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A mini review on theories and measures of interspecific associations

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Abstract

Ecological community is a self-organizing system. Interspecific association is the conceptual basis of direct or indirect interactions between species. In present paper we made a brief review on theories and methods of interspecific associations. Some measures for interspecific associations were given.

Keywords interspecific associations; measures; theories.

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1 Introduction

Interspecific association is an important feature of ecological communities. It is the foundation for the formation and evolution of ecological communities. To measure interspecific associations is of great significance for understanding the formation of spatial patterns of populations, population evolution and community succession (Clements, 1916; Callaway, 1995; Ollerton et al., 2003; Palmer et al., 2003; Kuželová and Chytrý, 2004; Bruno et al., 2003; Meyer, 2006; Waterman and Roth, 2007; Menzel et al., 2008; Meyer, 2006; Haugaasen and Peres, 2009; Hegland et al., 2009; Nansen et al., 2009; Desbiez et al., 2010; Oliveira and Dietz, 2011; Lan et al., 2012; Gonzalez-Moreno et al., 2013). Under the same environmental conditions, a positive association may implicit some degree of beneficial interaction, for example, mutualism or complementary resource-partitioning, while a negative association may indicate the detrimental interaction between two species, such as interspecific competition, or interspecific interference. Interspecific association is sourced from evolution. All species tend to maximally benefit from interspecific associations (e.g., improve feeding rate) while minimize the cost and risk led by interspecific associations (e.g., predation). There are many measures for interspecific associations (Qi, 2003; Zhang et al., 2004; Zhang, 2007, 2012a, 2012b, 2012c). Each measure has its own advantages and restrictions.

2 Theory and Methods of Interspecific Associations

Ecological communities are self-organizing systems (Zhang, 2013). They are important components in maintaining the stability of ecosystems. Ecosystems are maintained by interactions between the environment

and communities. So the mechanism of community dynamics and evolution has been an important topic in ecology studies. The core of this mechanism is interspecific associations. Interspecific associations are affected by the environment, and vice versa. So far, a variety of measures and theory for interspecific associations have been proposed. Here interspecific associations is a broadly defined terminology, which refers to interspecific, inter-ecosystem and other types of associations.

The theories and methods of interspecific associations are different for animal communities and plant communities. Comparing to plant communities, interspecific associations in animal communities are usually more complex and more un-deterministic. Interspecific associations in animal communities occur at various trophic levels. However, they occur mostly at the same trophic level in plant communities. Regardless of the methods used, we always focus on negative/positive/no significant associations, and the extent of these associations.

2.1 Overall interspecific associations of plant species

Research on interspecific associations of plant species will help to reveal the mechanism of interspecific replacement in the community succession, and to provide theoretical basis for vegetation restoration and reconstruction. Most of research on interspecific associations of plant species focuses on trees in the forests. Researchers have measured the change of interspecific associations between seedling stage, growth stage and adult trees and found that interspecific associations and aggregation degree from seedling stage, growth stage, onto adult trees decreased gradually. The positive interspecific associations between adult trees were guessed to be a result of facilitation (Lan et al., 2012).

For plant communities, measured interspecific associations are largely influenced by sample size and sampling coverage. Interspecific associations measured in the local area are relatively significant, but as the increase of sampling scale, they decrease or even change from positive (negative) to negative (positive).

Different from animals, plants usually disseminate their seeds through gravity, wind, and some animals as insects in order to reproduce themselves. Therefore their interspecific associations are distinct from animals.

Researchers always detect the whole interspecific associations of all species within a certain geographical area by using statistic methods (Fang et al., 2012). The overall interspecific associations are static relationships and can not only reflect the stability of communities but also include spatial distribution information.

A positive interspecific association of plant species may implicit two possibilities. The first possibility is that two species have similar living phenotypes and resource utilization patterns, and thus they compete with each other strongly. Ecological niches of the two species are highly overlapped. However, as the advance of community succession, a species will replace another one and become dominant species. The second possibility is that two species are dependent on each other during the long period of co-evolution. The two species cooperate to utilize resources and result in the mutualism. A negative interspecific association means that two species have different resource-utilizing patterns. They require different habitats and their ecological niches are separated. The co-existence of the two species in the same community is nearly impossible.

2.2 Interspecific associations in community succession

Interspecific associations determine the direction and speed of community succession. They can represent the type and phase of a community succession.

Conventional theory held that primitive species tend to generate positive interspecific associations and the species at degraded phase tend to generate negative or no significant interspecific associations. Modern theory maintains that positive interspecific associations will increase as the advance of community succession in order to guarantee the stable co-existence of species. Nevertheless, Wang and Yu (2005) argued that too many associations, including positive associations, are detrimental to the stability of communities. So far, there is no unified and convincing theory on the relationship between interspecific associations and community

succession.

2.3 Interspecific associations of animal species

Animals can move and demonstrate individualistic and population activities. Interspecific associations are usually measured for species in different habitats. Most of studies focus on the risk and benefits resulted from interspecific associations. Ecological niches of the species with positive/negative associations do not fully overlap. At least one of two species will benefit from these associations. It should be noted that an interspecific association might be asymmetric (Menzel et al., 2008).

For animal species, interspecific associations may reduce the predation risk (Oliveira and Dietz, 2011), and the risk of competition for foraging and reproduction. Some species may associate to reduce predation risk and to increase foraging benefit.

2.4 Measures for interspecific associations

2.4.1 Point correlation (χ^2 test)

Point correlation is defined as (Zhang, 2007)

$$p_{ij} = (ad - bc) / ((a+b)(c+d)(a+c)(b+d))^{1/2}$$

where $-1 \leq p_{ij} \leq 1$, both species i and species j take values 0 (no occurrence) or 1 (occurrence). a is number of samples that both species i and species j take value 0, b is number of samples that species i takes 0 and species j takes 1, c is number of samples that species i takes 1 and species j takes 0, and d is number of samples that both species i and species j take value 1. The χ^2 -test value of point correlation is

$$\chi^2 = n(ad - bc)^2 / [(a+b)(c+d)(a+c)(b+d)].$$

If $\chi^2 > \chi^2_{\alpha}(1)$ ($\chi^2_{0.01}(1) = 6.64$, $\chi^2_{0.05}(1) = 3.84$), then interspecific association is statistically significant; $p > 0$, positive association; $p < 0$, negative association.

2.4.2 Some Boolean measures

Quadratic correlation, two angular cosine functions, and Jaccard coefficient are as follows (Zhang, 2007, 2011a)

$$\begin{aligned} z_{ij} &= 1 - (ad - bc) / ((a+b)(c+d)(a+c)(b+d))^{1/2} \\ z_{ij} &= 1 - \sin((a+d - (b+c)) / (a+b+c+d) * 3.1415926/2) \\ z_{ij} &= 1 - (a * a / ((a+b)(a+c)))^{1/2} \\ z_{ij} &= 1 - (a * a * d * d / ((a+b)(a+c)(b+d)(c+d)))^{1/2} \\ z_{ij} &= (b+c) / (b+c+d) \end{aligned}$$

where both species i and species j take values 0 (no occurrence) or 1 (occurrence). a is number of samples that both species i and species j take value 0, b is number of samples that species i takes 0 and species j takes 1, c is number of samples that species i takes 1 and species j takes 0, and d is number of samples that both species i and species j take value 1.

2.4.3 VR (Variance Ratio) measure

$VR > 1$, positive association; $VR < 0$, negative association.

2.4.4 Ochiai Index (OI)

OI is defined as

$$OI = \frac{a}{\sqrt{a+b}\sqrt{a+c}}$$

where n : sample size, a : number of samples that both species are found; b, c : number of samples that one of two species occurs; d : number of samples that both species do not occur. A high OI implies a larger probability for positive association. $ad > bc$, positive association; $ad < bc$, negative association.

2.4.5 Pearson correlation

Pearson correlation between species i and j is

$$r_{ij} = \frac{\sum_{k=1}^n ((a_{ik} - a_{i\bar{k}})(a_{jk} - a_{j\bar{k}}))}{[\sum_{k=1}^n (a_{ik} - a_{i\bar{k}})^2 \sum_{k=1}^n (a_{jk} - a_{j\bar{k}})^2]^{1/2}}$$

where, $-1 \leq r_{ij} \leq 1$, a_{ik} and a_{jk} are k -th sample of sampling set of species i and j respectively, $a_{i\bar{k}}$ and $a_{j\bar{k}}$ are means of a_{ik} and a_{jk} respectively, n is the number of samples. The t -test values of Pearson correlation is

$$t = r_{ij} / [(1 - r_{ij}^2) / (n - 2)]^{1/2}$$

where m is the number of species (families). If $t > t_{\alpha}$, then the interspecific correlation (association) is statistically significant; $r_{ij} > 0$, positive correlation (association); $r_{ij} < 0$, negative correlation (association).

2.4.6 Spearman rank correlation

Spearman rank correlation is defined as (Spearman, 1904; Schoenly and Zhang, 1999; Zhang, 2011b, 2012a, 2012b)

$$r_{ij} = 1 - 6 * \sum d^2 / [n(n^2 - 1)]$$

where $-1 \leq r_{ij} \leq 1$, $d = r(i) - r(j)$, and $r(i)$ and $r(j)$ are rank of an element in the sampling set of species i and j , from the smaller to the larger values in n elements. The above t -test can be used in the significance test of Spearman rank correlation. If $t > t_{\alpha}$, then the interspecific correlation (association) is statistically significant; $r_{ij} > 0$, positive correlation (association); $r_{ij} < 0$, negative correlation (association).

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