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Spatial pattern model of herbaceous plant mass at species level

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ABSTRACT

Individual plant species distribute according to their own spatial pattern in a community. In this study, we proposed an index for measuring the spatial heterogeneity in mass (dry weight) of individual plant species. First, we showed that the frequency distributions for mass of individual plant species per quadrat in a plant community are expressed using the gamma distribution with two parameters of λ (mean) and *p*. The parameter *p* is a measure indicating the level of spatial heterogeneity of plant mass as follows: (1) when $p = 1$, the plant mass per quadrat has a random pattern; (2) when $p > 1$, the plant mass has a spatial pattern with a lower heterogeneity than would be expected in the random pattern; and (3) when $p < 1$, the plant mass has a spatial pattern with a higher heterogeneity than would be expected in the random pattern. The *p* value for a given species can easily be calculated by the following equation if we use the moment method: (mean plant mass among quadrats)^2 / (variance of plant mass among quadrats). The scatter diagram of (λ, *p*) for individual plant species, exhibits the spatial characteristics of each species in the community. We illustrated two examples of the (λ, *p*) diagram from data for individual species composing actual communities in a semi-natural grassland and a weedy grassland. Frequency distributions for the plant mass of individual species per quadrat followed the gamma distribution, and indi vidual species exhibited an inherent level of spatial heterogeneity.

1. Introduction

Small-scale spatial patterns in vegetation are formed by various external factors, such as small-scale spatial variations in nutrient concentrations, water conditions, soil salinity, soil pH, grazing by animals, and plant diseases (e.g., Gokalp et al., 2010; Mallants et al., 1996; Yasuda et al., 2003). The development of spatial patterns is also related to internal factors in vegetation, such as species-to-species interactions (e.g., Kull and Zobel, 1991; van der Maarel and Sykes, 1993; van der Maarel et al., 1995; Zobel et al., 2000). Silvertown and Charlesworth (2001) reviewed the biological mechanisms leading to plant heterogeneity and classified the factors causing spatial patterns into the following six types: (1) niche separation processes, (2) spatial segregation processes, (3) recruitment limitation processes, (4) pest-pressure processes, (5) storage effect processes and (6) density independent processes. Small-scale spatial patterns of vegetation are, in general, measured by determining the frequency of occurrence, density of individuals, plant cover and biomass (Bonham, 2013). Through these measures, the vegetation structure, such as species richness and species composition, can be evaluated numerically (Shiyomi et al., 2010).

We divide the research methods of spatial pattern formation in a community into two categories: the first involves the frequency distributions of plant abundance such as the frequency of occurrence and density per unit ground area (e.g., Greig-Smith, 1964; Harte et al., 2005; Pielou, 1977; Shiyomi, 1981), and the second uses various measures of spatial series, such as fractal analysis and semivariance analysis (e.g., Manurer, 1994; Palmer, 1988; Roe et al., 2011; Schabenberger and Gotway, 2005). In this study, we refer to the first of the two methods, and focus on the frequency distribution of the mass (dry weight) of individual plant species per unit ground area.

To determine the spatial pattern of vegetation, the criterion that expresses the standard pattern of spatial distribution must be elucidated. In many cases, the standard is "random spatial pattern"; for example, in a classic index by David and Moore (1954), $I = \text{variance/mean} - 1 = 0$ indicates a random pattern in 'count' data, such as the number of aphids per plant, and in the index of Morisita (1962), $I_\delta = 1$ indicates a random pattern in count data of individuals.

Since the spatial pattern of a single plant species in a community is influenced by 'continuous' variables such as cover and plant mass (weight), these continuous variables also have to have criteria to determine the pattern. In this paper, we propose a criterion to determine the spatial pattern of mass for a plant species and accordingly consider a model of the spatial pattern.

Shiyomi et al. (1983) attempted to fit a frequency model of total plant mass constructing a plant community per unit ground area using a gamma distribution. The frequency distributions of the mass of pooled plant species per unit ground area were recorded under various stocking rates, and were fitted to the gamma distribution. Chen et al. (2008) reported that the gamma distribution that described the

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frequency distribution of plant mass per unit ground area could be derived from the beta distribution that described the frequency distribution of plant cover per unit ground area.

In this paper, we derive and use the gamma distribution to measure the spatial heterogeneity in mass of individual plant species. We first define ‘a random spatial pattern for mass of a single plant species’, and show that the spatial pattern of plant mass is expressed using a parameter contained in the gamma distribution. Second, we determine whether plant mass of a herbaceous species population is spatially distributed according to a pattern more or less heterogeneous than the random pattern. Next we determine whether the gamma distribution and its parameters adequately describe the spatial heterogeneity in the mass of a herbaceous plant species making up a community, based on two examples from a semi-natural grassland and a weedy grassland.

2. Model of spatial pattern for mass of a single plant species

2.1. Random pattern in mass of a plant species

For simplicity, we consider a line segment with a given length of θ (>0). Then, suppose that the line segment is cut at n random points, each of whose length from the origin is $x_1, x_2, \ldots, x_n$ ($0 \le x_i \le \theta$; $i = 1, 2, \ldots, n$), where x follows a uniform distribution and is generally referred to as a random length (Fig. 1a shows an example for $n = 3$). The density function of x, $f(x)$, is expressed as:

$$f(x) = \theta^{-1} \text{for } 0 \le x \le \theta \\ = 0, \text{otherwise}. \quad (1)$$

The $n + 1$ short segments are formed on the line segment (Fig. 1a). The small segment, y, intercepted by the adjacent two random points follows the power distribution according to the theory of order statistics (e.g., Zwillinger and Kokoska 2000). That is, y is a new random length following the power distribution. The density function of y, $f(y)$, is expressed by the following form:

$$f(y) = n(\theta - y)^{n-1}\theta^{-1} \text{for } 0 \le y \le \theta \\ = 0, \text{ otherwise}. \quad (2)$$

The mean and variance of Eq. (2) are expressed as $\theta(n+1)^{-1}$ and $n\theta^2 (n+1)^{-2}(n+2)^{-1}$, respectively.

Now, under the condition of $\theta n^{-1} = \lambda$: constant, for $\theta \to \infty$

$$f(y) = n(\theta - y)^{n-1}\theta^{-1} \to e^{-y/\lambda}\lambda^{-1}, \text{ for } y \ge 0, \lambda > 0, \quad (3)$$

in which the short segment of y with a random length approaches asymptotically a random distribution according to the exponential distribution (Eq. (3)) (Fig. 1b), and the mean and variance of the right side of Eq. (3) approach: $\theta(n+1)^{-1} \to \lambda$ and $n\theta^2 (n+1)^{-2} (n+2)^{-1} \to \lambda^2$, respectively. Therefore, in Eq. (3), [mean]^2 / [variance] = 1. We define the following three situations in spatial pattern of y: (1) if [mean]^2 / [variance] = 1, y randomly distributes spatially based on the above definition; (2) if [mean]^2 / [variance] > 1 (i.e., the standard deviation is relatively small compared to the mean), y distributes with a lower spatial heterogeneity than would be expected in a random case (the larger [mean]^2 / [variance], the lower the heterogeneity is) and; (3) if [mean]^2 / [variance] < 1 (i.e., the standard deviation is relatively large compared to the mean), y distributes with a higher

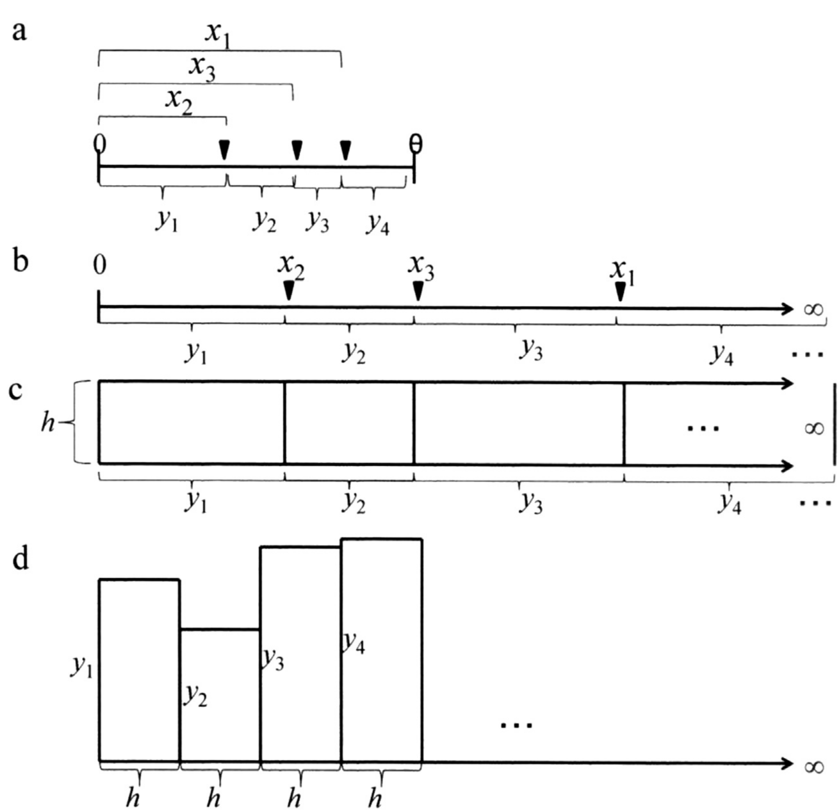

Fig. 1. The random spatial pattern of plant mass. (a) Three lengths, x_1, x_2 and x_3, generated according to the uniform distribution from the origin on a line segment with finite length of θ (Eq. (1)). Four small segments with lengths of y_1, y_2, y_3 and y_4, in that order from the origin follow a power distribution (Eq. (2)). (b) An extension of the line segment of length θ to a half-line with an infinite length. Short line segments of y_1, y_2, … (in order from the origin) follow an exponential distribution. (c) When the same plant mass, h, lies at any point of the half-line, the area of each small rectangle with a given height h on the half-line, i.e. $h \times y_i$, represents the plant mass on a small segment of y_i, and follows the exponential distribution, which is random according to the exponential distribution. (d) Let us exchange the height and width of each rectangle in Fig. 1c, that is, suppose that $y_i \times h = z_i$ indicates (the plant mass density) × (the quadrat size on the ith quadrat). Then, each z_i follows an exponential distribution.