of β -diversity are also included, and defined as by Koleff *et al.* (2003).

In order to test the sensitivity of these different measures to modelled ecological processes, we use data from stochastic individual-based models of a plant community which provide multispecies spatial patterns under neutral, niche, lottery, Janzen-Connell and heteromyopia assumptions. These were chosen as the principal theorised mechanisms of species coexistence in diverse plant communities.

n_j	number of individuals belonging to species j per unit area
n_k	number of individuals belonging to species k per unit area
$N_{jj}(r)$	number of conspecifics within a defined radius
$N_{ij}(r)$	number of heterospecifics within a defined radius
$N_{jk}(r)$	number of individuals belonging to species k within a defined radius
$N_{jk}(R)$	number of pairs of individuals belonging to species j and k separated by distance R (in practice, within range $(r + dr)$)
A_c	area considered in count of points

Table 1: Separate pieces of information used in spatial measures considered here

3. Results

It is on the species level that most measures of spatial structure operate, making use of the numerous pieces of information which describe species-specific behaviour (Table 1). However, the differences these measures detect between models are often clearer when expressed at the community level. An example is the xPOD, which can be defined as:

$$A_{jk} = \int \log\left(\frac{N_{jk}(R)}{n_j n_k A_c}\right)$$

with terms as shown in Table 1. This measure describes the spatial overlap of all pairs of abundant species (with a threshold of 500 individuals) in a community, and shows substantial differences between models. Specifically, it shows that a far wider range of behaviour is produced by the niche and lottery models than any other, and the smallest range produced by the Janzen-Connell model. This suggests that species in the Janzen-Connell model are more mingled than under neutrality, and species in temporal or spatial niche models more segregated, on average.

These findings are confirmed by almost all of the other measures which we consider, and agree with theoretical predictions from each modelled process. Importantly, those measures which detect differences between the models all find higher levels of conspecific clumping and lower levels of heterospecific mingling in the niche and lottery models, and the opposite signals in the Janzen-Connell model. In addition, these signals are found in single pieces of information gathered at or averaged to the species level, prior to their combination to produce complete measures of spatial structure.

4. Concluding Remarks

In almost all measures (and at all levels), some aspect of the same behaviour is detected. In particular, the niche and lottery models produce clumped species which are not mingled, the neutral and heteromyopia models produce very similar spatial properties, and the Janzen-Connell model produces the least clumped and most mingled species. These findings are also apparent in single low-level pieces of information such as the proportion of conspecific neighbours, when expressed at the species or community level. In terms of β -diversity, those measures which emphasise simple counts of species unique to pairs of quadrats find the largest differences between models. This suggests both that the potential for distinguishing the modelled processes is limited to the spatial

characteristics listed above, and that relatively simple measures of spatial structure, operating at an appropriate level, have similar discriminatory power as those which are far more complex.

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