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Effects of management on vegetation dynamics and associated nutrient cycling in a karst area, Yunnan, SW China

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Abstract The legacies of land use (such as plantations, pastures and coppices) in the Shilin karst area of central Yunnan, SW China have strongly influenced the plant communities' structure, dynamics, species diversity, litter nutrients inputs, and soil chemical properties. To evaluate the effects of various restoration approaches on ecosystem recovery in the area, we analyzed vegetation characteristics of a *Pinus* plantation, natural successional plant communities (the shrubland, the secondary forest and the natural premature forest), and their leaf litter nutrients and soil chemical properties. The natural successional plant communities had better regeneration, higher species diversity, higher litter nutrient input, and higher soil fertility as compared with the *Pinus* plantation. The results indicate that the natural secondary succession facilitates regeneration to young and old secondary forests, promotes recovery of plant diversity and cycling of litter-soil-nutrients, yielding greater ecological benefits. The study will provide guidance for restoration of the vegetation and for forest management planning in this fragile mountainous ecosystem.

Keywords Litter nutrient inputs · Plantations · Regeneration dynamics · Secondary succession · Shilin karst area · Soil properties · Species diversity

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Introduction

Restoration of degraded land may be achieved by establishing plantations or may be left to natural succession. Succession plays an important role in vegetation recovery, community structure, and dynamics in post-disturbance landscapes (Drake 1990; Oliver and Larson 1990). Secondary succession is a complex multifactorial process (Bazzaz 1990; Peet 1992). Regeneration dynamics vary with the intensity of disturbances, natural and man-made. *Pinus* afforestation has occurred in many regions of the world (FAO 2007). Plantations will not match the composition and structure of the original forest cover (Chazdon 2008). Studies have reported that monocultural plantations have reduced biodiversity in many regions such as southwestern (Tang et al. 2007, 2010a) and northern China (Jiang et al. 2003) and in Japan (Nagaike 2000; Ito et al. 2003), while pine plantations in degraded land have provided conditions for rehabilitation of natural vegetation in Thailand (Oberhauser 1997), Sri Lanka (Ashton et al. 1997), and northern China (Zhang et al. 2010). Plant litter production is an important process controlling nutrient cycling within forest ecosystems, being the main mechanism of transfer of dead organic matter (OM) and nutrients from living biomass to soils (Vitousek and Sanford 1986; Arunachalam et al. 1998). Needles of some *Pinus* species hinder regeneration of native plants and influence ecosystem processes by affecting the soil nutrient cycling, the water, and light regimes, or by allelopathic effects (Facelli and Pickett 1991; Eckstein and Donath 2005; Nektarios et al. 2005; Navarro-Cano et al. 2010).

Rocky desertification in southwestern China has resulted from severe ecological and environmental degradation through depletion of biodiversity, destruction of habitats, and deterioration of soil due to large-scale tree cutting, pasture creation, slash-and-burn agriculture, and the collection of fuelwood (Cao et al. 2003; Wang and Liu 2004; Zhang et al. 2006). A government policy of ''returning the agricultural land to the forests'' was implemented between the mid-1980s and late 1990s in China, and included abandonment of agricultural land and a vast project of sowing *Pinus* seeds from airplanes. Since then the secondary plant communities (also called the naturally regenerated plant communities) have been in the process of succeeding toward the state of the original natural forests (Tang 2010; Tang et al. 2010b). Widespread loss and habitat degradation of natural forests in the karst areas have motivated previous studies on plant communities (Yu et al. 2002; Su and Li 2003; Shen et al. 2005), species diversity (Tang et al. 2010a) and soil chemistry (Li et al. 2005; Hu et al. 2009). However, studies have not been done on the influence of natural successional plant communities and *Pinus* plantations on ecosystem restorative processes in the karst area. To make recommendations for restoration of the ecosystem, we need to evaluate the recovery seen in the post-disturbance karst landscape.

Based upon a detailed examination of secondary successional plant communities and a *Pinus* plantation, comparisons of the plant communities, litter, and soil nutrient dynamics were made among all the representative vegetation of the local landscape, according to their recent history of disturbances and management. Our aim was to study effects of management on vegetation dynamics and associated nutrient cycling, to answer the question: What are the effects of natural secondary succession, as compared to a *Pinus* plantation, on ecosystems as seen in the plant diversity, regeneration dynamics, litter nutrients inputs, and soil chemical properties of soils?

Methods

Study area

This study was carried out in the Shilin karst area (24°38′–24°58′N, 103°11′–103°29′E, alt. 1600–2203 m) of central Yunnan (Fig. 1). The area covers about 900 km^2 underlain by Permian carbonate rocks, of which more than 400 km^2 have developed into karst and related landforms. The climate is subtropical, with a mean annual temperature of 16.2 °C (mean maximum temperature is 20.7 °C in July and mean minimum temperature is 8.2 °C in January), and a mean annual precipitation of 967.9 mm, 80 % of which falls between May and October. The land consists of rock gaps, rock ditches, small rock caves and rock slots, all of which are surrounded by soil. The soil is shallow and patchily distributed on or between these various rock surfaces. The ratio of outcrops to soil ranges from 0.3 to 1.3. Soil types were originally the same in all the study sites, based on the same climatic conditions and the same mineralogical and textural character of surface and subsurface soils. The differences among present-day soil properties are attributed to plant litter traits reflecting different plants, diverse plant communities, and varied disturbances or human activities.

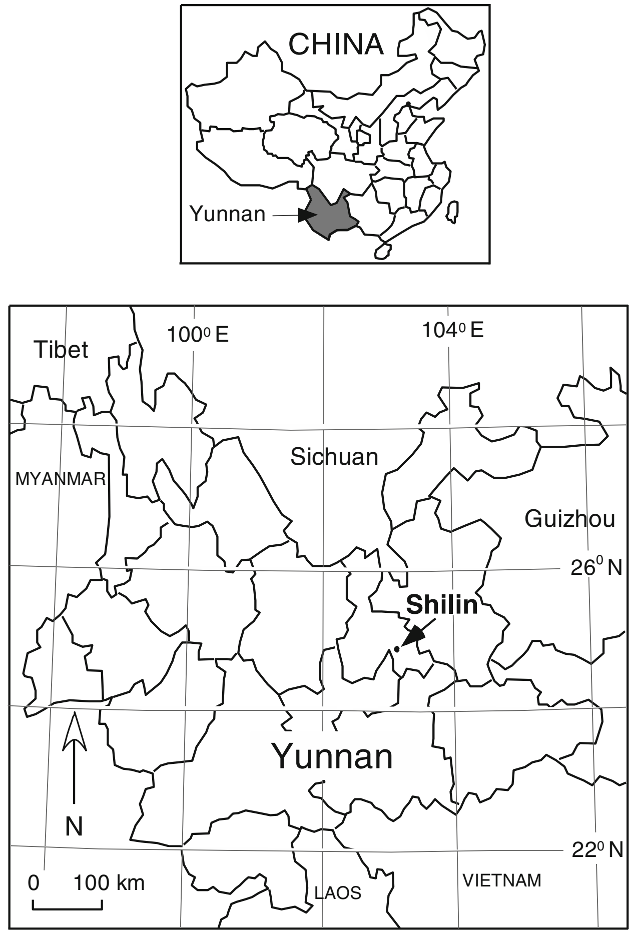


Fig. 1 The location of the study area (Shilin) in central Yunnan, China

The original vegetation in the area was semi-humid evergreen broad-leaved forest dominated by evergreen species of *Cyclobalanopsis* (a sub-genus of Quercus), *Castanopsis* and *Lithocarpus* of Fagaceae (Wu et al. 1987; Tang and Ohsawa 2009; Tang et al. 2013). Most of this forest had previously been utilized as coppices for fuelwood or pastures, but since the 1980s some of the pastures and bare land have been replaced by plantations of *Pinus yunnanensis*. Other remnant coppices and pastures were abandoned in the 1980s and have since regenerated naturally, with secondary stands consisting of evergreen and deciduous broad-leaved trees or shrubs. These secondary woodlands and *Pinus* plantations have been unmanaged since they were either abandoned or planted. The landscapes appear as dynamic habitats comprised of mosaics of diverse stands in various stages of vegetation recovery.

Data collection and analysis

The plant communities are heterogeneous in structure and species composition. We surveyed all the vegetation patches in the area. Based on management history and disturbance intensity we established transects for natural secondary plant communities including the shrubland (4 transects) in Naigushan, the secondary forest (4 transects) in Yuehu and the natural premature forest in Soyishan (6 transects) to represent different periods of natural secondary succession, and for a plantation (4 transects) in Songlinhoushan. The intensity of disturbances' influence is defined based on disturbance type, disturbance severity, and time since the last disturbance. It was evaluated subjectively by scores assigned as follows: 1, limited cutting of fuelwood before 1975, protected from human activity since then; 5, cutting of fuelwood ceased in 1980; 10, clear-cutting 40 years ago and use as a pasture until late 1980s; and 15, *Pinus* plantation (Uotila and Kouki 2005; Tang et al. 2010b). The age for each type of plant community was determined from known management history or tree-rings of dominant tree species with large DBHs in transects. Within the secondary forest, 2 transects were selected for a 40 year-old forest and a 50 year-old forest, respectively. Within the premature forest, 2 transects were selected each for an 80 year-old forest, a 105 year-old forest and a 120 year-old forest. Since the shrubland was unified as 20 year-old after pasture abandonment and the *Pinus* plantation was unified as 30 year-old after seed dispersal by airplanes, 4 transects for each of them were randomly chosen to ensure the representativeness of the sampling sites. A transect of arbitrary length was selected and divided into 10 m × 10 m quadrats. In view of the relationship between the minimal area of a transect and the maximum number of species, our quadrat sampling was continued at each transect until no newly appeared species were encountered in three contiguous quadrats. A total of 2.06 ha were sampled. In studying the overstory of the plant communities, a tree inventory was carried out for all the individuals at least 1.3 m high in each quadrat. All were tagged with numbered tape, recorded with species name, whether living or dead, diameter at breast height (DBH) (including all stem stumps and sprouts) and tree height (*H*). We randomly selected two 2 m × 2 m plots in each quadrat to investigate the woody species ($H < 1.3$ m) in the understory. Seedlings (30 cm $< H <$ 130 cm) of each species were counted. For herbaceous species investigation, we randomly selected two 1 m × 1 m subplots in each quadrat. All the species were identified and the number of individuals was counted. The diversity indices for woody and herbaceous species were calculated using the Shannon–Wiener index (H') (Pielou 1969).

In each transect, 4 quadrats were randomly chosen for soil samples. In each quadrat, we randomly collected soil samples (0–20 cm depth) from five locations, and then mixed them to represent the soil of the quadrat. The soil samples were air-dried, and passed through 1.0 and 0.25 mm sieves. We performed soil chemical analysis following standard methods of the Forestry Bureau of China (1999) as follows. Soil acidity (pH) was measured using a glass electrode (1:5 soil:water ratio). Soil OM by the oil bath $K_2Cr_2O_7$ titration method after digestion, and total nitrogen (TN) by the Kjeldahl method. The concentration of the following total elements was determined after treating samples in solution composed of 5 ml perchloric acid ($HClO_4$) and 5 ml hydrofluoric acid (HF), then dissolving and cooling them in 50 ml solution of diluted hydrochloric acid (HCl) to get sample solutions for analysis; total phosphorus (TP) by molybdenum blue colorimetry, total potassium (TK) by flame photometry, total calcium (TCa) and total magnesium (TMg) by atomic absorption spectrometry. Hydrolyzable nitrogen was considered as available nitrogen (AN) in this study as per the Forestry Bureau of China (1999) and determined by using a micro-diffusion technique after alkaline hydrolysis. Available phosphorus (AP) was determined by the Olsen method. Exchangeable potassium (EK) was determined by the atomic absorption spectrometry on 1 mol/L ammonium acetate (NH_4OAc) extract. Exchangeable calcium (ECa) and exchangeable magnesium (EMg) were determined after treating samples with 1 mol/L NH_4-OAc and a standardizing solution of 250 ml to exclude organic substances for analysis by Inductively coupled plasma atomic-emission spectrometry (ICP-AES) on 1 mol/L sodium bicarbonate ($NaHCO_3$) (pH = 7) extract. In each transect 10 L traps (each 0.25 m^2) were installed. The litter traps were made of plastic material with 1.2 mm mesh. Each trap was supported on four legs so that the top was 30 cm above the soil. Aboveground litterfall was collected every month from November 2009 to October 2010. The material that fell into the traps included leaves, flowers, fruits and twigs (<2 cm), and was, therefore, equivalent to the fine litter of Vitousek (1984) and the small litter of (Proctor

1983). At each collection date the content of each trap was placed in paper bags, brought to the field laboratory and dried at 65 °C to a constant weight. N, P, and K concentrations of litter samples were determined after being wet digested in a $H_2SO_4 + H_2O_2$ (with a Se + $CuSO_4$ catalyst) acid mixture. The semi-micro Kjeldahl procedure was applied for determination of N, and P was measured spectrophotometrically after a reaction with ammonium molybdate + ammonium vanadium, and K was determined by flame photometry. Ca and Mg were determined by atomic absorption spectrometry after digestion of ground samples in concentrated $H_2SO_4 + HClO_4 + HNO_3$. At each collection date, nutrient pools in litterfall were calculated by multiplying the mass of each trap by its corresponding nutrient concentration. To estimate forest-floor mass, 10 replicates of a 50 cm × 50 cm plot were randomly placed on the forest-floor of each transect every month, and all forest-floor material inside the plot was removed. It was then separated into leaves, cones, fruit, flowers, and bark plus branches (<2 cm diameter), and dried at 105 °C to a constant weight.

Litter turnover (k) as calculated as annual litterfall divided by floor litter matter (litter standing crop) on the soil surface, or alternatively an exponential decay constant (k), was fitted to the rates at which confined leaves lost weight (Vitousek and Sanford 1986). Nutrient concentration of litterfall was used to determine potential nutrient inputs to each site. Potential nutrient inputs were determined by multiplying total values of litterfall by the corresponding nutrient concentration.

Species basal area (BA, cm^2) of plants was calculated from DBH (diameter at breast height) data for all the stems of woody species, and the relative proportion of BA was calculated for the species (RBA, %). To determine which woody species were dominant, dominance analysis (Ohsawa 1984) was applied. We categorized species according to their light requirements as light-demanding, intermediate (somewhat light-demanding, somewhat shade-tolerant), and shade-tolerant. Designation of species traits was based on the information from Tang et al. (2010a).

Differences in species diversity, in forest floor mass, leaf litter nutrient inputs and soil chemical properties among plant communities were tested by the non-parametric Kruskal–Wallis all-pairwise comparisons test, using Analyse-it software (Analyse-it Software, Ltd., UK).

Results

Characteristics of plant communities

Table 1 provides a summary of the characteristics of the 4 plant community types with the intensity (score) of disturbances, including the *Pinus* plantation (PP), the shrubland (SL), the secondary forest (SF), and the natural premature forest (NF), which were taken as representative mosaics of patchy vegetation in the Shilin area. In total, 64 woody species (trees and shrubs) were found in the four communities. The community structure varied among the four community types, as follows.

1. The *Pinus* plantation (PP) in Songlinhoushan was exclusively dominated by *Pinus yunnanensis*, which grew after seed dispersal by airplanes in 1980. The maximum height was 15 m with 26.8 cm DBH.
2. The shrubland (SL) in Naigushan was dominated by pioneer light-demanding evergreen broad-leaved *Neolitsea homilantha*, which began to grow after the abandonment of a pasture in 1989. It represented the early successional plant community. The maximum height was 8.5 m with 9 cm DBH.
3. The secondary forest (SF) in Yuehu was dominated by shade-tolerant evergreen broad-leaved *Cyclobalanopsis glaucoides* and *Olea yunnanensis*, as well as light-demanding deciduous *Pistacia weinmannifolia*, representing a natural process formed from an abandoned coppice that was utilized for fuelwood cutting until 1990. It represented the middle successional forest. The maximum height of trees reached 14 m with 33.4 cm DBH. Many sprouts in the secondary forest were the result of fuelwood cutting in the past.
4. Natural premature forest (PF) in Soyishan was dominated by shade-tolerant evergreen *Cyclobalanopsis glaucoides*, *Olea yunnanensis* and light-demanding deciduous *Pistacia weinmannifolia* in the canopy layer, constituting a premature stage of a typical semi-humid evergreen broad-leaved forest in central Yunnan. This plant community was partially cut for fuelwood 25 years ago, but there has been no human activity since then. True primary forests are practically nonexistent in the area. The natural premature forest represented the late successional forest. The maximum height and DBH were 25 m and 68.2 cm, respectively.

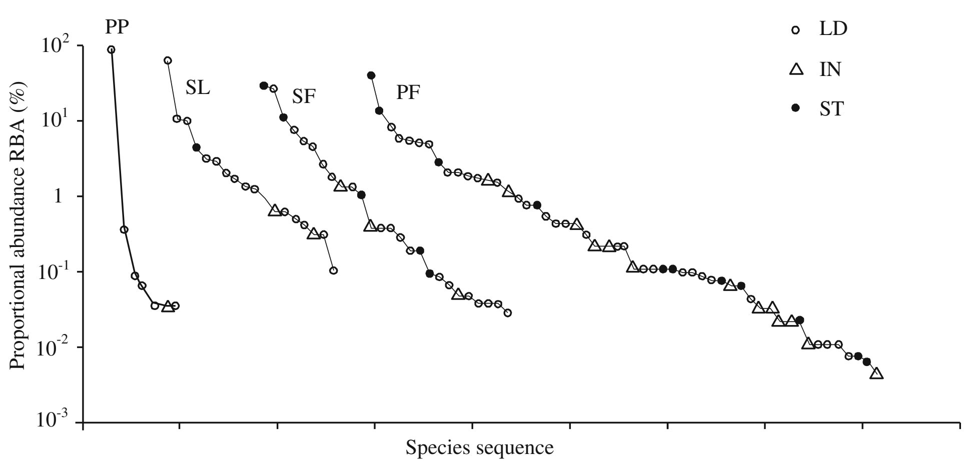
The natural premature forest had significantly higher numbers of woody species and herbaceous species. The Shannon–Weiner index (H') of woody species significantly increased from the *Pinus* plantation to the shrubland, then to the secondary forest, finally to the premature natural forest, while the H' of herbaceous species did not significantly differ among the four community types (Table 1). To ascertain diversity structure in relation to species traits (i.e., light-demanding, intermediate and shade-tolerant species) of all the four communities, dominance-diversity curves are drawn in Fig. 2. The abundance of each species was plotted on a logarithmic scale from the most to the least abundant species. In the secondary forest (SF) and the

Table 1 Characteristics of each plant community

Community type	*Pinus* plantation (PP)	Shrubland (SL)	Secondary forest (SF)	Natural premature forest (PF)
No. of transects	4	4	4	6
Transect area (m^2)	4800	4000	4000	7800
Stand age (year)	30	15–20	40–50	80–120
Land use history	Grew after seed dispersal by airplane in 1980	Area used as pasture until late 1980s	Cutting of fuelwood ceased in 1980	Limited cutting of fuelwood before 1975, protected from human activity since then
Intensity (score) of disturbances	15	10	5	1
Dominant species	*Pinus yunnanensis*	*Neolitsea homilantha*	*Cyclobalanopsis glaucoides*, *Olea yunnanensis*, *Pistacia weinmannifolia*	*Cyclobalanopsis glaucoides*, *Olea yunnanensis*, *Pistacia weinmannifolia*
No. of woody species	13.5 ± 2.89^{d}	23.5 ± 7^{c}	29.2 ± 3.11^{b}	48.6 ± 4.04^{a}
H' for woody species	2.49 ± 0.4^{d}	3.14 ± 0.09^{c}	3.45 ± 0.1^{b}	3.81 ± 0.3^{a}
No. of herbaceous species	22.75 ± 4.35^{b}	26.25 ± 3.3^{b}	28.6 ± 5.86^{b}	43.8 ± 7.12^{a}
H' for herbaceous species	3.11 ± 0.16^{a}	3.26 ± 0.57^{a}	3.77 ± 0.42^{a}	3.67 ± 0.48^{a}
Basal area at breast height (m^2/ha)	4.7	1.3	11.3	19.2
No. of stems (>1.3 m high) per ha	594	881	3748	2437
Max. height (m)	15	8.5	14	25
Max. DBH (cm)	26.8	9	33.4	68.2
Mean height (m)	5.7	2.8	3.4	5
Mean DBH (cm)	8.1	3.3	5.3	7.9

The transect area is for the total area of the transects in each plant community type. Significant differences of number (±SE) of species and Shannon Weiner index (H') (±SE) are indicated by different superscript letters ($p < 0.05$)

Fig. 2 Dominance-diversity curves of the four plant communities. Species traits are distinguished with marks. *PP* *Pinus* plantation, *SL* shrubland, *SF* secondary forest, *PF* natural premature forest, *LD* light-demanding, *IN* intermediate, *ST* shade-tolerant



natural premature forest (PF), many species had similar RBA, and there were several co-dominant species. Hence, the diversity was higher in the SF and PF. In the shrubland, the patterns became steeper. In the *Pinus* plantation, the top dominant (*Pinus yunnanensis*) became conspicuous. The diversity curves could represent the relative importance of the species in the community as well as illustrate the role played by certain species in determining community structure. The woody species ($H \geq 1.3$ high) composition is shown in Appendix 1.

Regeneration dynamics in the various plant communities

We consider a species to be an important one if it dominates at least one community. Figure 3 indicates the regeneration dynamics of five important species. They show inverse-J, sporadic and unimodal types of DBH size frequency distribution. The inverse-J type, having the highest frequency in small DBH classes with gradual decrease in the number of individuals toward the large size-classes, suggests that regeneration is active. The sporadic type, with more than one peak in the size-classes, indicates the possibility of weak or strong regeneration. The unimodal type, with a single peak in the intermediate or large DBH size-classes and fewer if any individuals in small-size classes, suggests a weak regeneration pattern. In the *Pinus* plantaion (PP) *Pinus yunnanensis* was of the inverse-J type. Only a few individuals of *Pistacia weinmannifolia* of 5–10 cm DBH were found at the forest edge. In the shrubland, *Neolitsea homilantha*, *Olea yunnanensis* and *Pistacia weinmannifolia* fell into the inverse-J type; seedlings of shade-tolerant *Cyclobalanopsis glaucoides* were found in the understory, though none were taller than 1.3 m of this species. In the secondary forest (SF), *Olea yunnanensis*, *Pistacia weinmannifolia*, and *Cyclobalanopsis glaucoides* were in good regeneration of the inverse-J type, while *Neolitsea homilantha* had a week generation pattern of the unimodal type. In the natural premature forest (PF), *Cyclobalanopsis glaucoides* was in very good regeneration of the inverse-J type; by contrast *Neolitsea homilantha* and *Pistacia weinmannifolia* were represented by the unimodal type and *Olea yunnanensis* by the sporadic type, with weak regeneration.

Nutrient dynamics in the various plant communities

Litter production and nutrient inputs

In the late successional premature forest (PF) and the middle (seral) successional secondary forest (SF), the litter production and forest floor mass were significantly higher than those in the early successional shrubland (SL) and *Pinus* plantation (PP) (Table 2). Litter turnover coefficient (k) in the premature forest (0.38 year^{-1}), the secondary forest (0.36 year^{-1}) and the shrubland (0.32 year^{-1}) had significantly higher values than that in the *Pinus* plantation (0.24 year^{-1}). The concentrations of leaf litter nitrogen (ranging from 10.76 to 12.83 g/kg), phosphorous (from 1.24 to 1.53 g/kg) and potassium (from 5.55 to 7.51 g/kg) in all the secondary successional plant communities showed significantly higher values than those in the *Pinus* plantation. Leaf N (9.91 kg ha^{-1} year^{-1}), P (1.62 kg ha^{-1} year^{-1}), and K (4.69 kg ha^{-1} year^{-1}) inputs in the *Pinus* plantation showed significantly lower values than those in the successional communities. Leaf litter *Pinus* plantation had the lowest value compared with the other plant communities. Leaf litter Ca and Mg inputs in both of the *Pinus* plantation and the shubland were low, but they did not significantly differ from each other.

Soil chemical properties

Table 3 shows soil chemical properties among the four plant communities. The soil pH values varied from 5.1 to 7 among these communities. In the natural premature forest (PF) and the secondary forest (SF), the OM (ranging from 10.66 to 13.73 %), organic C (ranging from 6.31 to 7.96 %), total N (ranging from 0.45 to 0.55 %), available N (ranging from 313.6 to 436 mg/kg), available P (ranging from 4.18 to 4.51 mg/kg), and available K (ranging from 129.67 to 144 mg/kg) were higher than those in the shrubland (SL) and the *Pinus* plantation (PP). The shrubland had significantly higher concentrations of total N (0.35 %), total P (0.07 %) and available N (268 mg/kg), available P (3.88 mg/kg) than those in the *Pinus* plantation. The concentrations of total Ca, and exchangeable Ca tended to be higher in the secondary forest and the shrubland than in the other plant communities. The ratio of organic C to total N in the *Pinus* plantation was the highest (19.41) among all the plant communities.

Age-related patterns of leaf litter nutrient inputs and soil available nutrients were observed across the natural secondary successional plant communities (Fig. 4a–f). The concentrations of leaf litter N, P and K inputs and soil available N increased with increasing plant community ages. In contrast, the 30-year-old *Pinus* plantation hindered the soil development via low leaf litter nutrient input.

Discussion

Ecosystem processes

As for the degraded ecosystem, its recovery relies on the increase of species diversity, litterfall production, litter nutrient input and rehabilitation of soil fertility. The *Pinus* plantation as a human restoration effort has resulted in poor species diversity because the densely planted *Pinus yunnanensis* occupied the available space, hindering other species' regeneration. In contrast, a number of light-demanding species, colonized in the shrubland, have con-

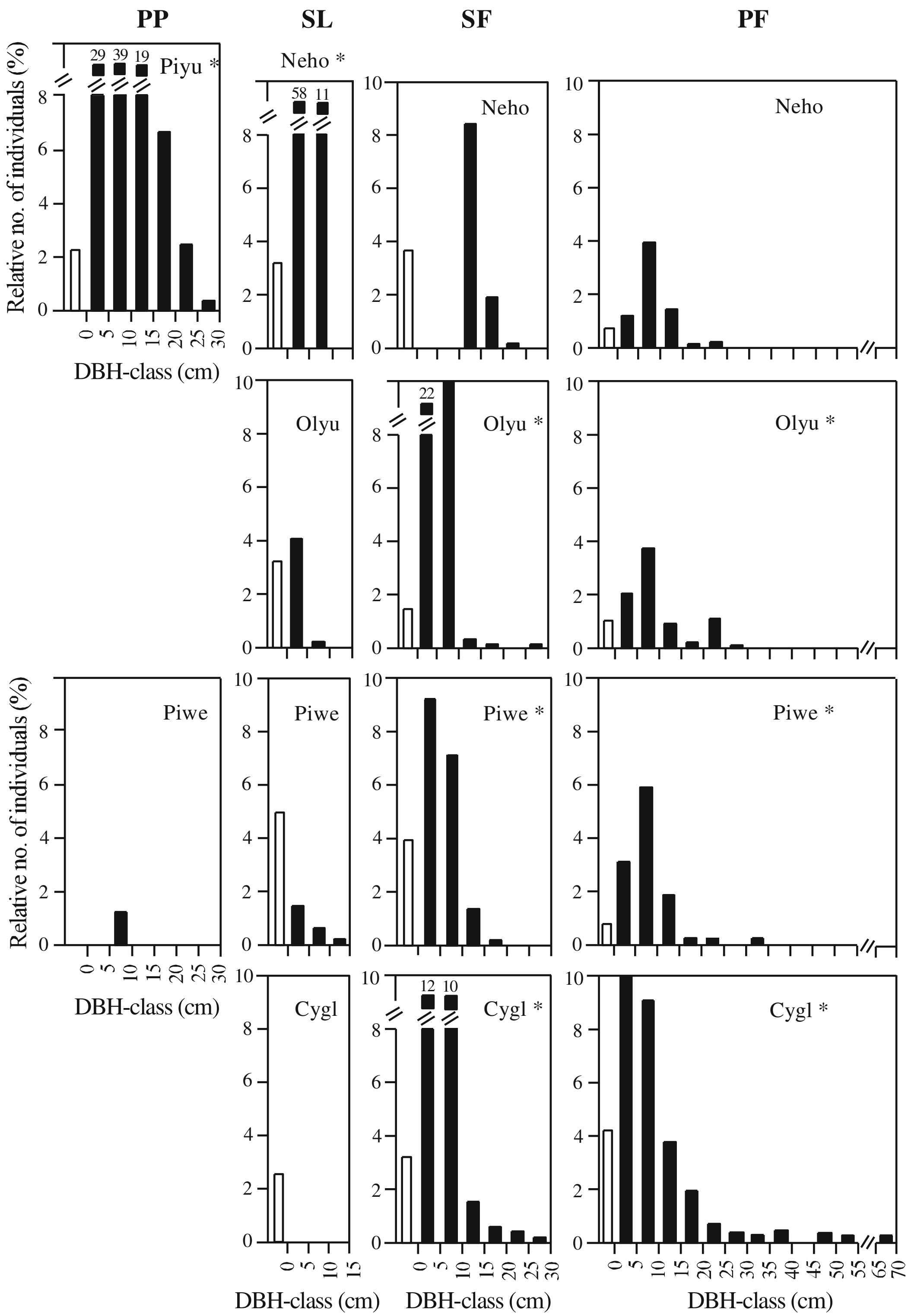


Fig. 3 The DBH-class frequency distribution and seedlings for major species. Dominant species are indicated by an *asterisk*. The number of seedlings (30 cm < *H* < 130 cm) is represented by an *empty bar*. *PP Pinus* plantation, *SL* shrubland, *SF* secondary forest, *PF* natural premature forest, Piyu, *Pinus yunnanensis*; Neho, *Neolitsea homilantha*; Olyu, *Olea yunnanensis*; Piwe, *Pistacia weinmannifolia*; Cygl, *Cyclobalanopsis glaucoides*

Table 2 Litterfall, forest floor mass, litter turnover coefficient, turnover time, and nutrients concentrations of leaf litterfall and leaf litter nutrients input in the four plant communities (±SD)

	PP	SL	SF	PF
Litterfall (t ha^{-1} $year^{-1}$)	1.49 ± 0.52^{c}	1.6 ± 0.69^{c}	3.31 ± 0.82^{b}	4.59 ± 1.04^{a}
Forest floor mass (t ha^{-1})	6.48 ± 1.17^{c}	4.91 ± 1.06^{c}	9.25 ± 1.07^{b}	12.29 ± 2.03^{a}
Litter turnover coefficient (k) ($year^{-1}$)	0.24 ± 0.12^{c}	0.32 ± 0.09^{b}	0.36 ± 0.06^{a}	0.38 ± 0.1^{a}
Turnover time (1/k) (year)	4.76 ± 2.43^{a}	3.34 ± 0.87^{b}	2.88 ± 0.53^{c}	2.76 ± 0.68^{c}
Leaf litter N (g/kg)	6.64 ± 0.98^{c}	10.76 ± 1.84^{b}	11.64 ± 2.59^{ab}	12.83 ± 1.2^{a}
Leaf litter P (g/kg)	1.09 ± 0.45^{c}	1.24 ± 0.26^{b}	1.41 ± 0.38^{ab}	1.53 ± 0.42^{a}
Leaf litter K (g/kg)	3.15 ± 2.32^{c}	7.51 ± 4.44^{a}	5.55 ± 2.74^{b}	6.12 ± 3.29^{b}
Leaf litter Ca (g/kg)	3 ± 2.85^{c}	2.89 ± 1.04^{c}	5.03 ± 2.23^{b}	7.85 ± 1.53^{a}
Leaf litter Mg (g/kg)	4.83 ± 1.24^{b}	3.57 ± 0.73^{b}	9.13 ± 2.26^{a}	11.06 ± 4.24^{a}
Leaf litter N input (kg ha^{-1} $year^{-1}$)	9.91 ± 2.75^{d}	17.22 ± 7.81^{c}	38.53 ± 9.56^{b}	58.88 ± 13.03^{a}
Leaf litter P input (kg ha^{-1} $year^{-1}$)	1.62 ± 0.56^{c}	1.98 ± 0.86^{c}	4.67 ± 1.12^{b}	7.01 ± 1.31^{a}
Leaf litter K input (kg ha^{-1} $year^{-1}$)	4.69 ± 1.38^{d}	12.02 ± 5.04^{c}	18.36 ± 4.56^{b}	28.08 ± 6.33^{a}
Leaf litter Ca input (kg ha^{-1} $year^{-1}$)	4.47 ± 1.55^{c}	4.62 ± 2^{c}	16.64 ± 4.13^{b}	36 ± 8.54^{a}
Leaf litter Mg input (kg ha^{-1} $year^{-1}$)	7.19 ± 2.31^{b}	5.71 ± 2.76^{b}	30.2 ± 8.51^{a}	50.81 ± 11.5^{a}

Values followed by different letters are significantly different at $p < 0.05$. *PP Pinus* plantation, *SL* shrubland, *SF* secondary forest, *PF* natural premature forest

Table 3 Soil properties in each plant community (±SD)

	PP	SL	SF	PF
pH	6.0 ± 0.47^{b}	7.0 ± 0.2^{a}	6.5 ± 0.4^{ab}	5.1 ± 0.18^{c}
OM (%)	7.38 ± 1.26^{b}	7.57 ± 2.04^{b}	10.66 ± 4.1^{a}	13.73 ± 0.9^{a}
OC (%)	4.28 ± 0.75^{b}	4.71 ± 1.17^{b}	6.31 ± 2.27^{a}	7.96 ± 0.53^{a}
TN (%)	0.23 ± 0.09^{c}	0.35 ± 0.08^{b}	0.45 ± 0.18^{a}	0.55 ± 0.03^{a}
C/N	19.41 ± 6.52^{a}	13.44 ± 1.82^{b}	15.12 ± 7.25^{b}	14.56 ± 0.32^{b}
TP (%)	0.03 ± 0.01^{c}	0.07 ± 0.02^{ab}	0.06 ± 0.03^{b}	0.08 ± 0.01^{a}
TK (%)	0.58 ± 0.2^{b}	0.3 ± 0.06^{c}	0.73 ± 0.14^{a}	0.28 ± 0.03^{c}
TCa (%)	0.69 ± 0.14^{b}	1.02 ± 0.23^{a}	1.1 ± 0.27^{a}	0.5 ± 0.1^{b}
TMg (%)	0.39 ± 0.17^{b}	0.63 ± 0.05^{a}	0.57 ± 0.08^{a}	0.36 ± 0.05^{b}
AN (mg/kg)	150.3 ± 72.05^{d}	268 ± 73.2^{c}	313.6 ± 160.5^{b}	436 ± 74.98^{a}
AP (mg/kg)	3.42 ± 1.04^{c}	3.88 ± 1.67^{b}	4.51 ± 1.73^{a}	4.18 ± 0.76^{ab}
AK (mg/kg)	103 ± 32.77^{b}	105.17 ± 25.18^{b}	144 ± 46.04^{a}	129.67 ± 24.93^{a}
ECa [cmol (1/2Ca^{2+})/kg]	23 ± 5.71^{b}	32.5 ± 6.24^{a}	30.03 ± 8.1^{a}	18.9 ± 5.59^{c}
EMg [cmol (1/2 Mg^{2+})/kg]	1.82 ± 0.41^{b}	4.79 ± 1.05^{a}	1.73 ± 0.74^{b}	1.12 ± 0.42^{b}

PP Pinus plantation, *SL* shrubland, *SF* secondary forest, *PF* natural pre-mature forest, *OM* organic matter, *OC* organic carbon, *TN* total nitrogen, *AN* available nitrogen, *TP* total phosphorus, *AK* available potassium, *TK* total potassium, *TCa* total calcium, *ECa* exchangeable calcium, *TMg* total magnesium, *EMg* exchangeable magnesium

Different letters in a row differ significantly ($p < 0.05$)

tributed to higher species diversity. Analysis of the population dynamics of a plant community provides information on habitat suitability and ecosystem productivity, helping to predict successional pathways (Jones et al. 2004; Silver et al. 2004). The present 30-year-old *Pinus* plantation with the disturbance score 15, is overwhelmingly dominated by *Pinus yunnanensis*, making it difficult to predict its future successional trend. In the shrubland with the disturbance score 10, however, seedlings of late-successional species *Cyclobalanopsis glaucoides* have begun to appear in the understory. In the secondary forest with the disturbance score 5, when the plant community achieves more closure, shade-tolerant *Cyclobalanopsis glaucoides* can establish themselves. In the natural premature forest with the disturbance score only 1, gradual replacement of light-demanding pioneer *Neolitsea homilantha* and *Pistacia weinmannifolia* by *Cyclobalanopsis glaucoides* is clearly seen in its dominance in the understory and overstory (Fig. 3). Space-for-time substitution can approximate successional trends (Foster and Tilman 2000; Molles 2002). Tang et al. (2010b) studied plant communities of central Yunnan resembling these of the Shilin area, providing a secondary successional model for central Yunnan: the abandoned farmland, pasture, or clear-cut forest would in c. 15–50 years form a pioneer woody community dominated by light-demanding deciduous or evergreen broad-leaved or coniferous species, then at 40–80 years the early successional community would establish a mixed evergreen and deciduous broad-leaved or coniferous forest dominated by both light-demanding and shade-tolerant tree species,

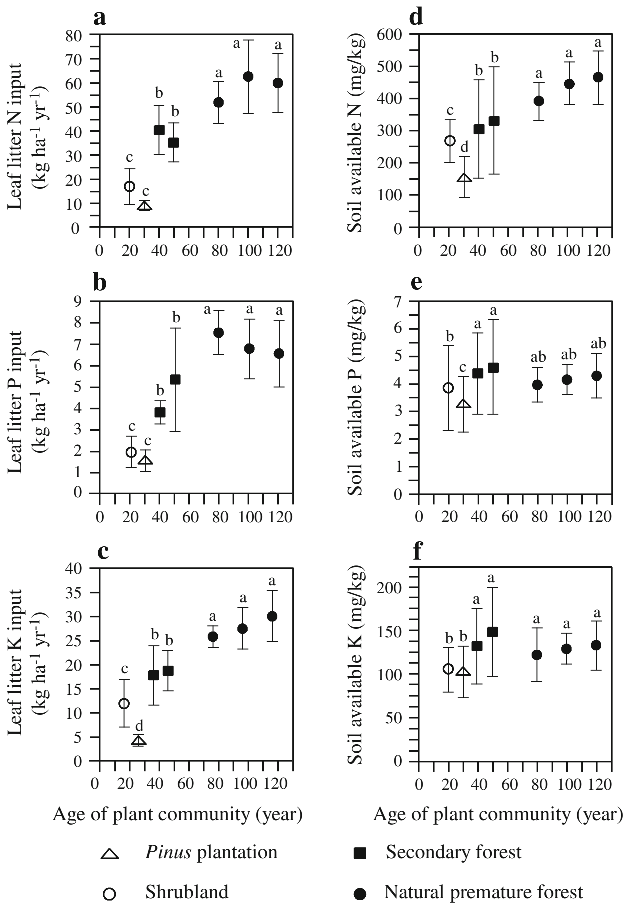


Fig. 4 Changes in leaf litter nutrient inputs and soil available nutrients with different ages of successional plant communities and the *Pinus* plantation. *Different letters* indicate significant differences ($p < 0.05$); *vertical bars* indicate standard deviation

finally after another 40–100 years to succeeding to a natural semi-humid evergreen broad-leaved forest dominated by species of *Cyclobalanopsis* or *Castanopsis*. The regeneration dynamics of the plant communities in Shilin here under study suggest a possible secondary successional pathway from the pioneer shrubland to the deciduous and evergreen broad-leaved mixed secondary forest, then to the natural premature forest and finally, towards the natural mature semi-humid evergreen broad-leaved forest, if no dramatic disturbances occur in future. Community structure and species composition tend to increase in complexity as the succession proceeds. Litterfall production in a forest ecosystem is determined by climatic condition, species composition, and successional stage (Haase 1999; Sundarapandian and Swamy 1999; Vogt et al. 1986). Litter accumulation during succession has been traditionally considered an ecosystem process with significant impact on carbon and nutrient cycles (Odum 1960; Mellinger and McNaughton 1975; Holland and Coleman 1987). Our study shows the same trend, that broad-leaved trees had higher litterfall production than coniferous trees in the subtropics (Deng et al. 1993; Xu and Hirata 2002).

Litterfall and decomposition are critical processes for transferring nutrients from aboveground forest biomass to soils (Golley et al. 1975; Swift et al. 1979). Litter nutrient inputs varied with differing successional plant communities, as changes in species assemblages would be expected to alter nutrient cycling. With increasing age in the various successional communities, leaf litter N, P, K, Ca and Mg inputs increase, showing a relationship between leaf litter nutrient inputs and soil nutrient storage. In the *Pinus* plantation, those inputs have been very low, due to the low concentration of nutrients in the pine needles and their low litter decomposition rate (showing the high ratio of organic C to total N in the soil of the *Pinus* plantation) on the forest floor. Considering N dynamics under all the plant communities, the lowest N concentration (6.64 g/kg) is found in pine litter, and the lowest value (150.3 mg/kg) of soil available N in the *Pinus* plantation. However, in the *Pinus* plantation under study, the soil available N concentration is much higher than those in a *Pinus* plantation of Mouding (70 mg/kg from Hou et al. 2010), and Luquan (35.8 mg/kg from Tang et al. 2010b), central Yunnan. This is because *Albizia mollis* is present in the *Pinus* plantation of current study (Appendix 1), and has a nitrification function.

In Korea, after abandonment of rice paddy fields, natural habitat recovery generally appears sufficiently robust through natural succession to achieve restoration of native plant community without intervention (Lee et al. 2002). Our study concludes that vegetation, plant diversity, litter nutrient input and soil nutrient storage are more efficiently recovered by letting plant communities grow back naturally than by establishing a *Pinus* plantation. Natural succession promotes nutrient cycling and yields the best ecological benefits.

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Appendix

See Table 4

Table 4 Woody species ($H \geq 1.3$ m high) composition in the overstory of each plant community

Species	Traits	PP	SL	SF	PF
Pinus yunnanensis Fr.	LD	**99.3**	9.6		
Albizia mollis (Wall.) Boiv.	LD	0.41		8	1.6
Pistacia weinmannifolia J. Poisoon ex Fr.	LD	0.1	1.2	**28.1**	**8.1**
Pistacia chinensis Bunge	LD	0.07	1.9	5.7	4.7
Rhamnus leptophylus Schneid	LD	0.04		0.3	0.9
Dichotomanthes tristaniaecarpa Kurz	IN	0.04	0.3	1.4	0.1
Cotoneaster franchetii Bois	LD	0.04		0.2	
Neolitsea homilantha Allen	LD		**60.5**	4.8	4.4
Diospyros mollifolia Rehd. et Wils.	LD		10.1		0.1
Olea yunnanensis Hand.-Mazz.	ST		4.1	**11.7**	**12.5**
Rhamnella martini (Levl) Schneid	LD		3	1.9	0.01
Mallotus philippinensis (Lam.) Muell.-Arg.	LD		2.8		
Dalbergia mimosoides Franch.	LD		1.6	1.4	0.1
Prunus zippeliana Miq.	LD		1.3		1.9
Toxicodendron succedaneum (L.) O. Kuntze	LD		0.9	0.04	0.7
Morus australis Poir.	IN		0.6		0.2
Sageretia theezans L.	LD		0.6		0.09
Celtis bungeana Bl.	LD		0.5		0.09
Nothapodytes tomentosa C. Y. Wu	LD		0.4		0.08
Pyrus pashia Buch.-Ham. ex. D. Don	LD		0.3		0.01
Prunus persica (L.) Bartsch	LD		0.1		
Cyclobalanopsis glaucoides Shottky	ST			**30.7**	**39.8**
Toxicodendron griffithii (Hook. F.) Wall. Ex. D. Don	LD			2.8	1.9
Machilus yunnanensis Leocomie	ST			1.1	2.6
Osyris wightiana Wall.	IN			0.4	
Juniperus formosanna Hayata	LD			0.4	
Keteleeria evelyniana Mast.	LD			0.4	
Photinia glomerata Rehd. ex Wils	ST			0.2	0.02
Photinia sp.	ST			0.1	0.1
Rhus chinensis Mill	LD			0.09	0.04
Campylotropis polyyantha (Franch.) A. K. Schind	LD			0.07	
Pentapanax henryi Harms	IN			0.05	0.2
Quercus dentata Th.	LD			0.05	
Celtis tetrandra Roxb.	LD			0.04	1.4
Rosa banksiae R. Br	LD			0.04	
Cornus paucinervis Hance	LD			0.03	
Ilex macrocarpa Oliv.	LD				5
Carpinus mobeigiana Hand.-Mazz	LD				4.5
Xylosma racemosum (Sieb et Zucc.) Miq.	LD				1.7
Lindera communis Hemsl	IN				1.5
Jasminum humile L.	IN				1.1
Pittosporum brevicalyx (Oliv.)	ST				0.7
Zhanthoxylum scandens Bl.	LD				0.5
Distyliopsis laurifolia (Hemsl.) Endress	LD				0.4
Quercus variabilis Bl.	LD				0.4
Ficus virens Ait.	IN				0.4
Milletia dielsiana Harms	LD				0.3
Dalbergia collettii Prein	LD				0.2
Milletia reticulata Benth.	LD				0.2
Myrsine semiserrata Wall.	ST				0.1
Schoepfia jasminodora S. et. Z.	LD				0.07
Ficus pandurata Hance	ST				0.07
Lonicera japonica Thunb.	IN				0.06
Lithocarpus confinis Hunag et Chang	ST				0.06
Fortunella sagittifolia Feng et Mao	IN				0.03
Indigofera cinerascens Franch.	IN				0.03
Leptodermis potaninii Batain	IN				0.02
Paederia scandens (Lour.) Merr.	IN				0.02
Elaeagnus lanceolata Walb.	IN				0.01
Debregeasia edulis (Sieb. et Zucc.) Wedd.	LD				0.01
Crataegus scabrifolia (Franch.) Rehd.	LD				0.007
Euonymus fortunei Maxim.	ST				0.007
Ficus chartacea Wall. ex King	ST				0.006
Buddleia officinalis Maxium	IN				0.004

Values are relative basal area (RBA) of each species. Dominant species are shown in boldface

PP Pinus plantation, *SL* shrubland, *SF* secondary forest, *PF* natural pre-mature forest, *LD* light-demanding, *IN* intermediate, *ST* shade-tolerant

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