Article

Research advances in theories and methods of community assembly and succession

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Abstract

Community succession refers to the regular and predictable process of species replacement in the environment that all species had been eliminated or that had been disturbed. Community assembly is the process that species growth and interact to establish a community. Community assembly stresses the change of community over a single phase. So far a lot of theories and methods have been proposed for community assembly and succession. In present article I introduced research advances in theories and methods of community assembly and succession. Finally, continuing my past propositions, I further proposed the unified theory and methodology on community assembly and succession. I suggested that community assembly and succession is a process of self-organization. It follows the major principles and mechanisms of self-organization. Agent-based modeling was suggested being used to describe the dynamics of community assembly and succession.

Keywords community; assembly; succession; theory; methodology; research advances.

1 Introduction

There are not control and organizing centres in the evolution of community succession and assembly (Whittaker, 1979). It is in essence a self-organizing process (Zhang, 2014b). According to Young et al. (2001), community succession refers to the regular and predictable process of replacement of species composition in the environment that all species had been eliminated or that had been disturbed. Succession likely leads to the restoration of the community to the previous non-disturbing state. Community assembly is the process that species growth and interact to establish a community. Community assembly stresses the change of community over a single phase (Warren et al., 2003). Community assembly may likely lead to a diverse and stable community.

Different from the power-law mechanism of node growth in the network, which species can join the community and how much species can be contained in a community is determined by specific mechanism.

Theory on community assembly provides basic rules for species assembly (Chase, 2003; Zhang, 2012c). Community assembly rule was firstly proposed by Diamond in 1975. He held that community assembly is the process that species in the regional species bank join the local community through the multiple-layer filtering of the environment and biological interactions (Diamond, 1975; Wang et al., 2014; Zhang, 2014b). Wilson and Roxburgh (1994) maintained that the rules for plant community assembly are a series of potential rules restricting the presence or increase of species. So far, many rules have proposed. However, the most accepted rule is species co-occurrence hypothesis proposed by Diamond (1975). About the community assembly mechanism, Fukami (2010) defined the mechanism of community assembly as a construction and conservation process of local community through sequential arrival of species from the external species bank and increase/extinction of species in the community. Ecological niche theory and neutral theory are two important interpretations of the community assembly mechanism. Methods used in community assembly include establishing research plots, indoor simulation, etc. In addition, methods of community succession can be used in community assembly research.

Community succession is one the most important topics in ecology. It was firstly discussed by Clements in 1916. Community succession is suggested to be studied at landscape level (spatial heterogeneity and disturbance, etc.) (Margalef, 1968). The rules and directions of community succession have been disputed among ecologists (Connel and Slatyer, 1977). Major theories on community succession include relay floristic hypothesis, initial floristic composition hypothesis, C-S hypothesis, life history strategy hypothesis, resource ratio hypothesis, Odum-Magelef's ecosystem development hypothesis, McMahon system concept model, shifting mosaic steady state hypothesis, and scale and hierarchical system hypothesis, etc. Research of community succession can be performed in two ways: a long period of survey in the same research plot, or multi-site sampling in a large area to replace time costing survey in the same plot.

The theory of community assembly holds that ecological drift and niche differentiation lead to the formation of the community. However, the theory of community succession maintains that the formation of a community is predictable. It is a process towards a certain direction. Young (2001) suggested that both of them try to understand the mechanism of community formation; they emphasize the history of community formation; both recognize that the community tends to be stable over the time, and both of them recognized the role of interspecific interactions, in particular competition.

2 Theories and Methods on Community Assembly

2.1 Concept of community assembly

Community assembly can be divided into two categories, habitat filtering and micro-environment/resource blocking. Micro-environment/resource herein generally can restrict similar species in the community (Cornwell and Ackerly, 2009). Community assembly might be constrained by local (abiotic characteristics of habitat) or regional (composition of species pool, habitat isolation) factors (Bossuyt et al., 2005).

2.2 Theories on community assembly

2.2.1 Ecological niche theory

As early as in the 1895, Warming pointed out that the similar phenotypes shared the same habitat. Niche theory holds that the similar habitats in different regions will finally harbor the plants with similar physiological characteristics. And plant phenotypes may match their environments in a predictable way. The theory emphasizes that the differences in habitat or resource requirements of species and in environmental influences greatly affect the outcome of interspecific interactions (Chase and Leibold, 2003).

Competitive exclusion principle, proposed by Gauss, has become one of the core paradigms in community ecology. It points out that two species with the similar ecological niche requirements will be

impossible to live together. Competition between the species with the similar fundamental eco-niches constrains their long term co-existence (Maherali and Klironomos, 2007). Differentiation in habitat, food spectrum, activity time or other biological habits will occur if they live in the same environment. It means that some species will extinct if a species successfully joins the community (Weiher and Keddy, 1999). The species belonging to the same family might be impossible to survive in the same habitat. The community with more niche resources may accommodate more species (Bossuyt et al., 2005).

2.2.2 Neutral theory

Ecological niche theory is unable to explain the extreme biodiversity in the rain forests. Thus the neutral theory, i.e., neutral mutation and random genetic drift, originated from molecular evolution, was used to describe community assembly. This theory states that most molecular mutations contributing to the evolution are neutral or nearly neutral in the sense of natural selection; the evolution of neutral mutations is a process of random genetic drift: they may be fixed in the population or disappear. It assumes that all species and individuals at the same trophic level are completely equivalent. Random walk and richness of species in the community are dependent upon the dynamic equilibrium between species formation, extinction and immigration. In this situation, the relative abundance of every species coincides with logarithmic series distribution (for assembly communities that speciation by point mutations) or polynomial distribution (pervasion constrained local community or randomly species formed assembly community). In general, neutral theory emphasizes the equivalence of individuals at the same trophic level rather than species differences in ecological niches.

The unified neutral theory was proposed by adding speciation rate in the neutral theory (Chisholm and Burgman, 2004). It assumes that all individuals in the community are equivalent. Nevertheless, neglection of interspecific differences cannot explain species differences in environmental response and invasion capacity.

2.2.3 Incorporation of niche theory and neutral theory

Assembly and construction is probably the outcome of joined action of random ecological drift and niche differentiation. So niche theory and neutral theory can be incorporated to interpret the mechanism of community assembly (Chase, 2005; Gravel et al., 2006). Harte (2004) suggested treating neutral theory as the null model of community assembly. Gravel (2006) put forward the neutral - niche continuum hypothesis. It predicts that when the community saturates due to niche complementary, the immigration of propagules will preserve the redundancy of species in the community, and ecological drift can increase species richness (Purves and Pacala, 2005; Leibold and McPeek, 2006). Random niche theory, proposed by Tilman in 2004, holds that the community assembly is in essence a process of continuous species invasion.

2.2.4 Assembly historical

Assembly history is particularly important to small communities, probably due to the priority effect of earlier arrived species (Fukami, 2004). Assembly history is also significant to community structure.

2.3 Research methods of community assembly

2.3.1 Agent-based modeling

Zhang (2012a, 2013, 2014a, 2014c) pointed out that agent-based modeling (ABM) should be used as the core methodology for community assembly, and methodological details for constructing communities using ABM were discussed. The mechanisms represented by both neutral theory and niche theory are seamlessly incorporated in agent-based modelling: species are the parental agents and individuals are offspring agents.

2.3.2 Phylogenetic analysis

Using phylogenetic analysis method to approach assembly rules of local forest communities is a research focus. Ge et al. (2012) used the three fragments (rbcL, matK and psbA-trnH) commonly used in plant barcodes, the plant DNA barcodes and Phylomatic method to build the phylogenetic relationship of 183 woody plant species

in a forest community of Dinghushan. The results revealed that the closely related species coexisted in low-elevation habitats and habitat filtering may play a leading role; the species being phylogenetically distant coexisted in high-elevation habitats and competitive exclusion may play a leading role.

2.3.3 Network analysis

Ecosystems are highly self-organizing and self-developing network systems. An ecological network is a network of interactions for material, energy flows between different compartments. Structural network analysis has become effective tool to study structural and internal changes in ecosystems (Bailey, 2004; Fath, 2004; Fath et al., 2007; Zhang, 2012a).

Some researchers have built the predation structures of some communities using network analysis, in which primary producers, herbivores, and carnivores were included but they lacked of decomposers and detritivores. Therefore, the networks lacked of matter circulation. These networks include cascade model (Cohen and Newman, 1985) and habitat model (Williams and Martinez, 2000). Some other networks included energy flows and functional groups and thus are relatively perfect models (Fath et al., 2007).
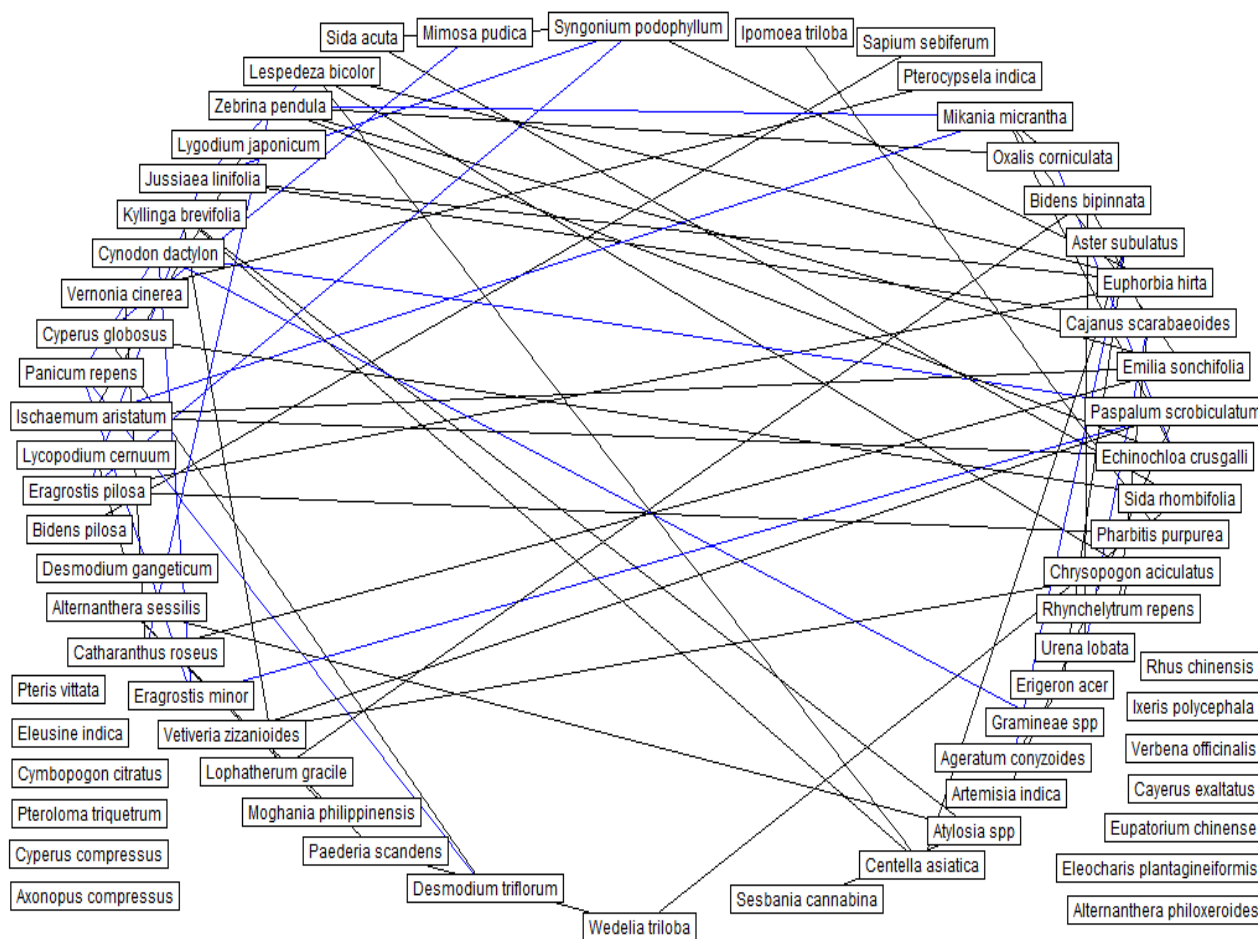

Fig. 1 Interspecific association network, constructed from partial linear correlation measure. Blue lines denote negative associations and black lines denote positive associations (From Zhang, 2012b).

For those networks without full knowledge on interspecific associations, in particular the large scale food webs, Zhang (2011, 2012b, 2014b) used interspecific correlation measures to construct networks with indirect or direct interactions, and proposed the concept, theory and methodology of statistic networks (Fig. 1).

Moreover, Zhang (2012b, 2014b) found that many species in a community are redundant species and they are important for robustness of the community.

2.3.4 Species - area relationship analysis

Using species - area relationship analysis, Gong et al. (2011) found that the importance of the same species was different at different phases for different communities.

2.3.5 Spatial pattern analysis

Spatial distribution patterns may reflect the situation of interspecific interactions (Li et al., 2014).

2.3.6 Pedigree structure analysis

With the rapid development of techniques in molecular biology, the methods of systematic evolution have been applied to the studies of community ecology. Pedigree structure analysis is used in the community assembly for two reasons: (1) one is that community assembly is treated as a process of random ecological drift of equivalent individuals (Hubbell, 2001), and the null hypothesis of this theory is that the assembled community is composed of species (the number of species is equal to the observed richness of the community) randomly selected from species pool, which is in essence similar to the neutral theory; (2) the aggregation or divergence of pedigree structure means the habitat filtering or competitive exclusion, which emphasizes the non-equivalence of different species and thus acknowledges niche theory. Therefore pedigree structure analysis can be used to analyse the major factors of community assembly by analysing phylogenetic linkages between species and to explore the effect of historical factors on the community (Webb et al., 2002). Pedigree structure analysis is considered as a combined solution of neutral theory and niche theory (Cavender-Bares et al., 2009).

3 Theories and Methods on Community Succession

3.1 Concept of community succession

Community succession is a phenomenon or process by which an ecological community undergoes more or less orderly and predictable changes following a disturbance or initial colonization of new habitat (Connell and Slatyer, 1977). It is the observed process of change in the species structure of an ecological community over time. The community begins with relatively few pioneering plants and animals and develops through increasing complexity until it becomes stable or self-perpetuating as a climax community (Wikipedia: http://en.wikipedia.org/wiki/Ecological_succession; Fig. 2). In general, succession is composed of three phases: (1) invasion and colonization. Some pioneer species invade and colonize in the barren land, change the environment, and thus lay basis for successive invasions of other species. (2) Competition and equilibrium. Some species survive in the competition and some species extinct. The coexisting species reach an equilibrium state in utilizing resources. (3) Relatively stable state. Species composition and abundance are relatively fixed. Food web is complex and stable. However, so far there is not widely recognized pattern and theory on community succession (Lebrija-Trejos et al., 2010).

3.1.1 Types of community succession

There are two kinds of successions, i.e., primary succession and secondary succession. Succession that begins in new habitats that uninfluenced by pre-existing communities is primary succession, whereas succession that follows disruption of a pre-existing community is secondary succession. Succession can be classified as century succession, long term succession and short term succession. It can also be identified as autotrophic succession, heterotrophic succession and relatively stable climax.

3.1.2 Influential factors of community succession

External natural factors dominating community succession include fire, drought, CO_2, storm, volcano eruption, etc.

Fig. 2 A birch forest community in Mohe County, Heilongjiang Province, China.

3.2 Theories on community succession

3.2.1 Promotion theory

Promotion theory was first proposed by Clements in 1916. The theory held that the plant community is a super-organism. This organism is highly integrated. Through succession, a community can develop into a single climax community. Development of community is orderly and successive. It develops from a pioneer community into a complex climax community. Succession is powered mainly by the interactions between organisms and between organisms and the environment. The development of the present phase will promote the development of the next phase. The succession is directional and predictable. Species composition and environmental characteristics are predictable. The winner species in the competition becomes the dominant species, but after a certain time, the new species with stronger competition capacity will become the new dominant species.

3.2.2 Initial floristic composition theory

The theory argued that succession is highly heterogeneous (Egler, 1954). It will not certainly proceed towards a climax community. Succession is a continuum and it is a species replacing process rather than community replacing process. Succession process is determined by the initial floristic composition at the earlier phase of the succession. The species in the initial floristic composition are randomly occurred. Succession is unpredictable.

3.2.3 Resource-ratio hypothesis

Tilman (1985) maintained that the change in resource-ratio leads to the change of competion relationship and thus results in community succession.

3.2.4 Tolerance hypothesis

Connell and Slatyer (1977) suggested that succession occurs through facilitation, inhibition and tolerance between populations. They thought that the pioneer species are not important and any species can start succession. Species replacement reduces as the decrease of resources. And more tolerable species to resource deficiency will replace the sensitive species.

3.2.5 Life history strategy hypothesis

Grime (1988) thought that the pattern of species strategies in the succession is predictable. He argued that the secondary succession is predictable. R-strategy species (which are adaptable to the environment with abundant resources temporarily) are pioneer species, C-strategy species (which are adaptable to the environment with abundant resources eternally, and are thus called competitive species) occur in mid-succession, and S- strategy species (which are adaptable to the environment lacking of resources, and are thus called tolerance species) are dominant in the climax community.

3.2.6 Mosaic theory

Bormann and Likens (1979) proposed that community succession is free of external disturbance. It should be a sponteneuous and self-controlled process.

3.3 Research methods of community succession

3.3.1 Long-term observation of fixed plots

In this method, fixed plots are observed for dozens or even hundreds of years. Species composition, environmental factors and other data are recorded in detail.

3.3.2 Space-time replacement

The community succession in different regions will be similar to each other if the environmental conditions of these regions are similar (Ladislav, 2010). Thus we can record the full process of succession of a community over different regions.

3.3.3 Mathematical and GIS/GPS/RS methods

A typical mathematical method used in community succession is the state transition probability models, including Markov chain (Zhang and Wei, 2009). GIS, GPS and RS are powerful tools for community succession research.

4 A Unified Theory and Methodology on Community Assembly and Succession

Continuing my past propositions, here I further propose the unified theory and methodology on community assembly and succession. Community assembly and succession is a process of self-organization; it follows the major principles and mechanism of self-organization (Zhang, 2013, 2014c). Multi steady states are available for community succession. The community assembly and succession is unpredictable. Agent-based modeling can be used to describe the dynamics of community assembly and succession. Full details on self-organization and agent-based modelling, can be found in Zhang (2012a, 2013, 2014a, 2014c).

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