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Winners and losers among tree species in Xishuangbanna: which traits are most important?

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Abstract Massive human interference in natural ecosystems is resulting in a few "winners" and many "losers". However, the drivers of this winner–loser replacement pattern remain poorly understood. The aim of the study reported here was to identify winners among the tree flora of Xishuangbanna and compare their functional traits, specific leaf area (SLA), wood density (WD), seed mass (SM) and maximum height (MH) with previously identified losers (i.e., endangered species). Fifteen native tree species were identified as winners from expert opinion, plot-based surveys of secondary forests and plotless surveys along roads. Twelve endangered tree species for which trait information could be obtained were used for comparison. Traits were compared with a Wilcoxon rank-sum test. Winners had significantly higher SLA, but lower WD. SM and MH did not differ significantly between groups. When the effects of phylogeny were removed by using phylogenetic generalized least squares, the difference in SLA became marginally insignificant. Principal component analysis resulted in two overlapping groups, showing that the selected traits were insufficient to distinguish winners and losers. Our results suggest that the "few winners, many losers" paradigm applies to trees in Xishuangbanna, with 15 species accounting for most trees in the disturbed habitats sampled.

Keywords Human disturbance · Functional traits · Phylogeny · Conservation status · Tropical forests

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1 Introduction

Accumulating evidence shows that the "few winners and many losers" paradigm has become the emerging prospect for tropical forest biodiversity [1, 2]. The concept applies equally well to both plants and animals, but only plants are considered in this paper. As a result of the impact of human activities, including deforestation, fragmentation and overexploitation, a few "winner" species are able to increase their population densities and/or geographical ranges, while many "loser" species suffer reduced densities and ranges and may even become extinct [3, 4]. The winners are often alien cosmopolitans with r life history strategies, while the losers are native species with narrow ecological niches and k life history strategies [2, 5, 6], so the proliferation of alien species at the expense of native species in response to disturbance has received most attention in the literature [7–9]. Thus, a common view is that exotic winners succeed local losers within human-disturbed environments, leading to biotic homogenization [6, 7, 10]. However, in the human-dominated tropics, the invasive alien flora is dominated by herbs, climbers and shrubs, while the tree flora of disturbed sites consists largely or entirely of native species [11, 12]. Moreover, the alien species tend to be eliminated during succession. Tree winners are thus largely native, as are some of the non-tree species. Biotic homogenization therefore results not only from the success of alien species, but also from the rearrangement of the native flora under human impacts, favouring a few native species while harming most others [5, 13, 14].

The drivers of this winner–loser replacement process have been under-researched, especially for native trees. However, increasing evidence has shown that tree species with certain traits tend to decline in disturbed habitats, for example trees with extreme heights or inflexible stems [15–17], shade-tolerant species [18] or species with big seeds that require gut passage through vertebrates to germinate [19], whereas other species can survive serious anthropological disturbance, such as wind-dispersed species with small seeds [20], pioneers with relatively short life cycles and species with high fecundity [21, 22]. Researchers have also found that the mortality of disturbance-sensitive tree species rises sharply near forest edges in experimental forest fragments in Central Amazonia, because they are exposed to stronger winds and drought [23]. Soil moisture and microclimatic changes along forest margins cause many trees to lose their leaves and die standing [16, 24]. Collectively, changing forest composition through the loss of species and higher species turnover is the direct consequence of these effects [25, 26].

We define a winner tree species as one that is common in human-disturbed habitats and has therefore benefitted by the land-use changes of the last few decades. A loser, in contrast, is a plant species that grows only in habitats that have not been seriously disturbed by people and has consequently declined as such habitats have become restricted in recent decades. Winners are expected to dominate in forest edges, young secondary forests and in chronically disturbed areas, such as along roads, while losers will dominate in the interior of well-protected forest areas. The major aim of the study reported here was to assess why some tree species are winners and some losers. We focused on a comparison between their functional traits, since these are believed to be closely related to their life strategies, which in turn are likely to determine their capacity to adjust to the novel environments resulting from human activities. The losers in our study area have been identified as "endangered" or "critically endangered" in an earlier study of the conservation status of the entire angiosperm flora, but the winners were included within a broad "least concern" category that included 72 % of the flora (Pan et al. unpublished). We therefore attempted to answer three questions: (1) Which native tree species are winners in Xishuangbanna? (2) Do these species differ from losers in four key functional traits? and (3) Do these differences persist when the effects of phylogeny are removed?

2 Methods

2.1 Study area

All fieldwork was conducted in the 20,000-km^2 Xishuangbanna Dai Autonomous Prefecture, Yunnan Province, Southwest China, which is located in the biogeographical transitional zone between tropical Southeast Asia and temperate East Asia (21°08′–22°36′N, 99°56′–101°50′E) [27]. Xishuangbanna is a biodiversity hot spot in China with more than 3,500 native plant species. The terrain is steep, with elevation ranging from 475 to 2,420 m [28, 29]. Xishuangbanna has a monsoon climate with hot, wet summers and cool, dry winters. Monthly mean temperatures range from 15.7 to 25.8 °C at 558 m a.s.l., but frosts occur in winter at higher altitudes. Annual precipitation ranges from 1,200 to 1,556 mm, with more than 80 % between May and the end of October, but dense fog in the morning reduces water stress between November and February. Until recently, tropical rain forests occupied the lowest elevations and a variety of more seasonal forest formations occurred elsewhere [27].

However, the primary forests in Xishuangbanna have been under severe pressure from agricultural expansion over the last 30 years [30, 31]. Below 900 m a.s.l, most unprotected forest has been replaced by monoculture rubber plantations, which increased from 87,000 ha in 1992 to 424,000 ha in 2010 [31]. Other crops, such as tea, have replaced forests at higher altitudes. Three nature reserves protect 15.5 % of Xishuangbanna, including the largest forest patches, but numerous unprotected forest fragments of various sizes persist in the agricultural matrix.

2.2 Identification of losers and winners

The selection of winner and loser species was based on a combination of expert opinion from field botanists with many years' experience in Xishuangbanna and, for winners only, new field surveys. An initial survey of forest edges in the study area found them to be largely dominated by species from the interior of the primary forest, reflecting the continuing rapid retreat of the forest, which has not allowed the development of the distinct woody edge community found in more stable landscapes. Widespread winner species were therefore identified from secondary forests and the disturbed vegetation near roadsides. Three typical secondary forest stands of different ages (3, 7 and >10 years), each near to protected primary forest areas, were selected and three representative 20 m × 10 m plots established in each. Within each plot, all trees >150 cm in height were measured [diameter at breast height (d.b.h.) and height], tagged, identified and counted. Voucher specimens were collected for identification and future reference. Artificially planted trees were excluded, as were large trees (d.b.h. > 20 cm) which may have established before disturbance. Plotless sampling was used for the scattered trees in non-forest areas, since widely varying density and accessibility precluded the use of plots. Trees were investigated along roads in three directions from the Xishuangbanna Tropical Botanical Garden (XTBG) (Fig. 1). We stopped every 5 km and sampled the first 45 trees (the average number in each secondary forest plot) encountered that were >150 cm in height and <20 cm in diameter.

The total area sampled is only a tiny fraction of Xishuangbanna, so we used the expert opinions of experienced field botanists to help select 15 winner species that were not only common in our samples but also widespread in disturbed habitats in Xishuangbanna. We then selected 12 loser species from the 69 tree species classified as Endangered or Critically Endangered in a recent (2012–2014) assessment of the status of all angiosperms in Xishuangbanna (Pan et al. unpublished). This assessment was based on expert opinion, herbarium records and extensive field surveys. The final selection of species for trait measurement was based largely on their availability in cultivation in XTBG, since it was not practical to locate wild trees of most species (Tables 1, 2). The selected species have all almost certainly declined as a result of recent deforestation and their inability to colonize anthropogenic habitats.

2.3 Trait measurements

Four traits were selected to represent different aspects of the life history strategies of the tree species. Specific leaf area (SLA) is associated with shade tolerance [32, 33]. It can be used to distinguish the leaves of sun-loving "pioneer" species from those of shade-tolerant "climax" species, with the former associated with rapid growth and large, palatable leaves, while the latter have leaves that are smaller, thicker, denser and physically robust. Wood density (WD) is biomass invested per unit wood volume [33]. It reflects the trade-off between stem growth rate and mechanical strength, as well as tolerance of drought and shade. Seed mass (SM) is related to the dispersal and establishment of plant species [34]. Maximum height at maturity (MH) plays a fundamental role in access to light for adult trees. Trait measurements were taken according to standardized protocols [35].

For each winner species, we sampled five individuals haphazardly in the field. This was not possible for the loser species, which are rare in the field and usually also in the

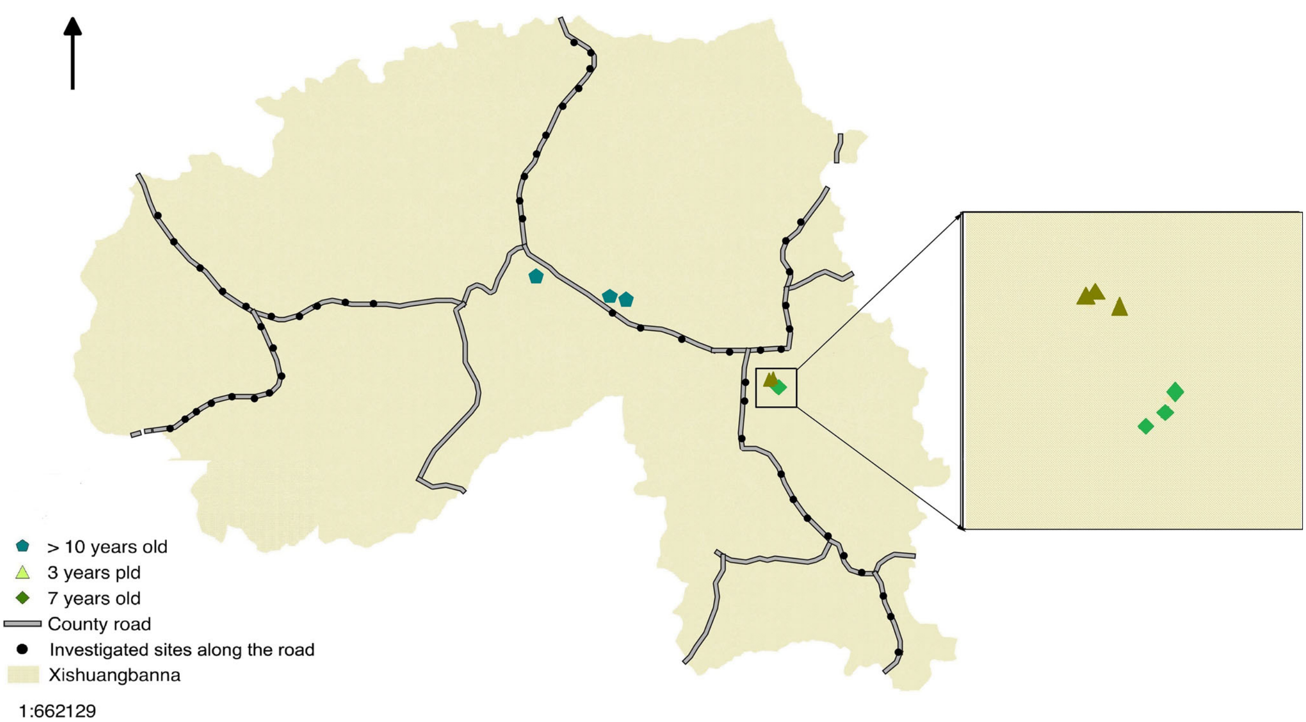

Fig. 1 (Color online) The sketch map of Xishuangbanna Dai Autonomous Prefecture showing locations of the nine sampling plots: pentagons represent >10-year secondary forest, quadrangles represent 7-year secondary forest, and triangles represent 3-year secondary forest. The black dots in the road represent the sites sampled in the roadside survey

Table 1 The numbers of the 15 winner tree species recorded during the field survey

Number	Winners	Families	Number in 3-year forest $n = 141$	Number in 7-year forest $n = 153$	Number in >10-year forest $n = 166$	Number in roadside survey $n = 2{,}340$	Presence in forest edges
1	*Macaranga denticulata* (Blume) Müll. Arg.	Euphorbiaceae	53		3	760	–
2	*Macaranga indica* Wight	Euphorbiaceae			2	149	–
3	*Toona ciliata* M. Roem.	Meliaceae			1	138	–
4	*Trema tomentosa* (Roxb.) H. Hara	Cannabaceae	3	9		108	–
5	*Ficus semicordata* Buch.-Ham. ex Sm.	Moraceae				102	–
6	*Mallotus paniculatus* (Lam.) Müll. Arg.	Euphorbiaceae			2	101	–
7	*Mallotus barbatus* Müll. Arg.	Euphorbiaceae			2	75	–
8	*Ficus auriculata* Lour.	Moraceae				67	+
9	*Rhus chinensis* Mill.	Anacardiaceae	6	22		53	–
10	*Macaranga pustulata* King ex Hook.f.	Euphorbiaceae		22		6	–
11	*Wendlandia tinctoria* (Roxb.) DC.	Rubiaceae	23	15	3	6	–
12	*Schima wallichii* Choisy	Theaceae	17	3	1	27	–
13	*Maesa indica* (Roxb.) A. DC.	Primulaceae		13	1	7	+
14	*Balakata baccata* (Roxb.) Esser	Euphorbiaceae		2	5	51	+
15	*Millettia leptobotrya* Dunn	Fabaceae			14	14	+

XTBG living collections, so only 1–3 individuals of each were sampled. Four leaves and three branches were taken from each individual. All the branches were fully exposed to the sun (except for species that are only found in shade), and fully expanded mature leaves without obvious damage were picked randomly from the branch. Each leaf with its petiole was scanned, and the area (cm^2) measured using ImageJ software [36] and then dried to a constant weight at 60 °C. SLA ($cm^2\ g^{-1}$) was calculated as the leaf blade area divided by the leaf dry mass [37]. The branches were cut into 2-cm-long segments, mixed and then subsampled. Three segments were chosen for each individual. The drainage method was used to measure the volume of each segment, which was then dried to a constant weight at 120 °C. WD (g cm^{-3}) was calculated as the wood dry mass divided by the volume of wood. SM (g) is the fresh weight of a single seed. Where fruiting individuals could be found (six species), as many mature seeds as possible were collected from multiple individuals and weighed in the laboratory. An additional 15 species were obtained from the XTBG Seed Bank, while data for the remaining nine species were obtained from the TRY plant trait database (http://www.try-db.org). MH (m) of mature tree was the maximum height given in the Flora of China. Locality information from the "Chinese Virtual Herbarium (http://www.cvh.org.cn/)" was used to assess the distribution of each species within China.

2.4 Phylogeny construction and data analysis

Total DNA was extracted from fresh leaf tissues of 15 winners and eight losers, following the modified hexadecyltrimethylammonium bromide (CTAB) procedure [38], and treated with RNaseA (Sigma). The primers for PCR amplification were used to acquire rbcL*b* sequences from genomic DNA according to Dong et al. [39]. PCR was performed using 94 °C for 30 s, 55 °C for 40 s and 72 °C for 1 min with 36 cycles, followed by a final extension at 72 °C for 10 min. The rbcL DNA sequences of *Trigonobalanus doichangensis* (gi|661916304), *Pterygota alata* (gi|452090514), *Dillenia triquetra* (gi|289599662) and *Pellacalyx saccardianus* (gi|2335174) were obtained from GenBank, with the latter two sequences substituting for the closely related *D. pentagyna* and *P. yunnanensis* (http://www.ncbi.nlm.nih.gov/Structure/cdd/wrpsb.cgi).

The 27 rbcL*b* sequences (23 PCR products and other four from GenBank) were aligned by Clustal X, and pairwise evolutionary distances were calculated with MEGA 5.0 [39, 40]. ModelGenerator v0.84 was used for calculating the amino acid substitution model, as the result "JTT+G+I" was selected as the optimal model [41]. Phylogenetic relationships were reconstructed using a maximum-likelihood (ML) method in MEGA version 5.0 program, with the APGIII phylogeny used as the backbone at the family level and above [42]. One thousand bootstrap

Table 2 Conservation status of the 12 loser tree species

Number	Losers	Families	Status
16	*Goniothalamus cheliensis* Hu	Annonaceae	CE
17	*Pterygota alata* (Roxb.) R.Br.	Malvaceae	CE
18	*Nyssa yunnanensis* W.Q. Yin ex H.N.Qin & Phengklai	Cornaceae	CE
19	*Ficus nervosa* B.Heyne ex Roth	Moraceae	CE
20	*Hydnocarpus annamensis* (Gagnep.) Lescot & Sleumer	Achariaceae	CE
21	*Trigonobalanus doichangensis* (A. Camus) Forman	Fagaceae	EN
22	*Magnolia hypolampra* (Dandy) Figlar	Magnoliaceae	EN
23	*Ficus geniculata* Kurz	Moraceae	EN
24	*Cryptocarya hainanensis* Merr.	Lauraceae	EN
25	*Pterospermum kingtungense* C.Y. Wu ex H.H. Hsue	Malvaceae	EN
26	*Dillenia pentagyna* Roxb.	Dilleniaceae	CE
27	*Pellacalyx yunnanensis* Hu	Rhizophoraceae	CE

CE critically endangered, *EN* endangered

replicates were performed in each analysis to obtain the confidence support [41, 42] (Fig. 2).

A Wilcoxon rank-sum test was used to compare the mean trait values between winners and losers. Phylogenetic generalized least squares (pGLS) were used to remove the effects of phylogeny and then compare the mean trait values between these two groups. Principal component analysis (PCA) of the traits was performed with R software v.3.1.2.

3 Results

Initial assessments based on the opinion of experienced experts identified 198 species of winners in Xishuangbanna from the previously assessed "least concern" category. The Lauraceae, Fabaceae, Euphorbiaceae, Moraceae and Malvaceae are the largest families of winners. In Hong Kong (22°N, 114°E), which has a similar climate and flora, but was deforested hundreds of years ago, the largest families of "very common" tree species are similar [43] (Table S1). The field survey recorded 2,800 trees, including 460 in the secondary forest plots and 2,340 along the roadsides (Table 1). The 15 winner species selected for trait measurements accounted for more than 50 % of the total individuals in each secondary forest plot and 62.5 % of all the trees surveyed in the study.

The four functional traits varied considerably across species: SLA by 2.6-fold, SM 350-fold, WD 3.5-fold and MH 7.5-fold (Fig. 2). There were significant differences between winners and losers for two traits, SLA ($W = 128$, $P = 0.013$) and WD ($W = 35$, $P = 0.006$): Winners tended to have higher SLA, but lower WD. SM and MH tended to be higher in losers, but these differences were not significant (SM, $W = 70$, $P = 0.347$; MH, $W = 61$, $P = 0.157$). When the effects of phylogeny were removed, the difference in WD remained significant ($F = 5.91$, $P = 0.023$), but the difference in SLA became marginally insignificant ($F = 3.56$, $P = 0.071$), although the absolute change in significance was small (Table 3). The winners and losers overlapped in the principal components analysis, separating relatively well along the first axis (eigenvalue 1.52, proportion explained 38.0 %; Fig. 3).

Herbarium records show that the winner species are more widespread in China than the losers (Fig. 4). Distributional information from the Flora of China confirms this pattern and also shows that winners are more widespread outside China (Table S2).

4 Discussion

This study shows that human activities in recent decades in Xishuangbanna have favored a few tree species and harmed many, in agreement with the "few winners and many losers paradigm." Out of a total native tree flora of 831 species, 198 were identified by experienced field botanists as having probably benefitted from recent disturbances. Fifteen of these accounted for more than half the individual trees sampled in secondary forests and disturbed roadside areas. A recent top-down assessment of the entire angiosperm flora of Xishuangbanna identified 37 tree species as Critically Endangered (CE), 32 as Endangered (EN), 187 as Vulnerable (VU) and 551 as Least Concern (LC) (Pan et al., unpublished). In this study, we selected the losers from among the 69 CE and EN species, but almost all VU species have also declined, as have the majority of LC species. Alien species are not a major

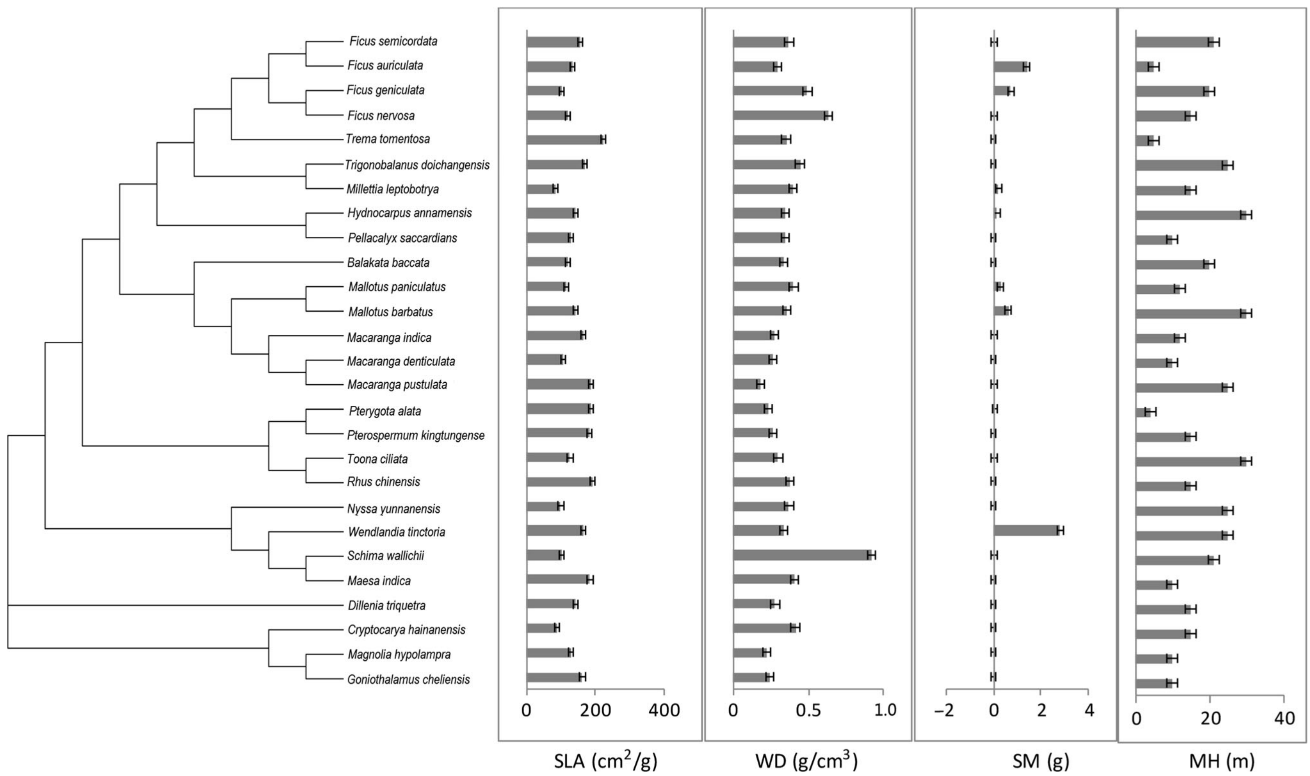

Fig. 2 Phylogenetic tree used for the 27 tree species along with trait values for specific leaf area (SLA), wood density (WD), seed mass (SM) and maximum height (MH)

Table 3 Difference between winners and losers for the four functional traits

Functional traits	Mean±SD		Wilcoxon rank-sum test		Phylogenetic generalized least squares (pGLS)	
	Winner	Loser	*W*	*P*	*F*	*P*
SLA	156.01±37.42	128.74±28.87	128	0.0132*	3.58	0.0698
WD	0.31±0.75	0.44±0.18	35	0.0063**	19.61	0.0002**
SM	0.21±0.72	0.27±0.44	70	0.3473	0.62	0.4368
MH	15.07±8.04	18.67±7.35	61	0.1569	3.46	0.0742

* $P < 0.05$; ** $P < 0.01$

component of the winner tree flora in Xishuangbanna. *Leucaena leucocephala* is common along roads, but has been widely sown there to provide rapid tree cover and it is not clear how common it is as a spontaneous tree. *Mimosa bimucronata* and *Piper aduncum* are present locally.

The winners identified in this study had higher SLA and lower wood density than the losers, while differences in seed mass and maximum height were not significant. High SLA is associated with high resource availability, particularly good illumination. Low-density wood is cheap to produce and is associated with rapid growth but low resistance to stress. When compared with loser species, winners tend to have large, soft foliage and lower woody density so that they can have high photosynthetic and respiratory rates allowing rapid growth [44, 45]. Many of the winners in the Xishuangbanna area are in the family Euphorbiaceae. They often have spreading crowns, which optimize sunlight capture. Their leaves have high metabolic rates and rapid abscission [46]. Resources used for rapid growth cannot be used for defense, so chemical and physical leaf defense is low and the leaves are often subject to high herbivory rates [47, 48]. In contrast, the losers mostly grow in closed-canopy forests, and must germinate and establish under canopy shade. In most cases, they have a relatively low growth rate and invest heavily in defense against mechanical damage and herbivory, resulting in dark and dense stem wood, closed crowns and tough long-lived leaves [44, 49].

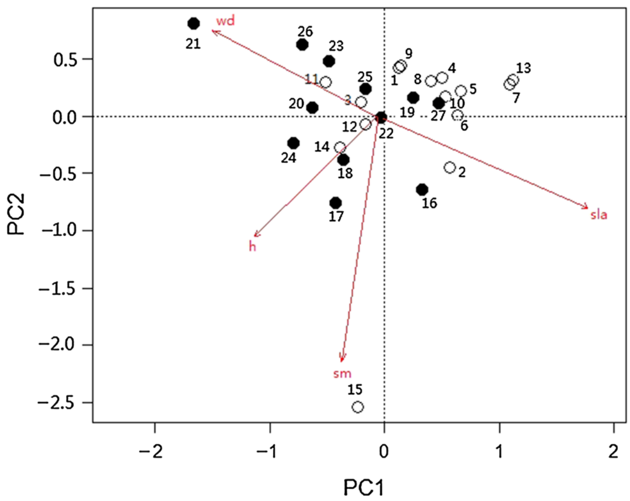

Fig. 3 (Color online) Principal component analysis (PCA) of four life history traits (specific leaf area, wood density, seed mass and maximum height): Winners and losers are indicated with blank and solid circles, respectively. The numbering of the species is the same as in Tables 1 and 2

Generally, tree species with pioneer characters tend to produce large amount of seeds but provide few resources for each [34]. Loser species are more likely to produce large and nutrient-rich seeds, which ensure they can establish under the deep shade [48, 50]. However, in tropical rainforest wind dispersal is a relatively minor strategy and as many as 85 % of woody species rely on birds and mammals [51]. Two-thirds of the winners in this study are dispersed by small birds and only three species (*Schima wallichii*, *Toona ciliata*, and *Wendlandia tinctoria*) by wind. Small birds are also important dispersal agents in native forests, so this helps explain why there was no significant difference in seed mass between winners and losers, although the losers include more large-seeded species. The rapid growth and low-density wood of most winners probably limits mature tree height, while the losers include both tall trees that compete for light in the canopy and shorter species that spend their whole lives in the subcanopy or understory, so a significant difference in height is not necessarily expected.

The removal of phylogenetic effects to assure statistical independence had little effect on the differences between winners and losers. The difference in SLA became marginally insignificant, but the absolute change was small. Future studies should investigate a larger number of both winner and loser species, to ensure a greater phylogenetic spread and increase statistical power. The overlap between winners and losers in the PCA also shows the need to investigate a wider range of traits, since the four in-

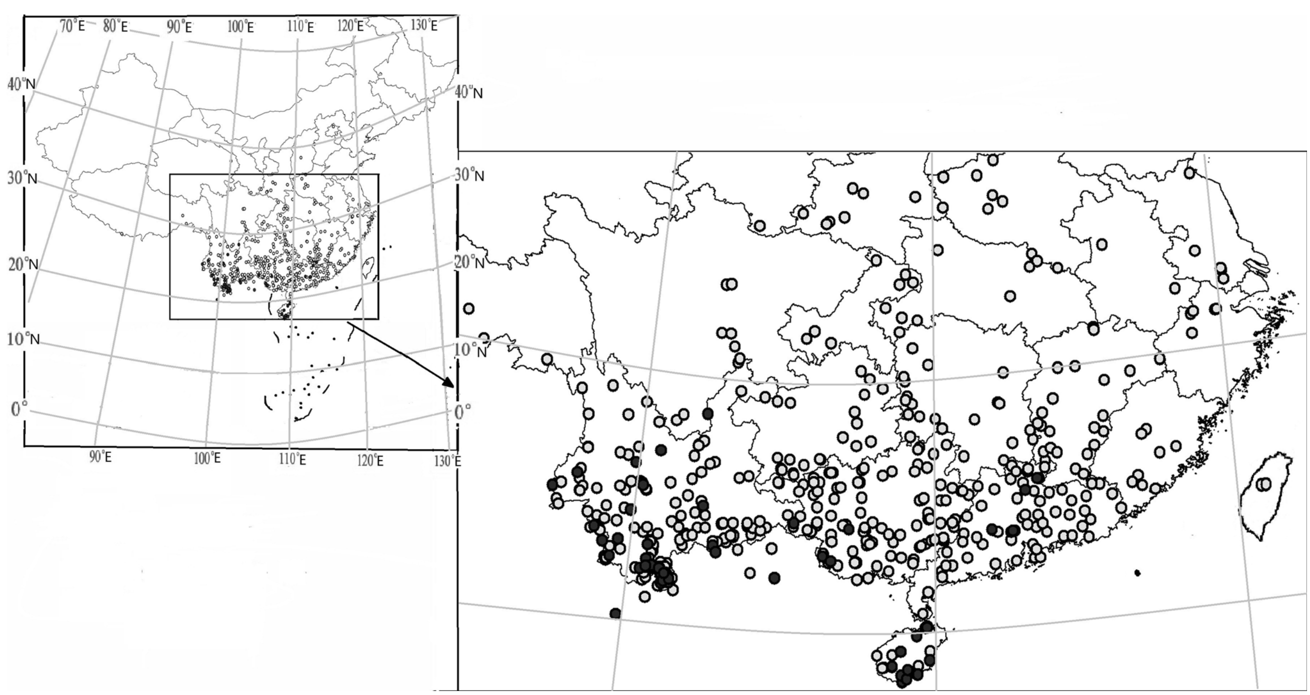

Fig. 4 The sketch map of the geographical distribution of the 27 species (1935–2000). The gray dots represent the winners, and black dots represent the losers

cluded in this study were not sufficient to predict the status of the species investigated.

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Conflict of interest The authors declare that they have no conflict of interest.

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