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Soil seed banks along elevational gradients in tropical, subtropical and subalpine forests in Yunnan Province, southwest China

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ABSTRACT

Soil seed banks are a vital part of ecosystems and influence community dynamics and regeneration. Although soil seed banks in different habitats have been reported, how soil seed banks vary with elevational gradients in different climatic zones is still unknown. This paper investigates seed density, species composition and nonconstituent species of forest soil seed banks in Yunnan Province, southwest China. Similarity between the soil seed bank and standing vegetation was also examined. We collected soil samples from sites spanning 12 elevations in tropical rain forests, subtropical evergreen broad-leaved forests and subalpine coniferous forests, and transported them to a glasshouse for germination trials for species identification. The soil seed banks of tropical and subtropical forests had much higher seed densities and species richness than those of subalpine forests. Seeds of woody species dominated the soil seed banks of tropical and subtropical forests, while herbs dominated those of subalpine forests. The nonconstituent species in the soil seed banks were all herbs and were most abundant in tropical forests, followed by subtropical forests but were completely absent from subalpine forests.

1. Introduction

The soil seed bank consists of seeds present on or in the soil, and it contributes to vegetation succession when dormancy-breaking and germination requirements of the seeds are met (Bakker et al., 1996; Funes et al., 2001; Erfanzadeh et al., 2013), especially in those ecosystems experiencing frequent disturbances (Davies and Waite, 1998; Li et al., 2004; Lin et al., 2006; Milberg, 1995; Willems and Bik, 1998).

The soil seed bank changes in seed density and species composition with vegetation succession (Cao et al., 1996, 2000a,b; Funes et al., 2003; Perera, 2005; Erfanzadeh et al., 2010; Tang et al., 1999). Ortega et al. (1997) found that both the richness and density of seeds in the soil seed bank decreased with elevation in mountain grasslands. Jalili et al. (2003) observed that seed density decreased with elevation in Iran, because the harsh environment at higher elevations reduced seed production and promoted vegetative reproduction of plants. Alternatively, Funes et al. (2003) showed that soil seed bank richness and density increase with elevation in Argentina as a result of two processes: the relatively warm conditions at the lower elevations which enhance seed predation, while the cold climate at the high elevations may favor the formation of persistent seed banks. Soil seed banks also had high variability in seed density and species composition among different forest types. In a study on the effects of elevational change (1500 m–3500 m) on soil seed banks in the Taibai Mountains of northern China, the number of species decreased with elevation, although seed density peaked at mid-elevation (2600 m) (Zhang and Fang, 2004a). Similar trends of species richness and seed density were also observed in soil seed banks of *Picea schrenkiana* forests in the Tianshan Mountains (1450–2750 m) in northwest China (Li et al., 2012). In the tropical forests of Xishuangbanna in southwest China, soil seed density ranged from 4585 seeds/m^2 (seasonal rain forest) to 65,665 seeds/m^2 (4-year-old secondary forest) in the top 10 cm of soil, while the number of species ranged from 50 to 59 (Cao et al., 2000a,b). Li et al. (2010) found that the soil seed density was 6160-22,760 seeds/m^2, with 29–62 species, in subtropical forests of

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Ailao Mountain, Yunnan, but only 185.5–1065.6 seeds/m^2 were reported in subalpine coniferous forests (Yin and Liu, 2004, 2005).

The similarity between soil seed banks and standing vegetation provides insight into the response of a community to disturbance (Hopfensperger, 2007). Many species in standing vegetation do not occur in soil seed banks, suggesting little similarity (Amiaud and Touzard, 2004; Esmailzadeh et al., 2011). Similarity was also lower in forest ecosystems than in grasslands and wetlands (Hopfensperger, 2007). Tang et al. (1999) found more seeds of common species in both the soil seed bank and standing vegetation at the initial stages of forest succession, but such a similarity in species decreased with succession. In five shrub communities in the Strandveld Succulent Karoo of South Africa, Sørensen indices between standing vegetation and soil seed bank averaged 47.9%, showing a relatively high similarity (Villiers et al., 2003). In subarctic plant communities in the early phase of regeneration in Finland, however, very low similarity occurred between the soil seed bank, seedlings emerging in the field, and standing vegetation (Welling et al., 2015). In the Tianshan Mountains (1750–2750 m) of northwest China, the Jaccard Index between the soil seed bank and standing vegetation decreased with elevation (Zhou et al., 2013). However, it has not been determined how soil seed banks respond to disturbance at different elevations.

Based on the study of soil seed banks in evergreen broad-leaved forests in Yunnan Province, southwest China, a new species group, i.e. nonconstituent species that occur in a natural landscape but are not native to it, has been recognized (Lin et al., 2006). In fragmented forests or disturbed forests, nonconstituent species may become established in habitats that differ from closed forests or their successional communities. Nonconstituent species are mostly exotics when considered in terms of both geographical and ecosystem scales and include exotic species or weeds from neighboring farmland. These species therefore tend to share some similar ecological traits, such as wind dispersal of seeds, small seed size, long life-span of seeds, and abundant seed production (Baker, 1974). This ecological similarity among nonconstituent species results in similar responses to anthropogenic disturbance; Thus, nonconstituent species in soil seed banks could serve as an ecosystem indicator of anthropogenic disturbance in forest ecosystems (Lin et al., 2006).

Although previous studies reported the distribution of forest soil seed banks in some mountains, these studies were conducted only in a single climatic zone and did not include elevational gradients in a continuous geographical gradient of different climatic zones. Yunnan Province is in the southwest of China, on the southeastern extension of the Himalayas, and it has tropical rain forest, subtropical evergreen broad-leaved forest and subalpine coniferous forest (Wu et al., 1987). However, the variation in the elevational distribution of soil seed banks in each climatic zone has received little attention. Therefore, the present study examines elevational changes of soil seed banks in tropical, subtropical and subalpine climatic zones of Yunnan Province. We aim to (1) determine how the size (seed density), species composition and richness of soil seed banks respond to variation in elevation in the three climatic zones; (2) analyze the variations in similarity between the soil seed bank and standing vegetation; and (3) explore the changes in nonconstituent species in soil seeds banks in these forests. We hypothesized that: 1) the size (seed density or abundance) and species richness of soil seed banks decrease with elevation in all three climatic zones; 2) similarity between soil seed bank and standing vegetation increases with elevation, because the species pool becomes smaller due to the harsher environment at high elevations; and 3) both seed abundance and species number of nonconstituent species decrease with elevation, as a consequence of reduced human activities in montane areas.

2. Materials and methods

2.1. Study area

This study was carried out in Yunnan Province, southwest China. Study sites were in tropical (Xishuangbanna – southwest Yunnan), subtropical (Ailao Mountains – central Yunnan) and subalpine (Lijiang – northwest Yunnan) zones (Fig. 1). Also, the sites represent geographical and climatic gradients of latitude, elevation, temperature and precipitation from south to north in this province (Table 1). In each vegetation zone, an elevational transect comprised of four points (elevations) at 200-m intervals from each other, was established. Five plots (20 m × 20 m) at each elevation were set up, and all the trees with DBH ≥ 5 cm in each plot were measured and identified to species.

Xishuangbanna lies on the northern edge of the tropics in southeast Asia and borders Laos and Myanmar to the south and west. This area has a tropical seasonal rain forest below 900 m a.s.l. due to monsoon climate with an alternation between a rainy (May–October) and dry (November–April) season (Cao et al., 1996, 2006). Dominant tree species in the tropical seasonal rain forest study site were *Parashorea chinensis*, *Pittosporopsis kerrii*, *Garcinia cowa*, *Castanopsis echidnocarpa*, *Mezzettiopsis creaghii*, and *Sloanea tomentosa* (Lan et al., 2009). On mountains over 1000 m, tropical montane evergreen broad-leaved forests occur (Zhu et al., 2006).

Ailao Mountain is located in the subtropical zone in central Yunnan Province. Subtropical middle montane moist evergreen broad-leaved forest is distributed between 2000 m–2600 m. The forest is dominated by *Castanopsis wattii*, *Lithocarpus hancei*, *Lithocarpus xylocarpus* and *L. truncates.*

Lijiang is in northwest Yunnan. Our study site is on Yulong Snow Mountain, which is the southeastern extension of the Tibetan Plateau (Niu et al., 2013). The major forest type between 3100 m–4000 m on this mountain is subalpine coniferous forest dominated by species of Pinaceae, such as *Abies forrestii* and *Abies georgei* (Wang et al., 2001).

2.2. Sampling methods

At each of the four elevations in each vegetation zone, we chose one of the five plots for soil sampling. Twenty soil cores (10 cm × 10 cm × 10 cm) were taken at 2 m intervals along two 20 m-long transects in the plot. Fresh litter on the soil surface was removed before sampling and discarded. Each soil core was sampled in three different layers (depths): 0–2 cm, 2–5 cm and 5–10 cm. This was completed by using two special flat shovels that were exactly 10 cm wide, along with a steel tape (Cao et al., 2000a,b). All samples from each soil core were placed separately in cloth bags and transported to Xishuangbanna Tropical Botanical Garden at Menglun Township, Xishuangbanna Prefecture for germination trials. The soil samples were collected at the end of the rainy season in 2013 for the Xishuangbanna site and in 2014 for the Ailao Mountain and Lijiang sites, when most seeds had dispersed (Zhang and Song, 2015; Yang et al., 2010).

2.3. Seed germination

Each soil sample was sieved with a 2-mm sieve to removed gravels and dead plant material buried in the soil. Soil samples were spread evenly into germination trays of different sizes to a depth of less than 2 cm. Before the soil was put into trays, the bottom of each tray was pierced to prevent the soil from becoming water-saturated (Li et al., 2010). All trays were put in a non-temperature controlled glasshouse to reduce contamination of seeds from the outside. Eight additional trays containing sterilized

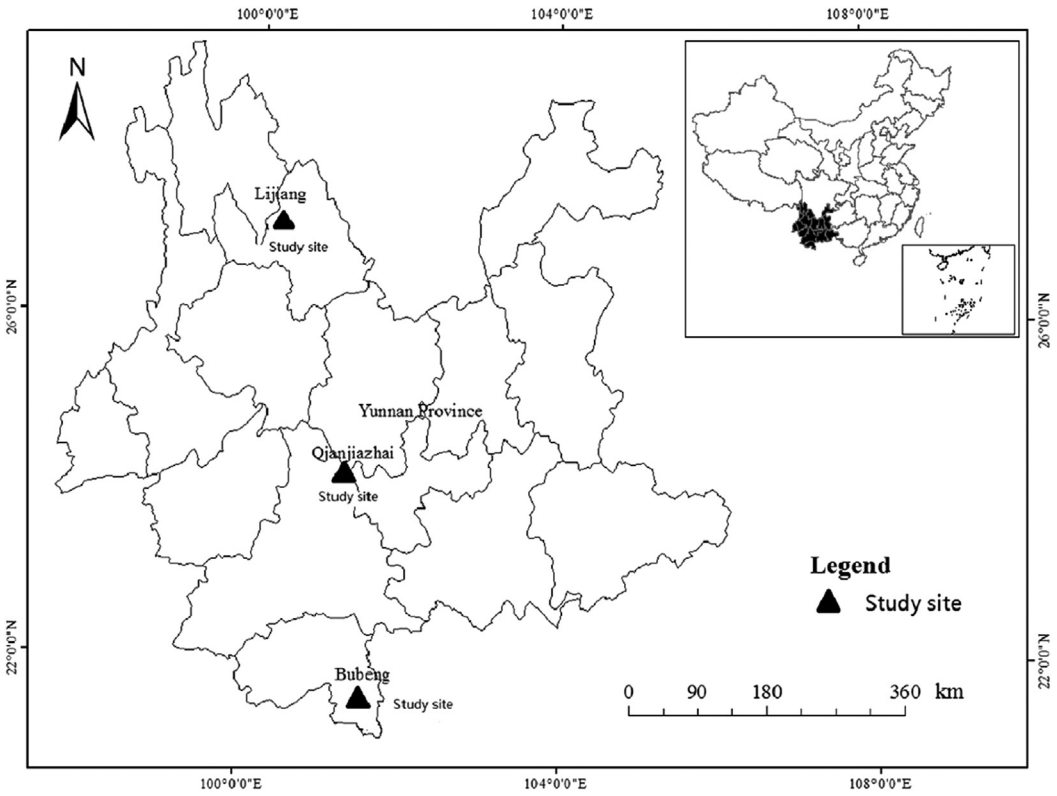

Fig. 1. Study sites in Yunnan Province, southwest China.

soil (105 °C for 12 h) were used as controls for testing seed contamination.

The germination trays were watered once or twice a day as needed to keep the soil samples moist. Seedlings were counted every 2 days during the first 60 days and then every 5–6 days afterwards. Seedlings were removed once they were identified. Seedlings that were difficult to distinguish were transplanted to separate containers for continued growth until they could be identified. After removing all seedlings within a tray, the soil sample was stirred and kept for germination until no more seedlings emerged for two weeks.

2.4. Data analysis

Seed density was calculated as the average number of emerged seedlings per square meter (at a depth of 10 cm) from soil samples. A one-way ANOVA followed by the Tukey–Kramer test (in SPSS 19.0) was used to analyze the differences in seed density among elevations. The level of significance was set at $p < 0.05$.

Species diversity indices of soil seed banks were measured based on the following formulas:

Shannon–Wiener diversity index: $H' = -\sum (P_i lnP_i)$ (Magurran, 1988)

Simpson diversity index: $D = 1-\sum (P_i)^2$ (Keylock, 2005) where P_i is the proportion of individuals of the ith species out of the total individuals at each elevation, i.e., $P_i = (N_i/N)$, where N is the total number of individuals recorded in the 20 soil samples at each elevation and N_i is the number of the individuals of the ith species in the 20 soil samples at each elevation.

Non-metric multi-dimensional scaling (NMDS) was used to explore the pattern of species composition of 20 soil samples at each elevation in R 3.2.2 using the package vegan (Legendre and Legendre, 1998).

Similarity between soil seed bank and standing vegetation was calculated using the Sørensen similarity index: $S = 2c/(a+b)$ (Sørensen, 1948), where a is the number of species of soil seed bank, b is the number of species of standing vegetation, and c is the number of species shared by both.

All the information on the soil seed banks for Xishuangbanna site (tropical forest) was analyzed based on the primary data of Zhang and Song (2015).

3. Results

3.1. Seed density

A total of 17,579 seeds germinated in the soil samples, and seed density varied among the three sites (Table 2). In the tropical forest, the soil seed bank at 800 m had more seeds than that at higher elevations, while the lowest seed density was observed at 1400 m. The highest seed density in soil seed banks of the subtropical forest occurred at 2000 m, although there was no significant difference in seed density between 2200 m, 2400 m and 2600 m ($p > 0.05$, Table 2). Therefore, both tropical and subtropical sites had the most abundant soil seed banks at the basal elevations (800 m and 2000 m, respectively). The subalpine forest had the highest seed density at 3400 m, but seed densities at the other three elevations did not differ significantly ($p > 0.05$). Looking at seed density of the basal elevation of the three sites (i.e. 800 m for tropical site, 2000 m for subtropical site and 3200 m for subalpine site), we observed that the soil seed bank at 2000 m (subtropical site) possessed the highest seed density, followed by tropical and subalpine sites (Table 2).

Table 1
Basic characteristics of the study sites.

Site	Elevation (m)	Latitude	Longitude	Forest type	Annual mean temperature (°C)	Annual mean precipitation (mm)	Dominant tree species	Mean DBH of trees (mm)	Tree density (trees ha^{-1})	Intensity of disturbance
Xishuangbanna	800	21°36′785″ N	101°34′799″ E	Tropical seasonal rain forest	21.5 (Mengla County, ele. 632 m)[a]	1520.5 (Mengla County, ele. 632 m)[a]	*Parashorea chinensis*, *Pittosporopsis kerrii*	135.8	1525	+
	1000	21°37′153″ N	101°34′425″ E	Tropical montane rain forest			*Actinodaphne henryi*, *Pittosporopsis kerrii*	44.0	1650	+
	1200	21°35′643″ N	101°33′620″ E	Tropical montane evergreen broad-leaved forest			*Castanopsis echinocarpa*, *Castanopsis mekongensis*	39.3	1275	+++
	1400	21°35′454″ N	101°32′966″ E	Tropical montane evergreen broad-leaved forest			*Castanopsis mekongensis*, *Schima argentea*	64.6	1150	++
Ailao Mountain	2000	24°16′209″ N	101°15′796″ E	Subtropical middle montane moist evergreen broad-leaved forest	18.7 (Zhenyuan County, ele. 1086 m)[a]	1237.2 (Zhenyuan County, ele. 1086 m)[a]	*Claoxylon khasianum*, *Ficus henryi*	55.6	1100	+++
	2200	24°16′621″ N	101°15′848″ E				*Manglietia insignis*, *Camellia assamica*	58.1	1300	++
	2400	24°17′066″ N	101°15′354″ E				*Lithocarpus xylocarpus*, *Eurya obliquifolia*	50.3	1850	+
	2600	24°17′143″ N	101°15′060″ E				*Castanopsis rufescens*, *Camellia forrestii*	78.1	1225	+
Lijiang	3200	27°08′363″ N	100°13′757″ E	Subalpine coniferous forest	12.8 (Lijiang County, ele. 2393 m)[b]	935.0 (Lijiang County, ele. 2393 m)[b]	*Abies forrestii*, *Sorbus rufopilosa*	59.4	500	++
	3400	27°09′784″ N	100°13′790″ E				*Abies georgei*, *Rhododendron yunnanense*	121.5	650	+++
	3600	27°10′244″ N	100°13′977″ E				*Abies georgei*, *Abies forrestii*, *Quercus pannosa*	86.5	1375	+
	3800	27°11′261″ N	100°13′174″ E				*Abies georgei*	92.2	825	+

[a] He, Y.L., Zhang, Y.P., 2005. Climate change from 1960 to 2000 in the Lancang River Valley, China. Mt. Res. Dev. 25, 341-348.
[b] Feng, J.M., Wang, R.P., Xu, C.D., Yang, Y.H., Fang, J.Y., 2006. Altitudinal patterns of plant species diversity and community structure on Yulong Mountains, Yunnan, China. J. Mt. Sci. 24, 110–116.

Table 2
Seed density along the three elevational gradients.

Site	Elevation (m)	Number of seeds				Seed density (seeds m^{-2})[a]
		0–2 cm	2–5 cm	5–10 cm	Total	
Xishuangbanna (Tropical forest)	800	928	433	747	2108	10,540 ± 1578 a
	1000	308	376	648	1332	6660 ± 479 bc
	1200	279	483	1051	1813	9065 ± 659 ab
	1400	170	341	554	1065	5325 ± 361 c
Ailao Mountain (Subtropical forest)	2000	1097	1080	1456	3633	18,165 ± 1408 a
	2200	586	496	527	1609	8045 ± 823 b
	2400	634	618	677	1929	9645 ± 621 b
	2600	491	510	539	1540	7700 ± 646 b
Lijiang (Subalpine forest)	3200	125	132	43	300	1500 ± 333 a
	3400	660	569	247	1476	7380 ± 844 b
	3600	102	148	132	382	1910 ± 367 a
	3800	72	105	215	392	1960 ± 194 a

[a] Mean ± standard error, $n = 20$; Different letters within a site denote significantly different as determined by Tukey–Kramer tests ($p < 0.05$).

3.2. Species composition

Soil samples from the tropical, subtropical and subalpine sites contained 129, 81 and 50 species (2540 unidentified seedlings excluded), respectively (Appendices 1-3), and number of species tended to decline with an increase in elevation. Among the three sites, soil seed bank at 800 m had the highest number of species, while that at 3800 m had the lowest (Fig. 2). However, the species diversity index was higher in the subtropical than in the tropical and subalpine forests when the three basal elevations (i.e. 800 m, 2000 m, and 3200 m, respectively) in each site were compared (Fig. 3).

Woody species (tree + shrub) dominated the soil seed banks in the tropical forest (Table 3), and the highest proportion of tree and shrub seeds occurred in soil at 800 m. In the subtropical forest, shrubs and herbs dominated the soil seed bank, and the highest proportion of tree and shrub species occurred at 2000 m. In the subalpine forest, however, herbs were dominant at all four

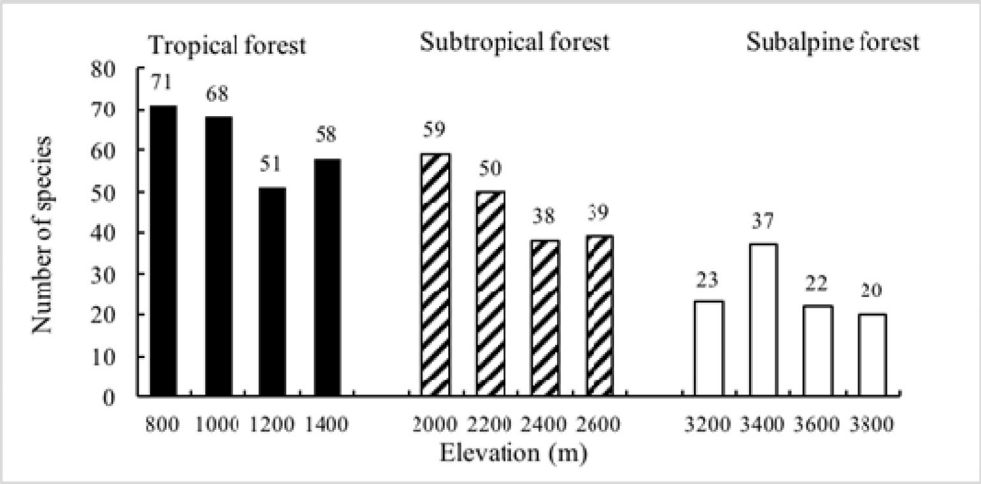

Fig. 2. Number of species in soil seed banks across different sites and elevations.

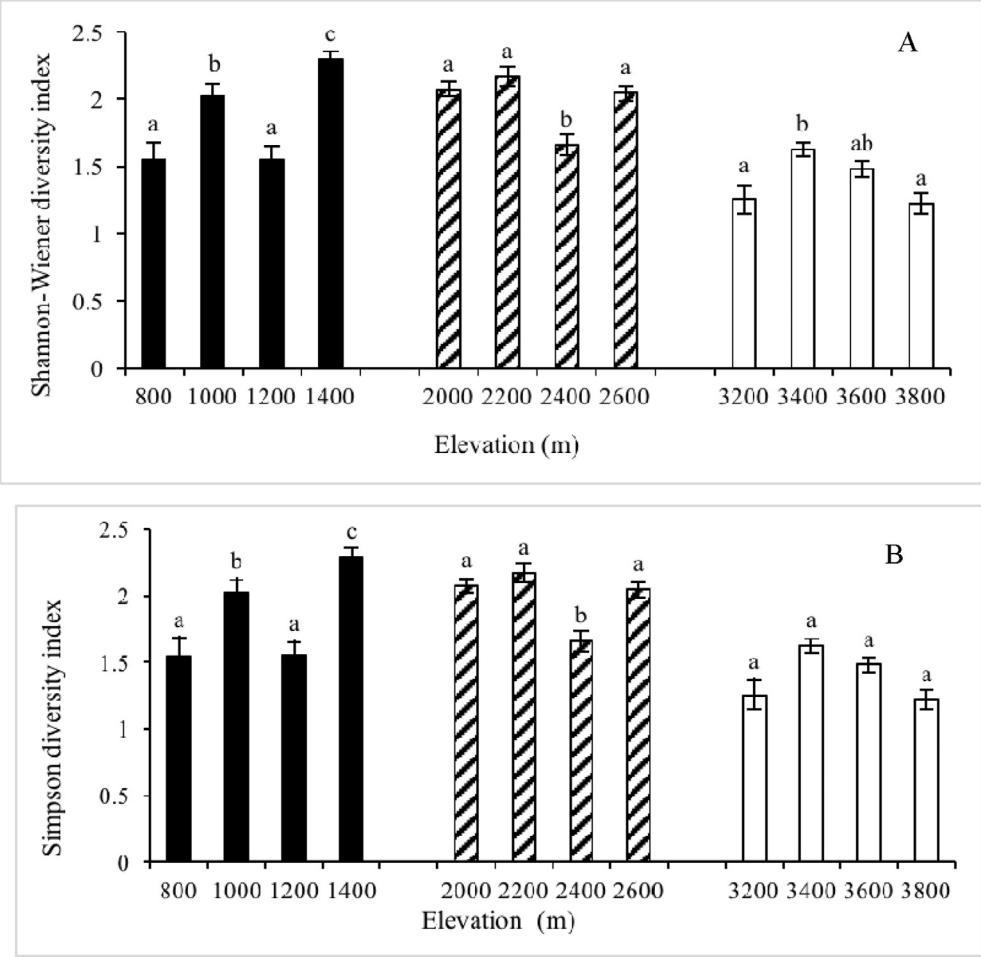

Fig. 3. Shannon–Wiener diversity index (A) and Simpson diversity index (B) along elevational gradients in tropical, subtropical and subalpine forests. Different letters indicate significant differences among elevations within a climatic zone.

elevations, and seeds of tree species were nearly absent from the soil seed bank (Table 3).

In the Xishuangbanna site, *Digitaria sanguinalis* obviously was dominant at the four elevations, although this species also commonly occurs in farm fields, roadsides and weedy places in subtropical and tropical areas. In contrast, *Neolamarckia cadamba* (formerly *Anthocephalus chinensis*), *Buddleja asiatica* and *Ludwigia hyssopifolia* only dominated at 800 m; *Ficus variegata* var. *chlorocarpa*, *Wendlandia uvariifolia* and *Crassocephalum crepidioides* were dominant only at 1000 m. At higher elevations (1200 m and

Table 3
Numbers of species germinated from the soil samples (20 samples for each elevation)[a].

Site	Elevation (m)	Life form				
		Tree	Shrub	Herb	Vine	Total
Xishuangbanna (Tropical forest)	800	22 (31.0%)	26 (36.6%)	16 (22.5%)	7 (9.9%)	71 (100.0%)
	1000	20 (29.4%)	24 (35.3%)	19 (27.9%)	5 (7.4%)	68 (100.0%)
	1200	13 (25.5%)	18 (35.3%)	16 (31.4%)	4 (7.8%)	51 (100.0%)
	1400	12 (20.7%)	21 (36.2%)	20 (34.5%)	5 (8.6%)	58 (100.0%)
Ailao Mountain (Subtropical forest)	2000	10 (16.9%)	19 (32.2%)	25 (42.4%)	5 (8.5%)	59 (100.0%)
	2200	9 (18.0%)	18 (36.0%)	19 (38.0%)	4 (8.0%)	50 (100.0%)
	2400	6 (15.8%)	15 (39.5%)	15 (39.5%)	2 (5.3%)	38 (100.0%)
	2600	7 (17.9%)	18 (46.2%)	13 (33.3%)	1 (2.6%)	39 (100.0%)
Lijiang (Subalpine forest)	3200		2 (8.7%)	21 (91.3%)		23 (100.0%)
	3400	1 (2.7%)	5 (13.5%)	31 (83.8%)		37 (100.0%)
	3600		3 (13.6%)	19 (86.4%)		22 (100.0%)
	3800		2 (10.0%)	18 (90.0%)		20 (100.0%)

[a] Figures in parentheses are percentages for the numbers of species out of the total number of species germinated from the 20 soil samples of each elevation.

Table 4
The five species with the most abundant seeds that germinated from the soil samples at each elevation (20 samples for each)[a].

Site	Species	Life form	Elevation (m)			
			800	1000	1200	1400
Xishuangbanna (Tropical forest)	*Neolamarckia cadamba*	Tree	1173 (55.65%)	18 (1.35%)		
	Ludwigia hyssopifolia	Herb	128 (6.07%)	20 (1.50%)	1 (0.06%)	
	Buddleja asiatica	Shrub	112 (5.31%)	12 (0.90%)		6 (0.56%)
	Digitaria sanguinalis	Herb	99 (4.70%)	391 (29.35%)	938 (51.74%)	197 (18.50%)
	Ficus semicordata	Tree	56 (2.66%)	183 (13.74%)	37 (2.04%)	118 (11.08%)
	Wendlandia uvariifolia	Shrub	3 (0.14%)	202 (15.17%)		
	Ficus variegata var. *chlorocarpa*	Tree	44 (2.09%)	72 (5.41%)	1 (0.06%)	24 (2.25%)
	Crassocephalum crepidioides	Herb	6 (0.28%)	31 (2.33%)	7 (0.39%)	10 (0.94%)
	Eurya pittosporifolia	Tree		15 (1.13%)	121 (6.67%)	117 (10.99%)
	Melastoma malabathricum	Shrub			167 (9.21%)	128 (12.02%)
	Wendlandia tinctoria	Shrub			124 (6.84%)	59 (5.54%)
	Maesa montana	Shrub		3 (0.23%)	**92 (5.07%)**	25 (2.35%)
Ailao Mountain (Subtropical forest)			**2000**	**2200**	**2400**	**2600**
	Debregeasia orientalis	Shrub	**1301 (35.81%)**	**129 (8.02%)**	3 (0.16%)	3 (0.19%)
	Maesa indica	Shrub	**475 (13.07%)**	6 (0.37%)		
	Ficus beipeiensis	Tree	**279 (7.68%)**	4 (0.25%)		
	Boehmeria clidemioides var. *diffusa*	Herb	**248 (6.83%)**	3 (0.19%)		
	Laggera alata	Herb	**224 (6.17%)**	1 (0.06%)		1 (0.06%)
	Elatostema laevissimum	Shrub	1 (0.03%)	**259 (16.10%)**	4 (0.21%)	44 (2.86%)
	Docynia delavayi	Tree	7 (0.19%)	**178 (11.06%)**	19 (0.98%)	19 (1.23%)
	Oxyspora paniculata	Shrub	40 (1.10%)	**119 (7.40%)**	66 (3.42%)	**66 (4.29%)**
	Laportea bulbifera	Herb	18 (0.50%)	**56 (3.48%)**	35 (1.81%)	34 (2.21%)
	Myrsine semiserrata	Shrub	18 (0.50%)	24 (1.49%)	**532 (27.58%)**	**226 (14.68%)**
	Scleria terrestris	Herb	20 (0.55%)	29 (1.80%)	**140 (7.26%)**	
	Agapetes mannii	Shrub	2 (0.06%)	44 (2.73%)	**92 (4.77%)**	**111 (7.21%)**
	Carex teinogyna	Herb	17 (0.47%)	19 (1.18%)	**85 (4.41%)**	7 (0.45%)
	Ilex corallina	Tree	13 (0.36%)	47 (2.92%)	**76 (3.94%)**	20 (1.30%)
	Rubus sumatranus	Shrub	6 (0.17%)	20 (1.24%)	40 (2.07%)	**85 (5.52%)**
	Eurya groffii	Tree	2 (0.06%)	23 (1.43%)	39 (2.02%)	**47 (3.05%)**
Lijiang (Subalpine forest)			**3200**	**3400**	**3600**	**3800**
	Carex nubigena	Herb	**120 (40.00%)**	17 (1.15%)	**22 (5.76%)**	**29 (7.40%)**
	Philadelphus delavayi	Shrub	**37 (12.33%)**	**370 (25.07%)**	15 (3.93%)	
	Pilea sinofasciata	Herb	**16 (5.33%)**	**340 (23.04%)**	19 (4.97%)	
	Stellaria vestita	Herb	**14 (4.67%)**	3 (0.20%)	17 (4.45%)	11 (2.81%)
	Myriactis wightii	Herb	**12 (4.00%)**	**186 (12.60%)**	21 (5.50%)	**23 (5.87%)**
	Ainsliaea latifolia	Herb	**12 (4.00%)**	**111 (7.52%)**		1 (0.26%)
	Clinopodium polycephalum	Herb	6 (2.00%)	**273 (18.50%)**		1 (0.26%)
	Rubus fockeanus	Herb	11 (3.67%)	22 (1.49%)	**83 (21.73%)**	
	Carex sp1.	Herb	2 (0.67%)	9 (0.61%)	**47 (12.30%)**	2 (0.51%)
	Ribes glaciale	Shrub	4 (1.33%)	4 (0.27%)	**43 (11.26%)**	3 (0.77%)
	Juncus effusus	Herb			**35 (9.16%)**	
	Astilbe chinensis	Herb				**76 (19.39%)**
	Ribes sp1.	Shrub		1 (0.07%)	1 (0.26%)	**71 (18.11%)**
	Polygonum runcinatum	Herb	1 (0.33%)			**33 (8.42%)**

[a] The number and proportion in bracket of each species in the soil seed bank at each elevation, the bold fonts were the five most abundant species at each elevation.

1400 m) where tropical montane evergreen broad-leaved forest occurs, *Melastoma malabathricum, Wendlandia tinctoria* and *Eurya pittosporifolia* dominated the soil seed banks, although *Maesa montana* was dominant only at 1200 m.

In the Ailao Mountain site, no species dominated at all four elevations. However, there were some species that were dominant at one elevation, such as *Maesa indica, Ficus beipeiensis, Boehmeria clidemioides* var. *diffusa* and *Laggera alata* at 2000 m; *Elatostema laevissimum, Docynia delavayi* and *Laportea bulbifera* at 2200 m; *Scleria terrestris, Carex teinogyna; Ilex coralline* at 2400 m; and *Rubus sumatranus and Eurya groffii* at 2600 m.

In the Lijiang site, the soil seed banks at 3200 m and 3400 m shared three dominant species, i.e. *Philadelphus delavayi, Pilea sinofasciata* and *Ainsliaea latifolia.* Four and three species were dominant at 3600 m and 3800 m, respectively. However, we did not observe tree species as dominants at the four elevations of the transect.

3.3. NMDS analysis

Species composition of 20 soil samples at each elevation tended to be more homogeneous than between elevations, as the 20 points representing 20 soil samples from same elevation aggregated in the NMDS plot (Fig. 4).

3.4. Similarity of woody species between soil seed bank and standing vegetation

In general, the values of Sørensen's index between soil seed bank and standing vegetation at low elevations were lower than those at high elevations in both tropical and subtropical sites. Further, the soil seed bank obviously had more woody species than the standing vegetation at all elevations (Table 5). However, the subalpine site had a completely different pattern, and here no woody species were shared by the standing vegetation and soil seed bank. Contrary to the tropical and subtropical sites, standing vegetation of the subalpine site had more woody species than the soil seed bank at 3200 m, 3400 m and 3600 m (Table 5).

3.5. Nonconstituent species in soil seed banks

Fifteen nonconstituent species germinated from soil samples of Xishuangbanna and four from those of Ailao Mountain, while none was found from those of Lijiang (Table 6). All the nonconstituent species from Xishuangbanna and Ailao Mountain were herbs. *D. sanguinalis* and *C. crepidioides* occurred at all elevations, and *D. sanguinalis* was the most abundant (1625), followed by *Ludwigia linifolia* (149) and *C. crepidioides* (54). In Ailao Mountain, *Ageratina adenophora, Laggera pterodonta* and *C. crepidioides* occurred at the four elevations, of which *A. adenophora* was the most abundant species (Table 6).

4. Discussion

4.1. Seed density and species composition

Overall, both tropical and subtropical forests had higher seed densities than subalpine forests (Table 2). Seed density at 800 m (10,540 ± 1577) was much higher than that of the same forest type 10 years ago (5415 ± 3232, Tang et al., 2006). This increase was

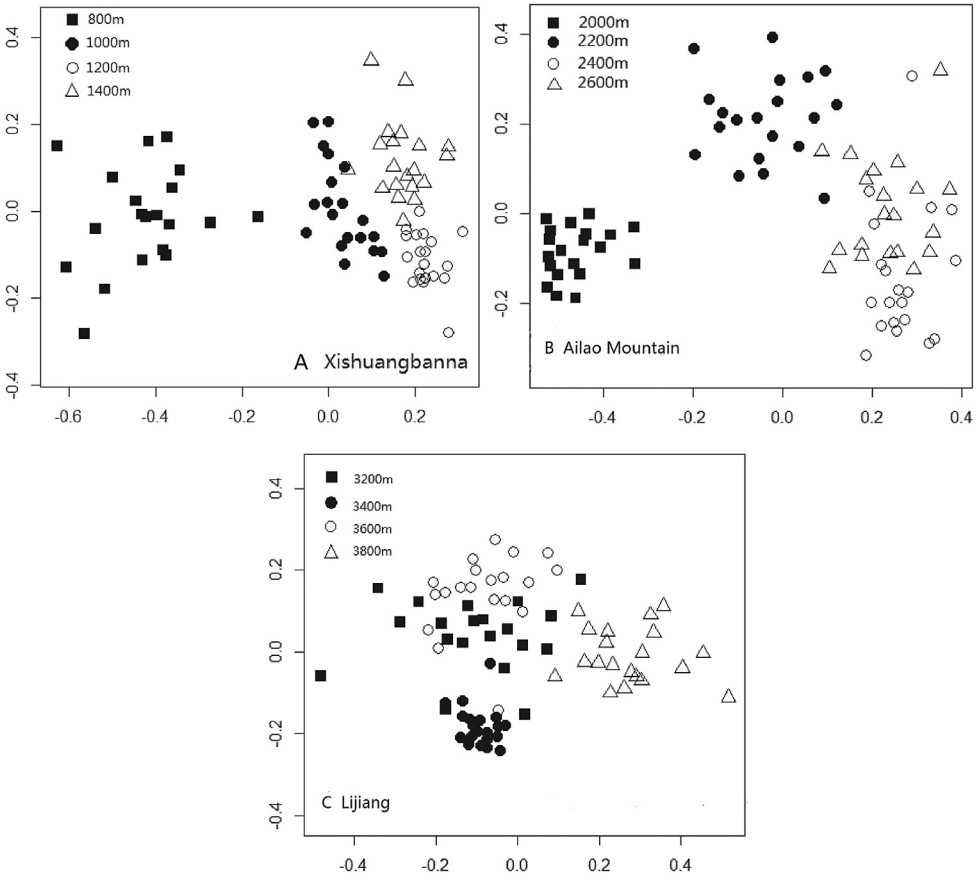

Fig. 4. Nonmetric multidimensional ordination based on composition of 20 soil samples among elevational gradients in A. Xishuangbanna, B. Ailao Mountain and C. Lijiang.

Table 5
Similarity of woody species composition between soil seed bank and standing vegetation.

Site	Elevation (m)	NWSAV	NWSIS	NCS	Sørensen's index
Xishuangbanna (Tropical forest)	800	24	53	0	0.00%
	1000	26	48	0	2.70%
	1200	11	34	2	8.89%
	1400	7	38	1	4.44%
Ailao Mountain (Subtropical forest)	2000	11	30	0	0.00%
	2200	14	28	1	4.76%
	2400	14	22	1	5.56%
	2600	13	25	2	10.53%
Lijiang (Subalpine forest)	3200	6	2	0	0.00%
	3400	7	6	0	0.00%
	3600	5	3	0	0.00%
	3800	1	2	0	0.00%

NWSAV: Number of woody species recorded in standing vegetation, NWSIS: Number of woody species in soil seed bank. NCS: Number of common woody species shared by both standing vegetation and soil seed bank.

Table 6
Nonconstituent species germinated from the 20 soil samples at each elevation.[a].

Site	Nonconstituent species	Life form	800 m	1000 m	1200 m	1400 m
Xishuangbanna (Tropical forest)	*Ludwigia linifolia*	Herb	128	20	1	
	Digitaria sanguinalis	Herb	99	391	938	197
	Crassocephalum crepidioides	Herb	6	31	7	10
	Ageratum conyzoides	Herb	3			
	Conyza canadensis	Herb	2	4		
	Chromolaena odorata	Herb	2	1		1
	Gnaphalium pensylvanicum	Herb	1	2		2
	Stachytarpheta jamaicensis	Herb	1			
	Mirabilis jalapa	Herb	1			
	Spermacoce remota	Herb		3	3	
	Hedyotis verticillata	Herb		3		
	Hedyotis diffusa	Herb		2		
	Hedyotis costata	Herb			37	8
	Lindernia crustacea	Herb			13	
	Lobelia nummularia	Herb			3	
	Total number		243	457	1002	218
	Percentage[b]		11.53%	34.31%	55.27%	20.47%
Ailao Mountain (Subtropical forest)	Nonconstituent species		2000 m	2200 m	2400 m	2600 m
	Ageratina adenophora	Herb	48	36	16	30
	Laggera pterodonta	Herb	35	1	3	5
	Crassocephalum crepidioides	Herb	14	7	1	5
	Crassocephalum rubens	Herb				5
	Total number		97	44	20	45
	Percentage[b]		2.67%	2.73%	1.04%	2.92%

[a] We did not find any nonconstituent species in the soil samples from Lijiang.
[b] Percentage of the total number of seeds of nonconstituent species from each elevation.

largely due to an increase in the number of *N. cadamba* seeds that germinated (1173 seeds germinated in our study and 81 in the study 10 years ago). This species is a common pioneer tree species in tropical Asian forests (Richards, 1996). Meanwhile, the number of species 10 years ago was 87, and it decreased to 71 in our study (Fig. 2).

Previous studies found that the seed density and species diversity of the soil seed bank peaked at an intermediate elevation (Zhang and Fang, 2004b; Li et al., 2012; Erfanzadeh et al., 2013). This seems to be true for the subalpine site in our study, but the tropical site had the highest seed bank species diversity at the highest elevation (1400 m). In addition, species diversity of subtropical soil seed bank did not show significant differences between 2000 m, 2200 m and 2600 m; however, species diversity for the subtropical seed soil bank at 2400 m was significantly lower than at the other three altitudes (Fig. 3).

With regard to the life form spectrum of the dominant species, a transition of tree + shrub → shrub + herb → herb was observed in the tropical, subtropical and subalpine sites (Tables 3 and 4). Some studies proposed that the occurrence of pioneer tree species in the soil seed bank plays an important role in forest dynamics, because the regeneration of forests depends on the alternation of climax species and pioneer species (Swaine and Whitmore, 1988; Whitmore, 1989; Richards, 1996). Thus, the dominance of some tree species such as *N. cadamba, Ficus semicordata* and *Wendlandia* spp. in the tropical soil seed bank serves as a species pool for future regeneration. In contrast, the subalpine site was dominated by herbs, and only one deciduous broad-leaved tree species (*Padus buergeriana*, 2 seeds) germinated from the soil seed bank. These results partially explain why the coniferous forest remains in the meadow stage of succession for a very long time after it is degraded (Liu et al., 2002). On the other hand, this result is different from that

obtained for a *P. schrenkiana* forest in the Tianshan Mountains, northwest China, where seeds of *P. schrenkiana* occurred in all the soil samples from 13 elevations ranging from 1500 m–2700 m (Li et al., 2012). A study on the soil seed banks in *Abies fargesii* and *Larix chinensis* forests in the Qinling Mountains, northern China, also found some seeds of the two tree species (Zhang and Fang, 2004b).

The tropical forest had the highest species richness, followed by the subtropical forest and subalpine forest. Further, species richness of the soil seed banks in tropical and subtropical forests tended to be larger at low than high elevations (Fig. 2). This result is in line with our expectations because tropical and subtropical sites have richer species pools than subalpine sites. However, tropical forests did not show the highest values of species diversity indices (Fig. 3), reflecting the uneven distribution of seed abundance.

4.2. Similarity between soil seed bank and standing vegetation

The similarity of woody species composition between the seed bank and standing vegetation was very low at all elevations and sites (below 11.00% in terms of Sørensen's index) (Table 5), suggesting a minor contribution of the woody species of the standing vegetation to the soil seed banks. This result is consistent with other findings for tropical forests (Tang et al., 1999), subtropical forests (An et al., 1996; Wei et al., 2005), temperate forests (Olano et al., 2002), subalpine and alpine forests (Erfanzadeh et al., 2010; Pei et al., 2012; Zhou et al., 2013) and grasslands (Funes et al., 2001), where the species composition of the soil seed bank differs greatly from that of the standing vegetation.

Some studies have found that species similarity between the soil seed bank and standing vegetation is very low (Hill and Stevens, 1981), especially in the late successional stage of the forest, which has a much lower similarity than early successional stages (Garwood, 1989; Huang et al., 1996; Xiong et al., 1992). The larger number of woody species in the soil seed bank than in the standing vegetation and thus the low similarity between the two can be explained by the fact that (1) the seed bank composition may be derived from a former successional stage (Thompson et al., 1998), (2) seeds from standing vegetation failed to remain viable in the soil seed bank, (3) seeds may germinate immediately once they fall into a moist habitat (Gross-Camp and Kaplin, 2005), and (4) the regeneration of forest depends on the cyclic replacement of different tree species groups (Whitmore, 1982, 1990).

We did not expect to obtain a "0" similarity between the soil seed bank and standing vegetation at the basal elevations of the tropical and subtropical sites. Furthermore, the subalpine site showed the same trends at all elevations ranging from 3200 m throughout 3400 m, 3600 m and 3800 m (Table 5). Does this suggest that none of the seeds of the canopy tree species remain viable in the soils under the forests? This merits long-term monitoring of these soil seed banks.

4.3. Nonconstituent species

A total of 15 nonconstituent species was recorded in the Xishuangbanna site, and seeds of these species accounted for an average of more than 30% of the total seeds that germinated in the samples, indicating disturbance to some extent. Four of the nonconstituent species were also found along four elevations in the Ailao Mountain site, of which *A. adenophora* (formerly *Eupatorium adenophorum*) was the most abundant alien species. This species appears to be very invasive to the native ecosystems in southwest China. Since it became colonized in the 1940s, its dispersal has been closely associated with human activities (Liu et al., 1985). This species has a persistent soil seed bank and can germinate after disturbance occurs in forests (Shen et al., 2006; Song et al., 2017). Lin and Cao, (2009) showed abundant seed storage of this species in the soils in the interior of a subtropical forest in Ailao Mountain because of edge effects, although no individuals of this species were observed in the understory vegetation. Impressively, another herbaceous species, *C. crepidioides* commonly occurred in both tropical and subtropical soil seed banks under the forests. This is a pantropical weed in fallow fields, on slopes, roadsides, streamsides and thickets in Africa, S and SE Asia, Australia, Central and South America, and the Pacific islands. It was previously recorded mostly below 300–1800 m in Jiangxi, Fujian, Hunan, Hubei, Guangdong, Guangxi, Guizhou, Yunnan, Sichuan, and Xizang provinces of China (Editing Committee of Flora of China, 1999), but we have observed it in the soils of the forest interior even up to 2600 m, indicating the potential colonization of this species at higher habitats in the event of disturbance.

We did not detect nonconstituent species in the forest soils in the subalpine site, but whether this is due to the harsh environment or inaccessibility of these species has not been determined.

5. Conclusions

The seed density of soil seed banks in tropical and subtropical sites peaked at low elevations (i.e. 800 m and 2000 m, respectively), but at intermediate elevation (3400 m) in the subalpine site. The tropical forest had the highest number of species in the soil seed bank, subtropical forest had a moderate number and subalpine forest had the lowest number. A transition in dominant life form in the soil seed banks was observed: tree + shrub for the tropical site → shrub + herb for the subtropical site → herb for the subalpine site. Tree seeds dominated the tropical soil seed banks, but they were very rare (only 2 seeds) in the subalpine soil seed banks, suggesting a longer regeneration after forest clearance compared with tropical and subtropical forests. Similarity (Sørensen index) of woody species composition between the soil seed bank and standing vegetation was very low at the lowest tropical and subtropical sites and decreased with an increase in elevation. In subalpine forests, there was no common woody species shared by the soil seed bank and standing vegetation. All the nonconstituent species occurring in soil seed banks were herbs, and seed abundance and species number decreased from tropical → subtropical → subalpine forests but not with an increase in elevation in either the tropical or subtropical sites. Nonconstituent species were completely absent from the soil seed bank of the subalpine site.

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Appendix 1
Species composition, life form, total number of each species and its proportion at each elevation in Xishuangbanna.

Species	Life form	800 m	1000 m	1200 m	1400 m
Acronychia pedunculata	Tree	1 (0.05%)			
Ageratum conyzoides	Herb	3 (0.14%)			
Aidia yunnanensis	Shrub	14 (0.66%)			
Alchornea davidii	Shrub	3 (0.14%)	6 (0.45%)	3 (0.17%)	12 (1.13%)
Alchornea tiliifolia	Tree			2 (0.11%)	1 (0.09%)
Alpinia conchigera	Herb				1 (0.09%)
Amischotolype hispida	Herb				1 (0.09%)
Aporosa yunnanensis	Tree		3 (0.23%)		
Baliospermum montanum	Shrub	9 (0.43%)			
Bauhinia glauca subsp. *tenuiflora*	Vine	1 (0.05%)			
Blumea lanceolaria	Herb	2 (0.09%)	7 (0.53%)	1 (0.06%)	13 (1.22%)
Boehmeria zollingeriana	Shrub	21 (1.00%)	2 (0.15%)	1 (0.06%)	2 (0.19%)
Breynia fruticosa	Shrub		2 (0.15%)		
Broussonetia papyifera	Tree		4 (0.30%)		1 (0.09%)
Buddleja asiatica	Shrub	112 (5.31%)	12 (0.90%)		6 (0.56%)
Cajanus grandiflorus	Vine		3 (0.23%)		4 (0.38%)
Callicarpa macrophylla	Shrub	2 (0.09%)		8 (0.44%)	9 (0.85%)
Campylotropis prainii	Shrub			2 (0.11%)	
Carex baccans	Herb	2 (0.09%)			
Carex cruciata	Herb				2 (0.19%)
Choerospondias axillaris var. *axillaris*	Tree		1 (0.08%)	2 (0.11%)	
Chromolaena odorata	Herb	2 (0.09%)	1 (0.08%)		1 (0.09%)
Cipadessa cinerascens	Tree		1 (0.08%)		
Colebrookea oppositifolia	Shrub			4 (0.22%)	34 (3.19%)
Colona thorelii	Tree	8 (0.38%)	7 (0.53%)		1 (0.09%)
Conyza canadensis	Herb	2 (0.09%)	4 (0.30%)		
Crassocephalum crepidioides	Herb	6 (0.28%)	31 (2.33%)	7 (0.39%)	10 (0.94%)
Croton kongensis	Shrub			6 (0.33%)	
Cyathula prostrata	Herb				1 (0.09%)
Cyperus duclouxii	Herb		1 (0.08%)	3 (0.17%)	14 (1.31%)
Dendrocnide basirotunda	Tree		11 (0.83%)		
Digitaria sanguinalis	Herb	99 (4.70%)	391 (29.35%)	938 (51.74%)	197 (18.50%)
Drypetes hoaensis	Tree			2 (0.11%)	
Elaeocarpus varunua	Tree	10 (0.47%)	3 (0.23%)		
Elsholtzia blanda	Herb		3 (0.23%)		
Elsholtzia rugulosa	Herb			4 (0.22%)	4 (0.38%)
Embelia subcoriacea	Shrub			2 (0.11%)	
Embelia vestita	Vine			9 (0.50%)	1 (0.09%)
Eriobotrya prinoides	Tree	1 (0.05%)	9 (0.68%)	2 (0.11%)	2 (0.19%)
Erythropalum scandens	Vine		4 (0.30%)	3 (0.17%)	
Euodia austro-sinensis	Tree	2 (0.09%)	3 (0.23%)	4 (0.22%)	
Eurya pittosporifolia	Tree		15 (1.13%)	121 (6.67%)	117 (10.99%)
Eurysolen gracilis	Shrub	3 (0.14%)			
Evodia lepta var. *lapta*	Shrub	2 (0.09%)		1 (0.06%)	2 (0.19%)
Ficus langkokensis	Tree	12 (0.57%)	15 (1.13%)	1 (0.06%)	1 (0.09%)
Ficus auriculata	Tree	1 (0.05%)			
Ficus cyrtophylla	Tree	8 (0.38%)	6 (0.45%)		19 (1.78%)
Ficus fistulosa	Tree	32 (1.52%)			
Ficus hirta var. *hirta*	Shrub		11 (0.83%)	5 (0.28%)	4 (0.38%)
Ficus hispida var. *hispida*	Shrub	2 (0.09%)	8 (0.60%)		
Ficus semicordata	Tree	56 (2.66%)	183 (13.74%)	37 (2.04%)	118 (11.08%)
Ficus subulata	Shrub	6 (0.28%)			
Ficus variegata var. *chlorocarpa*	Tree	44 (2.09%)	72 (5.41%)	1 (0.06%)	24 (2.25%)
Flueggea virosa	Tree	1 (0.05%)			
Garuga floribunda var. *gamblei*	Tree	2 (0.09%)			1 (0.09%)
Glochidion assamicum	Tree	1 (0.05%)			
Gnaphalium pensylvanicum	Herb	1 (0.05%)	2 (0.15%)		2 (0.19%)
Gomphostemma microdon	Vine	1 (0.05%)		2 (0.11%)	
Gynostemma pubescens	Herb	1 (0.05%)			
Hedyotis costata	Herb			37 (2.04%)	8 (0.75%)
Hedyotis diffusa	Herb		2 (0.15%)		
Hedyotis hedyotidea	Vine			2 (0.11%)	
Hedyotis scandens	Shrub	1 (0.05%)			
Hedyotis verticillata	Herb		3 (0.23%)		
Houttuynia cordata	Herb		2 (0.15%)		
Inula cappa	Shrub		17 (1.28%)		

Appendix 1 (*continued*)

Species	Life form	800 m	1000 m	1200 m	1400 m
Isachne globosa	Herb	1 (0.05%)	5 (0.38%)	1 (0.06%)	3 (0.28%)
Kydia calycina	Tree	3 (0.14%)			
Kyllinga monocephala	Herb		5 (0.38%)	8 (0.44%)	16 (1.50%)
Lindera metcalfiana var. *dictyophylla*	Tree			1 (0.06%)	1 (0.09%)
Lindernia crustacea	Herb			13 (0.72%)	
Lobelia nummularia	Herb			3 (0.17%)	10 (0.94%)
Ludwigia hyssopifolia	Herb	128 (6.07%)	20 (1.50%)	1 (0.06%)	
Lycianthes biflora	Shrub		2 (0.15%)		
Macaranga denticulata	Tree			4 (0.22%)	
Macropanax undulatus	Tree	3 (0.14%)			
Maesa indica	Shrub	14 (0.66%)	2 (0.15%)	16 (0.88%)	16 (1.50%)
Maesa montana	Shrub		3 (0.23%)	92 (5.07%)	25 (2.35%)
Mallotus paniculatus	Shrub		2 (0.15%)		
Mallotus philippensis	Shrub		2 (0.15%)		
Mallotus tetracoccus	Tree		1 (0.08%)		
Melastoma malabathricum	Shrub			167 (9.21%)	128 (12.02%)
Melia toosendan	Tree		1 (0.08%)		
Microstegium ciliatum	Herb			1 (0.06%)	8 (0.75%)
Millettia dielsiana	Vine				1 (0.09%)
Millettia pulchra	Shrub	1 (0.05%)			
Mirabilis jalapa	Herb	1 (0.05%)			
Musa acuminata	Herb	40 (1.90%)	9 (0.68%)		
Mussaenda macrophylla	Shrub	5 (0.24%)	25 (1.88%)	29 (1.60%)	33 (3.10%)
Mussaenda mollissima	Shrub			1 (0.06%)	8 (0.75%)
Mycetia gracilis	Shrub	2 (0.09%)			
Myrsine semiserrata	Shrub	1 (0.05%)	4 (0.30%)		1 (0.09%)
Neolamarckia cadamba	Tree	1173 (55.65%)	18 (1.35%)		
Ophiorrhiza repandicalyx	Herb		1 (0.08%)		
Oreocnide frutescens	Shrub	2 (0.09%)	8 (0.60%)	3 (0.17%)	3 (0.28%)
Parabaena sagittata	Vine	1 (0.05%)			
Parabarium micranthum	Vine	1 (0.05%)			
Paraphlomis javanica	Herb				2 (0.19%)
Phyllanthus reticulatus var. *reticulatus*	Shrub		3 (0.23%)		
Picria fel-terrae	Herb			2 (0.11%)	37 (3.47%)
Polygala japonica	Herb		2 (0.15%)	1 (0.06%)	3 (0.28%)
Premna fulva	Shrub		14 (1.05%)		
Psychotria morindoides	Shrub	2 (0.09%)			
Rhynchotechum ellipticum	Shrub	52 (2.47%)	1 (0.08%)		2 (0.19%)
Rubus alceifolius var. *alceaefolius*	Shrub	1 (0.05%)	1 (0.08%)	3 (0.17%)	28 (2.63%)
Rubus pirifolius	Shrub	1 (0.05%)	4 (0.30%)		2 (0.19%)
Saurauia yunnanensis	Shrub	6 (0.28%)			
Sida alnifolia	Shrub	1 (0.05%)	5 (0.38%)		
Smilax perfoliata	Vine	1 (0.05%)			
Smithia sensitiva	Herb				10 (0.94%)
Spermacoce remota	Herb		3 (0.23%)	3 (0.17%)	
Stachytarpheta jamaicensis	Herb	1 (0.05%)			
Stephania hernandiifolia	Vine	1 (0.05%)	1 (0.08%)		1 (0.09%)
Stereospermum colais	Tree	1 (0.05%)			
Steudnera colocacieafolia	Herb		4 (0.30%)		
Symphorema involucratum	Vine		1 (0.08%)		
Terminalia myriocarpa	Tree	43 (2.04%)			
Tetrameles nudiflora	Tree	1 (0.05%)	1 (0.08%)	1 (0.06%)	2 (0.19%)
Tetrastigma planicaule	Vine	2 (0.09%)	5 (0.38%)		2 (0.19%)
Torenia flava	Herb	1 (0.05%)			
Terma orientalis	Tree	2 (0.09%)	20 (1.50%)	13 (0.72%)	17 (1.60%)
Triumfetta annua	Herb	2 (0.09%)			
Triumfetta rhomboidea	Shrub	1 (0.05%)		2 (0.11%)	4 (0.38%)
Urophyllum chinense	Shrub	1 (0.05%)			
Vernonia cinerea	Herb		2 (0.15%)	4 (0.22%)	3 (0.28%)
Vernonia parishii	Tree	1 (0.05%)	3 (0.23%)		
Vernonia volkameriifolia	Shrub		1 (0.08%)		
Wendlandia tinctoria	Shrub			124 (6.84%)	59 (5.54%)
Wendlandia uvariifolia	Shrub	3 (0.14%)	202 (15.17%)		
Unidentified		134 (6.36%)	106 (7.96%)	110 (6.07%)	27 (2.54%)

Appendix 2
Species composition, life form, total number of each species and its proportion at each elevation in Ailao Mountain.

Species	Life form	2000 m	2200 m	2400 m	2600 m
Acalypha australis	Herb			1 (0.05%)	
Agapetes mannii	Shrub	2 (0.06%)	44 (2.73%)	92 (4.77%)	111 (7.21%)
Ageratina adenophora	Herb	48 (1.32%)	36 (2.24%)	16 (0.83%)	30 (1.95%)
Alpinia blepharocalyx	Herb	1 (0.03%)			
Amischotolype hispida	Herb	1 (0.03%)			
Aralia thomsonii	Shrub	1 (0.03%)			
Bidens pilosa	Herb			1 (0.05%)	
Boehmeria clidemioides var. *diffusa*	Herb	248 (6.83%)	3 (0.19%)		
Buddleja asiatica	Shrub	121 (3.33%)	38 (2.36%)	12 (0.62%)	9 (0.58%)
Buddleja macrostachya	Herb	11 (0.30%)	2 (0.12%)		
Cardamine hirsuta	Herb	2 (0.06%)			
Carex teinogyna	Herb	17 (0.47%)	19 (1.18%)	85 (4.41%)	7 (0.45%)
Conyza japonica	Herb	4 (0.11%)			
Crassocephalum rubens	Herb				5 (0.32%)
Crassocephalum crepidioides	Herb	14 (0.39%)	7 (0.44%)	1 (0.05%)	5 (0.32%)
Dactylicapnos scandens	Herb		4 (0.25%)	1 (0.05%)	4 (0.26%)
Debregeasia orientalis	Shrub	1301 (35.81%)	129 (8.02%)	3 (0.16%)	3 (0.19%)
Diplospora dubia	Shrub	47 (1.29%)	1 (0.06%)		1 (0.06%)
Docynia delavayi	Tree	7 (0.19%)	178 (11.06%)	19 (0.98%)	19 (1.23%)
Elatostema laevissimum	Shrub	1 (0.03%)	259 (16.10%)	4 (0.21%)	44 (2.86%)
Embelia ribes	Vine	9 (0.25%)			
Euonymus fortunei	Shrub				2 (0.13%)
Eurya groffii	Tree	2 (0.06%)	23 (1.43%)	39 (2.02%)	47 (3.05%)
Exbucklandia populnea	Tree		9 (0.56%)		1 (0.06%)
Ficus beipeiensis	Tree	279 (7.68%)	4 (0.25%)		
Ficus concinna	Tree		3 (0.19%)	5 (0.26%)	2 (0.13%)
Ficus pubigera	Shrub	32 (0.88%)	1 (0.06%)	2 (0.10%)	
Gaultheria leucocarpa	Shrub		1 (0.06%)		1 (0.06%)
Glochidion eriocarpum	Shrub	11 (0.30%)			
Gnaphalium affine	Herb	21 (0.58%)	22 (1.37%)	22 (1.14%)	25 (1.62%)
Gnaphalium pensylvanicum	Herb	10 (0.28%)	8 (0.50%)	5 (0.26%)	6 (0.39%)
Hedyotis scandens	Shrub	1 (0.03%)			
Ilex corallina	Tree	13 (0.36%)	47 (2.92%)	76 (3.94%)	20 (1.30%)
Ilex szechwanensis	Shrub			2 (0.10%)	8 (0.52%)
Ixeris denticulata	Herb		1 (0.06%)		
Laggera alata	Herb	224 (6.17%)	1 (0.06%)		1 (0.06%)
Laggera pterodonta	Herb	35 (0.96%)	1 (0.06%)	3 (0.16%)	5 (0.32%)
Laportea bulbifera	Herb	18 (0.50%)	56 (3.48%)	35 (1.81%)	34 (2.21%)
Laportea interrupta	Herb	8 (0.22%)		2 (0.10%)	1 (0.06%)
Litsea rubescens	Tree		2 (0.12%)		
Lobelia clavata	Herb		2 (0.12%)		
Luculia pinceana	Shrub	1 (0.03%)			
Macaranga pustulata	Tree	5 (0.14%)			
Maesa indica	Shrub	475 (13.07%)	6 (0.37%)		
Maesa perlarius	Shrub			2 (0.10%)	3 (0.19%)
Manglietia insignis	Tree	1 (0.03%)	10 (0.62%)	1 (0.05%)	1 (0.06%)
Meliosma arnottiana	Tree	1 (0.03%)			
Meliosma dumicola	Tree	3 (0.08%)	2 (0.12%)		
Miscanthus floridulus	Herb	1 (0.03%)			
Myrsine semiserrata	Shrub	18 (0.50%)	24 (1.49%)	532 (27.58%)	226 (14.68%)
Neanotis wightiana	Herb	1 (0.03%)	1 (0.06%)		
Oxalis corniculata	Herb	1 (0.03%)	1 (0.06%)		
Oxyspora paniculata	Shrub	40 (1.10%)	119 (7.40%)	66 (3.42%)	66 (4.29%)
Phytolacca acinosa	Herb		1 (0.06%)		
Pilea subcoriacea	Herb	202 (5.56%)			38 (2.47%)
Pogostemon glaber	Herb			1 (0.05%)	
Polygonum runcinatum	Herb	2 (0.06%)			
Rubus lineatus	Shrub				2 (0.13%)
Rubus pluribracteatus	Shrub	28 (0.77%)	38 (2.36%)	4 (0.21%)	4 (0.26%)
Rubus sumatranus	Shrub	6 (0.17%)	20 (1.24%)	40 (2.07%)	85 (5.52%)
Saurauia yunnanensis	Shrub	90 (2.48%)	8 (0.50%)	2 (0.10%)	3 (0.19%)
Scleria terrestris	Herb	20 (0.55%)	29 (1.80%)	140 (7.26%)	
Setaria plicata	Herb	6 (0.17%)	6 (0.37%)	2 (0.10%)	1 (0.06%)
Smilax china	Vine		1 (0.06%)		
Smilax myrtillus	Shrub		1 (0.06%)		4 (0.26%)
Solanum lyratum	Vine	2 (0.06%)			1 (0.06%)
Solanum nigrum	Herb	3 (0.08%)			
Spiraea japonica	Shrub	2 (0.06%)	3 (0.19%)	33 (1.71%)	
Styrax rugosus	Shrub	4 (0.11%)	3 (0.19%)		
Tetracentron sinense	Tree				1 (0.06%)
Tetrastigma henryi	Vine	3 (0.08%)	1 (0.06%)		

Appendix 2 (*continued*)

Species	Life form	2000 m	2200 m	2400 m	2600 m
Tetrastigma serrulatum	Vine		2 (0.12%)	3 (0.16%)	
Toddalia asiatica	Vine	3 (0.08%)	3 (0.19%)	3 (0.16%)	
Viburnum foetidum	Shrub	2 (0.06%)			
Viburnum foetidum var. *rectangulatum*	Shrub		3 (0.19%)	5 (0.26%)	1 (0.06%)
Viburnum sp.	Shrub		1 (0.06%)	15 (0.78%)	1 (0.06%)
Viola hossei	Herb	1 (0.03%)	6 (0.37%)	4 (0.21%)	
Wendlandia scabra	Tree	4 (0.11%)			
Zanthoxylum armatum	Tree	1 (0.03%)		1 (0.05%)	
Zehneria bodinieri	Vine	1 (0.03%)			
Unidentified		211 (5.81%)	419 (26.04%)	649 (33.64%)	712 (46.23%)

Appendix 3
Species composition, life form, total number of each species and its proportion at each elevation in Lijiang

Species	Life form	3200 m	3400 m	3600 m	3800 m
Ainsliaea latifolia	Herb	12 (4.00%)	111 (7.52%)		1 (0.26%)
Ainsliaea reflexa	Herb			1 (0.26%)	
Anaphalis sp.	Herb		1 (0.07%)		
Artemisia sp.		1 (0.33%)			
Astilbe chinensis	Herb				76 (19.39%)
Cardamine yunnanensis	Herb		2 (0.14%)		
Carex nubigena	Herb	120 (40.00%)	17 (1.15%)	22 (5.76%)	29 (7.40%)
Carex sp.1	Herb	2 (0.67%)	9 (0.61%)	47 (12.30%)	2 (0.51%)
Carex sp.2	Herb	1 (0.33%)			
Chrysosplenium davidianum	Herb		7 (0.47%)		1 (0.26%)
Circaea alpina	Herb	10 (3.33%)	2 (0.14%)	3 (0.79%)	
Clinopodium polycephalum	Herb	6 (2.00%)	273 (18.50%)		1 (0.26%)
Clinopodium sp.	Herb		8 (0.54%)		
Corydalis petrophila	Herb	1 (0.33%)	6 (0.41%)		1 (0.26%)
Cynoglossum amabile	Herb		2 (0.14%)		
Epilobium breuifolium	Herb	2 (0.67%)	7 (0.47%)	2 (0.52%)	1 (0.26%)
Epilobium brevifolium	Herb	2 (0.67%)			
Galium asperuloides	Herb		1 (0.07%)		
Galium elegans	Herb		2 (0.14%)		
Geranium sp.	Herb				4 (1.02%)
Gnaphalium affine	Herb	4 (1.33%)	7 (0.47%)	3 (0.79%)	1 (0.26%)
Gnaphalium pensylvanicum	Herb		1 (0.07%)		
Hemiphragma heterophyllum	Herb		9 (0.61%)	14 (3.66%)	1 (0.26%)
Hypericum acmosepalum	Shrub		1 (0.07%)		
Impatiens delavayi	Herb	1 (0.33%)	27 (1.83%)		
Juncus effusus	Herb			35 (9.16%)	
Laportea interrupta	Herb		3 (0.20%)	12 (3.14%)	1 (0.26%)
Luzula sp.	Herb		1 (0.07%)	2 (0.52%)	13 (3.32%)
Lysimachia violascens var. *robusta*	Herb		1 (0.07%)		
Myriactis wightii	Herb	12 (4.00%)	186 (12.60%)	21 (5.50%)	23 (5.87%)
Padus buergeriana	Tree		2 (0.14%)		
Parasenecio sp.	Herb				4 (1.02%)
Parnassia sp.	Herb			2 (0.52%)	
Philadelphus delavayi	Shrub	37 (12.33%)	370 (25.07%)	15 (3.93%)	
Pilea microphylla	Herb		2 (0.14%)		
Pilea sinofasciata	Herb	16 (5.33%)	340 (23.04%)	19 (4.97%)	
Pleurospermum camtschaticum	Herb				2 (0.51%)
Pogonatherum paniceum	Herb	3 (1.00%)	1 (0.07%)		
Polygonum runcinatum	Herb	1 (0.33%)			33 (8.42%)
Potentilla sp.	Herb			4 (1.05%)	
Ribes glaciale	Shrub	4 (1.33%)	4 (0.27%)	43 (11.26%)	3 (0.77%)
Ribes sp.	Shrub		1 (0.07%)	1 (0.26%)	71 (18.11%)
Rubia yunnanensis	Herb	4 (1.33%)	1 (0.07%)	4 (1.05%)	
Rubus fockeanus	Herb	11 (3.67%)	22 (1.49%)	83 (21.73%)	
Sambucus williamsii	Shrub		3 (0.20%)		
Sedum sp.	Herb	2 (0.67%)			
Stellaria vestita	Herb	14 (4.67%)	3 (0.20%)	17 (4.45%)	11 (2.81%)
Tripterospermum volubile	Herb		2 (0.14%)		
Veronica piroliformis	Herb	9 (3.00%)	28 (1.90%)	5 (1.31%)	
Viola biflora	Herb		2 (0.14%)	3 (0.79%)	
Unidentified		25 (8.33%)	11 (0.75%)	24 (6.28%)	113 (28.83%)

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