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Quantifying ecological memory during forest succession: A case study from lower subtropical forest ecosystems in South China

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ABSTRACT

The concept of ecological memory provides a new perspective for research on forest succession by including historical factors and the initial state of ecological processes. However, there are still significant gaps between the concept and its application. We selected nine proxy indicators (plant species, soil seed banks, soil microbes, soil animals, birds, soil age, soil pollen, soil mineral distribution, and light environment) and developed a method to quantify ecological memory and succession in a subtropical forest succession in South China. Taking the climax-monsoon evergreen broad-leaved forest as the reference ecosystem, we found that ecological memory increased nonlinearly and accumulated following a specific assembly rule during succession. Memory concerning major soil microbes and soil animals, which improve the soil substrate, mainly accumulated from the initial to the early successional stage. Memory concerning the number of bird species and the availability of light, which ensure a source of regenerative seeds and the survival of understory seedlings, mainly accumulated from the early to middle successional stages. Memory concerning vegetation and soil seed banks mainly accumulated late in succession, guaranteeing that the ecosystem would reach the regional climax stage. Prospective memory was greater than retrospective memory in every successional stage except the late stage, which indicated that all stages but the late stage were undergoing progressive succession. Our study demonstrates that the concept of ecological memory and the proposed evaluation framework are useful for guiding research on succession and restoration, and especially for assessing how "far" a restored ecosystem is from a reference ecosystem or how far a restored ecosystem has deviated from its natural succession trajectory.

1. Introduction

Ecological processes are strongly influenced by historical events (Levin, 1998; Scheffer et al., 2001). Past ecological states and experiences can influence the present or future responses of the community, consequently shaping the dynamic patterns of community coalescence and constraining the trajectory of an ecosystem (Dupouey et al., 2002; Egan and Howell, 2005). Ecological memory is the comprehensive assemblage of information encoded in remnant resources that can reflect the historical disturbance, current situation, and future trajectory of the community or ecosystem (Padisák, 1992; Nyström and Folke, 2001; Schaefer, 2009; Sun and Ren, 2011). The concept of ecological memory is fundamental to understanding spatial resilience and self-organization (Zinck and Grimm, 2009), the relationship between geomorphology and ecology (Stallins, 2006), the renewal cycle in succession (Bengtsson et al., 2003), landscape dynamics (Peterson, 2002), invasive species outbreaks, and urban ecosystem management (Andersson, 2006; Schaefer, 2009). Because it includes remnant resources, such as plants, animals, and the soil seed bank, ecological memory is likely to affect system development following disturbance.

Ecological memory was first defined as "the capacity of past states or experiences to influence present or future responses of the community" in the context of succession in freshwater ecosystems (Padisák, 1992), and subsequent papers focused on aquatic ecosystems (Arauzo and Alvarez Cobelas, 1994; Whillans, 1996; Holmlund and Hammer, 1999; Straile, 2000; Nyström and Folke, 2001). Peterson (2002) then used a simulation model to examine how ecological memory shaped landscape dynamics. A number

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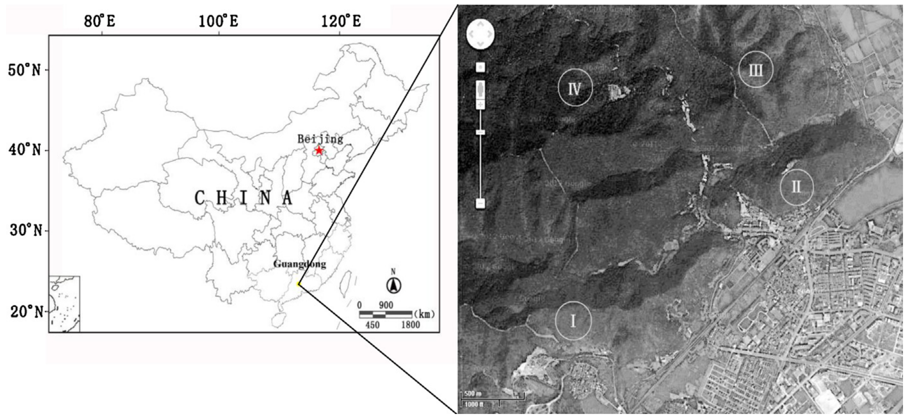

Fig. 1. Location of the study sites.

of terrestrial ecologists began to realize the value of the ecological memory concept for understanding how terrestrial systems absorb disturbances, reorganize, and maintain adaptive capacity (Moberg and Rönnbäck, 2003; Phillips and Marion, 2004; Walker et al., 2006). Ecological memory has now developed into a complex and comprehensive concept. It consists of external memory, internal memory, and mobile link species that occur on a spatial scale, and retrospective memory (reflecting the past disturbance) and prospective memory (reflecting the future trajectory) that occur on a temporal scale (Nyström and Folke, 2001; Bengtsson et al., 2003; Lundberg and Moberg, 2003; Sun and Ren, 2011).

The concept of ecological memory, however, has yet to be applied to the study of forest succession and restoration. The concept also lacks a specific indicator framework for assessing ecological memory. Moving from the concept to the establishment of indicators for the assessment of ecological memory has been a substantial challenge (Thompson et al., 2001; Golinski et al., 2008; Schaefer, 2009; Sun and Ren, 2011).

In the current study, we selected nine proxy indicators of ecological memory (plant species, soil seed banks, soil microbes, soil animals, soil mineral distribution, soil age, soil pollen, light environment, and birds) from previous conceptual definitions. We then quantified these indicators and integrated them into an evaluation framework. Finally, we tested the value of this evaluation framework for the study of a successional gradient in a lower subtropical forest in the Dinghushan Natural Reserve, South China. We used the framework to answer the following questions: (1) How does ecological memory accumulate during forest succession in lower subtropical areas? (2) How do retrospective and prospective memories affect forest succession?

2. Methods

2.1. Study sites

The study was conducted in the Dinghushan Natural Reserve (23°09′21″–23°11′30″ N, 112°30′39″–112°33′41″ E), Guangdong, South China (Fig. 1). The reserve was established in 1956. The region has a subtropical monsoon humid climate. The mean relative humidity is 80.8%. The annual mean temperature is 20.9 °C. The mean annual rainfall is 1927 mm, and more than 80% of this total occurs from April to September. The predominant soil types in this region are lateritic red-earth and yellow-earth (Huang et al., 1998). The study area is ideal for research on the succession of forest ecosystems because the typical forests in the area represent the forest successional sequence prevailing in subtropical China (Peng, 1996).

An abandoned grassland, a *Pinus massoniana* forest, a pine and broad-leaved mixed forest, and a monsoon evergreen broad-leaved forest were selected to represent the early (stage I), medium (stage II), late (stage III), and regional climax stage (stage IV) of forest succession, respectively (Fig. 1). The characteristics of these plant communities are listed in Table 1. Previous research demonstrated that the four stages represent a chronosequence of forest succession in subtropical China (Peng, 1996; Zhang et al., 2011).

2.2. Selection and integration of proxy indicators

2.2.1. Proxy indicator selection

Application of the ecological memory concept requires the selection of indicators of ecological memory. Ecological parameters and indicators span broad levels of biological, spatial, and temporal organization within ecosystems (Niemi and McDonald, 2004). The ideal suite of indicators should represent the key information about both the structure and function of an ecosystem; the ideal suite also should include key variables that affect ecosystem structure and function and should consist of indicators that can be easily and routinely measured (Dale and Beyeler, 2001; Gunderson and Holling, 2002). When used for the study of forest succession, indicators of ecological memory should be consistent with the concepts of both ecological memory and succession.

Schaefer (2009) concluded that "ecological memory consists of the species of an area and the ecological processes that will determine the trajectory for the ecosystem into the future". Ecological memory is generally encoded in the site history, soil properties, spores, seeds, stem fragments, mycorrhizae, species, populations, and other remnants. Based on previous definitions of ecological memory, the proxy indicators of ecological memory should also be concerned with the "evidences of processes and actions that prevailed in the past" (Whillans, 1996), the "composition and distribution of organisms and their interactions in space and time and life-history experience with environmental fluctuations" (Nyström and Folke, 2001), and the "combination of structures that make reorganization after disturbance possible" (Bengtsson et al., 2003).

Taking those previous works on ecological memory into account, we selected the following indicators to reflect the past vegetation and past ecological events of the ecosystem: soil age, soil pollen, and soil mineral distribution. The indicators chosen to reflect the present status of the community were plant species, soil microbes, soil animals, and the light environment. The soil seed bank was selected as the indicator reflecting the potential development of the ecosystem. We also selected birds as the mobile link species, which are those species whose movements in space can connect internal ecological memory and external ecological memory. All of the selected proxy indicators represent a special aspect