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Closed-Canopy Tropical Forests of Hainan, (China) Are Resilient against Invasive Herbs and Shrubs

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Abstract: The successful establishment of many plants in tropical forests often depends on species-specific adaptations related to light availability and forest successional stage. Species that are present in early successional stages generally do not occur in later successional stages. In this study, we documented the diversity, distribution, and abundance of terrestrial invasive plants across the (sub)tropical island of Hainan, China, and tested the germination of specific invasive plants in forested environments. In 97 transects positioned randomly across the island, we found nine invasive herb and shrub species were present in all human-modified habitats but not in intact forest interiors. In separate forest-specific transects, we documented a sharp drop in the abundance of invasive plants >5 m into the forest. High numbers of invasive plant seeds germinated from the soil seed bank sampled at the forest edge, but very few seeds germinated from soil sampled any distance into the forest. Finally, in experiments with four focal invasive plant species, overall germination rates were low; and much lower in shaded sites compared to full gap sites. In conclusion, our findings demonstrated that invasive herbs and shrubs do not yet form a serious threat to native species in the closed-canopy forests of Hainan.

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1. Introduction

Biological invasions can have serious environmental and economic impacts (Dennis 2004), for example through reduced forest productivity [1] and disrupted ecosystem services [2]. Nevertheless, biological invasions may also have positive impacts, including economic benefits from the introduction of new food sources for humans [3], improved soil microbial biomass and soil mineralization [4], and positive bottom-up effects on higher trophic levels [5]. Because of the many ways introduced species can impact ecosystem function, understanding the tradeoffs and establishment conditions of invasive species is vital for determining the resilience of vulnerable ecosystems against invasives.

In plant communities, invasive species can have detrimental effects on the native flora, either directly via competition, or indirectly by altering soil chemistry [6], nutrient cycling [7], or community assembly [8]. The mechanisms of plant invasion largely involve two major hypotheses: one based on the invasive ability of the exotic species [9–12], and another based on the invasibility of the habitat [13,14]. Based on succession theory, most

invasive species of forests are pioneers that can only survive in specific early successional stages (likewise for native pioneer species). Pioneer species are heliophilous plants that are generally characterized by rapid growth, shade-intolerance, fast reproductive cycles, and short lifespans (REFS). However, the development of the post-invasion community, especially during subsequent succession in tropical forests, remains largely unknown because of a lack of long-term monitoring of the communities affected by invasive plants [13–15].

Globally, there are approximately 289 invasive pioneer species documented to occur in the tropics and subtropics [16–19]. In general, tropical forests tend to be far less affected by invasive plant species than other forest types [20,21]. Complex forest communities and high connectivity, such as tropical forests, can resist invasion by exotic species through niche occupation and local adaptation [22–25]. Invasive species are often able to encroach on secondary habitats (e.g., abandoned fields and roadsides), secondary forests and forest gaps [26,27], and they could be well integrated in the local spatial-phylogenetic landscape [28], but few are able to establish within mature forest stands, suggesting that environmental barriers prevent their establishment there [29]. The seeds of exotic plants can reach the forest interior and remain in the soil seed bank, but subsequent germination and seedling growth are limited by environmental factors such as light availability [30,31].

The species richness and abundance of invasive species, both in the vegetation and the soil seed bank, generally decreases rapidly with increased distance from the forest edge [32]. However, the influence of edge effects on plant invasions may be confounded by other factors, such as disturbance, propagule source, physical barriers, and light intensity [29,33]. For example, invasive species can potentially colonize forest interiors following disturbance events [19], suggesting that the presence of invasive species in forest interiors could be limited by the process of forest succession [26]. Therefore, studies focusing on the distribution and abundance of invasive species along the forest succession gradient are necessary to ascertain the ecological limitations of plant invasions.

In 2012, the Chinese Ministry of Agriculture identified 20 invasive plant species as 'malignant' (That is, species that have caused huge losses and serious impacts on the economy or the ecological environment at the national level, and the invasion range exceeds more than one natural geographic area), including *Chromolaena odorata, Praxelis clematidea, Mimosa pudica, Parthenium hysterophorus, Mikania micrantha, Eichhornia crassipes, Pseudosorghum fasciculare, Sphagneticola trilobata, Conyza sumatrensis, Alternanthera philoxeroides, Lantana camara, Flaveria bidentis, Solanum rostratum, Lactuca serriola, Solidago canadensis, Sicyos angulatus, Ageratina adenophora, Ambrosia artemisiifolia, Cenchrus pauciflorus, Euphorbia dentate* [34]. Among these species, *Mikania micrantha* is an herbaceous vine that can reach the forest canopy and *Eichhornia crassipes* is an aquatic species found in freshwater wetlands. The remaining species are terrestrial invasive herbs and shrubs (TIHS) found in secondary habitats, but generally not in primary tropical rain forests [34].

In this study, we investigated the presence of TIHS in habitats of various successional stages in order to determine the ecological barriers that prevent the establishment of TIHS in tropical rain forests. Our study consisted of three components: (1) a survey of the diversity and distribution of TIHS across 97 plots distributed randomly across Hainan Island, (2) a study on the distribution of TIHS along forest edge gradients, and (3) an experiment to examine the germination and seedling vigor of TIHS under different canopy openness conditions in the forest interior of the Baiwang-lin Nature Reserve in Hainan Island. Specifically, we aimed to answer the following research questions: (1) Are TIHS present in the interior of tropical rain forests? (2) Does distance from the forest edge limit the occurrence of TIHS? (3) Does canopy shading negatively affect the germination rate and seedling vigor of TIHS?

2. Methods

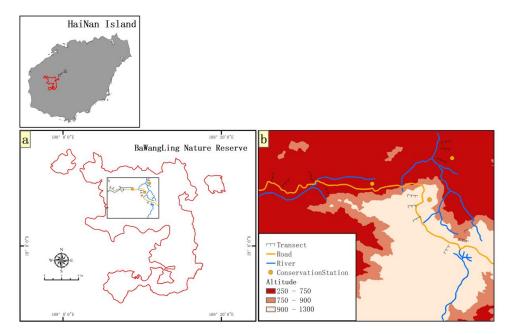### 2.1. Diversity and Distribution of Terrestrial Invasive Herbs and Shrubs in Hainan Island

We surveyed the species diversity and distribution of TIHS in Hainan Island, China, from 2011 to 2014. Hainan Island (33,000 km^2) is located at 18°10′–20°10′ N, 108°37′–111°03′ E. A total of 300 locations were randomly plotted on a map of the island. Of these, 203 turned out to be located inside towns, rural houses, or water bodies, and were discarded. The remaining 97 locations used for further study were located in abandoned fields, grasslands, road sides, plantations, rural vegetation, secondary forests, and old-growth forests. At each location, four 30-m transects were established that ran in North, East, South and West directions from a central point. Along each transect, five 2 × 2 m plots were established at 5-m intervals, resulting in a total of 20 survey plots per location. In each 2 × 2 m plot, the presence, number, and coverage of the following nine TIHS were recorded: *C. odorata*, *P. clematidea*, *M. pudica*, *P. hysterophorus*, *P. fasciculare*, *S. trilobata*, *C. sumatrensis*, *L. camara* and *A. philoxeroides* (Table 1).

Table 1. Study taxa and ecological traits.

Species	Code	Family	Growth Form	Dispersal Mechanism	Native to	Geographical Distribution
Chromolaena odorata (L.) R.M.King & H.Rob.	Co	Asteraceae	Herb	Wind	Americas	South America, Africa and tropical Asia
Praxelis clematidea (G.) R. M. King et H. Rob.	Pc	Asteraceae	Herb	Wind	South America	South America, tropical regions of the Eastern Hemisphere
Mimosa pudica Linn	Mp	Leguminous	Herb or subshrub	Wind	Americas	Tropical regions
Parthenium hysterophorus L.	Ph	Asteraceae	Herb	Wind	Americas	America, Northern Vietnam and Southern China
Pseudosorghum fasciculare (S.) A. Camus	Pf	Gramineae	Herb	Animals, farm tools, running water	Mediterranean	Tropical and subtropical regions from 55° N to 45° S
Sphagneticola trilobata	St	Asteraceae	Herb	Stolon	South America	South America, Southeast Asia and southern China
Alternanthera philoxeroides (M.) Griseb.	Ap	Amaranthaceae	Herb	Stolon	South America	South America, North America, Oceania, Southeast Asia, southern Europe and Africa
Conyza sumatrensis	Cs	Asteraceae	Herb	Wind	South America	Widely distributed in tropical and subtropical regions
Lantana camara L.	Lc	Verbenaceae	shrub	Animals	Americas	Widely distributed in tropical and subtropical regions

2.2. Forest Edge Effects on Distribution and Abundance of Terrestrial Invasive Herbs and Shrubs

During 2014–2015, we surveyed the distribution of TIHS along transects running along the forest edge of tropical rain forest in Baiwang-lin Nature Reserve in Hainan Island (18°52′–19°12′ N, 108°53′–109°20′ E). The Nature Reserve has a circumference road (3–6 m wide) of 26 km and covers an altitudinal range of 250 m to 1265 m. Baiwang-lin Nature Reserve consists of four forest types: rubber plantation, lowland tropical rain forest (low elevation, no clear dominant tree species), hillside tropical rain forest (intermediate to high elevation, dominant species *Dacrydium pierrei*), and tropical coniferous forest (intermediate to high elevation, dominated by *Pinus latteri*). We established 13 transects of 250 m length, spaced a minimum of 1 km apart, along forest edges, covering all three natural forest types (i.e., excluding the rubber plantations) (Figure 1). Along each transect we established three belt transects (2 m × 20 m) starting at and perpendicular to the forest edge. Each belt was subdivided into four quadrats (2 m × 5 m) at a distance of 0–5, 5–10, 10–15, 15–20 m from the forest edge. In each quadrat, the presence and abundance of TIHS were recorded, as well as environmental data such as elevation (measured with GPS), distance from forest edge, forest type, and canopy cover (arcsine-transformed). The canopy cover of the quadrat was estimated using a concave spherical crown densiometer (Lemmon, Bartesville, OR, USA). Readings were taken at approximately 1.5 m above ground as the percent cover in the center of the quadrat. While this method of canopy cover estimation can suffer from bias [35],

we were mainly interested in an index of relative canopy cover that could be compared between quadrats within this study. A two-sided Pearson correlation test was performed between the species richness and density of TIHS, and each environmental factor.

Figure 1. Location of soil sampling transects in Baiwang-lin Nature Reserve, Hainan Island, China. (**a**): Baiwang-lin Nature Reserve; (**b**): soil sample transects (dotted lines). The range in altitude of transects is 250–900 m. 13 transects of 250 m length were established, and along each transect there are three belt transects (2 m × 20 m) starting at and perpendicular to the forest edge.

2.3. Forest Edge Effects on Soil Seed Bank of Terrestrial Invasive Herbs and Shrubs

In each belt transect, five soil samples (volume = 20 × 20 × 10 cm) were taken at 0 m, 5 m, 10 m, 15 m, and 20 m from the forest edge, resulting in a total of 195 soil samples for all transects combined. Each soil sample was then placed in a 30 × 40 × 10 cm plastic frame for germination under full sun light in the greenhouse at Hainan University. Moisture of the soil samples was maintained and seed contamination was prevented by covering the trays with a fine sieve mesh. The number of species emerging was monitored daily and seedlings were removed from the tray once identified. The germination experiment lasted from 11 April to 11 June 2014 (60 days), after which date no new seedlings were recorded. The accumulated frequency of TIHS in the soil seed bank was calculated for each distance class as the number of soil samples with germinated seedlings/total number of soil samples. Seed density was calculated as the number of germinated plants per m^2.

2.4. Seed Germination of Terrestrial Invasive Herbs and Shrubs in Forest Gaps

During 2014–2015, we tested the seed germination rate in three forest gaps (I, II, and III, Table 2) in the hillside tropical rain forest at the Baiwang-lin Nature Reserve in Hainan Island. The seeds of *C. odorata*, *P. clematidea*, *Mimosa diplotricha* and *L. camara* were collected in Bawang-ling, Hainan. In each gap, a total of five seedling plots (1 m × 1 m) were set up: one in the center of the gap, two at the edge of the gap, and two in the understory next to the forest gap. Each seedling plot contained four plastic circular frames (radius = 10 cm, depth = 3 cm). Each frame was filled with local forest soil and filled with 50 seeds of each of the four TIHS species. Frames were watered regularly to avoid drying up of the soil. We recorded seed germination in the frames daily after sowing and continued monitoring the frames for 60 days.

Table 2. The three study forest gaps in Baiwang-lin of Hainan, China.

Forest Gap	Coordinate Point		Altitude
I	19°05′46.6″ E, 109°10′35″ N	17.5 × 16.0 m	1002 m
II	19°05′50.6″ E, 109°10′25″ N	14.5 × 15.0 m	1092 m
III	19°05′27.3″ E, 109°10′56″ N	12.6 × 13.3 m	1014 m

2.5. Statistical Analyses

To test if TIHS are present in the interior of tropical rain forests (Q1), we calculated the incidence of nine species of terrestrial invasive herbs or shrubs in different vegetation types on Hainan Island.

To test if distance from the forest edge limits the occurrence of TIHS (Q2), a two-sided Pearson correlation test was performed between the species richness and density of TIHS, and each environmental factor.

To test if canopy shading negatively affected the germination rate and seedling vigor of TIHS (Q3), we ran bivariate correlation analyses and distance correlation analyses using SPSS 19.0 (REF).

The Poisson generalized linear models (GLM) and negative binomial models (NBM) were used to analyze the influence of canopy rate and altitude on exotic plants (Table 3).

Table 3. The response variables included in the GLM models *.

Response Variable	Model Type	Forest Type	Dispersed Distance	Altitude	Canopy	Seed Mass	Seed Production
Canopy cover	Linear	+	+	+			
Pooled species richness	Poisson	+	+	+	+		
Pooled abundance	NegBin.	+	+	+	+	+	+
Dispersed distance	Linear	+		+	+	+	+
Presence in the soil seed bank	NegBin.	+	+	+	+		

* The model type (error distribution) and fixed effects considered for each response variable are shown ('+'); 'NegBin' denotes negative binomial.

3. Results

3.1. Species Diversity and Distribution of Terrestrial Invasive Herbs and Shrubs in Hainan Island

Across all 97 sample sites, the nine study species were detected in all habitat types except for the tropical rain forest interior (Table 4). Several TIHS were found in all non-rain forest habitats (e.g., Co, Cs and Lc) and others were found in fewer habitats (e.g., Ap, Pf, and Ph).

Table 4. Incidence of nine species of terrestrial invasive herbs or shrubs in different vegetation types in Hainan Island, China. For species codes, see Table 1 (+ = present, 0 = absent).

Habitat (N)	Ap	Co	Cs	Lc	Mp	Pc	Pf	Ph	St	Species Per Site (Mean ± Stdev)
Abandoned field (17)	+	+	+	+	+	+	+	+	+	4.6 ± 1.3
Plantation (20)	0	+	+	+	+	+	0	0	+	4.2 ± 1.0
Rural (14)	+	+	+	+	+	+	+	+	+	3.9 ±0.8
Grassland (11)	+	+	+	+	+	+	0	0	+	3.4 ± 0.9
Field (14)	+	+	+	+	+	+	+	+	+	3.6 ± 0.8
Forest edge (11)	0	+	+	+	+	+	0	0	+	2.7 ± 1.3
Rain forest (10)	0	0	0	0	0	0	0	0	0	0.0 ± 0.0

Of all invaded vegetation types, shrub land and forest edges had the lowest frequency of TIHS occurrence, while (abandoned) fields had the highest frequency (Table 5).
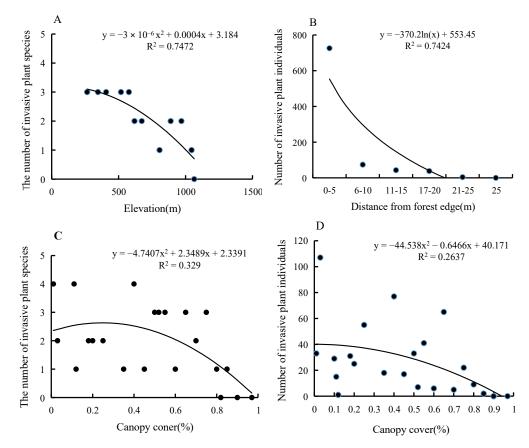
Table 5. Comparison of terrestrial invasive herbs and shrubs frequencies (TIHS/site) among invaded vegetation types (mean ± SE) *.

TIHS	Frequency of Terrestrial Invasive Herbs and Shrubs					
	AF (17)	PL (20)	RV (14)	SE (11)	FI (14)	GR (11)
Pc	0.700 ± 0.500 [a]	0.946 ± 0.472 [a]	0.485 ± 0.298 [b]	0.556 ± 0.529 [b,c]	0.790 ± 0.451 [b,c]	0.685 ± 0.218 [b]
Mp	0.502 ± 0.407 [a]	0.331 ± 0.357 [a]	0.274 ± 0.351 [a,b]	0.204 ± 0.430 [a]	0.592 ± 0.455 [c]	0.474 ± 0.250 [a,b]
Co	0.749 ± 0.493 [a]	0.701 ± 0.465 [a]	0.628 ± 0.326 [a]	0.556 ± 0.529 [a]	0.733 ± 0.459 [a]	0.771 ± 0.226 [a]
Cs	0.273 ± 0.431 [a]	0.339 ± 0.443 [a]	0.291 ± 0.394 [a]	0.186 ± 0.347 [a]	0.355 ± 0.527 [a]	0.191 ± 0.094 [a]
PF	0.118 ± 0.223 [a]	-	0.112 ± 0.185 [a]	-	0.051 ± 0.125 [a]	-
Lc	0.118 ± 0.311 [a]	0.025 ± 0.092 [a]	0.112 ± 0.185 [a]	0.099 ± 0.188 [a]	0.051 ± 0.125 [a]	0.092 ± 0.137 [a]
Ap	0.126 ± 0.211 [a]	0.022 ± 0.115 [a]	0.032 ± 0.105 [a]	-	0.091 ± 0.114 [a]	0.052 ± 0.137 [a]
St	0.126 ± 0.391 [a]	0.226 ± 0.173 [b]	0.029 ± 0.140 [a]	0.050 ± 0.169 [a]	0.179 ± 0.397 [a]	0.129 ± 0.140 [a]
Ph	0.085 ± 0.121 [a]	0.015 ± 0.002 [a]	0.112 ± 0.105 [a]	-	0.051 ± 0.125 [a]	0.092 ± 0.037 [a]
AFTIHS **	2.806	2.605	2.075	1.651	2.893	2.486

* Different lowercase letters indicate significant differences between invaded vegetation types ($p < 0.05$). ** AFTIHS: Accumulated frequency of invasive plants. AF: abandoned field, PL: plantation, RV: rural vegetation, SE: shurb and edge of tropical forest, FI: field, GR: grassland. Ap: *A. philoxeroides*, Co: *C. odorata*, Cs: *C. sumatrensis*, Lc: *L. camara*, Mp: *M. pudica*, Pc: *P. clematidea*, PF: *P. fasciculare*, Ph: *P. hysterophorus* and St: *S. trilobata*.
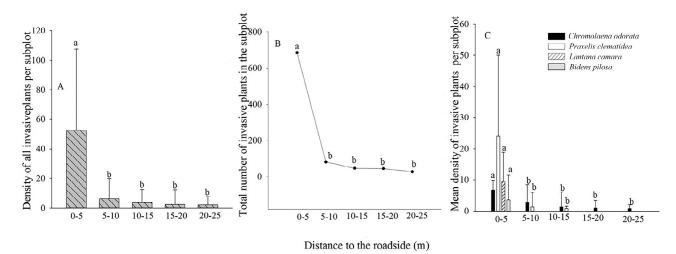
3.2. Forest Edge Effects on Terrestrial Invasive Herbs or Shrubs

Elevation and canopy cover had a significant negative correlation with TIHS species numbers (Figure 2A,C). In addition, distance to forest edge and canopy closure had a significant negative correlation with TIHS abundance (Figure 2B,D).

Figure 2. The relationship between the distribution characters and environmental factors. (**A**). The relationship between the number of invasive plant species and elevation; (**B**). The relationship between the number of invasive plant individuals and distance from forest edge; (**C**). The relationship between the number of invasive plant species and canopy coner; (**D**). The relationship between the number of invasive plant individuals and canopy cover.

Most TIHS individuals were found in sites 0–5 m from the forest edge, some at 5–10 m, and only a few at 10–15 m, 15–20 m, or 20–25 m (Figure 3A–C).
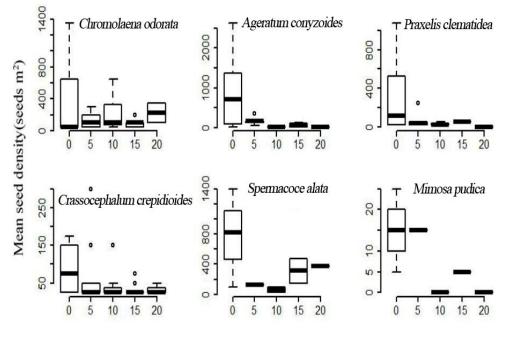
Figure 3. Abundance of terrestrial invasive herbs and shrubs in relation to distance from forest edge. (**A**). Density of invasive plants at different distances from forest edge; (**B**). The number of invasive plants at different distances from forest edge; (**C**). The density of four invasive plants at different distances from forest edge. Different lowercase letters indicate significant differences ($p < 0.05$).

A total of 57,138 individual seedlings from 72 plant species were germinated from the 195 soil samples collected from the Baiwang-lin Nature Reserve, among which 1545 seedlings of 12 TIHS were observed (2.7% of all seedlings). The 12 TIHS were *P. clematidea*, *C. odorata*, *L. camara*, *M. pudica*, *M. repens*, *M. diplotricha*, *Crassocephalum crepidioides*, *Tridax procumbens*, *Bidens pilosa*, *Spermacoce alata*, *Ageratum conyzoides*, and *Stachytarpheta jamaicensis*. Among these species, *P. clematidea*, *C. odorata*, *L. camara*, and *M. pudica* are classified as malignant TIHS in China (REF). The seed germination density of these TIHS ranged from 25 to 7000 seeds m^{-2} (Table 6). Seed density of the TIHS in the soil seed bank decreased rapidly with distance from the forest edge into the forest interior (Figure 4).
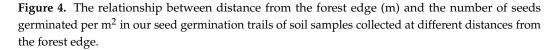
The best-supported model explaining the canopy cover included a significant effect of altitude (LRT: χ^2 = 27.234, df = 1, $p < 0.001$) and the distance from the forest edges (χ^2 = 6.1831, df = 1, $p = 0.129$) (Table 7). The canopy cover increased significantly as the distance from edge and altitude increased. The second best-supported model had similar AIC to the first model and also included the forest type, though the significance was marginal (χ^2 = 5.87, df = 3, $p = 0.08$). Low-stature forests generally had lower canopy cover than other forest types. Transects in higher areas in the study site usually had a more dense canopy cover (estimate of difference in higher altitude effect for the surveyed transects = 0.551; 95% confidence interval = 0.329, 0.774).

Table 6. Germination results of the terrestrial invasive herbs and shrubs seeds in the soil seed banks of tropical forest edges.

Species	Frequency (Presence/Soil Sample)	Furthest Distance Observed (m)	Range (Seedlings m^{-2})	Density (Seedlings m^{-2})	Total Germinated Seedlings of TIHS	Proportion of All Germinated Seedlings (57,138) (%)
A. conyzoides	0.138	20	25–625	501.9 ± 697.0	542	0.95
P. clematidea	0.159	20	25–7000	192.5 ± 267.0	511	0.89
B. latifolia	0.041	20	25–1400	387.5 ± 483.8	143	0.25
C. odorata	0.149	20	25–2900	104.5 ± 139.0	117	0.2
R. repen	0.015	0	225–1375	783.3 ± 575.0	94	0.16
C. crepidioide	0.185	20	25–300	54.9 ± 59.7	79	0.14
M. diplotricha	0.015	10	25–275	166.5 ± 128.0	20	0.04
M. pudica	0.036	15	25–125	67.9 ± 37.4	19	0.03
S. jamaicensis	0.010	20	25–175	100.0 ± 106.1	8	0.01
B. pilosa	0.015	15	25–75	41.6 ± 28.8	5	0.01
L. camara	0.021	0	25	25.0	4	0.01
T. procumbens	0.015	10	25	25.0	3	0.01
Total					1545	2.7

Figure 4. The relationship between distance from the forest edge (m) and the number of seeds germinated per m² in our seed germination trails of soil samples collected at different distances from the forest edge.
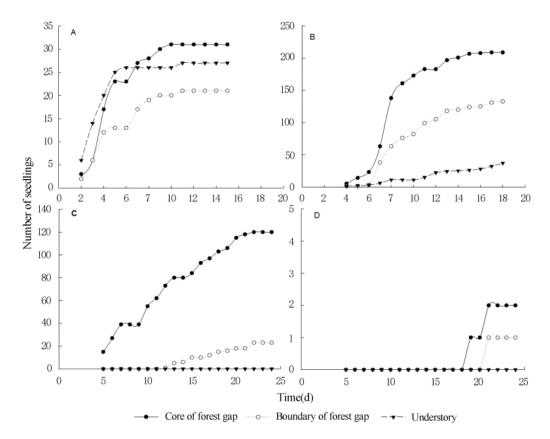
Table 7. The best-supported models explaining (A) the pooled species richness of exotic species and (B) the pooled abundance of exotic species (C) the presence of exotic plants in the soil seed bank. Parameter estimates and their standard errors are shown, as are standard deviations of model random effects.

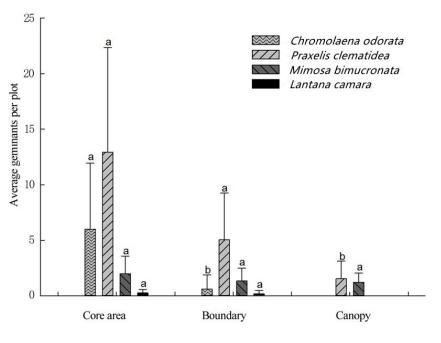| Effects	Parameter	Estimate (±1 SE)
(A) Pooled species richness of exotic species ~ Distance from edge + Canopy	Intercept	1.114 (0.212)
	Distance from the edge	−0.780 (0.383)
	Canopy cover	−0.796 (0.453)
(B) Pooled abundance of exotic seeds ~Distance from edge + Canopy cover + seed mass	Intercept	3.455 (0.302)
	Distance from the edge	−4.291 (0.650)
	seed mass	−2.151 (0.715)
	Canopy cover	−0.526 (0.361)
(C) Presence of exotic plants in the soil seed bank ~Distance from edge + Canopy cover	Intercept	6.910 (2.867)
	Distance from the edge	−2.627 (0.741)
	Canopy cover	0.265 (0.820)

For the pooled abundance of alien plants in the soil seed bank, the best-fitting model according to Akaike weights retained the significant effects of the distance from the edge ($\chi^2 = 46.81$, df = 1, $p < 0.001$), and the seed mass of the alien plants ($\chi^2 = 8.682$, df = 1, $p = 0.003$; Table 4), as well as a weak effect of canopy cover ($\chi^2 = 1.802$, df = 1, $p = 0.179$), while the second best model had similar AIC values to the first model and included the influence of altitude besides canopy cover and distance from edge (Table 7). For all the surveyed forests, the pooled abundance of alien species declined markedly with increasing distance from the edge. The seed traits of the exotic plants significantly affected their abundance in the soil seed bank. Light-seeded species were more abundant compared with the large-seeded species. We also found that species with lower seed mass usually have a higher chance of occurrence in the soil seed banks. This may suggest a biological barrier for the large-seeded exotic species to penetrate into the forest interior.

3.3. Seed Germination and Seedling Survival of Terrestrial Invasive Herbs and Shrubs in Forest Gaps

The average germination rate of TIHS was very low, being only 12.1%, 5.9%, and 2.1% in the gap core area (CA), boundary of forest gap (EA), and understory near the forest gap (UA), respectively. The germination rates for all TIHS were higher in the center of the gaps, lower at the edge of the gap, and even lower at the forest interior (Table 4, Figures 5 and 6), except for *M. diplotricha*. The seed germination of *M. diplotricha* occurred within 2 to 10 days after sowing, with 31, 21, and 27 seedlings in CA, EA, and UA, respectively. The seed germination of *P. clematidea* occurred within 5 to 15 days after sowing, with 209, 133, and 37 seedlings in CA, EA, and UA, respectively. The seed germination of *C. odorata* occurred within 6 to 25 days after sowing, with 120, 23, and no seedlings in CA, EA, and UA, respectively. The seed germination of *L. camara* occurred within 20 to 30 days after sowing, with two, one, and no seedling(s) in CA, EA, and UA, respectively. All seedlings died within a year.

Figure 5. The germination rates of four species of terrestrial invasive herbs and shrubs in different locations of the forest gap ((**A**): *M. diplotricha*, (**B**): *P. clematidea*, (**C**): *C. odorata*, (**D**): *L. camara*).

Figure 6. Comparison of mean germinants per plot of four species of terrestrial invasive herbs and shrubs in three different positions in the forest gap. Different lowercase letters indicate significant differences ($p < 0.05$).

4. Discussion

Most of the 289 globally recognized invasive species are heliophilous plants with a preference for early successional vegetation [16]. In China, approximately 100 invasive species are known to be heliophilous plants [17]. From a classical forest succession perspective, plants are usually adapted to specific successional stages, i.e., heliophilous pioneer species will generally be replaced by mid- or late-successional species as succession progresses [36,37]. Pioneer species, both invasive and native, occur at early forest successional stages and may occupy a broad range of novel habitats [38]. The presence of these species is limited in mature forests, as they are usually replaced by other species during succession. However, some shade-tolerant invasive species are found in both disturbed and undisturbed habitats. For example, *Microstegium vimineum*, an exotic annual grass, is highly shade tolerant and found in both open and shady forest [16]. Nevertheless, our results from the randomly assigned survey sites across Hainan Island found no evidence of TIHS in forest interiors, indicating that none of the invasive species presently occurring in Hainan has been able to adapt to late-successional forest. Similar patterns were found for other studies conducted in tropical lowland forests [32].

The absence of TIHS from mature forest has been attributed to the presence of functionally diverse plant communities that are locally adapted and have a strong resistance towards biological invasion [24,39,40]. However, our results indicate that light conditions may be the main factor responsible for the absence of invasives in intact forest understories. Almost all our study species were found near forest edges where light conditions were favorable for them. Additionally, most invasives only managed to establish and maintain themselves under high-light conditions. Even species that did germinate in low-light conditions, did not survive for long unless there was enough light available (such as forest edges and in forest gaps). Therefore, the present set of exotic species in Hainan are unlikely to penetrate into tropical forest interiors. The depth that exotics were able to penetrate into tropical forest edges was associated with forest identity on Hainan, with exotic species concentrated within 5 m of the forest edge in mountain rain forest edges, but up to 15–25 m depth in rubber plantations.

The distribution survey and the germination study both further showed that TIHS grew rampantly in secondary habitats such as abandoned fields and roadsides, less so at forest edges, but were almost completely absent in forests interiors (>20 m from edges into forest). It was evident from our findings that TIHS were excluded from forest interior through low seed germination resulting from high canopy cover. The seed germination rate and seedling vigor of invasive species could be limited by weak light intensity [27,30,31]. Even though moderate germination was observed in our study for some invasive species, all the seedlings eventually died. Therefore, it is essential to consider the relationship between invasive species and forest succession stages when evaluating the environmental destruction of invasive plants.

5. Conclusions

In this study, we demonstrated that in Hainan Island, China, terrestrial invasive herbs and shrubs are widespread pioneer plants but are restricted to gaps in forest habitats. The TIHS mostly colonized and thrived in disturbed environments and their expansion was restricted by forest canopy cover. During forest succession, TIHS are likely replaced by native mid- to late-successional species, further limiting their growth in the understory of tropical rain forests. Thus, TIHS are likely not an immediate threat to the native species of the intact interiors of most tropical rain forests.

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