Science of the Total Environment 874 (2023) 162505

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Diversified land conversion deepens understanding of impacts of rapid rubber plantation expansion on plant diversity in the tropics

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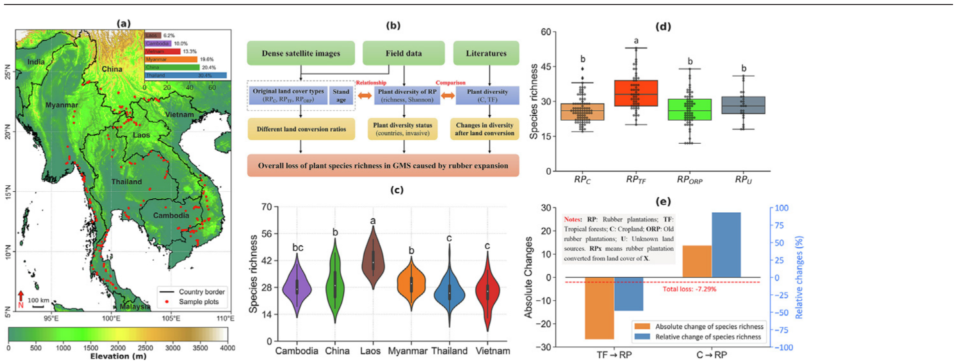
HIGHLIGHTS

- Mean plant species richness of rubber plantations across countries is ~25 to ~42.
- New rubber plantation mainly come from cropland, old rubber plantation, and forest.
- Plant species halved from forest to rubber but doubled when converted from cropland.
- Most rubber plantations can maintain plant diversity in a 30-year rotation.
- Rubber expansion leads to 7.29 % species loss considering diverse land conversions.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Paulo Pereira

Keywords:
Plant species richness
Rubber plantations
Original land cover types
Stand age
Greater Mekong Subregion

ABSTRACT

Understanding the status and changes of plant diversity in rubber (*Hevea brasiliensis*) plantations is essential for sustainable plantation management in the context of rapid rubber expansion in the tropics, but remains very limited at the continental scale. In this study, we investigated plant diversity from 10-meter quadrats in 240 different rubber plantations in the six countries of the Great Mekong Subregion (GMS)—where nearly half of the world's rubber plantations are located—and analyzed the influence of original land cover types and stand age on plant diversity using Landsat and Sentinel-2 satellite imagery since the late 1980s. The results indicate that the average plant species richness of rubber plantations is 28.69 ± 7.35 (1061 species in total, of which 11.22 % are invasive), approximating half the species richness of tropical forests but roughly double that of the intensively managed croplands. Time-series satellite imagery analysis revealed that rubber plantations were primarily established in place of cropland (RP_C, 37.72 %), old rubber plantations (RP_{ORP}, 27.63 %), and tropical forests (RP_{TF}, 24.12 %). Plant species richness in RP_{TF} (34.02 ± 7.62) was significantly ($p < 0.001$) higher than that in RP_{ORP} (26.41 ± 7.02) and RP_C (26.34 ± 5.37). More importantly,

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http://dx.doi.org/10.1016/j.scitotenv.2023.162505
Received 2 August 2022; Received in revised form 23 February 2023; Accepted 23 February 2023
Available online 1 March 2023
0048-9697/© 2023 Published by Elsevier B.V.

species richness can be maintained for the duration of the 30-year economic cycle, and the number of invasive species decreases as the stand ages. Given diverse land conversions and changes in stand age, the total loss of species richness due to rapid rubber expansion in the GMS was 7.29 %, which is far below the traditional estimates that only consider tropical forest conversion. In general, maintaining higher species richness at the earliest stages of cultivation has significant implications for biodiversity conservation in rubber plantations.

1. Introduction

Natural rubber, obtained mainly from the rubber tree (*Hevea brasiliensis* Muell. Arg) native to the Amazon basin and having an economic cycle of about 30 years, is a valuable commodity worldwide. Rapidly growing demand for natural rubber has led to a dramatic expansion of rubber plantations in the tropics in recent decades, particularly in biodiversity hotspots such as the Great Mekong Subregion (GMS), where about half of the world's rubber acreage is located (ANRPC, 2021). The Food and Agriculture Organization of the United Nations (FAO) reported that the area of rubber plantations in the GMS countries increased from 2.1 million hectares in 1990 to 2.5 million hectares in 2000, 3.7 million hectares in 2010, and 6.17 million hectares in 2019 (Fig. S1). It has been reported that rubber plantations in the GMS have expanded primarily in potentially suboptimal environments in nontraditional growing regions (Li and Fox, 2012; Chen et al., 2016).

Rubber plantations are often established in place of tropical forests and are therefore considered a major cause of deforestation and biodiversity loss in the tropics (Sodhi et al., 2010; Warren-Thomas et al., 2015; Hughes, 2017; Warren-Thomas et al., 2018; Grogan et al., 2019; Grass et al., 2020; Wang et al., 2020; Feng et al., 2021). Approximately 30 % of rubber plantations in Sumatra, Indonesia's largest natural rubber producer and one of the most deforested tropical hotspots, were established through tropical forest destruction between 1990 and 2013 (Grass et al., 2020). Between 2001 and 2015, 23.2 % of Cambodia's cleared forests were converted to rubber plantations (Grogan et al., 2019). Due to their high ecological and economic value, tropical forests, particularly tropical rainforests, are frequently used as comparators in studies of biodiversity loss caused by the expansion of rubber plantations. As a key component of biodiversity, plant diversity serves important ecological functions (Blicharska et al., 2019; Schaub et al., 2020; Wan et al., 2020; Chen et al., 2021; Furey and Tilman, 2021), and numerous studies have been conducted on rubber plantations (Lawrence, 1996; Beukema and van Noordwijk, 2004; Beukema et al., 2007; Katja et al., 2017; Lan et al., 2017). In China, a field survey of 120 plots at 10 × 10 m quadrats in rubber plantations revealed 916 plant species belonging to 539 genera and 144 families (Chen et al., 2019). However, the distribution ratio of common plants such as Gramineae and Rubiaceae is much higher than in tropical forests, and invasive alien plants are relatively severe in hilly rubber plantations (Gong et al., 2022). In Jambi Province, Indonesia, eight monoculture rubber plantations contained 230 vascular plant species, far fewer than jungle rubber plantations (652) and tropical rainforests (963) of the same plot size in (Katja et al., 2017). The majority of studies indicate that plant diversity in rubber plantations—whether in the form of alpha, beta, or gamma diversity—is significantly lower than in tropical rainforests, and that between 33 % and 76 % of plant species were lost when tropical rainforests were converted to monoculture rubber plantations (Alkemade et al., 2013; Katja et al., 2017; Singh et al., 2021). However, the spatial scale of the aforementioned studies on plant diversity in rubber plantations is quite small, i.e., less than or at county scale. The studies in China are relatively complete (Chen et al., 2019), whereas large-scale studies in Southeast Asia, the primary producing region of global natural rubber, are still very scarce. In addition, because the sampling methods of existing studies vary widely, it is difficult to combine them for a comprehensive assessment, so there is still a lack of knowledge regarding the status of plant diversity in rubber plantations at the continental scale.

A scientific and objective assessment of the impact of rubber plantation expansion on plant diversity in recent decades is critical for both rubber practitioners and the scientific community (Häuser, 2015; He and Martin, 2015; Singh et al., 2021). This requires a combination of many factors, such as understanding the effects of land conversion and changes in plant diversity with the stand age of rubber plantations (Gerstner et al., 2014; Jung et al., 2019). The status of plant diversity is most likely directly tied to the diversity of rubber plantations prior to their development, and is greatly influenced by the original land cover type (Ziegler et al., 2009; Wang et al., 2022). It is vital to understand the cost of plant diversity loss following conversion of tropical rainforests to rubber plantations (Kusuma et al., 2018), but assessment is susceptible to bias if conversion of other land cover to rubber plantations is overlooked. This bias can easily make rubber a detrimental crop, even though it provides an indispensable industrial raw material (Ziegler et al., 2009; Tan et al., 2011). In fact, rubber plantations have diverse land sources besides tropical forests, such as old rubber plantations and cropland (Chen et al., 2018; Hurni and Fox, 2018; Vrignon-Brenas et al., 2019). In regions where rubber has been cultivated for a long time, rubber plantations often continue even after the old rubber plantations have been cleared (Grass et al., 2020). According to a comprehensive study in Hainan Island, the second largest rubber-producing province in China, old rubber plantations were the largest source of new rubber plantations, followed by croplands and tropical forests (Chen et al., 2018). After rubber prices increased dramatically tenfold in the 2000s (Grogan et al., 2019), large amounts of cropland such as cassava and sugarcane plantations were converted to rubber plantations (Peerawat et al., 2018; Grass et al., 2020). Although rubber plantations have substantially less plant diversity than tropical forests, a number of studies indicate that it is significantly higher than intensively managed croplands and somewhat superior to some perennial plantations, such as oil palm and eucalyptus (Koh and Wilcove, 2008; Xiang et al., 2012; Xing et al., 2012; Botha et al., 2015). In addition, whether plant diversity can be maintained over the economic cycle (approximately 30 years) is a critical consideration in evaluating the impact of rapid expansion on plant diversity. In Thailand, for example, aging rubber plantations had a greater impact on soil biodiversity than land-use conversion, and most biotic parameters, composition, abundance, and activity levels changed significantly seven years after plantations establishment (e.g., old rubber plantations harbored the highest microbial and macrofaunal biomass) (Peerawat et al., 2018). Unfortunately, in addition to the widespread concern about plant diversity loss following conversion of tropical forests to rubber plantations, there have been very few studies on the conversion of other land types to rubber plantations and how plant diversity changes as rubber stands age, let alone large-scale, comprehensive studies.

In 2018, we conducted extensive field surveys in the GMS and collected data on plant diversity in 240 rubber plantations with varying stand ages. Using dense time series of satellite imagery from Landsat and Sentinel-2 since the late 1980s, we were able to determine the date of rubber plantation establishment (relative to stand age) and land cover types prior to plantation establishment (Gorelick et al., 2017; Chen et al., 2018; Tamiminia et al., 2020), allowing us to more comprehensively assess the impact of rapid expansion on plant diversity. In this study, we aim to address the following objectives: 1) what is the current extent and status of plant diversity in rubber plantations, 2) how do the different original land cover types affect plant diversity in rubber plantations and how does it change with stand age, and 3) to what extent has the rapid expansion of rubber plantations affected plant diversity in the area, given the multiple conversions of land types and changes in plant diversity with stand age? Understanding the status of plant diversity and the effects of varied land use histories on plant diversity in rubber plantations has important implications for management.

2. Materials and methods

2.1. Study region

The GMS comprises six countries—Cambodia, the People's Republic of China (particularly, Yunnan Province and the Guangxi Zhuang Autonomous Region), Lao People's Democratic Republic (referred to as Laos), Myanmar, Thailand, and Vietnam—that share Southeast Asia's longest river, the Mekong (Fig. 1a). From its estuary in southern Vietnam to the northern boundary of the study region in China, the region features a complicated landform and considerable elevation changes, ranging from 0 to about 4000 m above sea level. The northwestern part of Thailand, the central portion of Vietnam, and the eastern parts of Myanmar, Laos, and Yunnan in China are essentially mountainous, with elevations around 1000 m above sea level. The remaining regions are mostly plains, low-lying, and relatively flat. Large geographical and topographic variations within the GMS inevitably result in vast climatic variations. The average annual rainfall ranges from about 500 mm in central Myanmar to about 3500 mm in some coastal regions (Chen et al., 2017). The GMS is a global biodiversity hotspot and currently hosts nearly half of the world's rubber plantations (Golbon et al., 2018). According to the Association of Natural Rubber Producing Countries (ANRPC), the harvest area under rubber cultivation in Thailand at the end of 2019 was 3.5 million hectares, followed by China, Vietnam, Myanmar, Cambodia, and Laos, with a gradual decrease from 1.16 to ~0.28 million hectares (ANRPC, 2021). Due to the rapid increase in the price of natural rubber, rubber plantations have expanded rapidly in all countries in this region since the early 2000s, with the total harvest area increasing from 2.5 million hectares in 2000 to 6.17 million hectares in 2019 (excluding Laos, for which data are unavailable) (Fig. S1).

2.2. Data and processing

2.2.1. Field data

Between April and November 2018, fieldwork was undertaken in Cambodia, Vietnam, Laos, Thailand, and Myanmar, while sampling in Yunnan Province occurred between July and October 2016 (no sampling was conducted in Guangxi, where there are almost no rubber plantations). The field survey area and routes were planned in advance under the guidance of staff from these national rubber research institutes who were knowledgeable with rubber distribution and covered most of the rubber plantation regions in these countries. In general, the number of samples in each country was determined by the overall area (Fig. S1) and spatial distribution (e.g., degree of concentration) of rubber plantations. Rubber plantations of varying ages were chosen at random for examination with the aid of these collaborators and very high resolution (VHR) Google Earth satellite imagery that was dynamically screened with smartphones. The name and areal extent (as determined by field estimations) of each species were recorded, and photographs of each species were taken in an area of 100 m^2 (10-m square) at a minimum distance of 30 m within the plantation boundary. Landscape photographs were taken in each plantation using a camera-CASIO H20G with integrated Global Positioning System (GPS), and possible original land cover types (tropical forest or cropland; determined by the plants remaining in the plantation and the different land covers in the vicinity of the plantation) and stand age (estimated to our knowledge, from tree size and height of the tapping scars on the trunk) were recorded. This field data was utilized to validate and correct the stand age and original land cover types of the rubber plantation, which had been automatically interpreted from dense time-series satellite imagery using a machine learning algorithm.

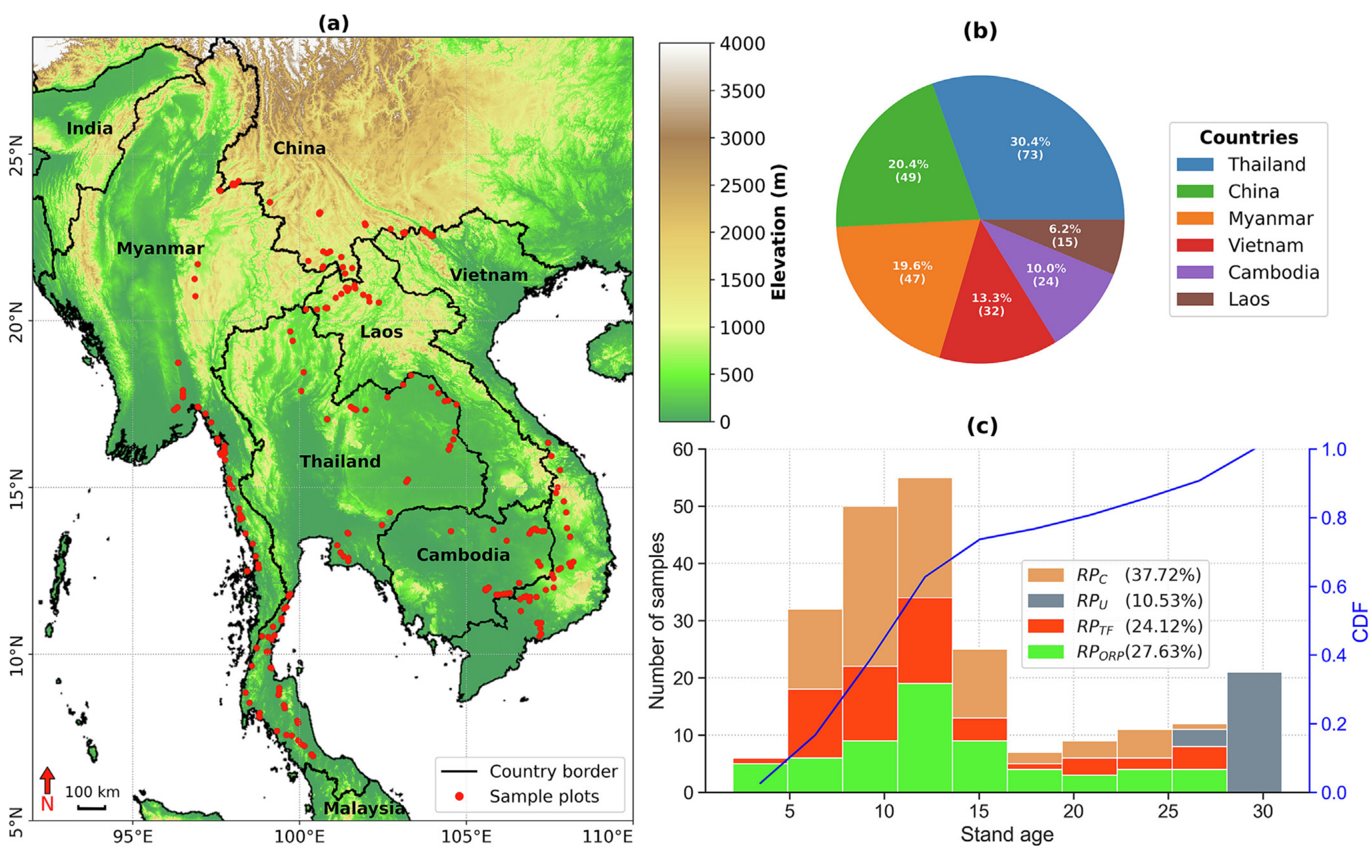

Fig. 1. Study area: (a) sampled rubber plantations, (b) number of sampled rubber plantations in different countries, and (c) stand age and original land cover types of rubber plantations. The RP_C, RP_{TF}, RP_{ORP}, and RP_U in figure (c) are rubber plantations converted from cropland, tropical forests, old rubber plantations, and unknown land sources, respectively. CDF is cumulative distribution function.

In total, we surveyed 240 rubber plantations, with 73, 49, 47, 32, 24, and 15 samples in Thailand, China, Myanmar, Vietnam, Cambodia, and Laos, respectively (Fig. 1b). With the exception of Vietnam, the number of samples in each country corresponds to the order of the rubber plantation area. Because rubber plantations in Vietnam are more densely distributed in the southern region, sampling is less extensive. Plants that were not recognized in the field were further identified by comparing field photos in the laboratory with information on the websites of the Global Biodiversity Information Facility (gbif.org) and Plant Plus of China (www.iplant.cn). After careful laboratory matching with Google Earth VHR imagery, 12 rubber plantations either had GPS coordinates inconsistent with their positions in the satellite imagery examined, or the area or shape of the plantations was not suitable for joint analysis with satellite imagery at 30 m spatial resolution. Therefore, these sampled plantations were excluded from the determination of stand age and original land cover types. However, they were still useful for species richness and invasive species analysis.

Species richness (S) was recorded as the total number of species within each plot. Shannon index (H') and Shannon evenness index (J') were calculated using Eqs. (1) and (2) for each plot (Pielou, 1975; Magrurran, 2004).

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \tag{1}$$

$$J' = H' / \ln(S) \tag{2}$$

where p_i is the proportion (n/N) of individuals of one particular species found (n) divided by the total number of individuals found (N), and S is species richness.

2.2.2. Satellite imagery

Landsat 5/7/8 Collection 1 top-of-atmosphere (TOA) reflectance data—Thematic Mapper (TM), Enhanced Thematic Mapper Plus (ETM+), and Operational Land Imager (OLI)—from the U.S. Geological Survey and Sentinel-2 Level-1C Multispectral Instrument (MSI) TOA data from the European Space Agency were used to determine the age and original land cover type of the surveyed rubber plantations. All Landsat and Sentinel-2 satellite imagery since the late 1980s were used for the analysis, approximately 1500 tiles for each plantation. These images were available on the Google Earth Engine (GEE) cloud computing platform and were processed with high geometric accuracy to reduce radiometric uncertainties between different acquisition dates and different sensors, such as ETM+ and OLI (Gorelick et al., 2017).

Clouds and cloud shadows in the Landsat imagery were masked with bitmasks generated from the associated quality assessment band using widely used C Function of Mask (CFMask) algorithm (Zhu et al., 2015); in the Sentinel-2 imagery, they were masked with cloud probability layers generated by Google. Three vegetation indices commonly used in land-use change monitoring, including normalized difference vegetation index (NDVI) (Tucker, 1979), land surface water index (LSWI) (Gao, 1996; Xiao et al., 2002), and normalized burn index (NBR) (Key and Benson, 1999), were calculated using Eqs. (2), (3), and (4), respectively.

$$NDVI = \frac{\rho_{NIR} - \rho_{red}}{\rho_{NIR} + \rho_{red}} \tag{3}$$

$$LSWI = \frac{\rho_{NIR} - \rho_{SWIR1}}{\rho_{NIR} + \rho_{SWIR1}} \tag{4}$$

$$NBR = \frac{\rho_{NIR} - \rho_{SWIR2}}{\rho_{NIR} + \rho_{SWIR2}} \tag{5}$$

where ρ_{red}, ρ_{NIR}, ρ_{SWIR1}, and ρ_{SWIR2} are red, near-infrared (NIR), shortwave infrared band 1 (SWIR), and SWIR band 2 of the Landsat and Sentinel-2 (LS2) images, respectively.

2.2.3. Terrain data

The digital surface model (DSM), AW3D30 (v3.2), provided by the Earth Observation Research Center, Japan Aerospace Exploration Agency (JAXA), was used to investigate the topographic distribution characteristics of the samples and explore the relationship between biodiversity and topography (Tadono et al., 2014). AW3D30 has a horizontal resolution of approximately 30 m (1 arcsecond mesh size). Elevation was obtained directly from AW3D30, and the corresponding slope was calculated in GEE.

2.3. Algorithms and data analysis

2.3.1. Identifying stand age and original land cover types of rubber plantations

Stand age (relative to the year of plantation establishment) was determined from signatures of exposed topsoil (determined from annual minimum LSWI values in images taken during rubber leaf greening season) at plantation establishment and linear increase in canopy closure (determined from annual average LSWI in images taken during rubber leaf greening season) that occurred during plantation maturation. LSWI time series prior to plantation establishment were used to examine original land cover types categorized as cropland (C), tropical forest (TF), old rubber plantation (ORP), and unknown (U) when historical satellite imagery prior to conversion was insufficient to determine original land cover types (Fig. 1c). A detailed description of the algorithms used to determine stand age and original land cover types is provided in our previous study (Chen et al., 2018). To achieve higher accuracy, stand age and original land cover types automatically determined by the algorithm were double conformed or corrected for each sampled plantation by visual inspection of the following data: 1) annual series of LSWI, NBR, and B5 with average and minimum values from 1987 to 2020 calculated from annual images taken during the rubber tree greening season (mid-April to late November) (Fig. 2a & b), 2) annual series of LSWI and NBR with minimum values from 1987 to 2020 calculated from annual images obtained during the rubber tree leaf-off and leaf-on seasons (January to mid-April) (Fig. 2c), 3) screenshots of cloud-free images and the median composite image created from annual images taken during rubber greening season (1987–2020) (Fig. 2d & e), 4) historical VHR images from Google Earth (Fig. 2f), and 5) landscape photos embedded in GPS, stand age, and/or field-estimated original land cover type (Fig. 2g).

2.3.2. Evaluating total plant diversity loss of rubber expansion

Data regarding the average plant richness of croplands and tropical forests were collected from scholarly literature found on reputable databases such as ScienceDirect, Web of Science, Google Scholar, and China National Knowledge Infrastructure (CNKI). The search was conducted using the relevant keywords “plant diversity” and “plant species richness” in the Topic/Title/Keywords/Abstract sections, and further refined by including the keywords “tropical/tropics” and “forest” or “cropland/crop/plantation”. It is worth noting that few studies utilized the same plot size and methodology as our study, particularly in context of tropical croplands. As a result, we were limited to using data from studies that adopted the most similar approaches to ours for comparison purposes. To eliminate differences between regions, we try to confine the studies used for comparison in the GMS, or in other regions but with larger area of rubber plantations near the plots. Finally, seven forest plots from the Smithsonian Center for Tropical Forest Science-Forest Global Earth Observatory (CTFS-ForestGEO) (LaManna et al., 2017), with latitudes ranging from 2.22°S to 17.04°N and average plant species richness spanning from 25.3 to 69.7 for each plot, were used for comparison (Table S1). Plant species richness of CTFS-ForestGEO was assessed using 20 × 20 m quadrats, but only trees were considered. Plant species richness of croplands was derived from five typical croplands (pineapple, cassava, sugarcane, rice, or their rotations) in Thailand, with plant species richness ranging from 9 to 18 for nested 10 × 10 m quadrats (Shrestha et al., 2010) (Table S2). Plant species richness in tropical forests and croplands was represented by the average values of species richness in the abovementioned tropical forests and cropland

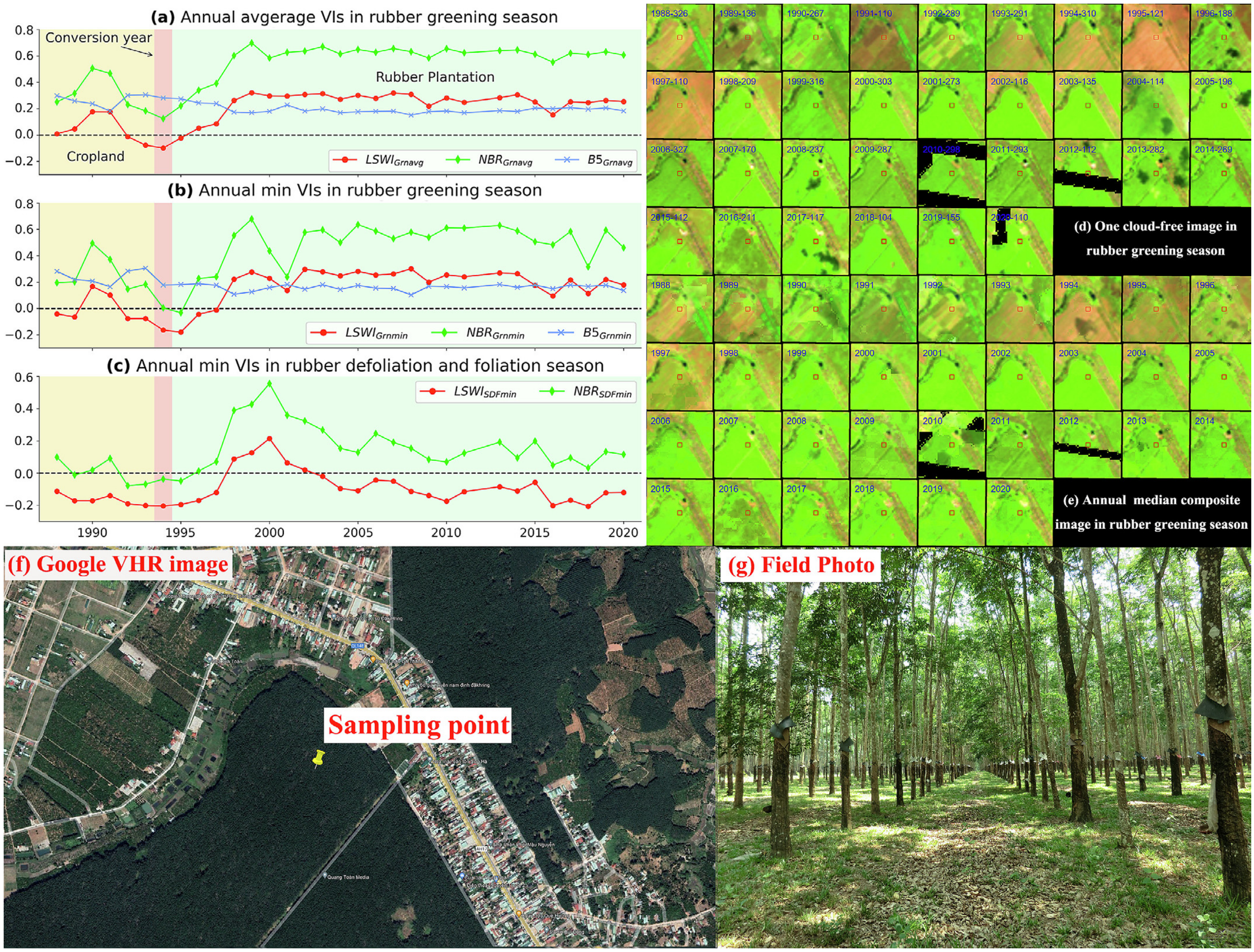

Fig. 2. Stand age and original land cover type of a rubber plantation near Kon Tum City, Vietnam (107.9150°E, 14.5854°N): a–c) time series of spectral indices, where a) and b) are annual mean and minimum values of LSWI, NBR, and B5 in rubber greening season, and c) is annual minimum LSWI and NBR in rubber defoliation and foliation season, respectively; d) and e) are annual cloud-free and median value composite imagery of the rubber plantation, respectively; f) Google satellite imagery, and g) a field photo.

samples, respectively. Plant species richness in rubber plantations was expressed by the average species richness of all sample plots in the GMS. The loss of plant diversity due to the rapid expansion of rubber plantations throughout the region was calculated using Eq. (5).

$$S_{loss}(\%) = \frac{\sum_{i=1}^{N}(S_i - S_{RP})p_i}{\sum_{i=1}^{N} S_i p_i} \times 100 \tag{6}$$

where S_{loss} is the percent loss of species richness, p_i is the percent of the i^{th} original land cover types converted to rubber plantation, S_i is the plant species richness of the i^{th} land cover type, such as cropland or tropical forest, S_{RP} is the plant species richness of the rubber plantation, and N is the number of original land cover types. Although there is a short-term loss of plant diversity when a rubber plantation is established (about one year), it recovers quickly and remains largely unchanged throughout its economic cycle (i.e., over a 30-year period) unless severe land clearing for latex tapping occurs. Therefore, we assume that the conversion of old rubber plantations to new rubber plantations did not result in a loss of plant diversity. Therefore, only the changes in RP_{TF} and RP_C were calculated when assessing the ultimate loss of plant diversity.

2.3.3. Statistical analysis

Histograms were used to examine distribution patterns of plant diversity for all sampled plantations, and violin diagrams were used to show differences in biodiversity among countries. Descriptive statistics (minimum, maximum, mean, and standard deviation) of species richness and Shannon index were calculated with all samples, and their percentiles (e.g., 5th and 95th) were calculated grouped by country. Using *agricolae* (https://cran.r-project.org/web/packages/agricolae/index.html)—an R package of statistical procedures for agricultural research—to detect differences in plant species richness and Shannon index between different countries by least significant difference (LSD) multiple comparisons ($p < 0.05$). Before applying an LSD test, the Shapiro-Wilk test revealed that the plant diversity data were not normal distributed, so the Kruskal-Wallis test was performed to determine whether there is a significant difference in species richness between these countries. The curve of cumulative species richness against the number of plots was calculated. Similar analyzes were performed for invasive plants.

The rubber plantations were divided into four groups with 10-year increments in stand age (≤ 10, 11–20, 21–30, and ≥ 30 years), roughly corresponding to the young, middle-aged, old, and very old stages of rubber plantations. Differences in plant richness among age groups were explored by boxplots and examined by LSD multiple comparisons. The sample data were also grouped by original land cover types, and the differences in plant species richness in each group were explored by boxplots and examined by LSD multiple comparisons. Relationships between plant richness and stand age in each group of original land cover types was explored by scatterplots with linear regression and correlation analysis. We conducted a similar analysis for invasive plants, and added a comparative analysis of the proportion of invasive plants at the plot level.

Geemap (https://geemap.org/), a Python package for interactive mapping with GEE, was used to extract different time series of vegetation indices and download the annual screenshots of satellite images for different sampling plots (Wu, 2020). *Scipy* (https://scipy.org) was used for statistical analysis, *Matplotlib* (https://matplotlib.org) and *Seaborn* (https://seaborn.pydata.org) were used to plot various figures (Hunter, 2007; Waskom, 2021).

3. Results

3.1. The current extent and status of plant diversity in rubber plantations in the GMS

Species richness of sampled rubber plantations in the GMS ranged from 12 to 53, with a mean ± standard deviation (SD) of 28.69 ± 7.35 (Fig. 3a). 90 % of the rubber plantations had species richness >20 and 50 % had species richness >28. The frequent distribution of species richness was slightly left-skewed and varied widely among rubber plantations. The Shannon index was slightly right-skewed, with a mean of 3.06 ± 0.32, and >90 % of rubber plantations had a Shannon index >2.68 (Fig. S2a). The Shannon evenness index ranged from 0.75 to 0.99, with a mean value of 0.92 and about 50 % of them >0.93 (Fig. S3a). Plant diversity also varied greatly among the six countries (Fig. 3b). The Kruskal-Wallis test showed that the H statistic is 55.19 ($p < 0.001$). The average species richness in Laos was much higher than ($p < 0.001$) the other countries, with a value of 42.27 ± 6.03. This was followed by Myanmar, China, and Cambodia with an average species richness of 30.08 ± 4.58, 29.92 ± 8.22, and 28.33 ± 5.38, respectively. Thailand had an average species richness of 25.84 ± 5.47, while Vietnam had the lowest species richness of 25.19 ± 6.82, with no significant differences in average species richness between these two countries. Among the countries studied, rubber plantations in China and Vietnam had the greatest variation in species richness, with a range between the 5th and 95th percentiles of 25.60 and 23.35, respectively, while the range for the other four countries was 13.00 (Myanmar) to 17.60 (Laos). The Shannon index for the countries studied showed a similar pattern to species richness, but the differences among the different countries were slightly larger than species richness (Fig. S2b). The greatest variation in the Shannon index was found in Vietnam, where the range between the 5th and 95th percentiles was 1.37, much higher ($p < 0.001$) than in the other countries, which ranged from 0.61 (Myanmar) to 1.10 (China) (Fig. S2b). The Shannon evenness index differed slightly among the different countries. Myanmar had the highest average value of about 0.94, followed by China, Laos, Cambodia, Thailand, and Vietnam. The Shannon evenness indices of rubber plantations in Myanmar and China were significantly higher than those of Thailand and Vietnam (Fig. S3b).

Field investigations showed that most rubber plantations had varying degrees of invasive plants. About 20 % of the sampled rubber plantations had three (about 10 % of the average plot-level plants recorded) or fewer invasive plants, and 50 % of the plantations had five (19.05 % of the average plot-level plants recorded, Fig. S4) or fewer species (Fig. 3c). The total number of species observed initially increased rapidly as the number of plots increased, exceeding 400 when the number of plots reached 50, and reaching approximately 700 when the number of plots reached 100 (Fig. 3d). The increase in species number slowed significantly when the number of plots exceeded 100. The total number of plant species we recorded in this region was 1061. A total of 119 invasive species were found in rubber plantations in the GMS, accounting for 11.22 % of the total species observed there (Fig. 3d).

3.2. Age structure and original land cover types of rubber plantations

Stand age was determined from all Landsat and Sentinel-2 time-series satellite imagery since the late 1980s (about 1500 satellite images for

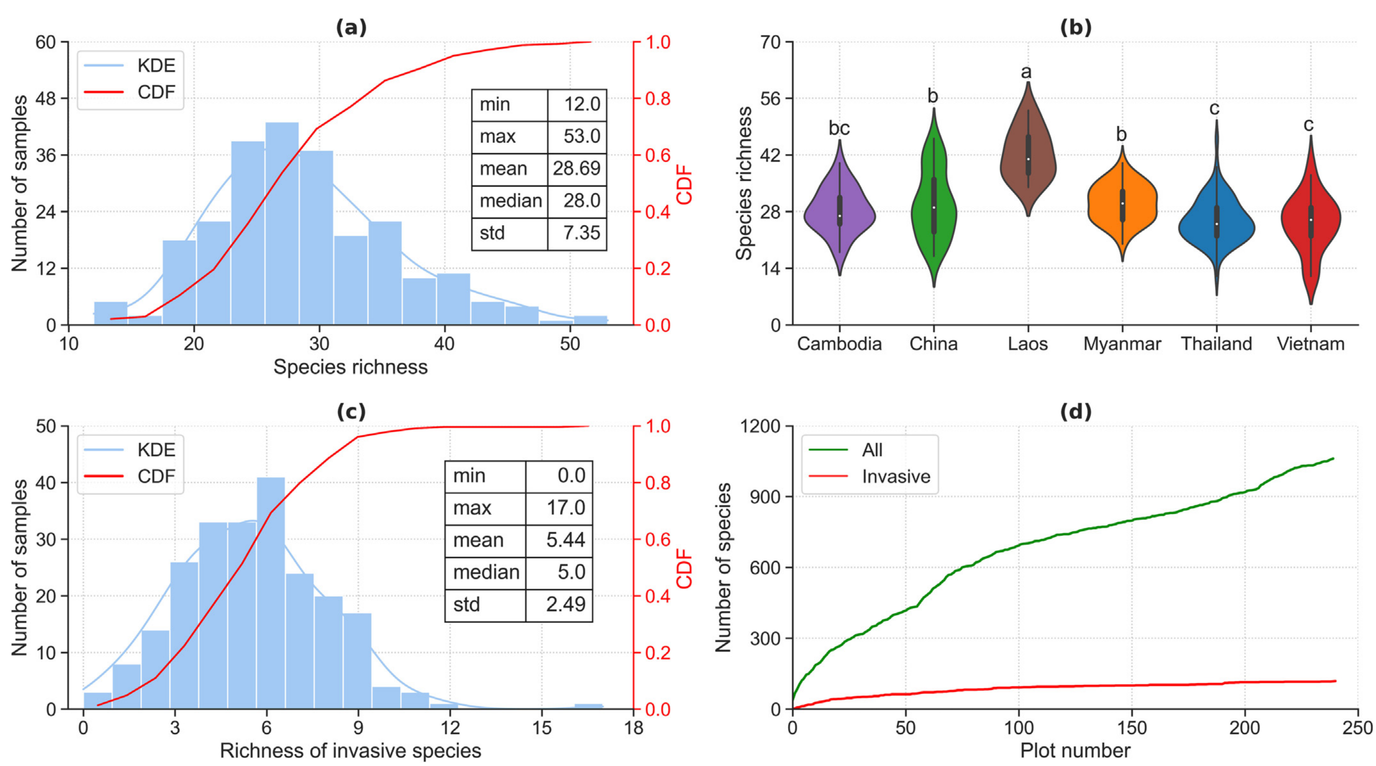

Fig. 3. Plant diversity of rubber plantations in the GMS at plot level: (a) histogram of all species richness, (b) species richness among different countries, (c) histogram of invasive species richness, and (d) species-accumulation curves of all and invasive species with observed data. CDF: Cumulative distribution function, KDE: Kernel density estimation.

each plantation surveyed). It was found that 50 % of the rubber plantations studied were <12 years old and 70 % were <15 years old (Fig. 1c). There were very few rubber plantations around 20 years old. A total of 86 rubber plantations were established on croplands (RP_C), which accounted for 37.72 % of the total samples, followed by rubber plantations on old rubber plantations (RP_{ORP}; 63 samples, 27.63 %), tropical forests (RP_{TF}; 55 samples, 24.12 %), and unknown land cover types (RP_U; 24 samples, 10.53 %), which could not be identified due to lack of historical satellite imagery (Fig. 1c).

3.3. Variation of plant species richness with stand age

The results of long-term observations on fixed plots were not available, so the species richness of rubber plantations of different ages was used to assess this variation. The boxplot in Fig. 4a showed that plant species richness of rubber plantations was very stable throughout the economic cycle, with very little decrease in species richness over 30 years. Species richness of plantations <20 years old showed a relatively wide range of variation, with interquartile ranges (IQR) much larger than those of rubber plantations older than 20 years. The species richness of RP_C and RP_{TF} decreased slightly with increasing stand age, while the species richness of RP_{ORP} remained almost unchanged (Fig. 4b–d). The number of invasive species in rubber plantations in the GMS decreased with increasing stand age, and the slope of the linear fit was −0.27 (Fig. 5a). Compared to RP_{TF}, the number of invasive plants in RP_C and RP_{ORP} decreased more rapidly with increasing stand age, and the slope of the linear fit was −0.49 (Fig. S5).

3.4. Evaluating the impacts of original land cover types and overall expansion

Variable plant diversity was observed in rubber plantations converted from different land cover types (Fig. 6a). RP_{TF} had the highest species richness with an average value of 34.02 ± 7.62, which was significantly higher ($p < 0.001$) than RP_U (28.33 ± 6.78), RP_{ORP} (26.41 ± 7.02), and RP_C (26.34 ± 5.37), respectively. RP_{TF} and RP_{ORP} had greater variation in species richness than RP_C and RP_U, with IRQs of 11 and 9, respectively (Fig. 6a). RP_C had the highest average richness of invasive species (5.79 ± 2.75), followed by RP_{ORP} (5.43 ± 2.49), RP_{TF} (5.16 ± 1.94), and RP_U (4.83 ± 2.62), respectively (Fig. 5b). Although the number of invasive species did not differ significantly, the proportions of total species richness varied significantly. The average proportion of invasive species in RP_C and RP_{ORP} (22.36 ± 9.87 % and 21.38 ± 10.11 %, respectively) was significantly higher ($p < 0.001$) than in RP_U (16.65 ± 8.87 %) and RP_{TF} (15.78 ± 6.17 %) (Fig. 5c).

The average plant species richness of tropical forests and croplands (e.g., cassava and sugarcane) at comparable levels from the literature review was 55.14 ± 17.42 and 15.00 ± 3.41, respectively. The former was significantly higher ($p < 0.001$) than the average plant species richness of the studied rubber plantations in the GMS (28.42 ± 7.26, Fig. 6b), while the latter was significantly lower ($p < 0.001$) than the studied rubber plantation. Conversion of tropical forests to rubber plantations resulted in an average net loss of 26.72 plant species, representing a relative decline of 48.46 %. In contrast, conversion of croplands to rubber plantations contributed to an average net increase in species richness of 13.42, corresponding to a relative increase of 89.47 %. According to our study, 24.12 % of the surveyed plantations were RP_{TF}, while 37.72 % were RP_C (Fig. 1c). Disregarding the variation in species richness during the 30-year rotation cycle (slight decrease, Fig. 4b–d) and the effects of RP_U (loss cannot be calculated), the total loss of species richness due to rubber plantation expansion in the GMS, after netting net losses and net gains, was only 7.29 %, which was 15.05 % of the estimated loss when the original land cover types of rubber plantations were considered as tropical forests only.

4. Discussion

4.1. Plant diversity of rubber plantations in the GMS

Our quadrat survey, the most comprehensive survey of plant species in rubber plantations in the GMS to date using a uniform survey method,

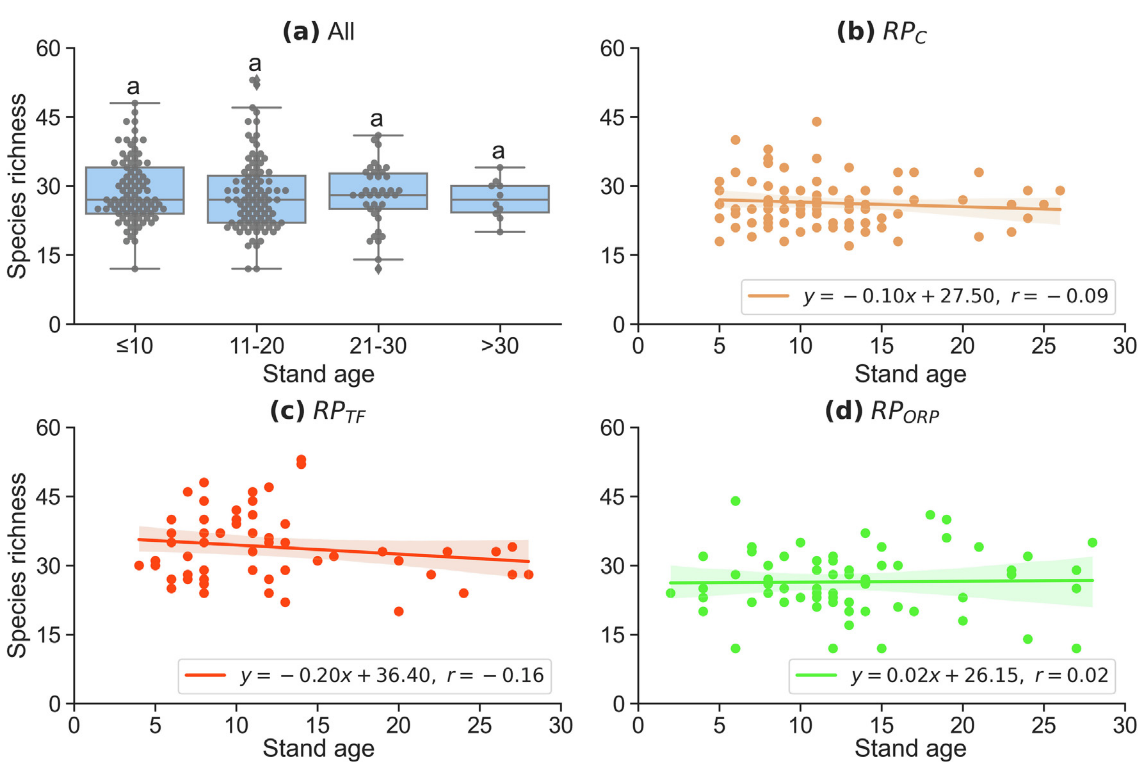

Fig. 4. Plant species richness of rubber plantations against stand age: a) all samples, b) samples of RP_C, c) samples of RP_{TF}, and d) samples of RP_{ORP}. The dots denote the species richness of each sample plot, while the hanging bars, upper fence, lower fence, and line inside the box chart indicate the range of the data beyond the box, the Q3 + 1.5 × IQR, Q1–1.5 × IQR, and the median value, where Q1 and Q3 are the first and third quartiles, respectively, and IQR is the interquartile range.

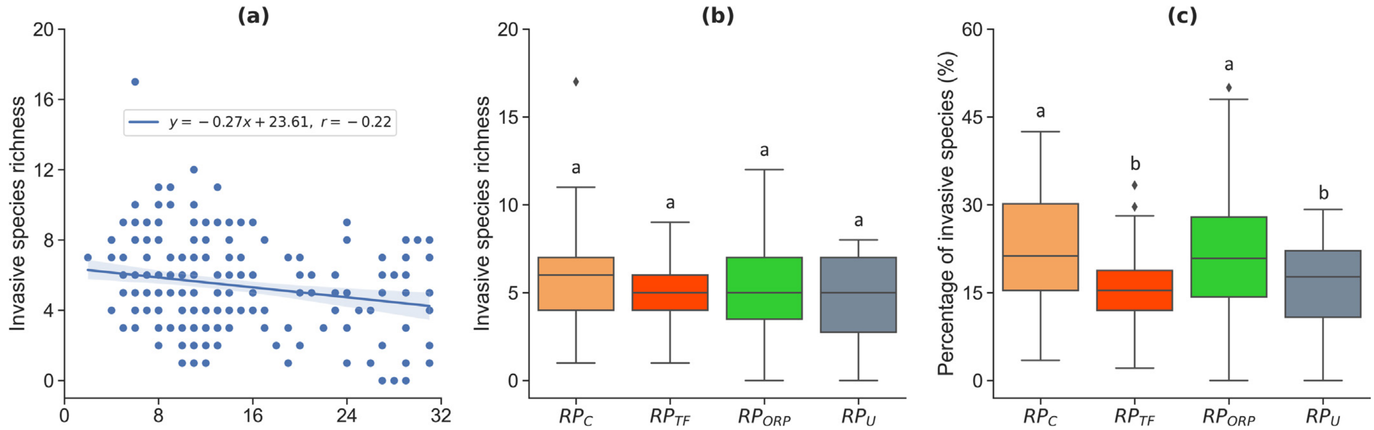

Fig. 5. Changes in invasive species against stand age of rubber plantations and comparison of invasive species between different original land cover types: a) invasive species richness against stand age, b) invasive species richness against original land cover types, c) percentage of invasive plants against original land cover types. The meaning of the hanging bars, upper fence, lower fence and line inside the box chat is the same as in Fig. 4a.

revealed that plant diversity in rubber plantations is at a moderate level (mean species richness at 10 × 10 m quadrats was 28.42 ± 7.26 and the total number of plants observed was 1061). It can serve as the first quantitative basis for the current status of plant diversity in rubber plantations in the GMS, since most previous plot-level studies were unable to quantify and compare the plant diversity status due to variable sampling methods or plot sizes (Katja et al., 2017; Adnan et al., 2020). A high Shannon Evenness Index (closer to 0.92 on average, Fig. S3a) indicated that many species in the rubber plantation occur at more-or-less similar frequencies on the plot, corroborating earlier findings that a drop in management intensity leads to reduced species evenness (Aavik et al., 2008; Reitalu et al., 2009). Intensive human disturbance in rubber plantations presumably decreases the frequency of competitively dominating plant species, hence increasing species evenness. Regarding plant diversity, numerous studies have demonstrated, and we must acknowledge, that the plant diversity of monoculture rubber plantations cannot be compared to that of tropical rainforests (He and Martin, 2015; Katja et al., 2017; Kusuma et al., 2018). Even rubber agroforest (or jungle rubber), which once covered >2 million hectares in Indonesia but has virtually disappeared in the 21st century due to low economic returns, can only be compared to tropical secondary forests (Gouyon et al., 1993; Beukema et al., 2007; Grass et al., 2020). Nonetheless, it is notable that the plant species richness of rubber plantations in this region is typically double or more than that of croplands such as sugarcane, cassava, and pineapple plantations, and that they have a much longer rotation period than these annual crops (Shrestha et al., 2010). With population increase and economic development, cropland has displaced a substantial amount of tropical forests and expanded to the highlands (Zeng et al., 2018; Folberth et al., 2020; Yang et al., 2022), increasing intensification (Egli et al., 2018), all of which poses a threat to biodiversity (Zabel et al., 2019). From a biodiversity conservation perspective, converting tropical forests or intensified croplands to rubber plantations with a 30-year economic life cycle is superior to converting forests to cropland or leaving cropland in its existing state (Peerawat et al., 2018).

There were two aspects that merited special consideration. First, rubber plantations in some regions or countries had very low plant diversity (as few as 12 plants). In Vietnam, for instance, the average species richness was 25.19 ± 6.82, and >10 % of rubber plantations had species richness of <15. At the time of the field visit, the analysis indicated that this was primarily due to intensive agricultural management, such as the excessive use of herbicides (Lan et al., 2022). Second, the plant invasion in rubber plantations was serious. Even though invasive species comprised only 11.22 % of all species surveyed, the average proportion of invasive species per plot reached 19.88 % (Fig. 3d). Previous study conducted in China's Yunnan Province determined that hilly rubber plantations are also highly invasive. There was a total of 82 invasive species discovered, 50 % of which were intentionally introduced and classified as malignant or

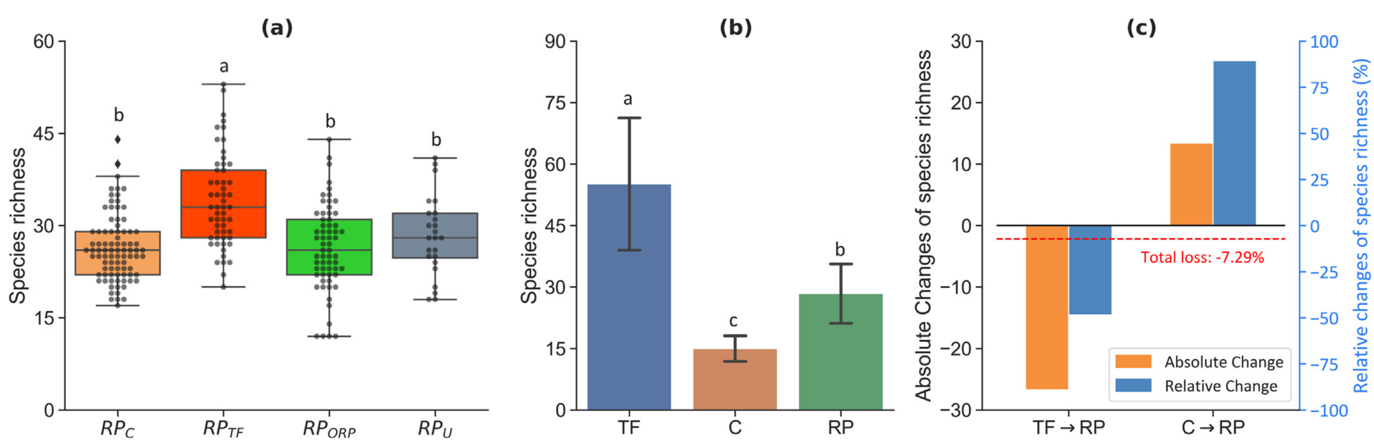

Fig. 6. Plant species richness of different land use types and effects of land use change: (a) rubber plantations converted from different land cover types, (b) comparison between tropical forests (TF), croplands (C), and rubber plantations (RP), and (c) changes in plant species richness when tropical forests and croplands were converted to rubber plantations. Species richness of tropical forests and croplands were derived from the literature, and that of rubber plantations from field surveys in the GMS. The red dot line in (c) shows the estimated loss of plant species richness in the GMS due to the rapid expansion of rubber plantations. The meaning of the hanging bars, upper fence, lower fence and line inside the box chat a) is the same as in Fig. 4a, while the hanging bars in b) represent the standard deviation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

extremely invasive (Gong et al., 2022). Similar results were discovered in Europe, indicating that tree-plantations are hotspots for plant invasions in landscapes with heterogeneous land use (Csecserits et al., 2016). In general, rubber plantations have an urgent need to strengthen plant diversity protection and invasive plant control.

4.2. The influence of stand age and original land cover type on plant diversity

Similar to a previous study on Hainan Island (Liu et al., 2006), we observed a slight decline in plant species richness with stand age in all samples examined in the rubber plantations of the GMS (Fig. 4). It was discovered that the plant species richness of rubber plantations decreased gradually over a period of 5 to 15 years, increased slowly up to the age of 25 years, and then decreased slightly again, indicating a slight downward trend in general. However, another study showed that the plant richness of old rubber plantations (11 plots) was marginally greater than that of young rubber plantations (10 plots), but the difference was not statistically significant (Xing et al., 2012). This trend of change observed in the GMS also differs from a global review of the impacts of tree plantations on the diversity of flora, fauna and microorganisms from 1980 to 2020, which revealed that the biodiversity of reforestation increases with the age of reforestation (Wang et al., 2022). Reforestation includes the conversion of tropical forests to rubber plantations or the continued cultivation of rubber in old rubber plantations. Consequently, when we combine our observations with those of previous studies such as cited above, we can assert that rubber plantations can maintain or even increase plant diversity throughout their 30-year economic life cycle. Given the vast areas that rubber plantations cover, the ability to preserve plant species diversity is very encouraging. In mature rubber plantations, the high intensity of human interventions, such as regular latex harvesting, can account for the slight decline in plant richness with increasing stand age (Lan et al., 2017; Adnan et al., 2020). Average species richness and IQR were also relatively high in young plantations <10 years old (Fig. 4a), which can be explained by canopy characteristics, original land cover types, and human interventions (Hougni et al., 2018). The open canopy of young plantations promotes plant growth, and different land cover types result in different-size seed banks, but intercropping in some young plantations and production management (e.g., weeding and fertilizing) would reduce plant species richness to some extent (Chen et al., 2018; Jung et al., 2019; Lan et al., 2022). Moreover, the species richness of invasive plants decreased with increasing stand age, and the decline rate during the economic cycle was faster than that of total species richness (Figs. 5a & S5), indicating that the plant community of rubber plantations is evolving toward a higher quality. In general, the pursuit of higher species richness in the early cultivation phase has a significant impact on the maintenance of plant diversity throughout the economic cycle in rubber plantations.

It was discovered that the plant diversity of rubber plantations is closely related to the original land cover types. As anticipated, RP_{TF} had the highest species richness, as large number of seed banks in tropical forests can maintain a high level of plant diversity (Yang et al., 2021). However, we also discovered that plant species richness was below 30 at some RP_{TF}, resulting in a higher IQR compared to RP_{ORP} and RP_{C}. Analysis revealed that these RP_{TF} sites were distributed in areas with much lower elevation and slope (about 110 m average elevation and 7° average slope) than rubber plantations with plant richness exceeding 30 (average elevation of about 360 m and slope of about 13°; Fig. S6). Due to favorable geographic conditions, these RP_{TF} are more susceptible to human interventions, such as intercropping with cassava at immature stage (Xing et al., 2012; Hougni et al., 2018). Additional analysis confirmed that 50 % of these plantations were <9.5 years old, indicating that human interventions have a significant impact on plant species richness, even in RP_{TF} with high plant diversity potential (Lan et al., 2022). RP_{U} had the second highest plant species on average, which can be explained by the rise in litter and forest gaps, as well as the decline in human intervention (Lyu et al., 2022). The management intensity of these RP_{U} (very old rubber plantations) is generally lower because economic benefits decline after 20 years and gaps and litter gradually increase due to natural disasters such as hurricanes, drought, and disease (Chen et al., 2012; Olaniyi and Szulczyk, 2022), which all promote the development of understory plants. RP_{C} had the lowest average species richness (26.34 ± 5.37) and the highest proportion of invasive species (22.36 ± 9.87 %, Fig. 5c), which could be attribute to the fact that croplands are managed more intensively (e.g., plowing, weeding, and harvesting) and invasive plants are more likely to be introduced during management (Shrestha et al., 2010; Katja et al., 2017; Hougni et al., 2018).

4.3. Assessing the impact of rubber plantation expansion on plant diversity

Numerous studies have shown that conversion of tropical rainforests to rubber plantations has led to severe declines in plant diversity (Koh and Wilcove, 2008; He and Martin, 2015; Panda and Sarkar, 2020; Singh et al., 2021). However, if other land-use changes are ignored when assessing the impact of rubber plantation expansion on biodiversity, rubber will inevitably be viewed as a detrimental crop, even though it provides an indispensable raw material for various industries. In fact, studies in Hainan and Sumatra islands, Cambodia, or our sample area in the GMS have consistently shown that RP_{TF} accounted for less than or approximately 30 % of the area of new rubber plantations established during the same period (Chen et al., 2018; Grogan et al., 2019; Grass et al., 2020). New rubber plantations were most frequently established on old rubber plantations (Hainan Island and Sumatra) and croplands (37.72 % of the samples in the GMS, Fig. 1c). Moreover, the proportion of RP_{ORP} is likely to increase in the future as more and more land is converted to rubber plantations, while the proportion of RP_{TF} will change in the opposite direction as forest protection measures are gradually strengthened. The conversion of intensively managed croplands to perennial rubber plantations has been of great benefit in maintaining plant diversity. As FAO statistics on the composition of major croplands show (Fig. S7), these croplands would likely continue to be used to grow short-term crops such as cassava, sugarcane, maize, and soybeans if they were not converted to rubber plantations. Croplands typically harbors half or fewer of the plant species found in rubber plantations (Shrestha et al., 2010; Botha et al., 2015), and intensification of crop management poses a major threat to biodiversity (Kehoe et al., 2017; Egli et al., 2018). Even when croplands are converted to perennial oil palm or eucalypt plantations, their plant diversity is often lower than that of rubber plantations (Fitzherbert et al., 2008; Xiang et al., 2012; Xing et al., 2012). In addition, previous studies had shown that rubber plantations have a higher beta plant diversity and fewer alien species than oil palm plantations (Katja et al., 2017). Considering the diversity and proportion of original land cover types, we estimated that the total loss of plant richness due to rubber plantation expansion in the GMS area over the past 30 years was 7.29 %, which was 15.05 % of the loss caused by considering the original land cover types of rubber plantations as tropical forests only.

4.4. Uncertainties and limitations

Due to personnel and time constraints, we are unable to conduct very detailed surveys in the wild, so there will be some plants that have not been investigated. Secondly, although random samples were taken whenever possible, the actual survey tended to select rubber plantations that were relatively easy to visit. For example, a relatively flat plantation was chosen over a steeply sloping one, despite the latter having a higher species diversity (Fig. S6). Consequently, the average plant species richness of rubber plantations in the GMS is likely greater than the results presented here. Nevertheless, this fieldwork was conducted by the same teams and consistent methods in the GMS, so it can reflect the species richness of rubber plantations in the different countries at the same level.

Thirdly, when assessing the impact of rapid expansion of rubber plantations on plant diversity, the proportion of different land types that are converted has a substantial impact on the assessment results. Due to the complex climatic conditions and highly fragmented landforms in the tropics (Brinck et al., 2017; Taubert et al., 2018; Qiu et al., 2019), high-precision maps of rubber plantations and land conversion in the GMS region have not yet been developed using remote sensing (nor are such public datasets currently available). Therefore, these percentages can only be determined statistically using ground survey samples. In the future, it is critical to use big data from remote sensing to improve the monitoring of rubber plantation dynamics and land conversion in these regions, which can provide reliable baseline data for ecological impact assessment.

4.5. Policy implication for biodiversity conservation in rubber plantations

To protect and enhance plant diversity in rubber plantations, numerous conservation measures have been proposed, including semi-natural management (Lan et al., 2017), agroforestry with clonal varieties (Warren Thomas et al., 2019), preservation of forest fragments and buffer zones (Tata et al., 2011), and non-use of herbicides (He and Martin, 2015; Lan et al., 2022). Our study revealed that plant species richness in rubber plantations can be maintained essentially unchanged throughout the rotation cycle (Fig. 4), which provides new insights for plant diversity conservation, i.e., when establishing rubber plantations, maintain plant diversity as much as possible. Specific advices include avoiding the complete removal of existing vegetation and root systems of previous land cover while establishing new rubber plantations without significantly affecting rubber cultivation and management (Vrignon-Brenas et al., 2019). Intercropping is not recommended for new rubber plantations with poor growing conditions since it is difficult to achieve higher economic returns, and heavy human intervention leads to loss of plant species richness and increases the likelihood of plant invasion (Katja et al., 2017; Gong et al., 2022). Furthermore, in regions suitable for rubber cultivation, croplands with poor geographical conditions (e.g., mountainous and sloping land) are encouraged to be converted into rubber plantations. On the one hand, rubber plantations have ecological functions such as a longer rotation cycle, higher plant species richness, and better soil and water conservation compared to intensively managed croplands (Xiang et al., 2012); on the other hand, this measure also significantly reduces the pressure on tropical forests to be converted into rubber plantations (Grogan et al., 2019; Wang et al., 2020). The establishment of rubber plantations in the future may refer more to the United Nations Sustainable Development Goals (SDGs), which aim to manage landscapes to improve livelihoods while ensuring the conservation and sustainable use of terrestrial ecosystems (United Nations, 2015).

5. Conclusion

The rapid expansion of rubber plantations over the past few decades has contributed to the increased importance of the plantation ecosystem in the GMS, and its impacts on the ecological environment, such as biodiversity, have attracted considerable attention. Using data from extensive field surveys and dense time-series satellite imagery, the current status and extent of plant diversity in rubber plantations in the six GMS countries were examined, as well as the overall impact on plant diversity in this region. The results indicate that plant diversity on a 10-m quadrat in rubber plantations is 28.69 ± 7.35, approximating half and twice the richness of tropical forests and intensively managed croplands, respectively. The total number of plants observed in the GMS was 1061, but the proportion of invasive species was significant high, at 11.22 %. Analysis of 30 years of satellite imagery reveals that the majority of these plantations were established on cropland (RP_C, 37.72 %), old rubber plantations (RP_{ORP}, 27.63 %), and tropical forests (RP_{TF}, 24.12 %). Thankfully, the plant diversity of rubber plantations can remain essentially unchanged in a 30-year cycle, and the number of invasive plants diminishes as the age of the stand increases. Taking into account diverse land conversions and age-related changes in plant diversity, the total loss of species richness due to the rapid expansion of rubber plantations was 7.29 %, which is far below the traditional estimates based solely on tropical forest conversion. In general, maintaining higher species richness at early stages of cultivation has important implications for biodiversity conservation in rubber plantations. Feature assessments of the rapid expansion of rubber plantations on biodiversity in the GMS will require more detailed land-use data.

CRediT authorship contribution statement

Bangqian Chen: Conceptualization, Methodology, Software, Validation, Investigation, Writing – original draft, Writing – review & editing, Funding acquisition. **Jun Ma:** Formal analysis, Visualization, Writing – review & editing. **Chuan Yang:** Investigation, Validation, Resources. **Xiangming Xiao:** Conceptualization, Formal analysis. **Weili Kou:** Writing – review & editing. **Zhixiang Wu:** Investigation, Funding acquisition. **Ting Yun:** Writing – review & editing. **Zar Ni Zaw:** Investigation. **Piyada Nawan:** Investigation. **Ratchada Sengprakhon:** Investigation. **Jiannan Zhou:** Investigation. **Jikun Wang:** Investigation. **Rui Sun:** Investigation, Funding acquisition. **Xicai Zhang:** Investigation. **Guishui Xie:** Conceptualization. **Guoyu Lan:** Conceptualization, Methodology, Resources, Visualization, Supervision, Funding acquisition, Writing – review & editing.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This research was funded in part by the National Natural Science Foundation of China (42071418), and the Natural Science Foundation of Hainan Province (422CXTD527, 2019RC329), Earmarked Fund for China Agriculture Research System (CARS-33), and Central Public-interest Scientific Institution Basal Research Fund (NO. 1630022022003), and the Lancang–Mekong international cooperation project of the Ministry of Foreign Affairs (grant no. 081720203994192003). We thank the U.S Geological Survey (USGS) EROS Data Center and European Space Agency (ESA) for their data sources, Google for the GEE platform, and Dr. Wu Qiusheng for his excellent geospatial package.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.162505.

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