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Changes in biodiversity and ecosystem function during the restoration of a tropical forest in south China

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Tropical forests continue to vanish rapidly, but few long-term studies have ever examined if and how the lost forests can be restored. Based on a 45-year restoration study in south China, we found that a tropical rain forest, once completely destroyed, could not recover naturally without deliberate restoration efforts. We identified two kinds of thresholds that must be overcome with human ameliorative measures before the ecosystem was able to recover. The first threshold was imposed primarily by extreme physical conditions such as exceedingly high surface temperature and impoverished soil, while the second was characterized by a critical level of biodiversity and a landscape context that accommodates dispersal and colonization processes. Our three treatment catchments (un-restored barren land, single-species plantation, and mixed-forest stand) exhibited dramatically different changes in biodiversity and ecosystem functioning over 4 decades. The mixed forest, having the highest level of biodiversity and ecosystem functioning, possesses several major properties of tropical rain forest. These findings may have important implications for the restoration of many severely degraded or lost tropical forest ecosystems.

rainforest restoration, biodiversity conservation, ecosystem functioning, China

Tropical forests are home to two thirds of all plant species of the world[1], and play a vital role in maintaining global biodiversity and ecosystem functioning. Can a tropical rain forest recover naturally without human ameliorative efforts after being destroyed? How do biodiversity and ecosystem functioning change as a severely disturbed or completely destroyed ecosystem recovers? As 1.54×10^7 ha of tropical forests continue being lost each year[2], these questions must be addressed urgently and adequately. Although most studies on the recovery and restoration of tropical rain forests did not start until the 1990s, restoring these ecosystems has widely been recognized as one of the most important and pressing challenges facing humanity[1,3−5]. Numerous studies have shown that vegetation recovery from severely degraded areas in tropical rain forests (e.g., abandoned mining sites, bulldozed areas) usually follows a general pattern largely consistent with the facilitation model of succession (i.e., earlier species keep modifying the environment that progressively favors later species)[6−8], although the detailed trajectory and speed of succession can be significantly influenced by the landscape context and land use legacies[4,9,10]. On the other hand, it has been well documented that the initial composition of vegetation might have various effects on the trajectory and speed of later succession[11−14]. Long-

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term studies, particularly for the tropical rain forests, are needed to clarify these issues.

One of the traditional views in ecology is "nature knows best" and thus "let nature take its course," which is essentially based on the time-honored notion of balance of nature[14, 15]. This view seems to support the practice of restoring degraded land by natural processes[14,16]. However, we argue that, while natural processes are indispensable part of any successful ecosystem recovery, they alone will not be adequate for the restoration of extremely degraded ecosystems (e.g., denuded forests or desertified grasslands where top soils are completely lost). Here, we report on the results of a 45-year (1959—2004) ecological restoration study in a tropical rain forest region in south China, and examine how biodiversity and ecosystem functioning change during the restoration of a once-lost forest.

1 Methods

Our restoration study was initiated in 1959 at the Xiaoliang Tropical Forest Long-Term Ecosystem Research Station in a coastal area in Guangdong Province of China (110°54′18″E, 21°27′49″N). The climate of this region is strongly influenced by tropical monsoons, with annual temperature of 23℃, and annual precipitation of 1400—1700 mm[17]. Prior to human disturbance, the area was covered by evergreen broad-leaved seasonal rain forests. By the early 1950s about 400 km^2 of tropical seasonal forests had been denuded, with only small xeric shrubs, grasses, and vines sparsely found in ditches. This formerly forested area had experienced complete logging, firewood harvesting, and soil erosion for more than 100 years. With topsoil being completely lost, the bare surface was covered by coarse sands and mineral aggregates rich in ferrous and manganese. As a result, the maximum monthly temperature of soil surface was extremely high (47.5℃), nearly 17℃ higher than its ambient air temperature. The highest soil surface temperature recorded between 1959 and 2004 was 62.5℃ (July 15, 1989). The soil was low in water content (17.6% at the depth of 20 cm), and poor in nutrients, with soil organic matter of 0.60% and total N of 0.027%. These extreme soil conditions represent a physical threshold preventing vegetation from recovering by natural processes.

To explore whether such extremely degraded ecosystems could be restored and how, we started a long-term restoration experiment in 1959 by establishing one control and 3 restoration treatments in four geographically similar catchments[17,18]. For the control catchment (3.7 ha), the barren land was left alone without any human interference. The three treatments included a pine (*Pinus massoniana*) plantation (3.2 ha), eucalyptus (*Eucalyptus exserta*) plantation (3.9 ha), and broad-leaved mixed plantation (3.8 ha). All tree planting in the different catchments followed the same procedures by which seedlings of chosen species were planted in a manually created pit of roughly 1 m^3 in volume, with addition of compost in a porous plastic bag and water. The spatial location of each seedling was determined using a regular grid with a mesh size of 2.5 m by 2.5 m while shrubs and grasses were intercropped.

The mixed forest plantation started as a eucalyptus stand in 1959, and then 312 species were introduced between 1964 and 1975. This was because our previous trials had shown that a broad-leaved mixed forest could not be established in the extreme soil and microclimate conditions without the initial eucalyptus stage. That is, the whole area was covered initially by eucalyptus and then cut completely throughout the catchment. Twelve species, accounting for 80% of the individuals, were randomly planted at the cleared site, including *Castanopsis fissa*, *Cinnamomum camphora*, *Carallia brachiata*, *Aphanamixis polystachya*, *Ternstroemia pseudoverticillata*, *Acacia auriculaiformis*, *Cassia siamea*, *Albizia procera*, *Albizia odoratissima*, *Leucaena leucocephala*, *Aquilaria sinensis* (Lour.) Gilg, and *Chakrasia tabularis*. Besides a few broad-leaved mixed forest species obtained from local plantations, the other species were introduced from a nearby secondary natural forest as well as a tropical seasonal monsoon forest in the Hainan Island which is about 200 km southwest of Xiaoliang. Since 1959, we have periodically monitored climatic conditions (air temperature, air humidity, soil temperature, and soil moisture), surface runoff and soil loss, and other ecosystem properties (e.g., species composition of plants, animals, and microbes, plant biomass, soil organic matter, nitrogen). Field sampling and laboratory analyses followed the standard procedures commonly used in ecology [17,18].

In the runoff and soil loss measurement, a weir gauge, before which was a soil sedimentary pool, was established at the bottom of each catchment. Runoff and washed soil was recorded for each rainfall manually[19].

In the soil measurement, 3 composite samples composing of 10 soil cores of 20 cm height and 3 cm diameter were taken from each of catchments. The composite samples were air-dried, milled and determined for total nitrogen and organic matter[20]. For insect, bird and animal measurement, surveys were made periodically in the whole catchment of each type. Soil animals were determined by Tullgren method, Baermann method[21]. In microbial measurement, A-horizon soil samples were taken from 0 to 15 at 10 randomly selected points in each of the catchments. Each sample was used as a replicate. The samples were sieved, stored in polyethylene bags at 4℃, and then determined for bacteria, fungi and actinomycetes by plate counting in lab[22].

2 Results

The environmental conditions of the barren land were extremely harsh, and essentially no plants could grow without human intervention. According to data obtained during 1981—1990, the average soil water content of the site was only 13.21%. The water content between January and April (Figure 1(a)) was lower than 13% which was a minimum requirement for germination of seeds for most plant species in this region. Soil temperature on the barren land could reach nearly 60℃, lasting for 2—3 h of a day in summer. The maximum air and soil temperatures were clearly beyond the tolerance range of most if not all plant species (Figure 1(b)). In addition, the extremely low fertility of soil, combined with the deteriorated physical properties, was not able to provide sufficient nutrients for plant growth (Figure 1(c)).

After 45 years, the denuded land still showed no sign of vegetation recovery (Figure 2(a)). In three field surveys (1994, 1998, 2004), we found only 3 herbaceous species in only some parts of erosion gullies, covering a negligible portion of the catchment. In 2004, again, only scattered plants were found in the gullies, with addition of 5 more species, and the total plant cover still was less than 5%.

The pure pine stand grew well for the first few years, but died out completely in 1964 because of combined effects of insect (*Dendrolimus punctatas*) attacks and heat stress from soil surface temperature. The planted eucalyptus stand persisted throughout the 45 years (Figure 2(b)), but tree density has been decreasing (from 40

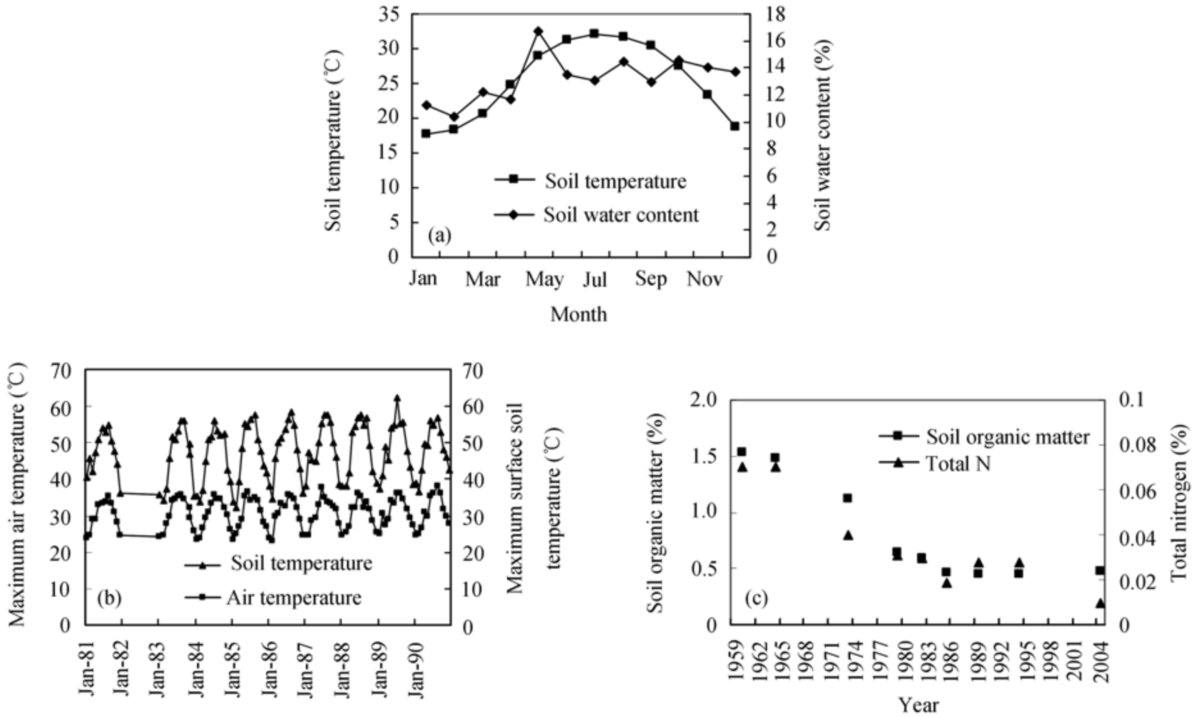

Figure 1 Physical and soil conditions of the barren land. (a) Monthly average soil temperature and soil water content; (b) average monthly maximum air and surface soil temperatures; (c) change in soil organic matter and total nitrogen.

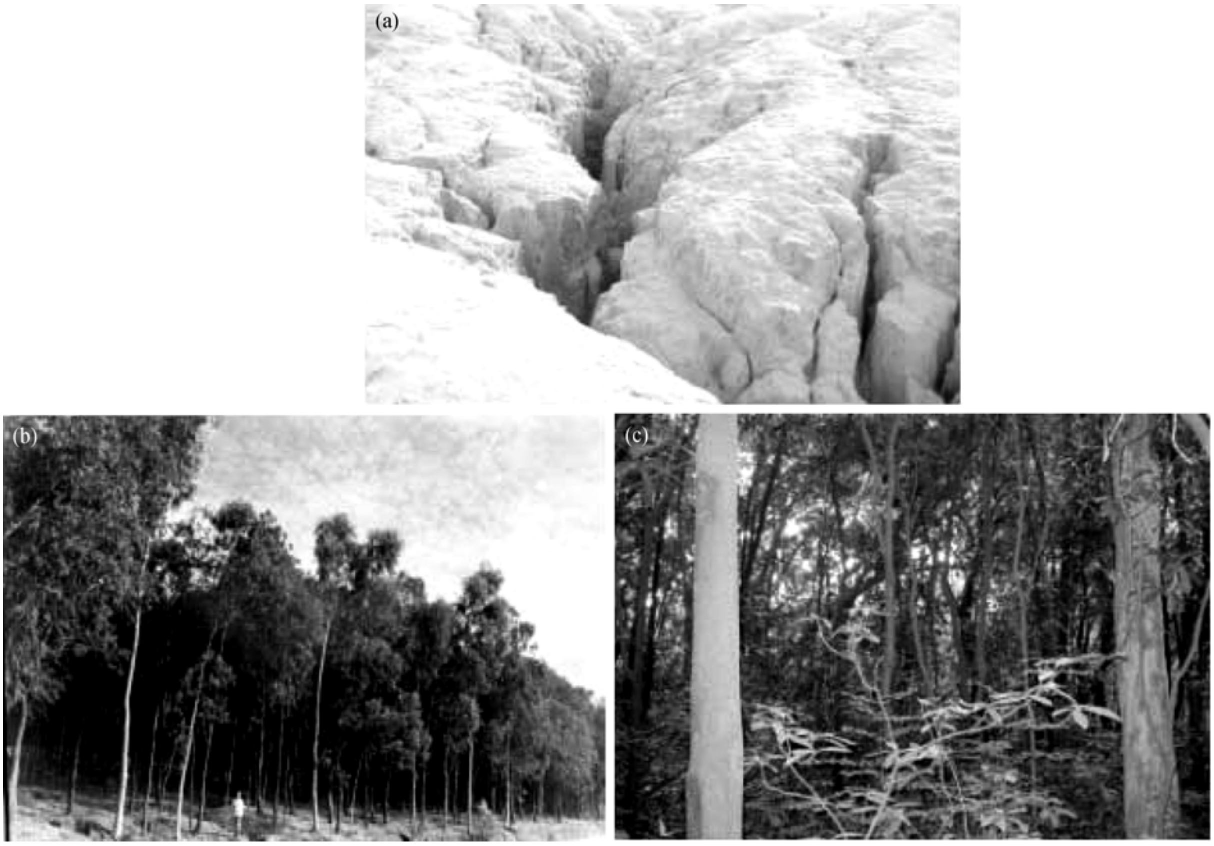

Figure 2 Photos of the barren land (control), eucalyptus forest, and mixed forest in 2004, 45 years since the onset of the restoration experiment.

individuals/100 m^2 in 1959 to about 25 individuals/100 m^2 in 2002). The understory of the eucalyptus forest was poorly developed, consisting of only one herbaceous plant (*Eriachne pallescens*). However, through improving the physical environmental conditions and soil developmental processes, the eucalyptus forest laid a necessary basis for broad-leaved mixed forest species to grow. In contrast with the barren land and the eucalyptus forest, the broad-leaved mixed forest catchment increased dramatically in species diversity of plants, animals, and microbes since the beginning of the restoration. Our field survey in 1994 indicated that 128 native species (47 trees, 57 shrubs, and 24 herbs) had colonized and established themselves in the mixed forest, although 120 of the 312 previously planted tree species had disappeared[18]. Also, the community structure was well developed with 3 distinctive tree layers as well as species-rich shrub and herbaceous layers (Figure 2(c)). Our 2004 field survey indicated that the broad-leaved mixed forest remained similar in plant species composition and canopy stratification. However, a number of community characteristics, typical of tropical seasonal rain forests, began to emerge. These included high biodiversity, complex community structure, cauliflory (tree trunks and large branches producing flowers and fruits), buttress roots, and woody vines. The species composition and community structure of the restored forest were quite similar to those of a nearby secondary natural forest. The two forest ecosystems shared several dominant species that characterize the forest biome in this geographic area, including *Syzygium levinei* (Merr.) Merr. et Perry, *Carallia brachiata* (Lour.) Merr., *Schefflera heptaphylla* (L.) D. G. Frodin, *Syzygium hancei* Merr. et Perry, *Psychotria rubra* (Lour.) Poir, and *Aporusa dioica* Muell. Arg[23]. Also, the Xiaoliang broad-leaved mixed forest possesses dominant species that are found in a tropical evergreen monsoon forest in the Hainan Island[24].

The animal biodiversity of the mixed forest community also increased progressively during ecosystem recovery. Between 1964 and 1972, about 50 insect species (belonging to 29 families and 11 orders) and 4 bird species were recorded. Soil fauna was dominated by nematodes[18, 25]. From 1974 to 1978, 8 species of phytophagous insects invaded the forest, and had a pervasive impact throughout the catchment, with many trees (particularly *Ailanthus menglunense* and *Chakrasia tabularis*) deprived of leaves. This outbreak of insect populations was suppressed by a rapid invasion of 16 insectivorous species (mainly birds and spiders) during 1979—1981. Avian species, including residential, migrant, and transient birds, increased from 9 in 1979, 18 in 1984, to about 100 in 2004 probably because of progressively more diversified flora and flowering phenology. The dramatic increase in bird diversity has undoubtedly contributed to the colonization of the large number of native plants. Soil animal diversity also increased from 8 orders in 1981, 25 in 1984, and to 32 in 1988[25]. The soil animal communities had a rapid increase stage in the first decade, a fluctuation stage in the second decade and then a stable stage. Soil animals developed with increase of soil fertility, especially soil organic matter[21]. Overall, changes in biodiversity of plants, animals, and microbes were closely related[26,27], and plant diversity seemed essential for the diversification of animals and soil microbes.

The recovery of vegetation was accompanied by the recovery of soil microbial biodiversity that is critical to ecosystem functioning. Our 1984 survey indicated that the mixed forest had the highest microbial abundance and diversity whereas barren land the lowest (Table 1). However, the estimated amount of microbes in the restored forest was lower than that of the secondary natural forest which had 13.33×10^6 individuals of microbes per gram of soil[23]. The microbial composition of the eucalyptus soil was characterized by low bacteria and high fungal contents, which was similar to that of the barren land, indicative of low soil fertility. The broad-leaved mixed forest soil had a combination of high bacteria, high actinomyces and low fungi contents. The higher microbial activity in the mixed forest promoted nutrient cycling and facilitated the growth of plants. The mixed forest also has developed a complex food web structure composed of three trophic levels and various groups of animals, including ants, termites, spiders, locusts, beetles, butterflies, insectivorous birds, tree frogs, and rodents (Figure 3). Evidently, the ecosystem still lacks top predators and large mammals commonly found in tropical seasonal rain forests. As compared to the mixed forest, the food web structure of the *Eucalyptus* forest was much simpler with only two trophic levels[28]. The level of food web complexity is an important indicator of ecosystem maturity, and the food web structure of the mixed forest is indicative of a fairly high degree of complex trophic interactions in this restored ecosystem.

Ecosystem functioning of the mixed forest also was improved significantly during the process of vegetation recovery. From 1959 to 2004, soil organic matter (SOM) increased from 0.64% to 2.95% and soil total N increased from 0.063% to 0.119% in the mixed forest (Figure 4(a)). Based on our field measurements between 1983 and 1989, the temporal pattern of surface runoff and soil loss for the barren land closely followed that of annual precipitation, and maintained the high level of soil loss (Figure 3(b),(c),and (d)). In contrast, the mixed forest has essentially eliminated surface runoff (<6 m^3 ha^{-1} y^{-1}; Figure 3(c)) and soil erosion (close to 0; Figure 3(d)) since 1986. Interestingly, the eucalyptus forest had even higher surface runoff than the barren land because of its somewhat impervious forest floor composed primarily of likes, but its soil loss was only 20% of that for the barren land (Figure 4(c) and (d)).

Table 1 Comparison of biodiversity in the barren, eucalyptus, and mixed forest catchments (Data were from a field survey in 1984, except for plants which were surveyed in 1994)

		Barren land	Eucalyptus	Mixed forest
Plants		3 (only in gullies; cover << 1%)	2	320
Avian species (including residential and transient birds)		4	7	18
Small mammals (no. of species)		0	2	8
Soil animals (no. of orders)		15	25	31
Soil animal biomass ($g\cdot m^{-2}$)		0.33	8.91	18.14
Insects (no. of families)		12	63	123
Microbes (individuals (10^6) per gram of dry soil)	Bacteria	0.09	1.80	4.22
	Fungi	0.29	1.96	0.65
	Actinomycetes	0.06	1.35	2.45
	Total	0.44	5.11	7.32

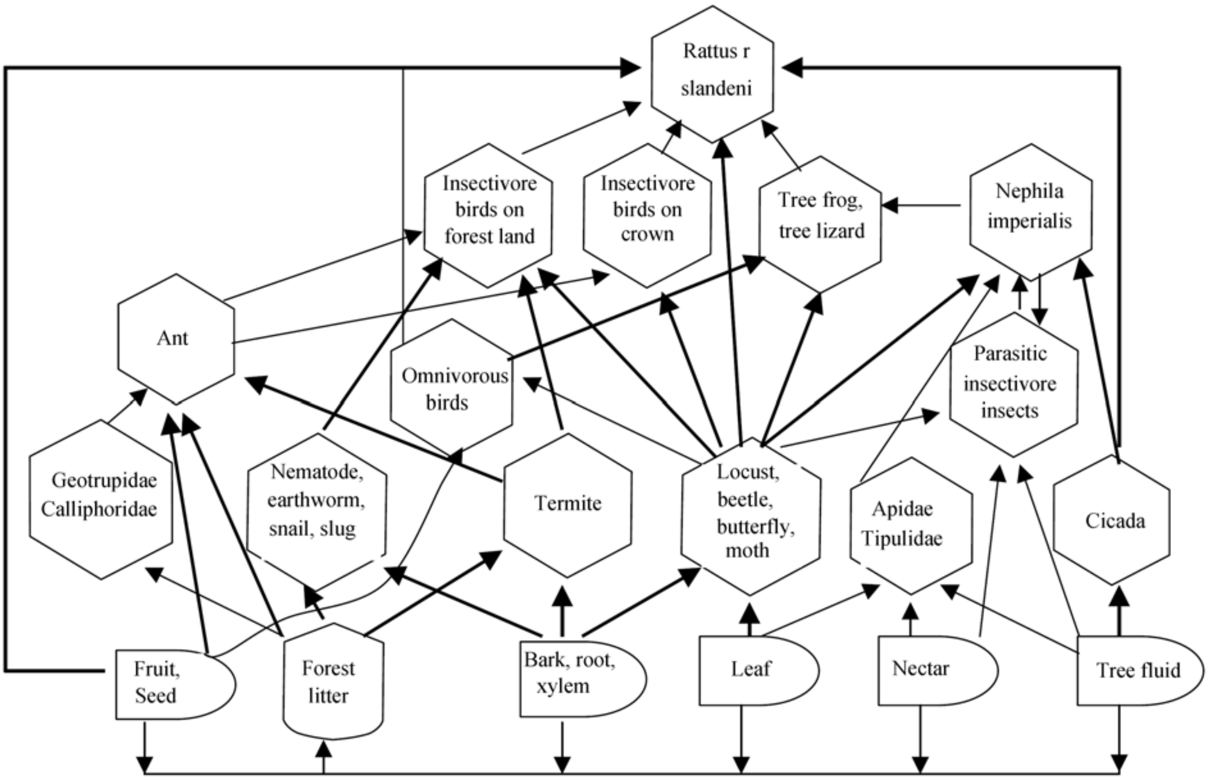

Figure 3 Food web structure of the broad-leaved mixed forest ecosystem. The thickness of connecting lines denotes the relative importance of the feeding relationships in the system.

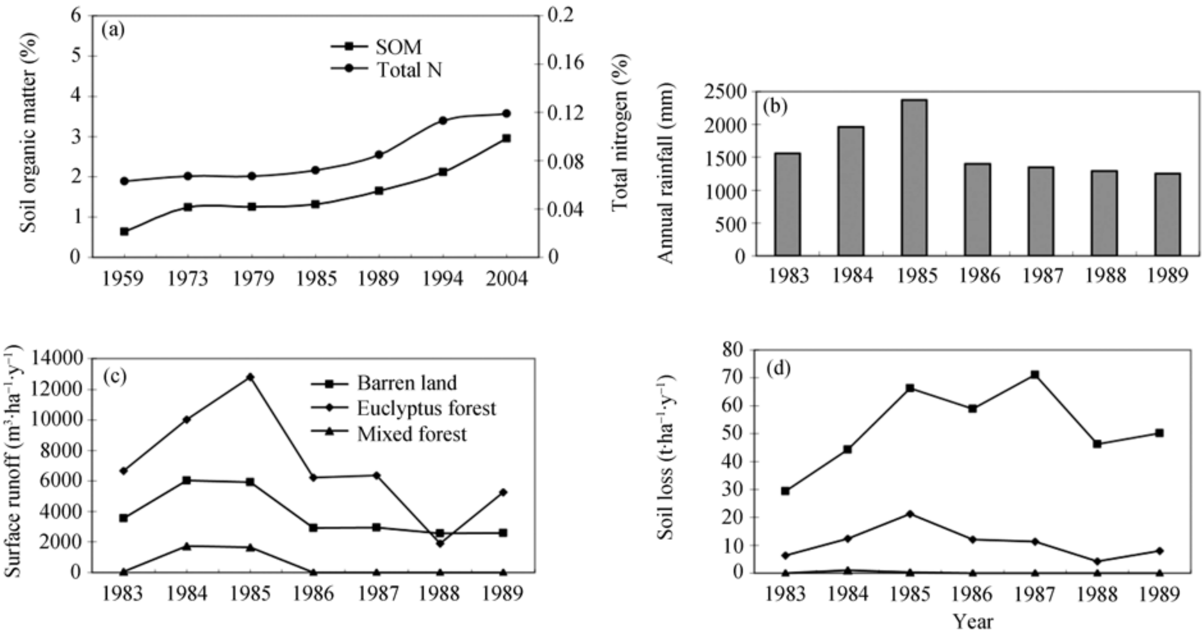

Figure 4 Changes in the ecosystem functioning of the three contrasting catchments: the barren land, eucalyptus forest, and mixed forest.

3 Discussion and conclusions

Our study provides several valuable lessons for restoring such barren lands in south China[17,18] and the rest of the world. First of all, there exist two kinds of thresholds during ecosystem restoration: the initial threshold characterized by extremely harsh physical environmental conditions and the secondary threshold controlled mainly by a critical level of biodiversity and dispersal-facilitating landscape context. In order for a severely degraded ecosystem to overcome these thresholds, human ameliorative efforts are needed. Such efforts should focus mainly on controlling soil and water loss from the system at the initial stage of restoration, since improvements in soil conditions are critically important to remove the physical barriers to seedling establishment. The choice of appropriate pioneer species is crucial in this initial stage as indicated by our study. Second, our study demonstrates that both the biodiversity and species composition at the initial stage of rehabilitation can have long-term effects on the successional trajectory of the ecosystem being restored[29]. Introduction of a single hardy species in an extremely degraded site, the eucalyptus forest in our case, may turn barren land into a forest, but this forest may never develop into an ecosystem similar to the pre-disturbance state. This corroborates the argument made by others that many mine reclamation efforts focusing on rapid-growing non-native species to control soil erosion may inhibit long-term ecosystem recovery[5, 30]. In our case, improper management practices of the single-species stand, such as removing litter from the forest floor, increased the loss of soil moisture and thus may have also reduced the possibility of native species getting established. On the other hand, planting a diversity of species can accelerate the restoration of biodiversity and ecosystem functioning as well as increase ecosystem stability. Once a relatively diversified forest is established, the forest could succeed naturally toward a zonal mature ecosystem with a complex food web, a stratified vegetation structure, enhanced soil fertility and a diverse soil microbial community. Third, because restoring severely degraded tropical lands requires extremely labor-intensive and costly ameliorative efforts, it is both ecologically and economically more sensible to prevent tropical rain forests from being denuded through proper ecosystem management measures.

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