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Using ecological memory as an indicator to monitor the ecological restoration of four forest plantations in subtropical China

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Abstract A large area of plantations has been established worldwide and especially in China. Evaluating the restoration status of these plantations is essential for their long-term management. Based on our previous work, we used an ecological memory (EM) approach to evaluate four 26-year-old plantations that represent four common kinds of plantations in subtropical China, i.e., mixed broad-leaved plantation (MBP), mixed coniferous plantation (MCP), eucalyptus plantation (EP), and mixed legume plantation (MLP). Comparing them with the regional climax community, i.e., monsoon evergreen broad-leaved forest (BF), all four plantations accumulated nearly the same pattern of EM during succession. EM was >50 % for soil minerals, light conditions, soil age, soil animals, and soil microbes. EM was about 25 % for soil pollen and 10 % for birds, soil seed bank, and plant species. The total EM value of the four plantations ranged from 50.96 to 52.54, which indicated that all four plantations were in the regional, natural trajectory of succession and between the early and medium successional stages. The results indicated that natural succession processes are unlikely to be accelerated by planting late-stage tree species without sufficient EM. The results also demonstrated that all four plantations were in positive successional trajectories, and the positive succession dynamics were greater in the MLP and MCP. We suggest that the entire natural succession trajectory be used to evaluate the restoration of a site and that the ultimate restoration target be divided into several milestones along the reference trajectory to monitor progress. Forest restoration may be accelerated by starting with a minimum dynamic unit supporting sufficient EM.

Keywords Evaluation approach · Forest restoration · Succession trajectory · Plantation · Ecosystem dynamic · Reference ecosystem

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Introduction

The area and quality of the world's forest resources have declined significantly in recent decades. The Food and

Agriculture Organization of the United Nations (2010) reported that approximately 13 million ha of forest have been converted to other uses or have lost their naturalness each year over the last decade. The extent of environmental degradation and deforestation underscores the urgent need for interventions to restore biodiversity, ecological functioning, and ecological services (Lamb et al. 2005). Many countries have carried out large afforestation or restoration projects to satisfy various ecological and social economic needs (Mansourian et al. 2005). These projects have achieved some positive results with respect to restoring biodiversity and ecological services. Restoration projects and large-scale afforestation, especially in China, have significantly reduced the net loss of global forests (Food and Agriculture Organization of the United Nations 2010). As of 2008, China's forest covered 195 million ha of which 62 million ha is plantation, an increase of 4.5 to 31.8 % from 1950 to 2008 (Ren et al. 2012) and the largest area of forest plantations in the world. However, this large area of artificial ecosystems raises a series of questions, which include the following: How should the success of forest restoration be evaluated? What are the ecological effects of different types of plantations? Do plantations develop along a natural trajectory or do they deviate toward novel ecosystems (Hobbs et al. 2014)? Many criteria or guidelines have been used to evaluate the success of efforts to restore forest plantations (Bautista et al. 2009). They are based on various qualitative and quantitative variables such as biodiversity, productivity, density, cover, abundance, species richness, growth, and biomass (Reay and Norton 1999; Vallauri et al. 2002; Martin et al. 2005; Ruiz-Jaen and Aide 2005). Some of these indicators, however, have weak theoretical support, and most of these approaches neglect the influences of historical events and the various initial circumstances of the communities. Ecological memory (EM) has recently received attention as an important variable in the evaluation of restoration success because it is closely related to ecosystem dynamics and resilience (Schaefer 2009; Sun and Ren 2011). EM is defined as the comprehensive assemblage of the information encoded in remnant resources at a location. It reflects the site's historical disturbance and current status and contributes to the future trajectory of the community or ecosystem (Padisák 1992; Nyström and Folke 2001; Schaefer 2009; Sun and Ren 2011). EM consists of internal memory, external memory, and mobile links in a spatial scale and of retrospective memory and prospective memory in a temporal scale (Nyström and Folke 2001; Sun and Ren 2011). Internal memory refers to ecological legacies within the ecosystem, i.e., those organisms, organic materials, and organically generated environmental patterns from the previous ecosystem that persists and can affect the development of the current and future ecosystems (Lundberg and Moberg 2003). External memory refers to refugia of organisms outside the disturbed area that can serve as sources of plants and animals for the recolonization of the disturbed area. Mobile link species are those components of external memory that can transport organisms into the disturbed area through immigration, i.e., that can transform external memory into internal memory. Retrospective memory (RM) and prospective memory (PM) exist in natural succession processes and have a close relationship with ecosystem dynamics (Sun et al. 2013). RM can "remember" the past ecological events and situation, which helps the disturbed ecosystem return to its previous stable stage. PM takes charge of "remembering" the succession direction and ensures that the ecosystem develops following a natural succession trajectory. The difference between RM and PM reflects the extent of resilience and dynamics of the ecosystem (Sun and Ren 2011). Unlike previous guidelines, the conceptual model of EM considers ecological hysteresis (the possibility that multiple states may exist under the same current environmental conditions) and provides a theoretical foundation to relate natural succession processes with forest restoration projects. Sun et al. (2013) selected nine proxy indicators (soil age, soil pollen, soil mineral distribution, plant species, soil microbes, soil animals, soil seed bank, light environment, and birds) for EM and integrated them into an evaluation framework that was used to evaluate the change of EM in subtropical forest succession. They found that EM might determine the character of early forest succession and it was a useful tool for guiding restoration efforts. In this paper, we used the EM framework which Sun et al.(2013) built to evaluate four 26-year-old restored forest plantations, and attempted to determine if EM can be used to guide efforts to restore forest ecosystems. We try to answer the following three questions: (1) Is the EM framework appropriate for evaluating restoration efforts? (2) To what degree has the four plantations achieved natural succession trajectory? (3) How to use EM approach to evaluate the restoration efforts and guide plantation management?

Methods

Study site

The study was conducted at the Dinghushan Natural Reserve (23° 09′ 21″–23° 11′ 30″ N, 112° 30′ 39″–112° 33′ 41″ E) and the Heshan National Field Research Station of Forest Ecosystem (112° 50′ E, 22° 34′ N) in Guangdong, South China. The two research sites are about 100 km apart and were established in 1956 and 1984, respectively (Fig. 1). The regional climate is subtropical monsoon, and the soils are acrisols. The mean annual rainfall is 1,534–1,927 mm, with nearly 80 % of the precipitation occurring in the wet season, i.e., from April to September. The mean annual temperature is 20.9–22.5 °C, and the regional climax plant community is a lower subtropical monsoon evergreen broad-leaved forest (Peng 1996). In this study, we selected one climax community, i.e., an evergreen broad-leaved forest (BF) that was about 400 years old, in the Dinghushan Nature Reserve as a natural reference ecosystem. Then, we used EM as an indicator to evaluate the progress of natural succession of the following four restored forest plantations at the Heshan National Field Research Station of Forest Ecosystems: a mixed broad-leaved plantation (MBP), a mixed coniferous plantation (MCP), a eucalyptus plantation (EP), and a mixed legume plantation (MLP). The four kinds of plantations are the most common artificial forests in South China. The selected four experimental plantations were established on a homogeneous degraded hilly substrate in 1984. The dominant tree species and properties of the communities are described in Table 1.

Indicator selection and integration method

Indicator selection

Sun et al. (2013) considered the following three principles in selecting the proxy indicators of EM: (1) the conceptual model and definitions of ecological memory (Whillans 1996; Schaefer 2009; Schaefer 2011; Fig. 2); (2) the applicability of the indicators to forest succession (Nyström and Folke 2001; Bengtsson et al. 2003); and (3) the measurability of the indicators. Soil ^{14}C age, soil mineral distribution, and soil pollen were selected as indicators to reflect the past status and events that happened in ecosystems. Plant species, soil animals, soil microbes, and the light environment were chosen as indicators to reflect the present situations of ecosystems. Soil seed bank was used as the indicator to predict the potential developmental trends of ecosystems. Birds, a crucial component of mobile link species, were selected to measure the potential for transforming external EM into internal EM (see details in Sun et al. 2013). Every selected proxy indicator has a close relationship with the conceptual model of EM and succession dynamics.

Integration method

Sun et al. (2013) considered one natural community as a successional "stable state" moving toward the regional climax community, because ecosystem development was usually accompanied by multiple stable states (May 1977; Levin 1998). They determined that EM in a community could be evaluated by the quantity of existing "remnant resources" of the natural reference ecosystem. In this paper, we use the term RM to describe the ecological memory between a plantation and the natural, adjacent, preceding successional stage, and we use the term PM to describe the ecological memory between a plantation and the natural, adjacent, following successional stage. As Sun et al. (2013) suggested, the Bray-Curtis similarity indicator can be used to indirectly measure each kind of resource overlap ratio (Clarke and Gorley 2006), and ecological memory can be calculated with the following equation:

$$\mathrm{EM} = \sum_{i-1}^{n} \frac{\omega_i S_i}{n} = \frac{100}{n} \sum_{i-1}^{n} \omega_i \left(1 - \frac{\sum_{i-1}^{n} |y_{i1} - y_{i1}|}{\sum_{i-1}^{n} y_{i1} + \sum_{i-1}^{n} y_{i2}} \right) \quad (1)$$

Here, EM is ecological memory, S_i is the Bray-Curtis similarity of the ith indicator between the selected two ecosystems, ω_i is the weight of S_i, y_{i1} is the value of the ith indicator of ecosystem 1, y_{i2} is the value of the ith indicator of ecosystem 2, and n is the number of proxy indicators. We used the climax community for the region as the reference ecosystem to calculate the total ecological memory for each plantation. At the same time, the successional stages preceding and following that of the plantation in question were used as the reference ecosystems to calculate the retrospective

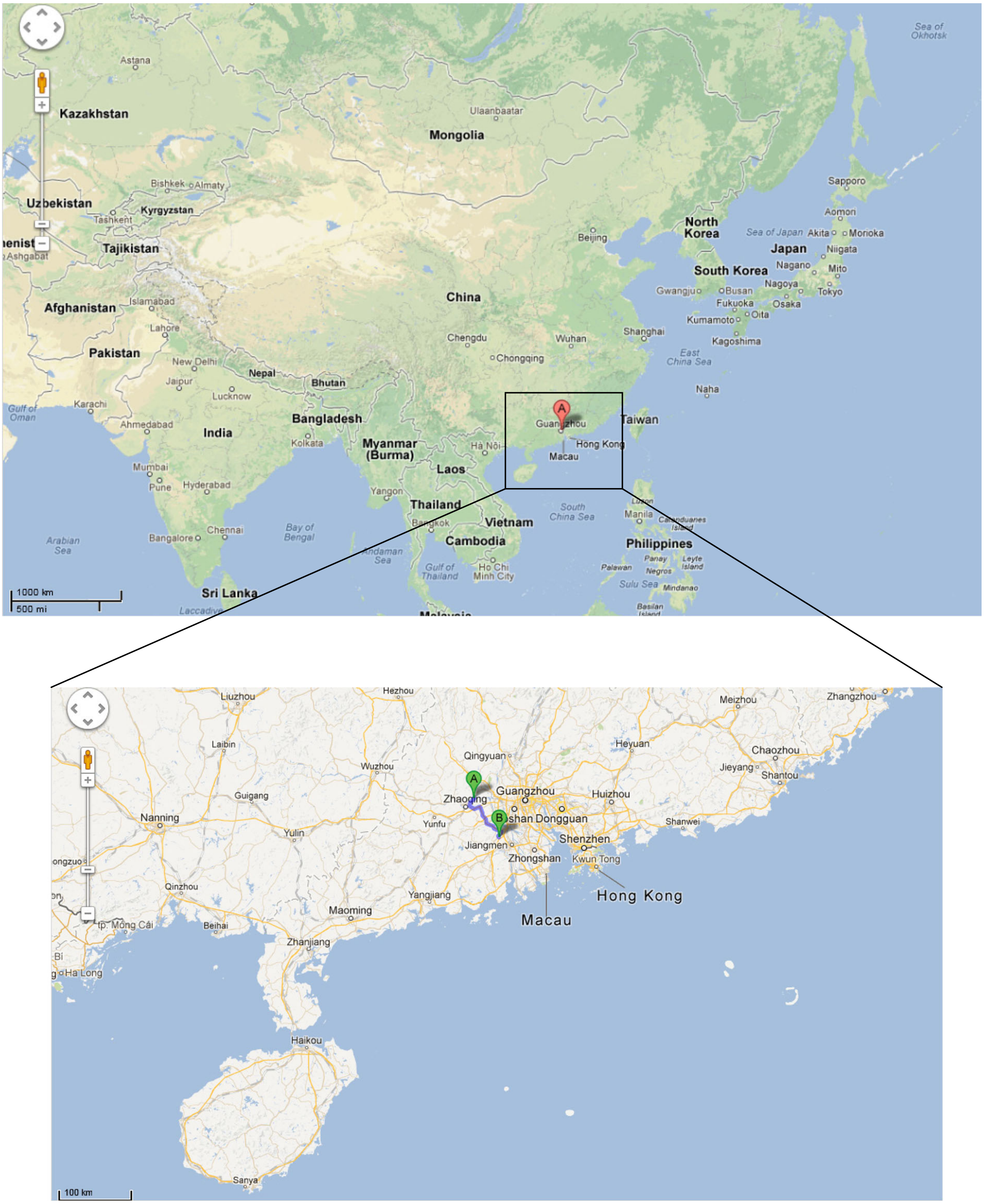

Fig. 1 The locations of the five forests. **a** Dinghushan Natural Reserve. **b** Heshan National Field Research Station of Forest Ecosystem

memory and prospective memory for each plantation. Being consistent with the research of Sun et al. (2013), we gave the same weight, "1," to each proxy indicator in this paper.

Table 1 The locations and geographic and vegetative characteristics of the five forests

Forest	Kind of plant community	Characteristic			
		Age in years	GPS coordinates	Elevation (m)	Dominant species/planted species
BF	Regional climax	About 400	112° 32′ E 23° 10′ N	230–350	*Cryptocarya concinna* Hance, *Aporusa yunnanensis* (Pax et Hoffm.) Metc., *Aidia canthioides* (Champ. ex Benth.) Masam., *Blastus cochinchinensis* Lour.
EP	Alien species plantation	26	112° 50′ E 22° 34′ N	60–70	*Eucalyptus urophylla* S.T. Blak., *Eucalyptus exserta* F.V. Muell.
MBP	Native species plantation	26	112° 50′ E 22° 34′ N	60–70	*Schima wallichii* (DC.) Choisy, *Schima superba* Gardn. et Champ., *Castanopsis hystrix* J.D. Hooker et Thomson ex A. De Candolle, *Michelia macclurei* Dandy var. *sublanea* Dandy
MLP	Alien species plantation	26	112° 50′ E 22° 34′ N	60–70	*Acacia auriculiformis* A. Cunn. ex Benth., *Acacia mangium* Willd., *Erythrophleum fordii* Oliv.
MCP	Native species plantation	26	112° 50′ E 22° 34′ N	60–70	*Pinus massoniana* Lamb., *Cunninghamia lanceolata* (Lamb.) Hook

BF broad-leaved forest, *EP* eucalyptus plantation, *MBP* mixed broad-leaved plantation, *MLP* mixed legume plantation, *MCP* mixed coniferous plantation

Data collection and analysis

Data in this research were gathered from two sources (Table 2). One source was the complementary data obtained from our field experiments carried out during 2010–2011. The other source was the general monitoring data sets of the Heshan National Field Research Station of Forest Ecosystem and relevant publications. Because the data from the second source were collected from 1990 to 2010, they might blur changes that occurred during the 20 year period and thereby reduce the precision of the EM calculation, especially with respect to succession. However, we are confident that our results largely reflect the general characteristics of the plantations because (1) ecosystem succession is a slow, long-term process lasting several decades or even hundreds of years; (2) the ecosystems in question have not crossed the successional threshold in the past 20 years; and (3) the data of the same indicator for the different ecosystems were collected in the same years. These factors should reduce any errors to an acceptable level.

Fig. 2 The procedures of the EM evaluation approach

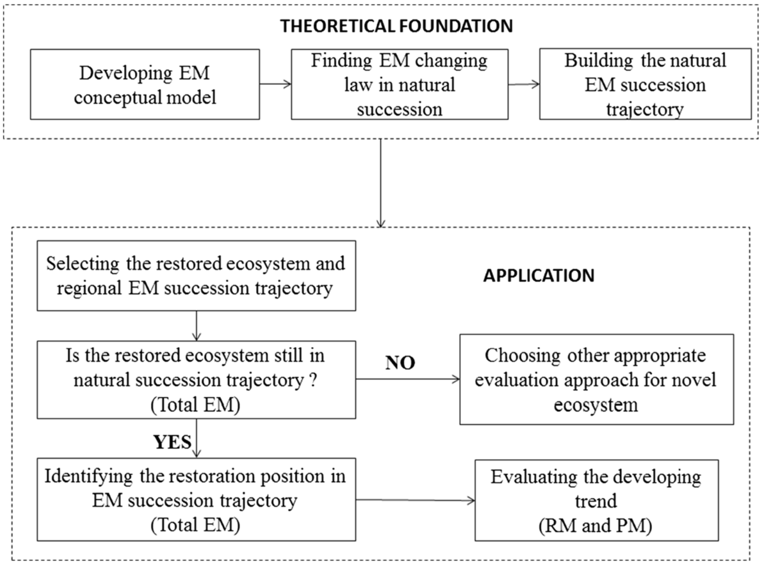

Table 2 The legacy type and data sources of the selected indicators of ecological memory

Legacy type	Indicators	Data source
Biological legacies	Plant species	The present study
	Soil seed bank	The present study
	Soil microbes	The present study
	Soil animals	Chen and Liao (1990), Liao et al. (1990)
	Birds	Zou and Yang (2005), Zhang et al. (2011)
Environmental legacies	Soil ^{14}C dating age	Shen et al. (2001)
	Soil pollen	The present study
	Light environment	The present study
	Soil mineral distribution	The present study

Vegetation investigation

Nine plots (10 m×10 m) were established in every plantation, and 20 plots (20 m×20 m) were established in the natural climax community, i.e., BF, for vegetation investigation in 2010 (see Table 2). We also randomly designated one subplot (5 m×5 m) in each plot to survey shrubs and one subplot (1 m×1 m) to survey herbs. All trees (diameter at breast height ≥1 cm) in every 10 m×10 m plot, shrubs in every 5 m×5 m subplot, and herbs in every 1 m×1 m subplot were identified and recorded. Four biodiversity indices were calculated, i.e., the Margalef index (*d*), the Shannon-Wiener index (*H*), the Simpson index (*D*), and the Pielou index (*J*).

Soil seed bank and soil microbes

Two parallel transects (5 m×25 m) 10 m apart were established on the same slope at each site in July 2010 and March 2011, which represent the typical wet and dry season in South China. Each transect was divided into five 5 m×5 m quadrats. Soil samples for analyzing the soil seed bank and soil microbes were then collected in each quadrat (see Table 2). Five soil samples of 10 cm×10 cm×10 cm (length×width×depth) were collected from each quadrat for characterizing soil seed bank. Because we focused on the seed "memory" in the soil, the seeds in the litter layer were not considered. Each sample was classified into subsamples of 0–5 and 5–10 cm depth. According to Ter Heerdt et al. (1996), the pooled samples were washed through a 2 mm sieve in order to remove soil and coarse debris. The remaining material was transferred into plastic trays with a layer of sterilized potting soil in the bottom. All trays were cultivated in an unheated greenhouse and treated with tap water. Over a 1 year period, the emerged seedlings were identified, counted, and removed as soon as possible. Soil microbes were characterized by phospholipid fatty acid (PLFA) analysis. Five quadrats that were not adjacent to each other in the two transects were sampled. In each quadrat, five soil cores (4 cm diameter and 20 cm depth, from the center and four corners of the quadrat) were collected. After litter was removed, the samples were classified into subsamples of 0–5 and 5–20 cm depth. The samples were extracted with a single-phase chloroform/methanol/buffer solution (1:2:0.8 *v*/*v*/*v*) for lipid extraction. After extraction, the lipids were separated into neutral, glycol, and phospholipids on a silicic acid column. Gas chromatography-mass spectrometry (GC-MS) (GCMS-QP2010PLUS, SHIMADZU, Japan) was used to separate and quantify the resultant phospholipid-linked fatty acid methyl esters (PL-FAME) after the methylation of phospholipids. PLFAs were classified into bacteria and fungi as suggested by Kaur et al. (2005).

Soil animals

The data of soil animals obtained in 1990 was collected from published papers identified in Table 2. In these studies, soil samples (15 cm depth) were collected with soil auger (8.5 cm diameter), and each sample was divided into three layers: 0–5, 5–10, and 10–15 cm. A Tullgren funnel was used for the collection of soil animals in the laboratory (Chen and Liao 1990; Liao et al. 1990).

Birds

The data of birds obtained in 2004 and 2010 were collected from the published papers. Point counts and mist-netting survey methods were adopted in the references (Zou and Yang 2005; Zhang et al. 2011). The species, sex, number, and activity for the surveyed birds were recorded from ten equidistant points in each forest. Ten mist nets were also randomly placed in the understory of each forest. The captured birds were banded with aluminum leg bands to calculate a capture rate.

Soil pollen, mineral elements, and age

Three soil profiles (80 cm depth) were excavated in 2011 at each research site. Soil samples at 0–5, 5–10, 10–20, 20–40, and 40–80 cm depths of each profile were collected. From each sample, we collected pollen, determined mineral composition, and performed ^{14}C dating analyses. Samples were first air-dried and then visible roots and stones were removed. Rootlets and coarse sand were subsequently removed by passing the soil through a 1 mm sieve (see Table 2). As suggested by Fægri et al. (1989), one *Lycopodium* tablet (27,673±200 grains) was added as tracer to a 2 g quantity of each sample. Then the samples were treated with 10 % HCl, 10 % NaOH, and 40 % HF and passed through a 7 μm screen. More than 200 pollen grains per sample were then identified with a microscope at ×400 magnification. Soil mineral composition was measured using the acid soluble-ICP emission spectrometric (Thomas 2004). Samples of 0.5±0.001 g of air-dried soil were heated and treated with HF, HNO_3, and $HClO_4$ in PTFE crucibles until the contents appeared as pastes. Then the pastes were transferred into a volumetric flask using dilute HNO_3. Minerals (K, Fe, Al, Na, Mg, Ca, and Mn) in the pastes were determined by an inductively coupled plasma emission spectrometer (Optima2000, PE, USA). The four plantations were relatively uniform in habitat because they were established on the same substrate and had the same disturbance history. As a result, we performed ^{14}C dating for one soil profile in the substrate of only one plantation (EP) and for only one soil profile from the reference ecosystem (Shen et al. 2001). Consistent with Ding et al. (2010), soil samples were first dried and the cohesive carbonate was eliminated with 2 M HCl, and then SOC was transformed into CO_2 in a muffle furnace (850 °C). The CO_2 was then purified in a vacuum system with liquid N_2 and liquid N_2 ethanol traps and then measured with a gas chromatograph (Agilent 6890N, Agilent Technologies, USA).

Light environment

We used the leaf area index (LAI) as an indicator to indirectly reflect the light environment of the plantation forests and reference ecosystem. The data were collected in 2010. A LAI-2000 plant canopy analyzer (LI-COR, Biosciences, Lincoln, NE, USA) was used to measure the LAI of the tree, shrub, and herb layer of each community. At each site, eight points along the same slope were selected to measure the LAI values. Five measurements were conducted in different directions in the tree, shrub, and herb layers at each point (see Table 2). The statistical software PRIMER V5.0 was used to calculate the Bray-Curtis similarity. SAS (SAS Institute Inc. 2011) was used to conduct one-way GLM and one-way ANOVA analyses.

Results

Plant species

A total of 4,289 individual plants belonging to 121 species were identified in the reference ecosystem (BF), and 9,129 individual plants of 95 species were identified in the four plantations. The species number in the tree layer was significantly higher in BF than in the four plantations, but species number did not significantly differ in the herb layer (Table 3). The values of d and H in the tree layer were significantly higher in BF than that in the four plantations, but these values did not significantly differ in the herb layer. Indices D and J in the tree and herb layers were similar in BF and four plantations. All diversity indices in the shrub layer were significantly lower in MCP than in the other forests (Table 3).

Soil seed banks

A total of 6,010 seedlings belonging to 81 species were identified, and 63 species were observed in all plantations. The number of species in the soil seed bank was larger in the plantations than in BF. In addition, the values of diversity indices tended to be slightly higher in EP than in the other plantations (Table 3). The composition of soil seed banks was less complex in plantations than in BF because, unlike BF, the plantation soil seed banks lacked vine species (Fig. 3a). The proportion of herb species in the soil seed banks was much higher in the four plantations than in BF, but the opposite was true for the proportions of shrub and tree species.

Soil microbes

Soil microbes were more abundant in the 0–5 cm soil layer than in the 5–20 cm soil layer in both the wet and dry seasons (Table 4). In the wet season, the contents of

Table 3 The number and diversity of plants, soil seed bank, soil animals, soil pollen, and birds in the five forests

Indicator	Characteristic	Layer	Forest type				
			BF	EP	MLP	MBP	MCP
Vegetation	No.	Tree	26.85±1.30a	11.44±0.84bc	7.67±0.55c	12.44±0.85b	11.11±0.45bc
		Shrub	9.50±0.88b	17.11±2.29a	15.89±1.43a	13.89±0.73ab	10.67±1.05b
		Herb	7.15±1.00a	4.67±0.67a	4±0.29a	5.78±0.6a	4.44±0.24a
	d	Tree	5.15±0.22a	2.71±0.2bc	1.93±0.14c	2.86±0.21b	2.51±0.13bc
		Shrub	2.50±0.18ab	3.11±0.4a	2.74±0.23ab	2.53±0.11ab	1.9±0.21b
		Herb	1.91±0.23a	1.14±0.22a	1.09±0.1a	1.46±0.16a	1.67±0.14a
	H	Tree	2.45±0.08a	1.93±0.08b	1.52±0.08c	1.9±0.08b	1.87±0.05b
		Shrub	1.71±0.07a	2.04±0.13a	2.03±0.08a	1.92±0.05a	1.3±0.12b
		Herb	1.51±0.14a	0.89±0.17a	0.95±0.09a	1.33±0.14a	1.24±0.08a
	D	Tree	0.84±0.02a	0.8±0.03ab	0.71±0.04b	0.8±0.02ab	0.8±0.01ab
		Shrub	0.78±0.02a	0.81±0.02a	0.81±0.02a	0.79±0.02a	0.57±0.05b
		Herb	0.72±0.05a	0.47±0.09a	0.54±0.06a	0.68±0.06a	0.76±0.07a
	J	Tree	0.75±0.02a	0.8±0.03a	0.76±0.04a	0.76±0.02a	0.78±0.01a
		Shrub	0.78±0.02a	0.74±0.01a	0.74±0.02a	0.73±0.02a	0.56±0.04b
		Herb	0.82±0.04a	0.6±0.09a	0.7±0.05a	0.77±0.04a	0.84±0.05a
Soil seed bank	No.	0–10 cm	23	33	31	33	37
	d	0–10 cm	4.61	4.83	4	4.58	4.66
	H	0–10 cm	2.71	2.27	1.78	1.66	1.86
	D	0–10 cm	0.92	0.85	0.76	0.65	0.74
	J	0–10 cm	0.86	0.65	0.52	0.47	0.51
Soil animals	No.	0–15 cm	27	20	23	20	19
	d	0–15 cm	2.46	1.86	2.12	1.82	1.7
	H	0–15 cm	1.49	0.82	0.82	0.83	0.71
	D	0–15 cm	0.7	0.37	0.4	0.4	0.34
	J	0–15 cm	0.45	0.28	0.26	0.28	0.24
Birds	No.	Tree, shrub, and herb	35	13	18	15	6
	d	Tree, shrub, and herb	4.74	2.78	3.77	3.14	1.00
	H	Tree, shrub, and herb	0.60	0.83	0.86	0.87	0.43
	D	Tree, shrub, and herb	2.13	2.12	2.48	2.36	0.76
	J	Tree, shrub, and herb	0.76	0.85	0.90	0.89	0.34
Soil pollen	No.	0–80 cm	38	43	36	46	36
	d	0–80 cm	3.98	4.39	3.7	4.45	3.66
	H	0–80 cm	1.92	1.85	1.92	1.67	1.79
	D	0–80 cm	0.79	0.79	0.8	0.74	0.77
	J	0–80 cm	0.53	0.49	0.54	0.44	0.50

Values are means±SE. Means within rows sharing the same letter are not significantly different ($P<0.05$)

BF broad-leaved forest, *EP* eucalyptus plantation, *MBP* mixed broad-leaved plantation, *MLP* mixed legume plantation, *MCP* mixed coniferous plantation, *No.* number of species, *d* Margalef index, *H* Shannon-Wiener index, *D* Simpson index, *J* Pielou index

total PLFAs, bacterial PLFAs, and fungal PLFAs in the 0–5 cm layer were lowest in MCP but did not differ between the other plantations and BF. Fungal PLFAs in the 5–20 cm layer were significantly higher in MLP than in BF, but bacterial PLFAs in the 5–20 cm layer did not differ significantly among the five forests. In the dry

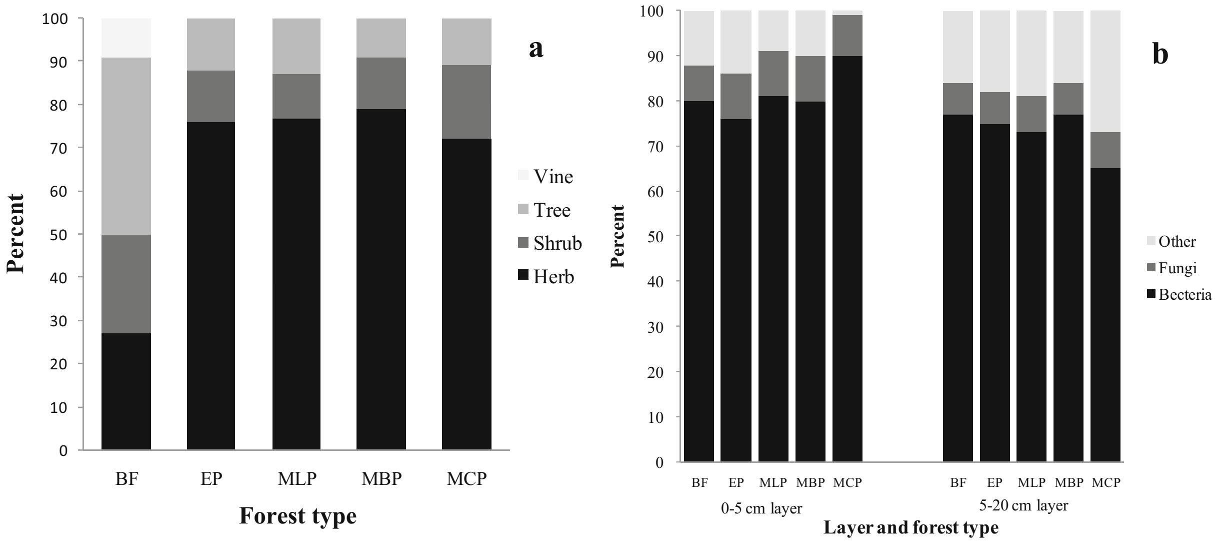

Fig. 3 The composition of soil seed banks and soil microbial communities in the five forests. *BF* broad-leaved forest, *EP* eucalyptus plantation, *MLP* mixed legume plantation, *MBP* mixed broad-leaved species plantation, *MCP* mixed coniferous plantation. **a** Composition of the soil seed banks. **b** Composition of the soil microbial community including protozoa and microalgae at two soil depths. Other: protozoa and microalgae

season, total, bacterial, and fungal PLFAs were significantly lower in BF than in the four plantations in the 0–5 cm layer but did not differ significantly in the 5–20 cm layer. The percentage of protozoa and microalgae in the 0–5 cm layer was much lower in MCP than in the other four forests but the opposite was true in the 5–20 cm layer (Fig. 3b). The soil microbial compositions of the other three plantations were similar to those of BF.

Soil animals

Soil animals were represented by 32 orders in all five forests and by 25 in four plantations. The number of orders and values for *d*, *H*, *D*, and *J* were higher in BF than in the plantations but tended to be similar among the plantations (Table 3).

Birds

A total of 59 bird species including nonforest species and forest-dependent species were recorded, and 29 species were recorded in the plantations. Species number and *d* value were highest in BF and lowest in MCP (Table 3). All diversity indices of the plantations other than MCP were higher than those in BF.

Soil age

We used one excavated soil profile to represent BF and a second profile to represent the degraded hilly substrate of the plantations because the substrate was similar among the four plantations. Soil C was older in the plantations than in BF except at 30–50 cm (Table 5). The age of soil C tended to increase with depth.

Soil pollen

A total of 64 genera were detected in the soil of the five forests, 57 genera of which were detected in the plantations. A high percentage of the pollen was from trees and shrubs (Fig. 4). In contrast to the soil profiles from the plantations, the BF soil profile contained a high percentage of *Castanopsis*/*Lithocarpus*, *Gironniera*, and *Aporusa* pollen. In addition, the percentage of *Poaceae* in the BF soil profile was relatively small. The percentages of *Eucalyptus*, *Schima*, and *Mallotus* pollen were high in the soil profiles of EP, MBP, and MLP. The pollen of *Pinus* and *Poaceae* were abundant in the soil profiles from all four plantations, and the percentage of *Poaceae* increased with soil depth. The number of pollen genera and the *d* value were higher in EP and MBP than in BF and the other two plantations. The other diversity indices tended to be similar among the five forests (Table 3).

Table 4 The content of total, bacterial, and fungal PLFAs (ng/g) in two soil layers of the five forests

Season	Layer (cm)	Category	Forest type				
			BF	EP	MLP	MBP	MCP
Wet season	0–5	Total PLFAs	5,625.63±362.73a	5,597.16±259.02a	5,893.8±317.95a	5,006.11±124.95ab	4,134.29±445.46b
		Bacteria	4,362.99±305.35a	4,367.32±213.17a	4,372.69±250.76a	3,624.95±66.62ab	2,975.83±389.44b
		Fungi	427.97±32.47ab	504.68±41.55a	527.67±50.27a	408.82±24.77ab	334.33±39.41b
	5–20	Total PLFAs	1,927.2±231.72ab	2,520.08±149.08a	2,597.49±55.27a	2,058.51±159.72ab	1,652.44±241.53b
		Bacteria	1,343.79±196.21a	1,823.38±120.45a	1,720.97±74.07a	1,480.44±116.43a	1,330.45±87.29a
		Fungi	107.9±15.96b	171.67±7.43ab	195.18±6.14a	129.78±6.74ab	129.54±8.44ab
Dry season	0–5	Total PLFAs	5,474.48±705.87b	8,980.62±204.38a	8,486.83±105.72a	9,000.08±641.23a	7,825.1±707.62a
		Bacteria	4,566.7±607.03b	6,694.51±297.4a	7,175.11±83.36a	7,620.5±554.78a	7,736.54±483.73a
		Fungi	423.66±80.24b	903.45±61.81a	943.86±11.3a	979.69±80.2a	791.39±98.84a
	5–20	Total PLFAs	3,802.58±702.2a	2,956.5±266.16a	3,019.77±123.39a	3,024.34±174.93a	3,270.01±663.01a
		Bacteria	3,055.09±607.31a	2,317.3±208.08a	2,350.15±92.89a	2,416.43±185.04a	1,895.99±99.33a
		Fungi	283.38±66.64a	201.84±12.89a	255.82±8.32a	224.78±8.78a	261.7±55.74a

Values are means±SE. Means within rows sharing the same letter are not significantly different ($P<0.05$)

BF broad-leaved forest, *EP* eucalyptus plantation, *MBP* mixed broad-leaved plantation, *MLP* mixed legume plantation, *MCP* mixed coniferous plantation

Light environment

The LAI averaged across all vegetation layers was significantly higher in BF than in the plantations, and most of the difference was explained by the tree layer (Table 6). The LAI of the tree layer was significantly higher in BF than in the plantations. The LAI of the shrub layer was significantly lower in MBP than in BF. The LAI of the herb layer was significantly higher in EP and MBP than in BF.

Table 5 ^{14}C dating (a BP) of soil profiles (0–80 cm depth) from the reference forest (BF) and from the four plantations (one profile was assumed to represent all four plantations)

Layer (cm)	Forest type	
	BF	Plantation
0–5	–	–
5–10	–	–
10–15	769	–
15–20	474	852
20–30	755	894
30–40	1,271	1,248
40–50	1,933	1,634
50–60	2,043	2,300
60–70	2,552	2,800
70–80	2,105	4,074

Soil mineral distribution

Fe content increased with soil depth in all five forests (Fig. 5). The contents of other mineral elements fluctuated with the depth, especially in the profiles from the plantations. The contents of K, Fe, and Ca were significantly higher in BF than in the plantations, while the contents of Mg and Na showed the opposite trend. The contents of all mineral elements were relatively constant from 10 to 80 cm depth in the plantation soils.

Ecological memory of the four study plantations

Taking the regional climax as the reference ecosystem, we calculated the EM of the four 26-year-old plantations based on Eq. 1 (Table 7). The total EM of the four plantations ranged from 50.96 to 52.54. Based on our previous research (Sun et al. 2013), the natural succession status of the four plantations increased from the grassland to coniferous forest stages

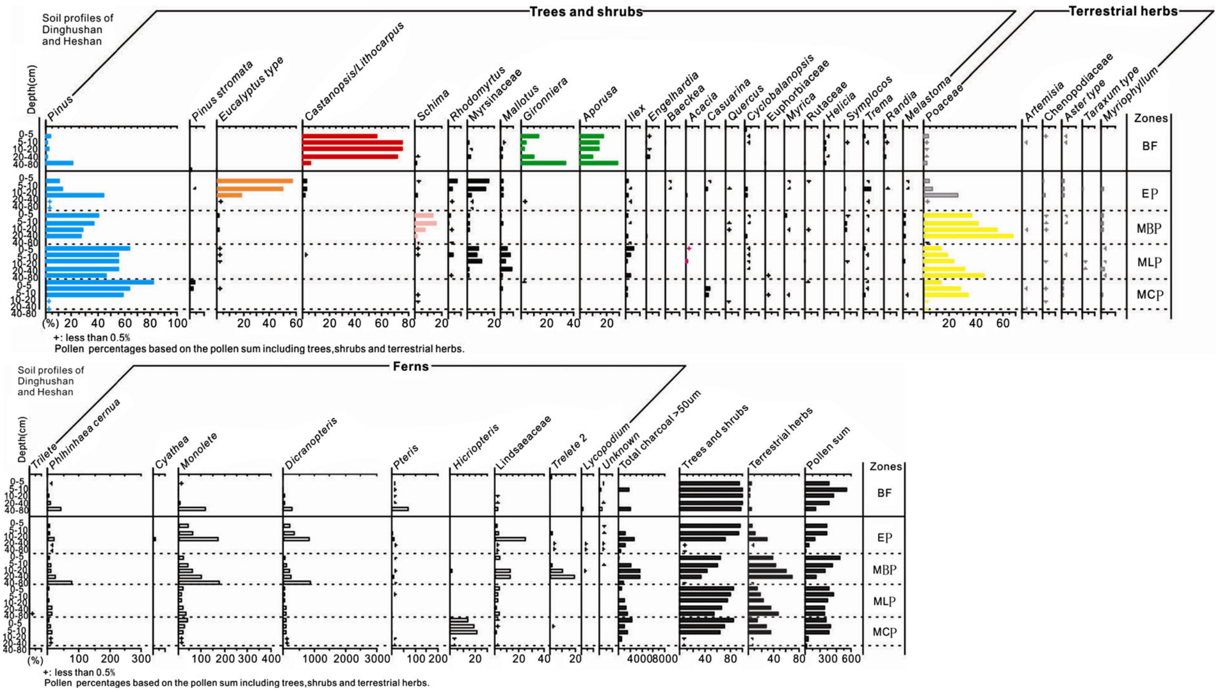

Fig. 4 Pollen diagram (0–80 cm soil depth) of the five forests. Percentages were calculated based on total number of pollen of all terrestrial seed plants. Notes: +<0.5 %. *BF* broad-leaved forest, *EP* eucalyptus plantation, *MLP* mixed legume plantation, *MBP* mixed broad-leaved species plantation, *MCP* mixed coniferous plantation

(46.55–59.8) in the natural succession trajectory. Therefore, we selected the grassland and coniferous forest stages as reference ecosystems to calculate PM (memory of the current ecosystem relative to the next successional stage) and RM (memory of the current ecosystem relative to the last successional stage) of each plantation (Table 7). The PM of every plantation was higher than for its RM. The difference between RM and PM was greater in the MCP and MLP than in the MBL and EP.

Patterns of ecological memory in plantations

The plantations retained about half of the total EM, and the pattern of memory retained and lost was similar for the plantations (Fig. 6 and Table 7). All plantations retained a low percentage of EM (<10 %) concerning vegetation, soil seed banks, and birds. The plantations had about 25 % of EM concerning soil pollen, but had >50 % of EM for soil microbes, soil age, soil animals, light environment, and soil mineral elements (Fig. 6 and Table 7).

Table 6 Leaf area index (LAI) of tree layer, shrub layer, herb layer, and all layers in the five forests

Layer	Forest type				
	BF	EP	MLP	MBP	MCP
All layers	5.59±0.12a	2.77±0.16d	4.57±0.09b	2.56±0.04d	3.14±0.15c
Tree	4.39±0.18a	0.83±0.14d	2.7±0.09b	1.27±0.15c	1.48±0.12c
Shrub	0.66±0.07a	0.64±0.13a	0.97±0.12a	0.23±0.08b	0.87±0.18a
Herb	0.54±0.10b	1.29±0.12a	0.9±0.12ab	1.07±0.13a	0.79±0.19ab

Values are means±SE. Means within rows sharing the same letter are not significantly different ($P<0.05$)

BF broad-leaved forest, *EP* eucalyptus plantation, *MBP* mixed broad-leaved plantation, *MLP* mixed legume plantation, *MCP* mixed coniferous plantation

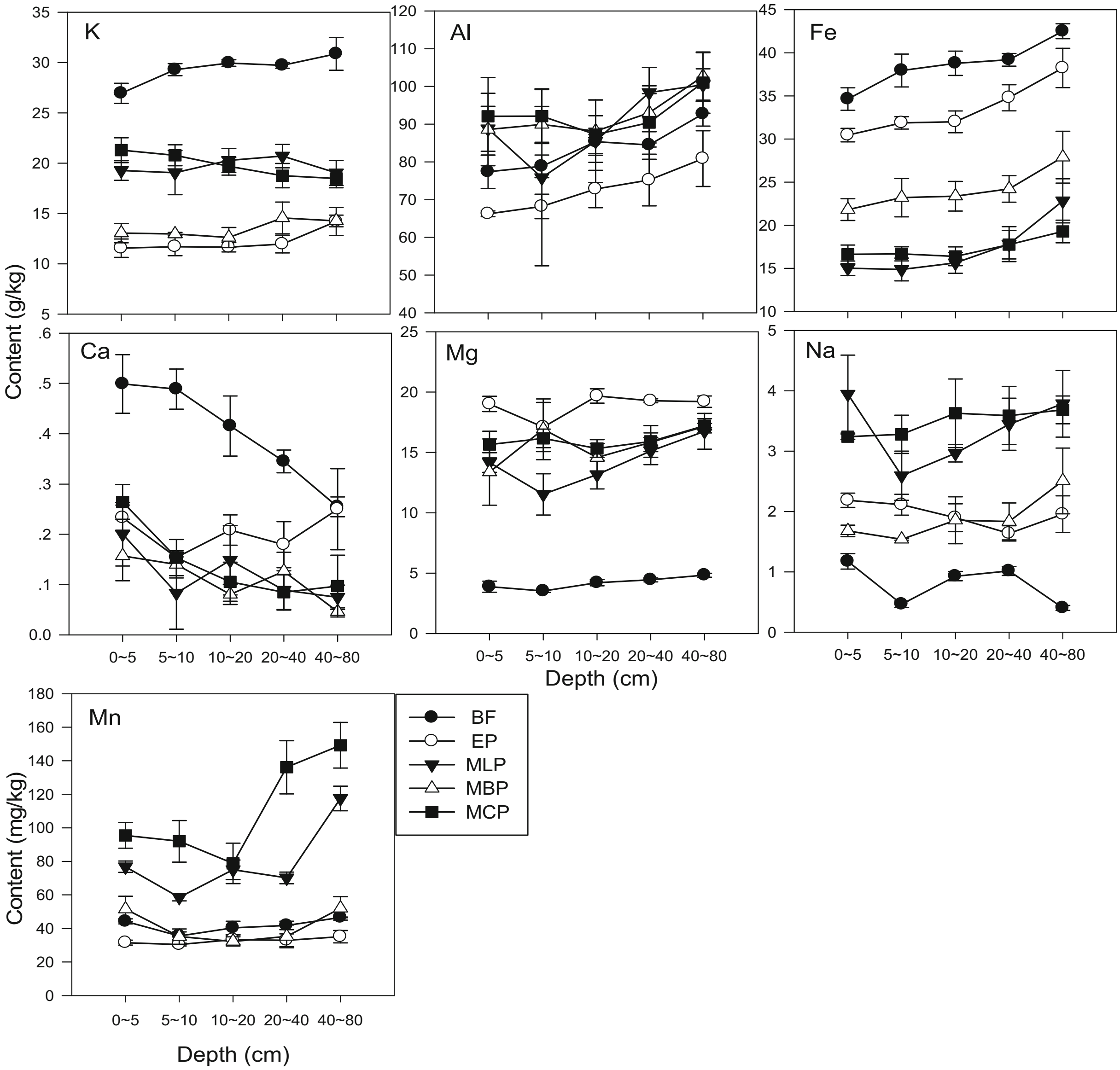

Fig. 5 The distribution of mineral elements with soil depth in the five forests. *BF* broad-leaved forest, *EP* eucalyptus plantation, *MLP* mixed legume plantation, *MBP* mixed broad-leaved species plantation, *MCP* mixed coniferous plantation

Discussion

The ecological memory approach and the assessment of forests

Based on the conceptual model of EM (Fig. 2), natural forest succession can be expressed as the "ball and cup" hypothesis (Gunderson 2000; Sun et al. 2013). The "ball and cup" model consists of a curve and a ball (Fig. 7). The curve represents the succession trajectory of forests, and the ball represents the community. The ball goes forward or backward along the curve, appearing as succession or degradation. If the succession trajectory could be expressed by a mathematical equation, no matter how simple or complex, it should contain two components: parameters and variables. The parameters determine the shape of the curve, and the values of the variables determine the points. In forest succession, parameters are those stable ecological factors, such as solar radiation, precipitation, effective accumulative temperature, monsoon, and geological factors. These determine the shape of the successional trajectory.

Table 7 The ecological memory of four plantations in terms of vegetation, soil seed bank, soil microbes, soil animals, soil age, soil pollen, soil mineral elements, light environment, and birds. Values can also represent the percentages relative to the reference system (BF)

Ecological memory type	Vegetation layer or soil depth	Forest type	Forest type				
			BF	EP	MLP	MBP	MCP
Vegetation memory	All layers	BF	100.00				
		EP	4.56	100.00			
		MLP	5.20	64.66	100.00		
		MBP	6.68	48.86	48.09	100.00	
		MCP	5.74	45.39	47.91	59.71	100.00
	Tree layer	BF	100.00				
		EP	2.95	100.00			
		MLP	2.77	45.98	100.00		
		MBP	5.61	19.25	17.71	100.00	
		MCP	1.88	27.48	32.76	42.04	100.00
	Shrub layer	BF	100.00				
		EP	4.32	100.00			
		MLP	5.47	68.98	100.00		
		MBP	5.72	54.44	49.55	100.00	
		MCP	6.28	48.28	48.71	66.24	100.00
	Herb layer	BF	100.00				
		EP	1.90	100.00			
		MLP	0.00	56.92	100.00		
		MBP	2.78	48.31	60.20	100.00	
		MCP	3.25	47.24	56.60	58.74	100.00
Soil seed memory	All depths	BF	100.00				
		EP	9.36	100.00			
		MLP	10.63	59.47	100.00		
		MBP	10.52	47.94	47.93	100.00	
		MCP	11.57	53.97	70.60	47.74	100.00
	0–5 cm	BF	100.00				
		EP	6.88	100.00			
		MLP	9.09	61.51	100.00		
		MBP	6.52	39.19	41.73	100.00	
		MCP	8.83	54.91	69.48	38.05	100.00
	5–10 cm	BF	100.00				
		EP	10.58	100.00			
		MLP	12.06	38.80	100.00		
		MBP	14.78	42.51	52.89	100.00	
		MCP	12.17	36.67	63.01	60.28	100.00
Soil microbes memory	All depths	BF	100.00				
		EP	93.32	100.00			
		MLP	93.80	97.81	100.00		
		MBP	91.71	94.96	96.04	100.00	
		MCP	93.74	91.39	91.92	93.82	100.00
	0–5 cm	BF	100.00				
		EP	94.64	100.00			

Table 7 (continued)

Ecological memory type	Vegetation layer or soil depth	Forest type	Forest type				
			BF	EP	MLP	MBP	MCP
		MLP	94.97	98.05	100.00		
		MBP	91.13	94.74	95.96	100.00	
		MCP	93.37	92.78	93.17	95.00	100.00
	5–20 cm	BF	100.00				
		EP	91.25	100.00			
		MLP	91.97	97.41	100.00		
		MBP	92.64	95.33	96.18	100.00	
		MCP	94.29	89.18	89.91	91.91	100.00
Soil animals memory	All depths	BF	100.00				
		EP	69.61	100.00			
		MLP	64.47	87.06	100.00		
		MBP	65.04	86.92	91.26	100.00	
		MCP	59.64	81.44	91.40	87.86	100.00
Birds memory	All layers	BF	100.00				
		EP	8.39	100.00			
		MLP	9.53	62.73	100.00		
		MBP	8.61	59.84	73.54	100.00	
		MCP	10.13	51.37	43.70	50.67	100.00
Soil ^{14}C dating memory	All depths	BF	100.00				
		EP	89.20				
		MLP	89.20	100.00			
		MBP	89.20	100.00	100.00		
		MCP	89.20	100.00	100.00	100.00	
Soil pollen memory	All depths	BF	100.00				
		EP	30.49	100.00			
		MLP	22.76	50.32	100.00		
		MBP	20.65	51.57	63.05	100.00	
		MCP	25.86	52.71	56.88	60.32	100.00
Light environment memory	All layers	BF	100.00				
		EP	78.16	100.00			
		MLP	90.91	84.57	100.00		
		MBP	76.92	91.98	83.48	100.00	
		MCP	83.87	91.49	91.41	90.49	100.00
Soil mineral memory	All depths	BF	100.00				
		EP	88.73	100.00			
		MLP	86.39	87.16	100.00		
		MBP	89.29	93.53	92.17	100.00	
		MCP	84.04	85.36	96.13	90.51	100.00
Total ecological memory	All layers/depths	BF	100.00				
		EP	52.42	100.00			
		MLP	52.54	77.09	100.00		
		MBP	50.96	75.07	77.28	100.00	
		MCP	51.53	72.57	76.66	75.68	100.00

Table 7 (continued)

Ecological memory type	Vegetation layer or soil depth	Forest type	Forest type				
			BF	EP	MLP	MBP	MCP
Retrospective memory	All layers/depths	Grassland	–	60.38	55.94	56.51	54.50
Prospective memory	All layers/depths	Coniferous forest	–	63.17	63.52	61.60	63.39

BF broad-leaved forest, *EP* eucalyptus plantation, *MBP* mixed broad-leaved plantation, *MLP* mixed legume plantation, *MCP* mixed coniferous plantation

Variables are those indices reflecting the structure and function of a community, such as species, productivity, density, and diversity. They determine the position of a community in the successional trajectory. In the conceptual model of EM, the total EM determines the position of the community in a succession trajectory, and the RM and PM determine if the community goes forward or backward. Novel ecosystems will emerge when the shape of the succession trajectory changes or the community breaks away from its successional trajectory. The former is led by the change of parameters that determine the succession trajectory for the region, such as climatic or geological disasters in the ecosystem (e.g., flood, earthquake, and tsunami). The latter is usually caused by human disturbances, such as over deforestation and species introduction, which cause variables to exceed their historical range of variability (Keane et al. 2009). The use of EM as an indicator for evaluating restored forests is demonstrated in Fig. 2. The comparison of the reference trajectory to the total EM can be

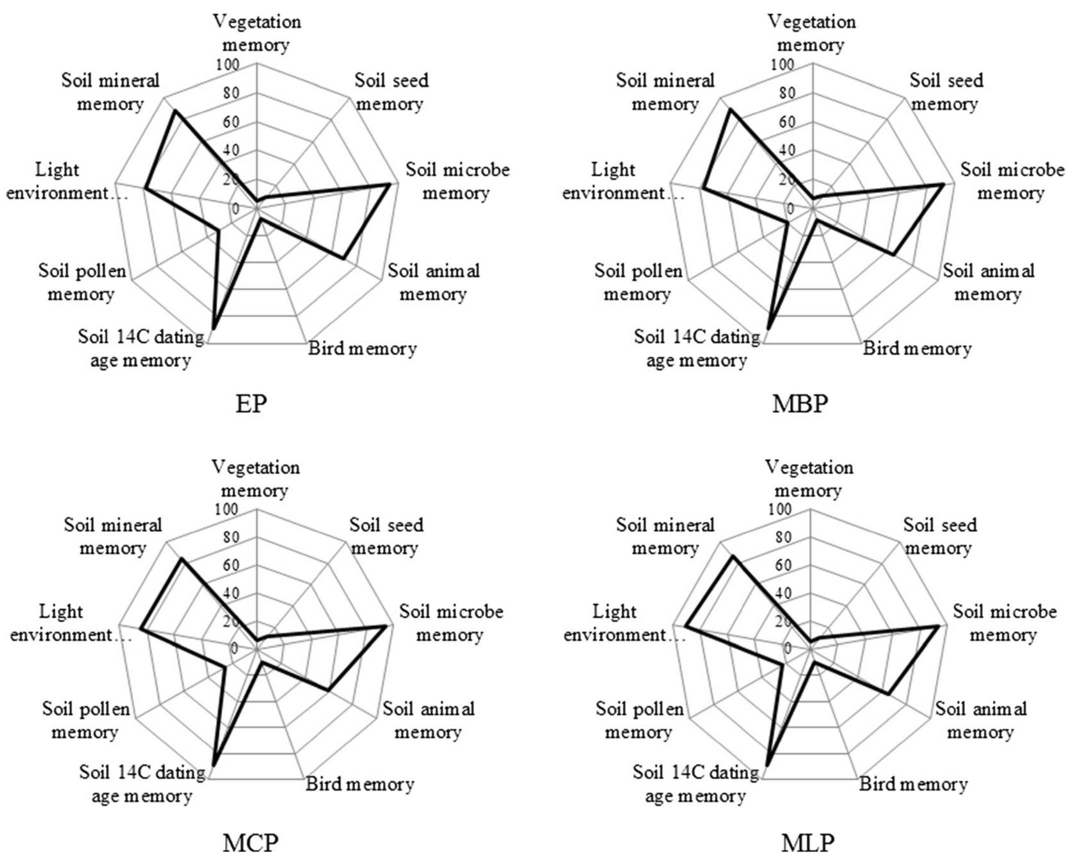

Fig. 6 The accumulation pattern of EM in the four plantations relative to the reference forest. Values from 0 to 100 indicate the percentage of the indicator relative to reference forest. *BF* broad-leaved forest, *EP* eucalyptus plantation, *MLP* mixed legume plantation, *MBP* mixed broad-leaved species plantation, *MCP* mixed coniferous plantation

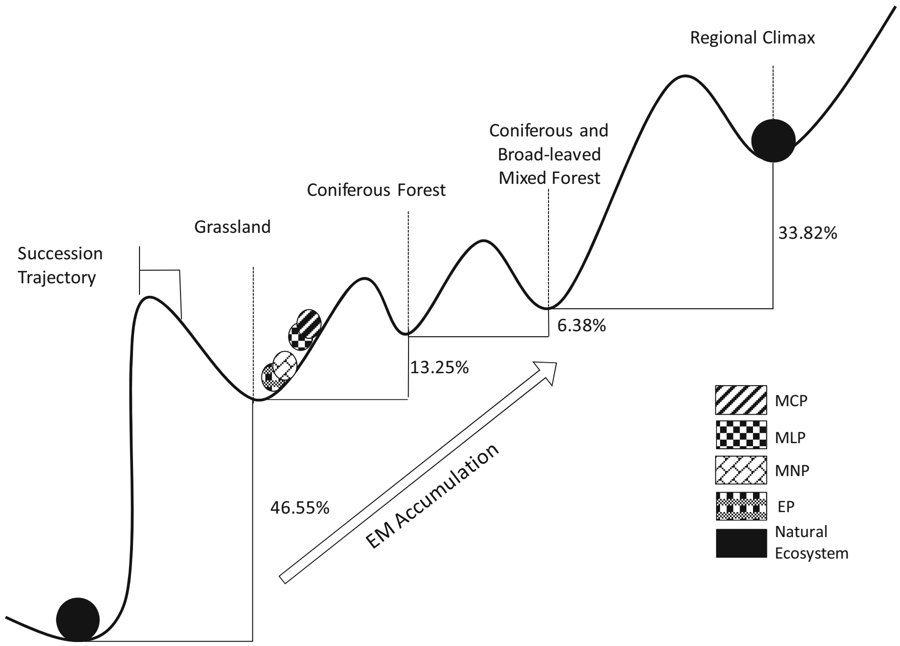

Fig. 7 The positions of the four plantations in the natural EM succession trajectory. The natural succession trajectory of EM was established in our previous study (Sun et al. 2013). EM accumulates nonlinearly during secondary succession. The valleys labeled with initial state, grassland, coniferous forest, coniferous, broad-leaved mixed forest, and regional climax forest represent successional stages of the subtropical forest. The positions of the balls in the valleys represent the restoration status and developing trend of the ecosystem. *BF* broad-leaved forest, *EP* eucalyptus plantation, *MLP* mixed legume plantation, *MBP* mixed broad-leaved species plantation, *MCP* mixed coniferous plantation

used to identify whether the plantations deviate from a natural successional trajectory. In the case of restored forests in South China, the initial successional stage is grassland and the final stage is broad-leaved forest (Fig. 7). If the EM of one ecosystem in this succession is greater than that of abandoned grassland, it means that the ecosystem is still in a natural successional trajectory. Total EM can also be used as an indicator of the position of a restored ecosystem in a natural successional trajectory. For instance, if total EM of a restored ecosystem is more than that of grassland and less than that of a coniferous forest, the natural successional status of the restored ecosystem is between grassland and coniferous forest successional stage. The difference between RM and PM reflects the ecological dynamics and the developmental trend of the plantations. If RM>PM, the evaluated ecosystem is in a retrogressive successional process. If RM<PM, the evaluated ecosystem is in a positive successional process. If RM=PM, the evaluated ecosystem is in a stable successional status (Fig. 7). The value of the difference represents the dynamics and instability of the ecosystem. The larger the difference between RM and PM, the more unstable the ecosystem.

The natural state of succession and patterns of ecological memory in plantations

We next consider whether the plantations in this study are following the natural successional trajectory and whether they have a positive or retrogressive successional trend. Grassland, coniferous forest, mixed coniferous and broad-leaved forest, and evergreen broad-leaved forest are four successional stages of forests in subtropical China (Peng 1996). In our previous study, we found that total EM increased with succession and that it accumulated from 46.55 to 59.80 from the grassland to the coniferous stage (Sun et al. 2013). The values of total EM for the four plantations are between 50.96 and 52.54, indicating that all plantations are in a natural succession trajectory between the grassland and coniferous forest stage (Fig. 7). Although the purpose of planting these four plantations was to accelerate succession by skipping the first two natural successional stages (grassland and coniferous forest), our results indicate that natural succession may actually not be accelerated by skipping these stages. The major factor limiting the ability of restored ecosystems to skip earlier successional stages may be insufficient ecological memory. The PM of every plantation was higher than its RM, which indicates that succession for all plantations was on a positive trajectory. The differences between RM and PM were higher in the mixed legume plantation and mixed coniferous plantation than in the mixed broad-leaved plantation and eucalyptus plantation, which indicates that the mixed legume and mixed coniferous plantations have stronger positive successional trends than the mixed broad-leaved and eucalyptus plantations. The pattern of total ecological memory accumulated was similar among the four plantations (Fig. 6). Three levels of EM among indicators were found in the plantations, i.e., a high level of memory (>50 % for soil minerals, light environment, soil age, soil animals, and soil microbes), a medium level of memory (about 25 % for soil pollen), and a low level of memory (about 10 % for birds, soil seed bank, and plant species). Since the pattern of EM accumulation in the four plantations was similar, it indicates that the identity of the initially planted species is not determinative in the accumulation of ecological memory. Changing one subvariable (e.g., plant species) of ecological memory may not alter the successional trajectory.

The naturalness minimum dynamic unit and forest restoration

Generally, the greater the naturalness of a forest, the greater the probability that its original constituent species will survive (Mansourian et al. 2005). Bautista et al. (2009) concluded that most evaluation approaches fall into three groups: (1) those that measure the achievement of specific goals and stages; (2) those that directly compare the restored site with reference sites or between restoration alternatives; and (3) those that assess ecosystem quality. Most of these approaches ignore evaluation of the naturalness of restored ecosystems. However, if the restored ecosystem breaks away from the natural succession trajectory and develops into a novel ecosystem, the evaluation approach should be reconsidered (Hobbs et al. 2006, 2009). In addition, reference to a single ecosystem or to a special goal might not be sufficient for evaluating the natural state of a restored ecosystem. A natural succession trajectory should be established as reference. In forest restoration, it is important to retain the various forms of EM present at different successional stages. Building the "minimum dynamic unit" that contains sufficient EM might be an effective way to accelerate forest restoration (Fig. 8). The minimum dynamic unit consists of abundant EM from all the successional stages and easy to be maintained. Given the proper condition, these various forms of EM would transform into internal EM and finally accelerate the restoration process (Nyström and Folke 2001).

Conclusions

We evaluated the restoration of four typical plantations in lower subtropical China by using an EM approach. The results indicated that the initial species planted did not significantly change the accumulation pattern of EM. The four plantations had similar EM values and almost the same accumulation pattern. All of them were within the natural succession trajectory and between the early and medium successional stage. Because total EM determines the early successional processes, attempts to

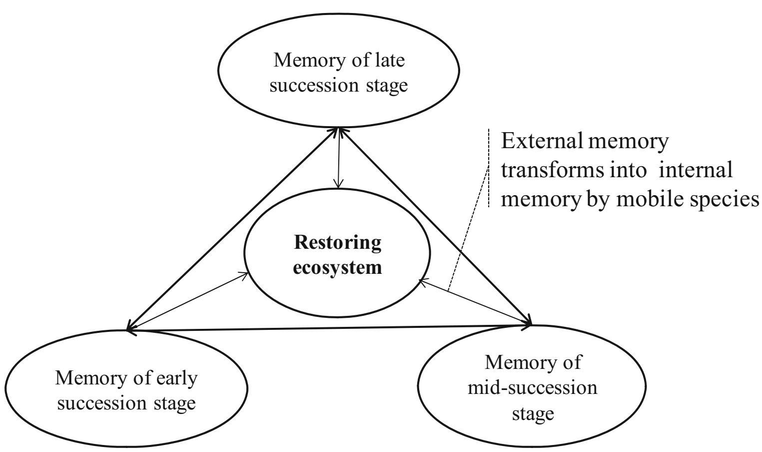

Fig. 8 Minimum dynamic unit with sufficient EM. The minimum dynamic unit with sufficient EM is one functional area, consisting of one restoring ecosystem and three neighboring communities with different kinds of successional memory (i.e., memory in early, mid-, and late-successional stages). The three communities around the restoring ecosystem provide external memory for the restoring ecosystem through mobile linking species. The transformed internal memory could accelerate restoration

skip several successional stages by planting later successional tree species might not accelerate succession. The comparison of RM and PM indicated that all four plantations were in positive successional trends. MLP and MCP had stronger positive developmental trends than EP and MBP. Based on EM, we suggest using the entire natural successional trajectory as the reference and dividing the restoration goal into several clear milestones along that reference trajectory. Finally, we address that restoration can be accelerated by starting with a minimum dynamic unit with sufficient EM.

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