Main drivers of plant diversity patterns of rubber plantations in the Greater Mekong Sub-region

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Running headline: Drivers of plant diversity of rubber plantations

Abstract:

The Greater Mekong Sub-region (GMS) is one the global biodiversity hotspots. However, the diversity has been seriously threatened due to environmental degradation and deforestation, especially by expansion of rubber plantations. Yet, little is known about the impact of expansion of rubber plantations on regional plant diversity as well as the drivers for plant diversity of rubber plantation in this region. In this study, we analyzed plant diversity patterns of rubber plantations in the GMS based on a ground survey of a large number of samples. We found that diversity varied across countries due to varying agricultural intensities. Laos had the highest diversity, then followed China, Myanmar, Cambodia. Plant species richness of Laos was about 1.5 times that of Vietnam. We uncovered latitudinal gradients in plant diversity across these artificial forests of rubber plantations and these gradients caused by environmental variables such as temperature. Results of RDA, multiple regression as well as random forests demonstrated that latitude and temperature were the two most important drivers for the composition and diversity of rubber plantations in GMS. Meanwhile, we also found that higher dominance of some exotic species (such as *Chromolaena odorata* and *Mimosa pudica*) were associated with a loss of plant diversity within rubber plantations, however, not all exotic plants cause the loss of plant diversity in rubber plantations. In conclusion, not only environmental factors (temperature), but also exotic species were the main factors affecting plant diversity of these artificial stands. Much more effort should be made to balance agricultural production with conservation goals in this region, particularly to minimize the diversity loss in Vietnam and Cambodia.

Keywords: Rubber plantation, Plant diversity, Exotic species, Mekong regions, Greater

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Mekong Sub-regions (GMS)

1. Introduction

Many tropical regions contain hotspots of biodiversity (Myers et al., 2000), especially for the Great Mekong Sub-region (GMS), threatened by agriculture (Delzeit et al., 2017; Egli et al., 2018; Shackelford et al., 2014; Kehoe et al., 2017). Much of the land has recently been converted from forest to agriculture (Li et al., 2007), and rubber plantations have quickly expanded throughout the region (Ziegler et al., 2009; Li et al., 2015; Ahrends et al., 2015) due to a surge in the global demand for natural rubber, driven largely by the growth of tire and automobile industries. For example, 23.5% of Cambodia's forest cover was destroyed between 2001 and 2015 make way for crops such as rubber (Figure S1h) and palm oil (Grogan et al., 2019). In southwest China, nearly 10% of the total area of nature reserves had been converted to rubber monoculture by 2010 (Chen et al., 2016). At present, GMS are globally important rubber-planting regions (Xiao et al., 2021).

Agricultural land-uses can exacerbate many infectious diseases in Southeast Asia (Shah et al., 2019) and reduce biodiversity (Xu, 2011; Warren-Thomas et al., 2018; Fitzherbert et al., 2018; Zabel et al., 2019; Singh et al., 2019). Previous study showed that rubber cultivation not only affect plant diversity (Hu et al., 2016), but also affects the soil fauna (Chaudhuri et al., 2013; Xiao et al., 2014), bird diversity (Aratrakorn et al., 2006; Li et al., 2013) as well as bat diversity (Phommexay et al., 2011). There is also a large body of literature on the effects of forest conversion from tropical forest to rubber plantations on soil microbial composition and diversity (Tripathi et al., 2012; Schneider et al., 2015; Kerfahi et al., 2016, Lan et al., 2017a; 2017b; 2017c; Cai et al., 2018; Lan et al., 2020a; 2020b; 2020c). However, the impact

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of expansion of rubber plantations on regional plant diversity as well as the drivers for plant diversity of rubber plantation in GMS are still unclear.

Latitudinal gradients in species diversity are well known (Mccoy and Connor, 1980), which holds that there is a fairly regular increase in the numbers of species of some higher taxon from the poles to the equator. It has been suggested that the latitudinal diversity gradient could be caused by environmental variables such as temperature and precipitation. Previous study also demonstrated temperature (Nottingham et al., 2018) and soil nutrients (Soons et al., 2017) as well as water resource utilization efficiency (Han et al., 2020), were the dominant drivers of plant diversity. However, whether latitudinal gradients in species-diversity exists in rubber plantation which is greatly affected by management measures, is still unknown. In addition, rubber plantations have lower biodiversity than natural forests (Chaudhary et al., 2016). Generally speaking, species rich zones showed a higher proportion of alien plant species in their flora (Stadler et al., 2000), thus exotic plants are ubiquitous in rubber plantations which in indicating that. Though exotic species invasion significantly decreased plant diversity (Xu et al., 2022) is universally known, we still do not have idea that whether exotic species are the main driver for the sharp decline of plant diversity in rubber plantation. Thus, we hypothesize that (1) latitudinal gradients in plant diversity would not exit in rubber plantation due to strong intensity of management; (2) exotic plants will result in a sharp decline in the plant diversity of rubber plantation because areas of low plant species richness may be invaded more easily than areas of high plant species richness (Stohlgren et al., 1999) and exotic species may results in loss of plant diversity (Xu et al., 2022). To testify these hypothesis, we surveyed a large number of plots on rubber plantations in the GMS to

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investigate plant diversity and analyzed the associated drivers. Our study provides an empirical case for understanding the effect of rubber plantations on plant diversity in the Greater Mekong region and the restoration and protection of biodiversity in this region.

2. Methods

2.1 Study area

The Mekong River Basin has a total length of 4880 km and a drainage area of 795000 square kilometers, with 326 million people living in the basin. The GMS encompasses a variety of climate types and geographical characteristics, and is rich in water and biological resources (Wu et al., 2020). Rubber plantations are one of the most widespread vegetation types in the region, and are distributed throughout the south of Yunnan province, almost all states of Thailand and Laos, the southern half of Vietnam and Myanmar, and the eastern half of Cambodia.

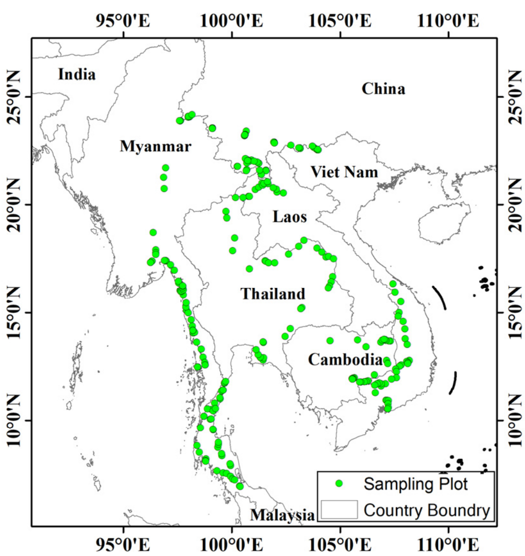

Figure 1 Sampling plot localities within rubber plantations in GMS

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2.2 Sampling methods

Before the field investigation, we first determined the investigation route according to the distribution of rubber plantation in this regions. Then, plots were randomly selected approximately equidistant from each other (every 10-20 km according to the actual situation) along the investigation route (Yaseen, 2013). We did not deliberately select plots according types of rubber plantation, thus these plots were independent from each other. Consequently, a total of 240 plots, each with an area of 100 m^2 (10 m × 10 m), were selected in the GMS, with 32 plots in Vietnam, 24 in Cambodia, 15 in Laos, 73 in Thailand, 47 in Myanmar, and 49 in China (Figure 1). We started the investigation only after the guide (local people) asked the farmer's consent. Plot measurements, such as longitude, latitude, elevation, slope degree, slope aspect, rubber tree height, and canopy density were recorded in detail (Table S1). Annual and perennial plant species, shrubs, trees and lianas as well as theirs seedlings were recorded. We do not investigate bryophytes, but ferns were investigated. Species information, such as species name, height and coverage, life form (non-woody, shrub, liana or tree) (Lan et al., 2014), from each plot in the rubber plantations were also recorded. We visually assigned a cover value to each species in each quadrant of the plot, using an ordinal cover class scale with class limits 0.5%, 1%, 2%, 5%, 10%, 15%, 20%, and thereafter every 10% up to 100%. The cover values for each species in the plot were then averaged across the four quadrants (Sabatini et al., 2016). Climate data, including annual average temperature and annual average precipitation, were obtained from WorldClim (http://worldclim.org) based on the geographic coordinates of each sample site.

2.3 Data analysis

Relative height (*RH*), relative dominance (*RD*, using coverage), and relative frequency (*RF*) were calculated for each species to estimate the importance value (*IV*). Importance value, as defined here, differs from previous studies (e.g., Curtis and Mcintosh 1950, 1951; Greig-Smith 1983; Linares-Palomino and Alvarez 2005) because most understory species are herbs, which make precise measure of abundance difficult. We define the importance value as:

Importance value: $IV_j = RF_j + RH_j + RD_j$, Relative frequency: $RF_j = 100 \times F_j / \sum_j F_j$

Relative height: $RH_j = 100 \times H_j / \sum_j H_j$, Relative dominance: $RD_j = 100 \times D_j / \sum_j D_j$

where F_j was the number of plots containing species *j*; D_j was the coverage of species *j*; and H_j was the height of species *j*. For local community, there was no frequency data, therefore importance value is defined as: $IV_j = RH_j + RD_j$.

Species richness, the Shannon index were used to measure α diversity of each plot. It should be noted that the importance values of each species were used to calculate the Shannon diversity (i.e., replace "abundance" or "number of individuals" with "important value"). Principal coordinates analysis (PCoA) based on Bray–Curtis distance of species IVs (importance values) was performed to compare plant species composition across countries using R package "amplicon". Analysis of similarity (ANOSIM) was used to test for differences in diversity indices among countries. Multiple linear regression was used to find whether there were positive or negative correlations between diversity (richness) and environmental variables including latitude, longitude, elevation, rainfall, temperature, slope degree, tree age, tree height as well as canopy density. Machine learning algorithm, Random forests, was used to model α diversity (richness) and rank the feature importance of

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where *S* is the total species richness of all samples and m。is the mean species richness of these samples.

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environmental factors with 999 iterations. In order to understand how plant compositions are structured by environmental factors, a redundancy analysis (RDA) for the importance value of species was carried out using the Vegan package in R environment. Statistical significance was assessed using Monte Carlo tests with 999 permutations.

3 Results

3.1 Plant composition of rubber plantations

A total of 949 plant species, representing 550 genera and 153 families, were recorded across rubber plantations of the six countries (Table 1 &Table S2). Our results also showed that 445 (46.89%) were herbs, with a largest number of Compositae (Table 1). Plant communities of rubber plantation tended to be dominated by Fabaceae, Euphorbiaceae, Poaceae, Rubiaceae, and Compositae (Table S3). The five most common species observed were *Cyrtococcum patens, Chromolaena odorata, Asystasia chelonoides, Axonopus compressus,* and *M. pudica* (Table S4). 237 plots containing exotic plant species, most of them were from tropical America. A total of 121 (12.75%) species were identified as exotic (belonging to 45 families and 91 genera). The five most common exotic species were *C. odorata*, *M. pudica*, *Axonopus compressus*, *Ageratum conyzoides*, and *Borreria latifolia*. *C. odorata* and *M. pudica* were recorded in almost every plot (Figure 2).

PCoA and ANOSIM were used to reveal the difference in plant compositions among these six countries. And the results showed that significant differences (R = 0.383, P = 0.001) in species composition among these countries (Figure 3a-b). Meanwhile, the first and second axes of RDA explained 5.95% and 3.11% of variation of species compositions, respectively (Figure 4a). All environmental factors explained 18.65% of the total variation (Figure 4b). Countries,

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删除的内容: There are 597 species of medicinal plants, 163 species of edible plants, 220 species of economic plants, 64 species of forage plants, 158 species of ornamental plants, 62 species of ecological plants, and 170 species of unidentified uses under rubber plantation in GMS (Table S3).

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latitude, longitude, canopy height as well as elevation all significantly impacted plant compositions of rubber plantations in GMS, and explained 5.62%, 3.37%, 3.14%, 1.11% and 1.10% of the total variations (Table 2).

Table 1 Composition of plants of rubber plantations in GMS

Types	No. of	Lifeform (%)	No. of families	No. of genera	No. of species
Ferns	76 (8.00)	Non-woody plant	86（38.05）	278（45.65）	445（46.89）
Gymnosperms	3 (0.32)	Liana	32（14.16）	62（10.18）	101（10.64）
Angiosperm	870 (91.68)	Shrub	42（18.58）	118（19.38）	192（20.23）
		Tree	66（29.20）	151（24.79）	211（22.23）
Total	949 (100)	Total	226（100.00）	609	949

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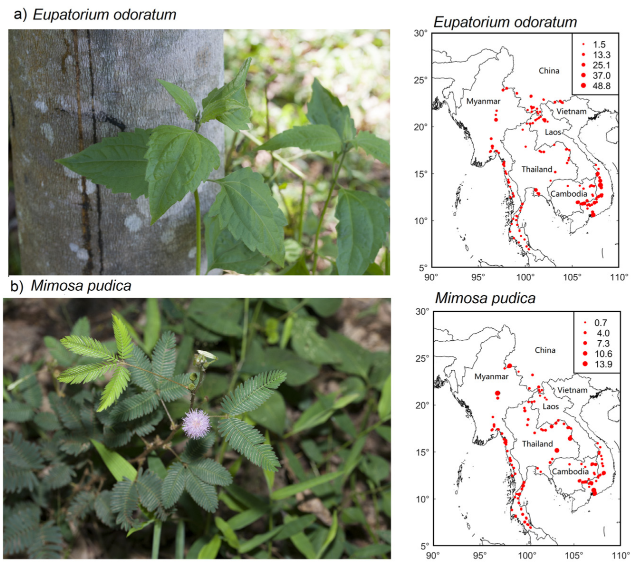

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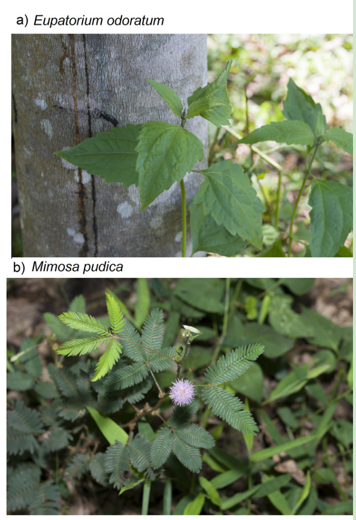

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Figure 2 Distribution maps of two common exotic species (a: *Chromolaena odorata*, b: *Mimosa pudica*) of rubber plantation in the GMS (circle size is proportional to importance value)

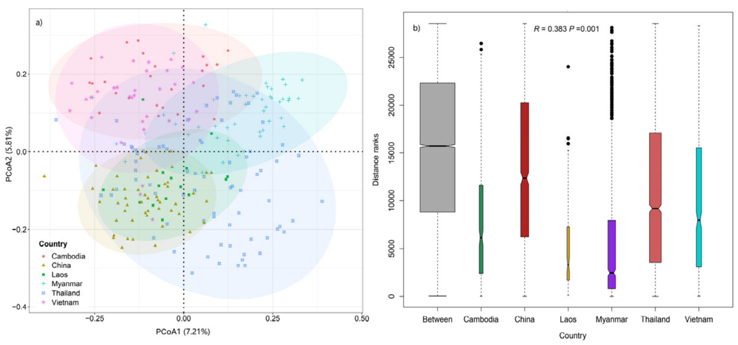

Figure 3 Significant difference in plant community compositions of rubber plantations among countries in GMS. a: Principal coordinate analysis (PCoA) based on Bray-curtis distance; b: Analysis of similarity among countries.

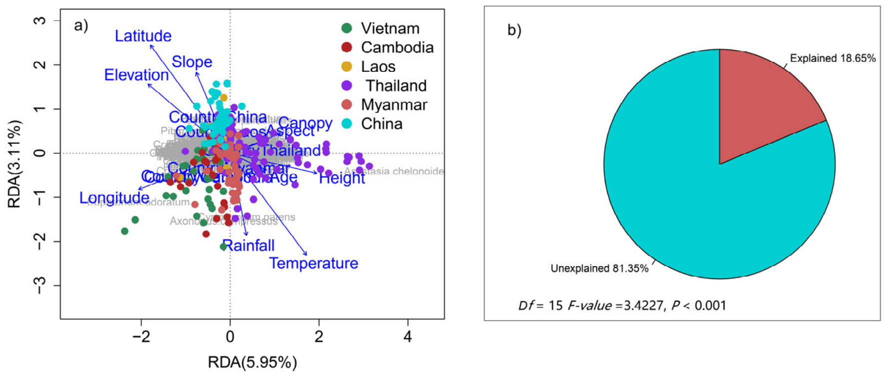

Figure 4 Redundancy analysis of plant community compositions of rubber plantation in the GMS (a: RDA ordination, b: Percentage of explained and unexplained by RDA results)

Table 2 Explained percentage of environmental factors on the variation of plant community compositions of rubber plantations in GMS based on the RDA results

Contents	Df	Variance	Explained (%)	F	Pr (> F)
Country	1	33.18	5.62	3.08	0.007 **

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Latitude	1	19.89	3.37	9.22	0.001 ***
Longitude	1	18.53	3.14	8.59	0.001 ***
Height	1	6.54	1.11	3.03	0.001 ***
Elevation	1	6.50	1.10	3.01	0.001 ***
Age	1	5.54	0.94	2.56	0.001 ***
Slope	1	5.01	0.85	2.32	0.002 ***
Temperature	2	4.63	0.78	2.16	0.005**
Rainfall	2	3.19	0.54	1.49	0.032*
Canopy	1	4.01	0.68	1.86	0.001 ***
Aspect	1	2.97	0.50	1.38	0.073
Residual	224	479.91	82.68		

3.2 Plant diversity of rubber plantations

Species richness of rubber plantations in Laos was the highest among the six countries, followed by China and Myanmar, while the richness of Thailand, Cambodia, and Vietnam were relatively lower (Figure 5a). The same was true for Shannon diversity (Figure 5b).

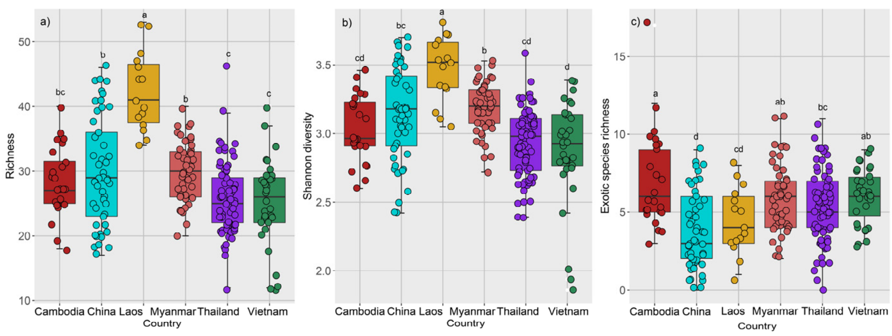

Figure 5 Plant species diversity of rubber plantations across countries in the GMS (a: species richness; b: Shannon diversity; c: Exotic species richness).

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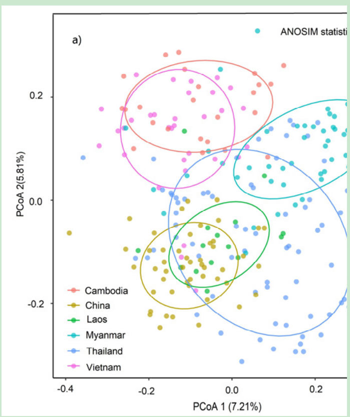

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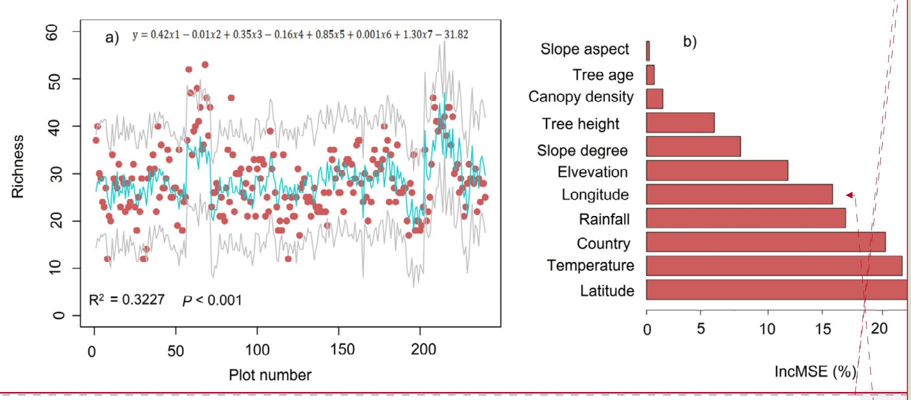

Figure 6 Factors affecting plant diversity of rubber plantation in GMS. a: Predicting species richness by using multiple linear regression (The red point was the observed richness, the green solid line was the estimated richness, and the grey solid line was the 95% confidence interval. y: Richness, $x1$: Latitude, $x2$: Elevation, $x3$: Slope, $x4$: Age, $x5$: Height, $x6$: Rainfall, $x7$: Temperature.) b: Predictions of the importance of environmental variables based on random forests.

The results of multiple linear regression (R^2 = 0.3227, P < 0.001) showed that temperature (P < 0.001), tree height (P < 0.001), latitude (P < 0.01) and slope degree (P < 0.001) were positively correlated with the species richness (Figure 6a). Among these factors, temperature (with the highest intercept 1.3) is the most important factor affecting plant diversity. Random forest results showed that high mean squared errors of latitude, temperature, and countries were the top three features affecting plant diversity of rubber plantation (Figure 6b).

3.3 Effects of exotic species on plant diversity of rubber plantations

The exotic species richness of rubber plantations was relatively higher in Cambodia, Vietnam, and Myanmar compared to China, Laos, and Thailand (Figure 3c). In order to clarify whether

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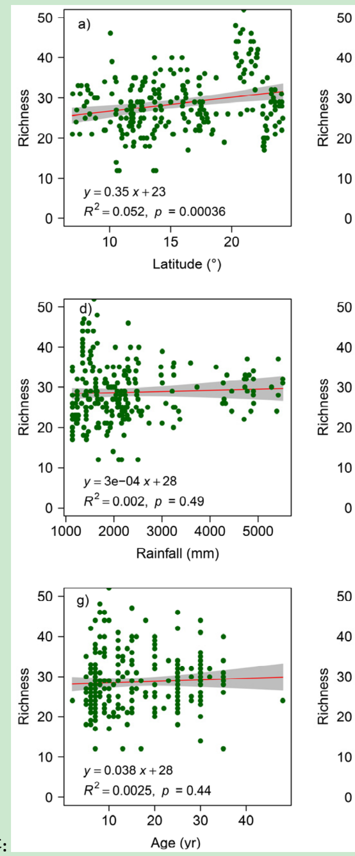

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exotic species can reduce plant diversity, we analyzed the relationship between the dominance of exotic species and the species richness in the plot. In view of the fact that *C. odorata* and *M. pudica* are the two most common exotic species in rubber plantations (Figure 7a) the two species were selected for analysis. The importance values of exotic species *C. odorata* (Figure S2a) and *M. pudica* (Figure S2b) were negatively correlated with species richness, suggesting that exotic species with high dominance will reduced rubber plantation diversity. However, exotic species richness was positively correlated with species richness (Figure 7c). Richness of communities where *C. odorata* (*M. pudica*) was present was not lower than those where it was absent (Figure 7b). In sum, diversity of the community was reduced only when the dominance of exotic species was high.

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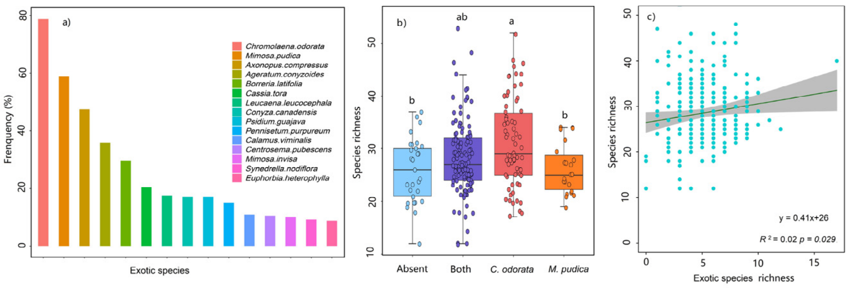

Figure 7 Effects of exotic species on plant diversity of rubber plantations in the GMS (a: Frequency of the most common exotic species; b: Richness comparison of different communities (sky blue bar: plots without *C. odorata* and *M. pudica*; blue bar: plots with both *C. odorata* and *M. pudica*; red bar: plots only with *C. odorata*; yellow bar: plots only with *M. pudica*) c: relationship between exotic species richness of given plot and species richness of given plot)

4. Discussion

4.1 Main drivers for plant composition and diversity of rubber plantations

Rubber plantations constitute one of the most important agro-ecosystems of tropical regions and play an important role in their carbon budgets (Chen et al., 2020). For, plant composition, latitude ranks the second (Table2) in terms of its impact on plant composition which indicating that latitude is an important driver of plant composition of rubber plantation. For plant diversity, both multiple linear regression and random forests showed that temperature was the most important factor for plant diversity of rubber plantations. Our results consistent with previous study which revealed that temperature is the main driver for plant diversity (Nottingham et al., 2018). We were surprised to find that understory plant diversity of artificial rubber plantations increased with latitude, similar to that of the global diversity patterns (Rohde 1992; Perrigo et al., 2013) that latitudinal gradients are known in which maximum diversity does not occur near the equator (Stehli, 1968). One suggest that the diversity of plant communities was directly affected by latitude (Li et al., 2019). Our results showed that elevation was not as important as other factors which is different from our previous cognition that elevation significantly affect plant species diversity (Li et al., 2019). Plant diversity of north Laos and south China was relatively higher than other countries. This observation may be due to the large variation in elevation in these areas, which translates into greater environmental heterogeneity. In addition, greater slope may increase environmental heterogeneity and expand niche space (Morrison-Whittle and Goddard, 2015). Anyway, the latitudinal diversity gradient and temperature, could largely contribute explaining composition and diversity patterns of artificial rubber plantations.

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已下移 [4]: In artificial forests such as rubber plantations, there is no doubt that management measures and agricultural intensity are two most important factors affecting plant diversity. For example, herbicide application causes low diversity of understory plants. This is especially true of rubber plantations of Vietnam (Figure S1f).

删除的内容: Usually, species richness increases with lower latitude. However, we found that species richness increases with higher latitude, peaking at about 25 degrees which was the highest latitude we studied.

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Plant diversity of north Laos and south China was relatively higher than other countries. This observation may be due to ... [20]

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4.2 Not all exotic plants cause the loss of plant diversity in rubber plantations

Rubber plantation expansion and intensification has occurred in many regions that are key for biodiversity conservation. Monoculture plantations have been promoted to restore the world's forested areas, but have done little to slow the loss of biodiversity (Zhang et al., 2021). It has been hypothesized that exotic species might more easily invade areas of low species diversity than areas of high species diversity (Stohlgren et al., 1999). A recent study shows exotic plants account for ~17% and ~35% of the total importance value indices of natural and human-modified ecosystems, respectively (Chandrasekaran et al., 2000). Here, in rubber plantations, exotic plants made up roughly 12% of the total recorded species and 22.80% of the coverage. *C. odorata* is a noxious perennial weed in many parts of the world (Kushwaha et al., 1981), and it is unsurprising that it was recorded in almost all plantation plots in our study. These indicated that invasion by exotic species has either already occurred or is inevitable in many systems (Stohlgren et al., 1999). *M. pudica*, the "sensitive plant", is a worldwide, pan-tropical invasive species (Melkonian et al., 2014). *M. pudica*, as many tropical grasses and herbs, is tolerant of low pH (Humphreys 1997, Paudel 2018), which explains its ubiquity in acidic rubber plantation soil.

More importantly, our study demonstrated that the diversity of the community reduced only when the importance value of exotic species is large enough and not all exotic species cause the loss of plant diversity in rubber plantations, which follow the theory that many species can coexist in spatially heterogeneous areas as long as nutrients and light are not limiting (Huston and DeAngelis, 1994). Our results also were consistent with idea that inhibition of plant diversity by exotic species invasion gradually weakened with increased

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precipitation (Xu et al., 2022) due to higher precipitation in GMS. In addition, management of rubber plantation reduces the dominance of exotic species to a great extent, thus providing space for the survival of other plants.

4.3 Plant composition and diversity is largely affected by of management

Forests that are intensively managed for production purposes generally have lower biodiversity than natural forests (Chaudhary et al., 2016), and this is especially true for rubber plantations (He and Martin, 2016). In artificial forests such as rubber plantations, there is no doubt that management measures and agricultural intensity are two most important factors affecting plant diversity. The application of herbicides and sprout control causes low diversity of understory plants, this is especially true of rubber plantations of Vietnam (Figure S1f). Also, it is not easy for farmers to clear understory plants on the steep slopes of rubber plantations at high elevation; thus high slope degree indirectly results in low agricultural intensity and high diversity. RDA analysis only explained 18.65% of the variation of community compositions, and multiple linear regression only explained 32.27% of the variation of plant diversity. Most of the unexplained variation are caused by management intensity and measures. In sum, plant compositions and diversity is largely affected by the measures and intensity of management.

In poor areas, we cannot just talk about ecological goals without first understanding local cultures and economies. Well-managed forests can alleviate poverty in rural areas, as outlined by the United Nations Sustainable Development Goals (Lewis et al., 2019). Previous study conducted in India demonstrated that a no-weeding practice in mature rubber plantations did not affect rubber yield (Abraham and Joseph, 2016). A similar study conducted in China also showed that natural management strategies can improve biodiversity without reducing latex

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production (Lan et al., 2017d). There is strong evidence that adopting more natural management strategies improves plant diversity without reducing latex production (Lan et al., 2017d). More innovative management measures, such as cease of weeding and herbicide application (He and Martin, 2015), must be implemented to improve the biodiversity of rubber plantations, so as to promote the biodiversity of the region.

5. Conclusion

We provide a large regional study on the plant diversity of rubber plantations in a global biodiversity hotspot. Plant diversity followed global trends with respect to latitude and temperature. Exotic species were very common in rubber plantations, especially where agricultural intensity was strong. However, not all exotic species directly drive the loss of biodiversity. Only higher dominance of some exotic species were associated with a loss of plant diversity within rubber plantations. We must make greater efforts to balance agricultural production with conservation goals in this region, particularly in Vietnams and Cambodia, to minimize the loss of biodiversity.

Code availability

Not applicable

Authors' contributions

Guoyu Lan: Conceptualization, Methodology, Writing, Reviewing and Editing; **Bangqian Chen**: Methodology, Reviewing and Editing, **Chuan Yang, Rui Sun, Bangqian Chen, Zhixiang Wu and Xicai Zhang**: Investigation

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Competing interests

The authors declared that they have no conflicts of interest to this study.

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Acknowledgements

We thank the help of the Rubber Research Bureau of Thailand, Perennial Crop Research Institute of Myanmar, the Rubber Research Institute of Cambodia, Vietnam Agricultural University, and the Yunnan Rubber Group. We would like to thank Prof. Fangliang He at University of Alberta and Dr. Ian Gilman at Yale University for his assistance with English language and grammatical editing.

Funding

This large-scale field investigation was supported by National Natural Science Foundation of China (42071418), the Lancang-Mekong international cooperation project of the Ministry of Foreign Affairs (081720203994192003) and the Earmarked Fund for China Agriculture Research System (CARS-33-ZP3).

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Figure captions

Figure 1 Sampling plot localities within rubber plantations in GMS

Figure 2 Distribution maps of two common exotic species (a: *Chromolaena odorata***,** b: *Mimosa pudica*) of rubber plantation in the GMS (circle size is proportional to importance value)

Figure 3 Significant difference in plant community compositions of rubber plantations among countries in GMS. a: Principal coordinate analysis (PCoA) based on Bray-curtis distance; b: Analysis of similarity among countries.

Figure 4 Redundancy analysis of plant community compositions of rubber plantation in the GMS (a: RDA ordination, b: Percentage of explained and unexplained by RDA results)

Figure 5 Plant species diversity of rubber plantations across countries in the GMS (a: species richness; b: Shannon diversity; c: Exotic species richness).

Figure 6 Factors affecting plant diversity of rubber plantation. a) Predicting species richness by using multiple linear regression (The red point was the observed richness, the green solid line was the estimated richness, and the grey solid line was the 95% confidence interval. y: Richness, $x1$: Latitude, $x2$: Elevation, $x3$: Slope, $x4$: Age, $x5$: Height, $x6$: Rainfall, $x7$: Temperature.) b)：Predictions of the importance of environmental variables based on random forests.

Figure 7 Effects of exotic species on plant diversity of rubber plantations in the GMS (a: Frequency of the most common exotic species; b: Richness comparison of different communities (sky blue bar: plots without *C. odorata* and *M. pudica*; blue bar: plots with both *C. odorata* and *M. pudica*; red bar: plots only with *C. odorata*; yellow bar: plots only with *M.*

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删除的内容: Linear regressions of species richness of rubber plantation with environmental variables (a: latitude; b: longitude; c: elevation; d: rainfall; e: temperature; f: slope degree; g: tree age, h: tree height; i: canopy density)

删除的内容: Figure 6 Divers of plantation community or rubber plantation in GMS (a: Predictions of the importance of environmental variables based on random forests; b: Boxplots showing the relative changes in deterministic and stochastic processes assessed by null deviation analysis. A null deviation close to zero suggests that stochastic processes are more important in structuring the community, whereas a null deviation larger than zero indicates that deterministic processes are more important) .

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pudica) c: relationship between exotic species richness of given plot and species richness of given plot)

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Conservation and management of forests in this area are difficult due to conflicting external social and economic factors. Cambodia, Laos, and Myanmar have been recognized among the least developed countries in the world by the United Nations. Meanwhile, the urban and rural development of Vietnam and Thailand is unbalanced, and there are still a large number of population under poverty line. Recently, the GMS has been identified as a major strategic source of raw, extractable materials in Asia (Zhou and Wei, 2009).

In the GMS, logging, mining, and slash and burn agriculture contribute to deforestation and forest degradation.

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Though rubber expansion caused deforestation, cultivated rubber plantations have helped alleviate poverty in low-income regions, and rubber cultivation is the main economic source of farmers in remote areas in some areas of the GMS, such as Laos, Myanmar and Cambodia (Figure S1c-e).

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For example, compared with natural forest, rubber plantations reduces the taxa richness of earthworm (Chaudhuri et al., 2013), about 30% nematode taxa richness (Xiao et al., 2014), 50-60 % bird species (Aratrakorn et al., 2006; Li et al., 2013) and bat species (Phommexay et al., 2011).

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Expansion of rubber plantations is a resurgent driver of deforestation, carbon emissions, and biodiversity loss in this region (Xu, 2011; Warren-Thomas et al., 2018). It is indisputable that the large-scale rubber cultivation in countries of the GMS has an outsized impact on the ecosystem of tropical regions.

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Compared to primary forests, agricultural systems tend to have higher bacterial richness but lower fungal richness (Lan et al., 2017a; Cai et al., 2018; Tripathi et al., 2012; Kerfahi et al., 2016).

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Figure 4 Beta diversity of rubber plantations in the GMS (a: PCoA ordination plot, b: Whittaker's beta diversity (circle size is proportional to beta diversity value))

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Linear regressions of species richness of rubber plantation with environmental variables (a: latitude; b: longitude; c: elevation; d: rainfall; e: temperature; f: slope degree; g: tree age, h: tree height; i: canopy density)

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Diversity was significantly correlated with latitude, longitude, and elevation (Figure 5a-c). Linear regressions showed that diversity indices of richness, Shannon diversity, and Simpson diversity significantly increased with latitude and elevation ($p < 0.05$), however deceased with longitude ($p < 0.001$). Slope ($p < 0.001$) (Figure 5f) and tree height ($p < 0.001$) (Figure 5h) also were also important factors influencing diversity of rubber plantations. Rubber tree ages, canopy density, rainfall, and temperature showed no effects on diversity ($p > 0.05$).

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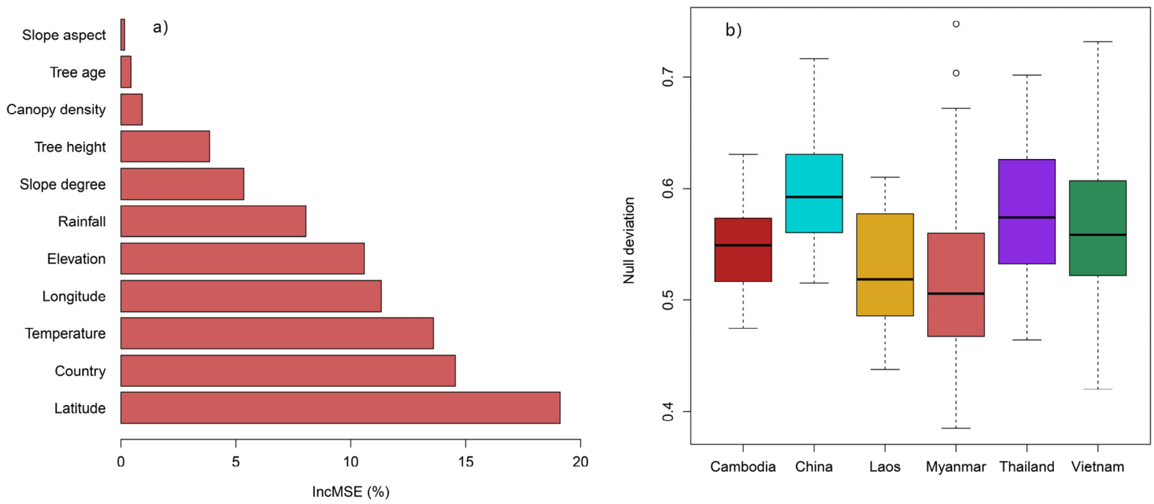

Figure 6 Divers of plantation community or rubber plantation in GMS (a: Predictions of the importance of environmental variables based on random forests; b: Boxplots showing the relative changes in deterministic and stochastic processes assessed by null deviation analysis. A null deviation close to zero suggests that stochastic processes are more important in structuring the community, whereas a null deviation larger than zero indicates that deterministic processes are more important)

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Plant diversity of north Laos and south China was relatively higher than other countries. This observation may be due to the large variation in elevation (for north Laos, elevation ranges from 300 to 900 m; for south China, elevation ranges from 100-1100 m) in these areas, which translates into greater environmental heterogeneity. We also found greater plant diversity at higher elevations (Figure 5c), which may be caused by the reduced agricultural activities on those terrains. It is not easy for farmers to clear understory plants on the steep slopes of rubber plantations at high elevation; thus high slope degree indirectly results in low agricultural intensity. In addition, greater slope may increase environmental heterogeneity and expand niche space (Morrison-Whittle and Goddard, 2015). In sum, the traditional ecological hypotheses, such as the latitudinal diversity gradient and niche partitioning, could also contribute to explaining diversity patterns of artificial rubber plantations. However, comparison of the diversity between rubber plantation and nearby natural forest needs further research.

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Many tropical regions, especially the GMS, contain hotspots of biodiversity that are threatened by agriculture (Delzeit et al., 2017, Egli et al., 2018; Shackelford et al., 2014, Kehoe et al., 2017). We must balance conservation with the economic goals of the GMS where the livelihood of many people rely on rubber plantations.

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Harvesting rubber latex may be the only way for many rural populations to generate stable income, but rubber production does not assume a comfortable living. For example, in Cambodia, many school children have to harvest rubber latex after classes to support their families (Figure S1e).

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Due to the low Human Development Index, people in GMS

must prioritize supporting their families before protecting the biodiversity of the region. It cannot fall squarely on local peoples to solve biodiversity crises.

In poor areas, we cannot just talk about ecological goals without first understanding local cultures and economies. The rubber industry has not made preserving forest biodiversity a major priority, and has struggled to meet conservation goals while minimizing economic loss (Lan et al., 2017). Our results showed that diversity of different countries varies significantly due to the variation in agricultural practice. In Vietnam, where diversity was low, rubber farmers clear the understory to facilitate tapping and other production activities (Figure S1f). The lower diversity in Cambodia may be due to the rubber plantations in northeastern which are managed by Vietnamese rubber companies. Vietnam and Cambodia, and regions that allow similar practices, augment the conflicts between agricultural production activities and biodiversity conservation. More effort must be given to balance agricultural production with biodiversity conservation goals in these regions. Thus, more innovative management measures, such as cease of weeding and herbicide application (He and Martin, 2015), must be implemented to improve the biodiversity of rubber plantations, so as to promote the biodiversity of the region. Previous study conducted in India demonstrated that a no-weeding practice in mature rubber plantations did not affect rubber yield (Abraham and Joseph, 2016). A similar study conducted in China also showed that natural management strategies can improve biodiversity without reducing latex production (Lan et al., 2017d). There is strong evidence that adopting more natural management strategies improves plant diversity without reducing latex production (Lan et al., 2017d). Thus, more innovative management measures must be implemented to improve the plant diversity of rubber plantations, so as to promote the biodiversity of the region.