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Grass Communities Differ Floristically Under Different Dominant Trees in Savannas in Thailand and Cambodia

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ABSTRACT

Southeast Asian savannas are some of the least studied ecosystems, with understanding of their function and resilience limited by a lack of understanding of grass species richness and composition. Since savannas are characterized by their grassy ground layer, we conducted field surveys in Thailand and Cambodia to assess grass community composition under different dominant tree genera. We conducted field surveys in four savanna ecosystems characterized by (i) *Dipterocarpus*, (ii) *Pinus*, (iii) *Pterocarpus*, and (iv) *Shorea* tree genera. In each, we recorded grass species composition and richness. We assessed differences in composition using PERMANOVA, patterns of grass species discovery using species accumulation curves, and common species with relative frequency distributions. In total, we recorded 160 unique grass species. These savannas support distinct grassy assemblages, with diverse patterns of species accumulation, richness, and overlap. Common grasses were frequently shared between ecosystems. Grass assemblages were functionally similar, comprising mostly C4 perennial species. Across the ecosystems, grass communities were mostly composed of tribe Andropogoneae, although we recorded common fire-adapted C3 grasses including *Vietnamosasa ciliata* (A. Camus) T.Q. Nguyen and *Vietnamosasa pusilla* (A. Chev. & A. Camus) T.Q. Nguyen. The savanna ecosystems of Thailand and Cambodia are characterized by *Dipterocarpus*, *Pinus*, *Pterocarpus*, and *Shorea* tree species, which support distinct grass assemblages. Diversity varies across savanna landscapes, with the highest grass species diversity found in the *Dipterocarpus* and *Shorea* savannas. Increased sampling is necessary to fully characterize the grass flora of Southeast Asian savannas and their responses to environment.

บทคัดย่อวัตถุประสงค์

สะวันนาในเอเชียตะวันออกเฉียงใต้เป็นหนึ่งในระบบนิเวศที่มีการศึกษาน้อยที่สุดในแง่ของหน้าที่และความยืดหยุ่นเชิงนิเวศวิทยา (resilience) ซึ่งถูกจำกัดโดยการขาดความเข้าใจในเรื่องของความหลากหลายและองค์ประกอบของพืชวงศ์หญ้า เนื่องจากสะวันนาถูกกำหนดคุณลักษณะโดยพืชพื้นล่างจำพวกพืชวงศ์หญ้าการสำรวจภาคสนามในประเทศไทยและกัมพูชาถูกใช้เพื่อประเมินองค์ประกอบของสังคมของพืชวงศ์หญ้าภายใต้สภาพของระบบนิเวศแบบสะวันนาที่มีสกุลของไม้ยืนต้นที่เป็นสกุลเด่นแตกต่างกัน วิธีการศึกษา:การสำรวจภาคสนามในระบบนิเวศแบบสะวันนาแบ่งออกเป็นสี่ประเภทตามไม้ยืนต้นที่เป็นไม้เด่น คือ พืชสกุลยางนา (*Dipterocarpus* C.F.Gaertn.) พืชสกุลสนเบา (*Pinus* L.) พืชสกุลประดู่(*Pterocarpus* Jacq.) และพืชสกุลสาละ (*Shorea* Roxb. ex C.F.Gaertn.) องค์ประกอบและความหลากหลายของพืชวงศ์หญ้าถูกบันทึกในระบบนิเวศแบบ

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สะวันนาแต่ละประเภท ความแตกต่างขององค์ประกอบของพืชวงศ์หญ้าถูกประเมินโดยใช้การวิเคราะห์ความแปรปรวนหลายตัวแปรแบบเรียงสับเปลี่ยน (PERMANOVA) และรูปแบบของการพบชนิดของพืชวงศ์หญ้า (species discovery) ในภาคสนามถูกแสดงโดยเส้นโค้งการสะสมชนิด (species accumulation curves) และการกระจายของความถี่สัมพัทธ์ของชนิดที่พบบ่อย (common species with relative frequency distributions) ผลการศึกษา:มีพืชวงศ์หญ้าทั้งหมด 160 ชนิดจากการสำรวจภาคสนาม ระบบนิเวศแบบสะวันนาแต่ละประเภทมีสังคมของพืชวงศ์หญ้าแตกต่างกันซึ่งแสดงให้เห็นจากเส้นโค้งการสะสมชนิด ความมากชนิด (species richness) และการซ้อนทับของชนิด (species overlap) ในรูปแบบที่หลากหลาย พืชวงศ์หญ้าที่พบบ่อยมักปรากฏร่วมกันในระบบนิเวศแบบสะวันนาแบบต่างๆ สังคมของพืชวงศ์หญ้าในสะวันนามีหน้าที่เชิงนิเวศวิทยาเหมือนกัน ซึ่งส่วนใหญ่ประกอบด้วยพืชวงศ์หญ้าหลายปีที่เป็นพืช C4 สังคมพืชวงศ์หญ้าส่วนใหญ่ระหว่างระบบนิเวศแบบสะวันนามักประกอบด้วยหญ้าในเผ่า Andropogoneae แม้ว่าจะพบไผ่โจด (*Vietnamosasa ciliata* (A.Camus) T.Q. Nguyen) และไผ่เพ็ก (*Vietnamosasa pusilla* (A.Chev. & A.Camus) T.Q. Nguyen) ซึ่งเป็นพืชวงศ์หญ้า C3 ที่พบได้ทั่วไปและมีการปรับตัวให้เข้ากับไฟได้เช่นกัน ข้อสรุป:ระบบนิเวศแบบสะวันนาในประเทศไทยและกัมพูชาถูกกำหนดคุณลักษณะโดยพืชสกุลยางนา พืชสกุลสนเบา พืชสกุลประดู่และพืชสกุลสาละ ซึ่งรองรับสังคมของพืชวงศ์หญ้าที่แตกต่างกัน ความหลากหลายของพืชวงศ์หญ้าสูงสุดในระบบนิเวศแบบสะวันนาที่มีไม้ยืนต้นสกุลประดู่และสกุลสาละเป็นไม้เด่น จากการศึกษาในครั้งนี้ชี้ให้เห็นว่า การสุ่มตัวอย่างที่มากขึ้นมีความจำเป็นในการกำหนดคุณลักษณะของพืชวงศ์หญ้าและการตอบสนองต่อสิ่งแวดล้อมของสะวันนาในเอเชียตะวันออกเฉียงใต้ให้สมบูรณ์.

1 | Introduction

The savannas of Southeast Asia are some of the most poorly known in the world and are threatened by conversion to agriculture, afforestation schemes (Joshi et al. 2018; Kumar et al. 2020) and accelerating climate change (Ratnam et al. 2016). These threats are exacerbated by the legacy of colonial perceptions of savannas as degraded forests (Ratnam et al. 2011). Savannas, which are maintained by fire (Bond and Keeley 2005) and/or herbivory (Staver et al. 2021), feature a more or less continuous grass cover (Bond and Parr 2010) and support tree cover from 0% to closed canopy formations (Archibald, Bond, et al. 2019; Archibald, Hempson, and Lehmann 2019), and are a dominant vegetation formation across mainland Southeast Asia (Mistry 2000). However, botanical research in Asian savannas has been limited, with even basic floristic surveys few in number and scope, and especially lacking in countries such as Laos and Cambodia, and Indonesian islands including the Lesser Sunda Islands (Middleton et al. 2019; Mistry 2000; Stott 1984, 1990).

Asian savannas support the livelihoods of millions of people, with many ecosystem services partially to fully dependent on the herbaceous layer (Mistry 2000). Such contributions include wallowing and grazing for livestock (BirdLife International Cambodia Programme 2012), watershed protection (Nguyen and Baker 2016), habitat for herbivores and birds (Rawat and Adhikari 2015; Sankaran 2009), and carbon sequestration (Kumar et al. 2021). While studies on Asian savanna systems have increased in recent years, these primarily focused on the tree component (e.g., Gopalakrishna et al. 2024; Nguyen et al. 2019; Nguyen and Baker 2016; Pletcher et al. 2022; Schwartz et al. 2025, but see Khaing et al. 2019; Sutomo et al. 2020; Sutomo and van Etten 2021) and understanding of their composition, function, and resilience remains limited, hampered by a lack of understanding of ground layer richness and diversity.

Asian savannas are distributed across a wide range of mean annual rainfall from 700 mm to 3200 mm (Ratnam et al. 2016), higher rainfall than savannas on other continents (Archibald, Bond, et al. 2019; Lehmann et al. 2011). These savannas are generally characterized by their dominant tree floras, such as the lontar savanna in Indonesia, named after the lontar palm (*Borassus flabellifer*) (Kurniawan and Yuniati 2015). Savannas in Asia can be separated into broad ecological categories such as deciduous, which in some areas includes the misclassified Deciduous Dipterocarp Forest (DDF) (Tornorsam et al. 2024) and spiny savanna (Ratnam et al. 2016), and coniferous, including pine savanna which is often interspersed with DDF. In Thailand and Cambodia, we focused on three classes of deciduous savannas, characterized by the genera *Dipterocarpus* C.F.Gaertn., *Pterocarpus* Jacq., and *Shorea* Roxb. ex C.F. Gaertn., and coniferous savanna dominated by the genus *Pinus* L. Details of this classification are provided in the Methods, but broadly follow Ratnam et al. (2016), where fire-maintained mixed deciduous savannas and *Pinus* savannas occur across East, South, and Southeast Asia. Tropical pine savanna systems are also scattered through North and Central America, and include extensive lowland pine savannas in Belize (Michelakis et al. 2014).

Across Southeast Asia, trees from different plant families dominate savannas. It is unknown whether this variability aligns with grass species richness and composition, however it is likely that between deciduous and pine savannas at least, large differences are present in part due to key differences in tree characteristics such as allometry and nutrient cycling (Ratnam et al. 2016). Where different savanna types are found, associations with distinct tree floras may result in distinct herbaceous floras, such as under the infertile soil conditions of pine savanna (Kellman and Miyanishi 1982) where ground layer flora display adaptations to low soil fertility as well as frequent fire, often resulting in high levels of endemism (Noss et al. 2015). Additionally, associations between tree and herbaceous floras may reflect not only their influence on soil fertility (Zhou et al. 2018) but also their joint responses to underlying environmental factors including soil conditions (Marage and Gégout 2009), climate, and disturbance regimes. While Asian pine savannas are likely to be functionally similar to those in tropical America (Ratnam et al. 2016), Asian deciduous savannas are more floristically similar to African

savannas and miombo (Dexter et al. 2015) perhaps due to historical herbivore assemblages of similar size classes (Ratnam et al. 2019).

Grass composition directly affects the physiognomic structure of the savanna (Solofondranohatra et al. 2018) as well as impacting landscape fire variability and herbivore consumption through trait differences (Archibald and Hempson 2016; Simpson et al. 2022). The grassy ground layer of Asian savannas contains considerable undescribed species diversity that, given current levels of unprecedented biodiversity loss and increasing land transformation (Zhao et al. 2006), is at risk of extinction before being described (Nerlekar et al. 2022). Further, the seasonal flowering of grassy taxa poses a challenge for recording species and accurately assessing species richness and composition, and this knowledge gap hinders management and protection of the ground layer (Bond and Parr 2010). We undertook surveys of the ground layer grassy flora in four savanna ecosystems across Cambodia and Thailand to characterize richness and composition.

We addressed the following questions:

1. Do grass communities in savannas differ depending on the dominant tree genera?
2. If grass communities differ, how many grass species are shared between the savanna ecosystems?

2 | Methods

2.1 | Study Regions and Sites

We conducted field surveys in four savanna ecosystems across Cambodia and Thailand to characterize the grass species composition and richness of these ecosystems.

We investigated the ground layer grass diversity and richness at 50 savanna sites in Northeastern Cambodia and Central and Eastern Thailand (Figure 1a). Sampling took place in October and November 2018 at the end of the rainy season to maximize grass flowering for species identification. Following Ratnam et al. (2016), we categorized sites to reflect differences in environment and tree composition to examine four distinct savannas (Table S1).

2.1.1 | *Dipterocarpus* Savanna (Dipterocarpaceae)

Dipterocarpus savanna was sampled in Cambodia in the BirdLife International-managed Western Siem Pang Protected Area. Western Siem Pang covers a 654 km^2 mosaic of savanna and forest which experiences fire (pers. obs.). The dominant tree species are *Dipterocarpus obtusifolius* Teijism. ex Miq., *Dipterocarpus tuberculatus* Roxb., *Dipterocarpus* sp., *Shorea siamensis*, and *Terminalia catappa* L (Figure 1b). The 10 sites in *Dipterocarpus* savannas span an altitude of 56–122 m (Table S1) and experience seasonal rainfall, with a mean rainfall of 2184 mm and a mean annual temperature of 26.7°C (Fick and Hijmans 2017) (Figure S1). Both *Shorea* and *Dipterocarpus* are in the family Dipterocarpaceae, but relative to the *Shorea* ecosystems sampled, the *Dipterocarpus* sites are characterized by higher rainfall and temperatures (Fick and Hijmans 2017). The soils in Western Siem Pang are old and shallow, often with a thick plinthite or even lateritic layer (BirdLife International Cambodia Programme 2012).

2.1.2 | *Pinus* Savanna (Pinaceae)

Pinus savanna, dominated by *Pinus merkusii* Jungh. & de Vriese or *Pinus kesiya* Royle ex. Gordon (Figure 1c), was sampled in Thailand in Phu Soi Dao and Thung Salaeng Luang National Parks which cover 340 and 487 km^2 respectively and experience fire (pers. obs.). The 10 *Pinus* savanna sites sampled span an altitude of 828 m–1547 m (Table S1), and have seasonal rainfall with a mean rainfall of 1124 mm and a mean annual temperature of 21.6°C (Fick and Hijmans 2017) (Figure S1). Soils in Phu Soi Dao vary from pH 4.78–6.20, and soil organic matter ranges from 0.89 to 10.70 (Pongthornpruek et al. 2013). The geology in Thung Salaeng Luang is shale and sandstone (Boonyanuphap and Hansawasdi 2011).

2.1.3 | *Pterocarpus* Savanna (Fabaceae)

Pterocarpus savanna, characterized by *Pterocarpus macrocarpus* and other *Pterocarpus* sp., *Buchanania lanzan* Spreng., and *Xylia* sp., was sampled in Thailand in Nam Nao and Phu Phan National Parks which cover 966 and 664 km^2, respectively, and experience fire (pers. obs.). The seven sites in *Pterocarpus* savanna (Figure 1d) span an altitude of 218–821 m (Table S1), and experience seasonal rainfall, with a mean rainfall of 1080 mm and a mean annual temperature of 21.6°C (Fick and Hijmans 2017) (Figure S1). The geology in Phu Phan is sandstone (Veeravinantanakul et al. 2018).

2.1.4 | *Shorea* Savanna (Dipterocarpaceae)

Shorea savanna, dominated by *Shorea obtusa* Wall. ex Blume, *Shorea siamensis* Miq., *Pterocarpus macrocarpus* Kurz, *Ochna integerrima* (Lour.) Merr., and *Vitex pinnata* L (Figure 1e), was sampled in Thailand in Nam Nao, Phu Phan, Phu Soi Dao and Thung Salaeng Luang National Parks which experience fire (pers. obs). The 23 sites in *Shorea* savanna span an altitude 218–752 m (Table S1), and experience seasonal rainfall with a mean rainfall of 1317 mm, and a mean annual temperature of 21.4°C (Fick and Hijmans 2017) (Figure S1). The geology in Phu Phan is sandstone (Veeravinantanakul et al. 2018) and the geology in Thung Salaeng Luang is shale and sandstone (Boonyanuphap and Hansawasdi 2011).

2.2 | Grass Richness and Composition

Grass species composition was collected following the protocol outlined in Vorontsova et al. (2016) and Lehmann et al. (2014). Each site comprised four transects each of 25 m radiating from the centre of a 0.25 ha area in North, South, East, and West directions. At the centre of a site, a circular plot 1 m in diameter

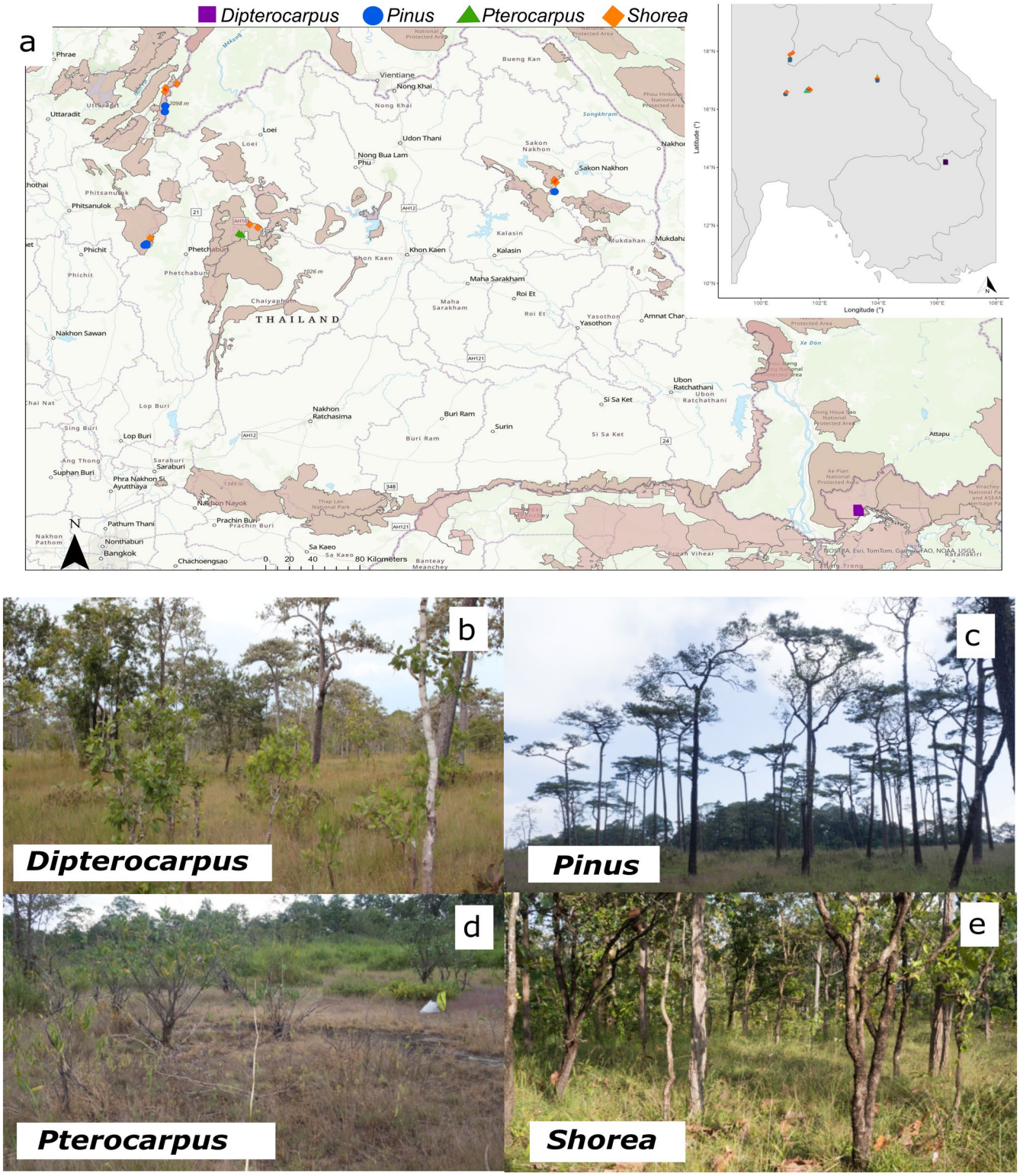


FIGURE 1 | (a) Map of Thailand and Cambodia that displays sites colored by savanna type, with protected areas in pink, protected area data from NEP-WCMC and IUCN (2024), Protected Planet: The World Database on Protected Areas (WDPA) and World Database on Other Effective Area-based Conservation Measures (WD-OECM) [Online], May 2024, Cambridge, UK: UNEP-WCMC and IUCN. Available at: http://www.protectedplanet.net/. Photo examples of each of the four savanna types sampled are depicted in (b) *Dipterocarpus*, (c) *Pinus*, (d) *Pterocarpus* and (e) *Shorea*. Photo credits: c, d and e by Watchara Arthan, b by Jess Rickenback.

was located. Circular plots are recommended for sampling grass and forb diversity (Lehmann et al. 2014) in part due to a circle containing less edge than a square (Packalen et al. 2023), thus reducing uncertainty regarding decisions over sampling inclusion. The circular plot method has successfully been used to examine ground layer plant composition across Madagascar (Vorontsova et al. 2016; Solofondranohatra et al. 2018, 2020) and Zambia (Wieczorkowski et al. 2024). One meter diameter

circular plots were placed at 5 m intervals along each of the four transects. In total, 21 × 1 m diameter plots constituted a site that assesses a total of 16.5 m^2 for herbaceous species richness and composition. In each plot, each species was recorded as present whether fertile or sterile. Data from a site therefore comprises counts of all grass species over 21 plots covering a 16.5 m^2 area that results in a frequency measure for each species at a site. Species were recorded a maximum of once per plot, and thus at each site, one species could be recorded a maximum of 21 times.

For Cambodian specimens, two vouchers per species were made and specimens deposited at the National Herbarium of Cambodia (RUPP) with duplicates deposited at the Royal Botanic Garden Edinburgh (E). For fertile Thai specimens, one voucher was made and deposited at Bangkok Forest Herbarium (BKF). To resolve genus- and species-level identifications, a combination of local floras, reference to herbarium specimens, and consultations with taxonomic experts at the Royal Botanic Garden Edinburgh and Royal Botanic Gardens, Kew was employed.

2.3 | Analyses of Grass Species Composition

To characterize the prevalence of grass species at each savanna type, and thus further infer patterns of species occupancy and functional composition, we identified the most common grasses by dividing the number of plots a species was recorded in by the overall number of plots in that savanna ecosystem to give a measure of relative frequency. We assigned these species to tribe, along with characterizing growth form as rhizomatous and/or caespitose and their life history as annual or perennial using GrassBase (Clayton et al. 2006), Plants of the World Online (POWO 2022), floras and peer-reviewed articles (Table S2). These taxonomic, morphological and life history characters have previously been shown to be important in understanding the responses of grass communities to disturbance (e.g., Solofondranohatra et al. 2021) and were visualized to show species common among savanna types both in composition but also in function.

To understand site level distinctiveness of grass species composition of the *Pinus*, *Pterocarpus*, *Shorea* and *Dipterocarpus* savannas, a permutational multivariate analysis of variance (PERMANOVA) in "vegan" v2.5-7 (Oksanen et al. 2020) was undertaken using grass species as present or absent via a community dissimilarity matrix created using the vegan package and the functions "adonis2" and "vegdist" using the "jaccard" method (appropriate for presence-absence data). To avoid pseudoreplication, presence/absence data were aggregated at the site level (21 plots per site). We also tested the assumption of homogeneity of multivariate dispersion using the "betadisper" function. We set the community dissimilarity matrix as the independent variable and savanna type as the dependent variable and conducted pairwise comparisons between the grass communities of all savanna types. In order to assess grass composition robustly we ran the analyses under different scenarios; first we retained all species to acknowledge the disproportionate contribution of rare species to patterns of local richness in other tropical ecosystems (Hubbell 2013). Second, we removed all singletons and doubletons—species recorded only once or twice in the dataset—to avoid a strong signal of difference caused stochastically. Finally, to assess the possibility of skewed results by the inclusion of 32 unknown species, analyses were undertaken both with the full data set and with unidentified species removed. We visualized the overall distinctiveness of grass communities between savanna types using Euler plots in "eulerr" v7.0.0 (Larsson 2022) where plots are area-proportional.

To determine how well our field collections characterized grass species assemblages among savanna types, the rank of grass species among sites was compiled by summing the number of sites in each savanna type where a unique species was recorded. On the basis of this, patterns of grass species discovery were calculated at a site level using the specaccum function in the package "vegan" v2.5-7 (Oksanen et al. 2020) to infer species accumulation curves with the random method, which adds sites in a random order for 100 permutations.

3 | Results

3.1 | Analyses of Grass Species Composition

3.1.1 | *Dipterocarpus* Savanna

Across the 10 sites, median richness was 10 grass species per site with 73 grasses recorded in total. Of these, 28 were identified to species (38%), 26 to genus (36%), and 19 were unknown (26%). None were found in all sites, and 34 were found at only one site. On the basis of relative frequency analyses, the top 25% most common grass species were the C3 grasses *Vietnamosasa ciliata* (A. Camus) T.Q. Nguyen and *Sacciolepis indica* Chase, and the C4 grasses *Eremochloa eriopoda* C.E. Hubb, a *Chrysopogon* sp., *Germainia capitata* Balansa & Piotr., *Heteropogon triticeus* (R.Br.) Stapf ex Craib, *Ischaemum muticum* L., and *Isachne puberula* Bor (Figure 2b). These are a mix of rhizomatous and caespitose forms and annual and perennial life histories (Table S2).

3.1.2 | *Pinus* Savanna

Across the 10 sites, median richness was eight grass species per site, with 37 grass species recorded in total. Of these, 18 were identified to species (49%), 14 to genus (38%) and five were unknown (14%). None were found in all sites, and 21 in only one site. On the basis of relative frequency analyses, the top 25% most common grass species were *Apocopis intermedia* (*A. Camus*) Chai-Anan, *Schizachyrium brevifolium* (Sw.) Nees ex Buse, *Schizachyrium sanguineum* (Retz.) Alston, *Arundinella setosa* Trin., *Themeda triandra* Forssk, and *Pseudopogonatherum speciosum* (Debeaux) Ohwi (Figure 2c), all of which use the C4 photosynthetic pathway, and which present as a mix of rhizomatous and caespitose, annual and perennial (Table S2).

3.1.3 | *Pterocarpus* Savanna

Across the seven sites examined, median richness was 10 grass species per site, with 34 grass species recorded in total. Of these, 28 were identified to species (82%), five to genus (15%) and one was unknown (3%). None were found in all sites, and 15 at only one site. On the basis of relative frequency analyses, the top 25% most common grass species were *Arundinella setosa*, *Tripogon*

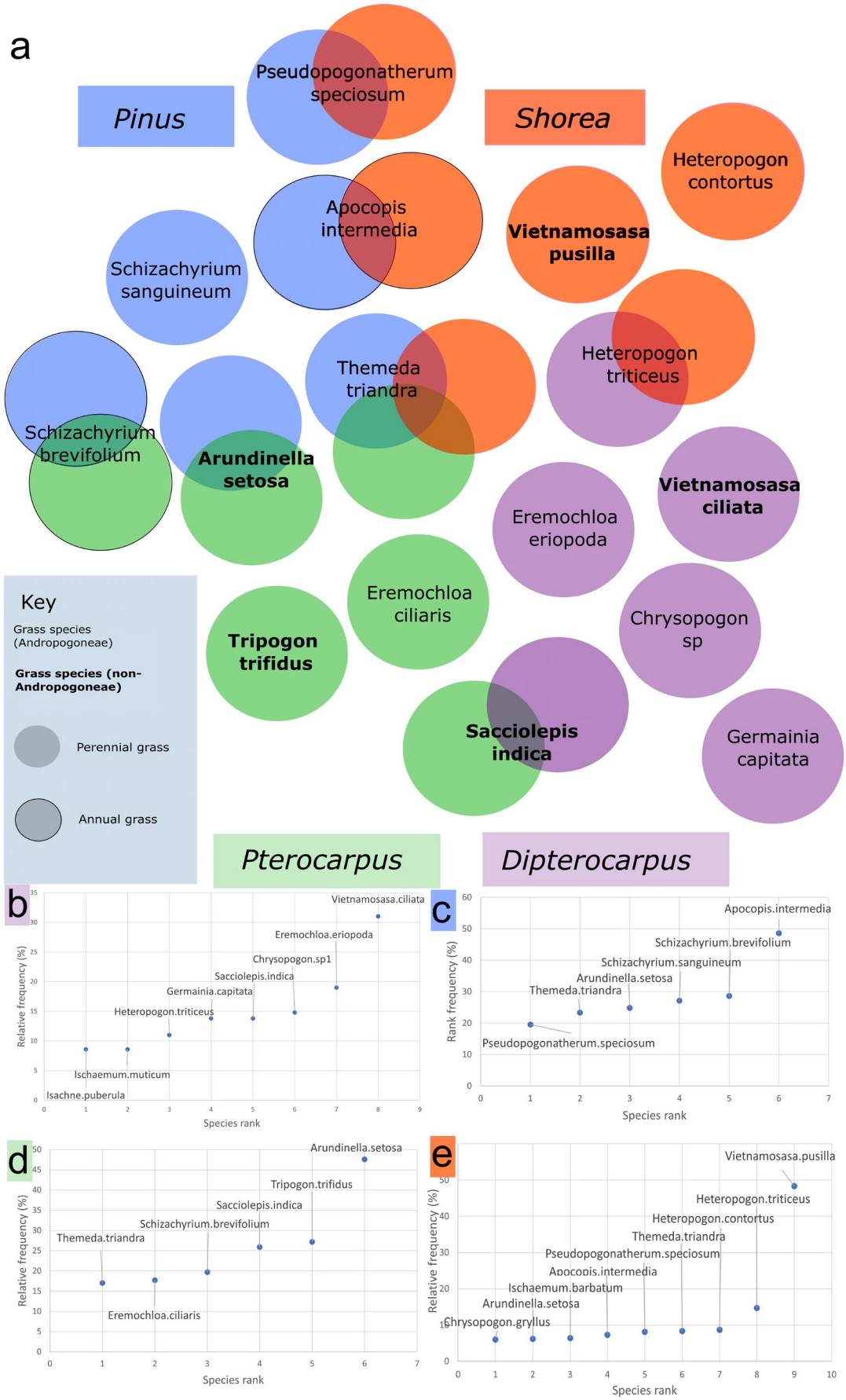


FIGURE 2 | Legend on next page.

FIGURE 2 | Representation of (a) the six most common grass species recorded in each savanna ecosystem based on relative frequency, and (b–e) the top 25% of species from relative frequency distributions underpinning the plot in (a). In (a), species shared between savanna types are depicted in overlapping circles. *Dipterocarpus* savannas (purple), *Pterocarpus* savannas (green), *Pinus* savannas (blue) and *Shorea* savannas (orange) have multiple shared common species. All grasses are from the tribe Andropogoneae except for those shown in bold (*Arundinella setosa* from Arundinelleae, *Vietnamosasa ciliata and Vietnamosasa pusilla* from Bambuseae, *Sacciolepis indica* from Panicoideae, and *Tripogon trifidus* from Cynodontideae). Annual grasses are indicated with a black outline. The relative frequency plots (b–e) show the most common 25% of grass species (C4 and C3 combined) by savanna type where relative frequency represents the number of plots a species was recorded in divided by the number of plots in that savanna type; (b) *Dipterocarpus*, (c) *Pinus*, (d) *Pterocarpus*, (e) *Shorea*.

TABLE 1 | Each savanna type is characterized by a unique grass community based on pairwise analyses of grass species composition (presence-absence) using a PERMANOVA in "vegan" v2.5-7 (Oksanen et al. 2020) using the "jaccard" method which is based on presence-absence data, with savanna type as the dependent variable.

Savanna type comparison	Regions	*p*	Pseudo *F*	R^2	Dispersion *p*
All savanna types	Cambodia and Thailand	0.001	2.53	0.14	0.003
Dipterocarpus vs. *Shorea*	Cambodia and Thailand	0.001	2.48	0.07	0.69
Shorea vs. *Pterocarpus*	Thailand	0.001	2.23	0.07	0.001
Shorea vs. *Pinus*	Thailand	0.004	2.46	0.07	0.02
Pinus vs. *Pterocarpus*	Thailand	0.001	3.29	0.18	0.42
Dipterocarpus vs. *Pinus*	Cambodia and Thailand	0.001	2.7	0.13	0.13
Dipterocarpus vs. *Pterocarpus*	Cambodia and Thailand	0.001	2.5	0.14	0.03

trifidus Munro ex Stapf, *Sacciolepis indica*, *Schizachyrium brevifolium*, *Eremochloa ciliata* Chinnock, and *Themeda triandra* (Figure 2d), of which all are C4 grasses except *Sacciolepis indica* and all of which present as a mix of rhizomatous and caespitose forms, and annual and perennial life histories (Table S2).

3.1.4 | *Shorea* Savanna

Across the 23 sites examined, median richness was eight grass species per site, with 72 grass species recorded in total. Of these, 41 were identified to species (57%), 21 to genus (29%), and 10 were unknown (14%). None were found in all sites, and 36 in only one site. On the basis of relative frequency analyses, the top 25% most common grass species were *Vietnamosasa pusilla* (A. Chev. & A. Camus) T.Q. Nguyen, *Heteropogon triticeus* (R.Br.) Stapf ex Craib, *Heteropogon contortus* (L.) P.Beauv. ex Roem. & Schult., *Themeda triandra*, *Pseudopogonatherum speciosum*, *Apocopis intermedia*, *Ischaemum barbatum*, *Arundinella setosa*, and *Chyrsopogon gryllus* (L.) Trin (Figure 2e). *Vietnamosasa pusilla* is a rhizomatous C3 bamboo and was by far the most common species within the *Shorea* savanna. The remaining common grass species are all C4 and present as a mix of rhizomatous and caespitose forms, and annual and perennial life histories (Table S2, Figure 2e).

3.2 | Distinctiveness of Grass Communities Among Savanna Types

Common species, as assigned based on relative frequency distributions, frequently occurred in more than one savanna ecosystem (Figure 2a). *Sacciolepis indica* was a common grass in both *Pterocarpus* and *Dipterocarpus* savannas. *Dipterocarpus* also shared the common grass *Heteropogon triticeus* with *Shorea* savanna. *Pinus* and *Shorea* savanna shared *Pseudopogonatherum speciosum* as well as *Apocopis intermedia*. *Schizachyrium brevifolium* and *Arundinella setosa* were shared common grasses in both *Pinus* and *Pterocarpus* savannas. Only one grass was common to more than two savanna ecosystems: *Themeda triandra* was common to *Pinus*, *Pterocarpus* and *Shorea* savannas.

PERMANOVA analyses including all grass species based on site level presence-absence data demonstrated significant differences among all pairwise comparisons of grass communities of the savanna types (Table 1). The exclusion of grass species unknown to genus level did not change the results, nor did the exclusion of singletons and doubletons (Table S3). Dispersion differed significantly in comparisons between *Dipterocarpus* and *Pterocarpus*, *Shorea* and *Pterocarpus*, and *Shorea* and *Pinus*.

Visualization of the full grass species composition in "eulerr" (Figure 3) indicates only three species found in all four savannas; *Arundinella setosa*, *Sacciolepis indica*, and *Schizachyrium brevifolium*, from subfamilies Arundinelleae, Paniceae, and Andropogoneae, respectively. Species found in three of the four savannas tend to be from the Andropogoneae, with only 1/10 of species found in 3/4 savannas from tribe Aristidoideae. Andropogoneae species dominate all shared savannas except species found in both *Pinus* and *Shorea* savannas which are dominated by Paniceae. Nine species are shared solely between *Pinus* and *Shorea* savannas, and seven between *Pterocarpus* and *Shorea* savannas. One species, *Dimeria falcata* Hack., is shared solely between *Pinus* and *Dipterocarpus* savannas, and *Mnesithea laevis* (Retz.) Kunth is shared between *Shorea* and *Dipterocarpus* savannas (Figure 3). Of the ecosystem-specific species—grasses

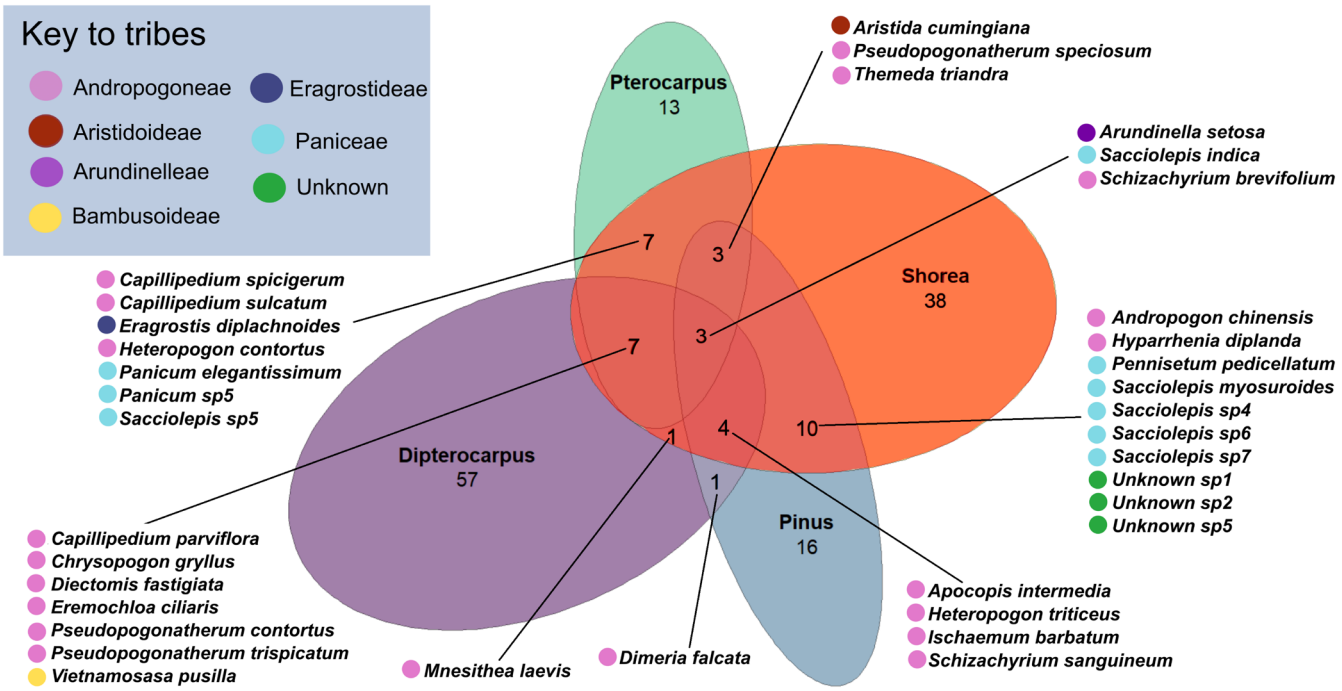


FIGURE 3 | Euler plot showing grass species richness per savanna type, overlap in species composition and number, and where species are shared between savannas, species name and tribe. Created using eulerr v7.0.0 (Larsson 2022).

TABLE 2 | Each savanna type supports over 50% ecosystem-specific (i.e., only found in one savanna ecosystem) Andropogoneae grass species. Data exclude unknown species.

Savanna	*Shorea*	*Dipterocarpus*	*Pterocarpus*	*Pinus*
% Andropogoneae	52	56	75	57

which are not shared between savannas—these are comprised of a greater diversity of tribes. Ecosystem-specific species are still mainly comprised of grasses from tribe Andropogoneae (57%), but a significant number of grasses are from tribe Paniceae (20%). This majority of Andropogoneae species holds true across the four savanna types (Table 2). In terms of subfamilies, 83% of grasses are from subfamily Panicoideae, which includes Andropogoneae, Paniceae, and Paspaleae (Table S4).

Grass species accumulation curves (Figure S2) indicate the need for increased sampling of all savanna types for a full quantification of grass species composition. While the pattern of species discovery demonstrates that much of the grass diversity has been captured within the sampling effort once unknown grasses are excluded (Figure S2b), sampling at the same intensity for all savanna ecosystems (20 sites) would have provided a fuller measure of grass composition.

4 | Discussion

Thai and Cambodian savannas support distinct grass communities with different patterns of richness and overlap. Our study sites in North and Central Thailand and Northeast Cambodia identified four savanna types differentiated by their grass assemblages as well as their tree assemblages (Table 1), irrespective of geographical proximity among the *Shorea*, *Pterocarpus*, and *Pinus* ecosystems (Figure 1a). Across the four savannas, we recorded 160 distinct grass species despite our data indicating that more surveys are needed to fully quantify grass diversity in Southeast Asian savannas (Figure S2). Further, sampling was limited to a single season, and species diversity is likely to be much higher given the nature of flowering in fire-driven ecosystems (Bond and Parr 2010). Grass species richness differs among savanna types, with the greatest richness in the *Shorea* and *Dipterocarpus* savannas. Thai *Pinus* savanna alone supports more than double the grass species diversity recorded in old-growth sites in Florida pine savannas by Diaz-Toribio, Carr, and Putz (2020). We show that common grasses, as ranked by relative frequency distributions, include species shared between savannas as well as those unique to individual savanna ecosystems. Finally, we show the dominance of C4 Andropogoneae grasses across all savanna ecosystems (Figure 3). Our data suggest that more field work in these regions is urgently needed to understand savanna ecosystems and their ground layer diversity patterns better.

We recorded significant differences in grass communities among the *Dipterocarpus*, *Pinus*, *Pterocarpus*, and *Shorea* savannas (Table 1). *Shorea* and *Dipterocarpus* savannas are both dominated by trees from the family Dipterocarpaceae, but the grass communities associated with these tree genera are some of the most distinct ($p = 0.001$). Different dominant tree associations, even when from the same family like the Dipterocarps, are likely to create and maintain distinct ecological niches through

habitat filtering, and may represent differences in underlying soil type, despite all sites being located on sandstone formations. However, it is possible that the strong differences in community composition between *Dipterocarpus* and *Shorea* savannas may be an artifact of the geographic separation between sites, with all *Shorea* sampling occurring in Thailand and all *Dipterocarpus* sampling in Cambodia (Figure 1a). Previous work has treated the Dipterocarpaceae savanna as dominated by *Shorea* and/or *Dipterocarpus* rather than differentiating between genera (Ratnam et al. 2016; Khaing et al. 2019). Under this approach, where *Dipterocarpus* and *Shorea* sampling are combined into Dipterocarpaceae savanna, our results support an even greater diversity of grasses across a wide geographical spread. For three of the pairwise comparisons, *Shorea* versus *Pinus*, *Shorea* versus *Pterocarpus*, and *Dipterocarpus* versus *Pterocarpus*, differences may be partially influenced by heterogeneity in beta diversity rather than compositional shifts alone.

Functional differentiation may underlie compositional differences, where different combinations of resistance-attraction-avoidance traits (Archibald, Hempson, and Lehmann 2019) may be associated with distinct savanna types. For example, *Pinus* savannas support more annual grasses than any other savanna ecosystem (Figure 2a). Annual grasses have been shown to be less resilient to fire exclusion than perennial species (Canales et al. 1994). By maintaining leaf cover year round, *Pinus* savannas may increase heterogeneity in light availability through canopy openings, which may increase species richness and alter composition (Crandall et al. 2024; Platt et al. 2016), perhaps by increased opportunities for fast-growing grasses. Frequent fires fueled by pyrogenic needles are likely to suppress caespitose clump-forming grasses, creating opportunities and physical space for other grasses such as annuals (Platt et al. 2016).

Fire regimes may also influence compositional differences. Grass composition in savannas directly affects the flammability of ecosystems (Cardoso et al. 2018) and dominant theory suggests that frequent fire should constrain grass richness (Archibald, Bond, et al. 2019; Archibald, Hempson, and Lehmann 2019). In the sites surveyed, the majority of shared common species (Figure 3) and ecosystem-specific species (Table S4) are from the C4 tribe Andropogoneae, where flammability traits have been previously associated with lineage (Ripley et al. 2015). Andropogoneae display a phylogenetic association with fire-prone environments (Ripley et al. 2015) and are characteristic of palaeotropical grassy biomes (Osborne 2008). However, research in the Dipterocarp landscapes of Myanmar found that fire frequency did not explain compositional differences between ground layer plant communities (Khaing et al. 2019).

Soil fertility or soil water availability is likely to influence patterns of plant compositional differences between savanna ecosystems. Low nutrient availability has been posited as an explanatory factor for the presence of savannas where the climate could support forests (Lehmann et al. 2011; Pellegrini 2016). In our study sites, and in general in mainland Southeast Asia, savannas are located on coarse sandy soils or soils with a laterite layer (Stott 1984, 1990). However, the interaction is likely complex, with low soil fertility maintaining slow rates of woody growth in between fires (Sankaran and Ratnam 2013). Our study sites experience seasonal precipitation regimes. Seasonal rainfall also slows woody growth (Lehmann et al. 2011) and increases the likelihood of fire (Archibald, Bond, et al. 2019; Archibald, Hempson, and Lehmann 2019).

While globally the predominant and characteristic savanna grasses use the C4 photosynthetic pathway (Edwards et al. 2010), the common grass species we recorded included some C3 as well as C4 grasses (Table S2). C3 Paniceae species have been shown to have similar post-fire recovery rates to C4 Andropogoneae, potentially because the reallocation to below-ground biomass recorded post-fire also provides an advantage for post-herbivory recovery (Ripley et al. 2015). The C3 grasses were *Sacciolepis indica* in *Dipterocarpus* and *Pterocarpus* savannas, *Isachne puberula* in *Dipterocarpus* savanna, as well as the bamboos *Vietnamosasa ciliata* and *V. pusilla* in *Dipterocarpus* and *Shorea* savannas (Figure 3b–e). The savannas studied here receive 1000–2100 mm precipitation per year, an amount comparable to Indonesian savannas, where the C3 grass *Calamagrostis australis* (Moritzi) Buse is widespread in Bali Barat savanna (Sutomo and van Etten 2021). Similarly, in wet African Miombo ecosystems, under late dry season fire conditions the C3 grass *Trichantecium nervatum* (Franch.) Zuloaga & Morrone is common (Wieczorkowski et al. 2024), and *Echinolaena inflexa* (Poir.) Chase is abundant in the Brazilian Cerrado where it is an important native C3 grass (Souza et al. 2010; Lannes et al. 2016). Increased precipitation leads to increased woody growth (Berry and Kulmatiski 2017), and perhaps therefore an understory adapted to shade as well as fire. C4 grasses are outcompeted in the shade by C3 grasses (Pilon et al. 2021), a dynamic reflected by the dominance of C3 bamboos (*V. pusilla* and *V. ciliata*) in *Shorea* and *Dipterocarpus* savannas at some sites. *Vietnamosasa pusilla* and *V. ciliata* have been widely recorded as the dominant flammable understory in Cambodian, Laos, Thai and Vietnamese Dipterocarpaceae savannas (Amma et al. 2018; Haevermans et al. 2013; Phengvichith and Hacker 2024; Ratnam et al. 2016; Sankaran and Ratnam 2013; Stott 1984; Wong 2004).

All four savanna types shared at least one of the 25% most common species with another savanna, but no species was common across all four savanna ecosystems (Figure 2a). Of the most common species, two were shared by *Pinus*, *Pterocarpus*, and *Shorea* savannas: *Arundinella setosa and Themeda triandra*. *Themeda triandra* is thought to have originated in South Asia (Dunning et al. 2017) and is an iconic grass with ecological and economic importance as a fire climax species (Snyman et al. 2013). *Arundinella setosa* is widely recorded across Indonesian savannas and dominates the Alas Purwo savanna (Sutomo and van Etten 2021). In line with the full grass composition data (Figure 3), the majority of shared top 25% most common species are from tribe Andropogoneae: *Apocopis intermedia*, *Heteropogon triticeus*, *Themeda triandra*, *Pseudopogonatherum speciosum*, and *Schizachyrium brevifolium* (Figure 2). The other shared common species are from tribe Arundinelleae—*Arundinella setosa*—and tribe Paniceae—*Sacciolepis indica*. The latter species is native to the Southeast Asian tropics (Barkworth et al. 2007), where it is common to savannas and grasslands (Thompson 2012).

While the most common grass species in each ecosystem differed, it is notable that all of them (*Apocopis intermedia*, *Arundinella setosa*, *Vietnamosasa ciliata*, and *V. pusilla*) are rhizomatous (Table S2). The rhizomatous strategy is a key growth form in

stressful climates (Thakur and Münzbergová 2022) enabling species persistence through below ground bud banks which can last for decades (Ott et al. 2019). Rhizomes also store nutrients and non-structural carbohydrates which facilitate new growth and structural support (Li et al. 2021). Indeed, rhizomes enable the strongest post-fire resprouting response of all the grass architectures (rhizomatous, caespitose, stoloniferous) (Pausas and Paula 2020). Being rhizomatous also helps grasses avoid self-shading, of significant benefit in the savanna biome (McGlone et al. 2014).

5 | Conclusions

The savanna ecosystems of Northeastern Cambodia and Central and Eastern Thailand are characterized by *Dipterocarpus*, *Pinus*, *Pterocarpus*, and *Shorea* tree species, and across this region they support distinct grass assemblages. Species accumulation curves indicate increased sampling is necessary to fully quantify and characterize savanna grasses, but despite this, we recorded 160 grass species, with richness highest in *Dipterocarpus* and *Shorea* savannas. We show that while some common grasses overlap between savannas, grass composition varies under different tree genera, suggesting that variation in tree flora, as well as abiotic conditions such as soil nutrients and fire, may maximize grass species diversity across savanna landscapes. Across the savanna ecosystems, while most grasses were from the C4 tribe Andropogoneae, common grasses in *Dipterocarpus*, *Pterocarpus*, and *Shorea* savannas included fire-adapted C3 species. Overall, our data suggest that increased sampling across multiple seasons and a greater geographic range is necessary to capture the functional and floristic diversity of Southeast Asian savannas. Given that grass communities differ so strongly between different savannas, future work should explore whether such compositional differences are reflected in the forb communities.

Author Contributions

J.R., W.A., R.T.P., M.S.V., and C.E.R.L. designed the research. J.R., W.A. and H.F. collected the data. Y.P., M.S.V., W.A., H.F., and J.R. identified collections, Y.P. facilitated specimen export and data collection. J.R. conducted analyses with support from C.E.R.L. J.R. wrote the manuscript with contributions from C.E.R.L. and R.T.P., and all authors read and commented on the manuscript.

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Disclosure

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in Edinburgh DataShare at https://doi.org/10.7488/ds/8066.

References

Amma, S., H. Toju, C. Wachrinrat, et al. 2018. "Composition and Diversity of Soil Fungi in Dipterocarpaceae-Dominated Seasonal Tropical Forests in Thailand." *Microbes and Environments* 33, no. 2: 135–143. https://doi.org/10.1264/jsme2.ME17168.

Archibald, S., W. J. Bond, W. Hoffmann, C. Lehmann, C. Staver, and N. Stevens. 2019. "Distribution and Determinants of Savannas." In *Savanna Woody Plants and Large Herbivores*, 1–24. John Wiley & Sons Ltd. https://doi.org/10.1002/9781119081111.ch1.

Archibald, S., and G. P. Hempson. 2016. "Competing Consumers: Contrasting the Patterns and Impacts of Fire and Mammalian Herbivory in Africa." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 371, no. 1703: 20150309.

Archibald, S., G. P. Hempson, and C. Lehmann. 2019. "A Unified Framework for Plant Life-History Strategies Shaped by Fire and Herbivory." *New Phytologist* 224, no. 4: 1490–1503. https://doi.org/10.1111/nph.15986.

Barkworth, M. E., L. K. Anderton, K. M. Capels, S. Long, and M. B. Piep. 2007. *Manual of Grasses for North America*. University Press of Colorado.

Berry, R. S., and A. Kulmatiski. 2017. "A Savanna Response to Precipitation Intensity." *PLoS One* 12, no. 4: e0175402. https://doi.org/10.1371/journal.pone.0175402.

BirdLife International Cambodia Programme. 2012. *The Biodiversity of the Proposed Western Siem Pang Protected Forest Stung Treng Province, Cambodia*. BirdLife International Cambodia Programme. https://data.opendevelopmentmekong.net/library_record/the-biodiversity-of-the-proposed-western-siem-pang-protected-forest-stung-treng-province-cambodia-/resource/09d97d7d-c902-4d2f-b163-ce7fe06c7b7b.

Bond, W. J., and J. E. Keeley. 2005. "Fire as a Global 'Herbivore': The Ecology and Evolution of Flammable Ecosystems." *Trends in Ecology & Evolution* 20, no. 7: 387–394. https://doi.org/10.1016/j.tree.2005.04.025.

Bond, W. J., and C. L. Parr. 2010. "Beyond the Forest Edge: Ecology, Diversity and Conservation of the Grassy Biomes." *Biological Conservation* 143, no. 10: 2395–2404. https://doi.org/10.1016/j.biocon.2009.12.012.

Boonyanuphap, J., and C. Hansawasdi. 2011. "Spatial Distribution of Beta Glucan Containing Wild Mushroom Communities in Subtropical Dry Forest, Thailand." *Fungal Diversity* 46, no. 1: 29–42. https://doi.org/10.1007/s13225-010-0067-8.

Canales, J., M. C. Trevisan, J. F. Silva, and H. Caswell. 1994. "A Demographic Study of an Annual Grass (*Andropogon brevifolius* Schwarz) in Burnt and Unburnt Savanna." *Acta Oecologica* 15, no. 3: 261–273.

Cardoso, A. W., I. Oliveras, K. A. Abernethy, et al. 2018. "Grass Species Flammability, Not Biomass, Drives Changes in Fire Behavior at Tropical Forest-Savanna Transitions." *Frontiers in Forests and Global Change* 1: 6. https://doi.org/10.3389/ffgc.2018.00006.

Clayton, W. D., M. S. Vorontsova, K. T. Harman, and H. Williamson. 2006. "GrassBase—The Online World Grass Flora." http://www.kew.org/data/grasses-db.html.

Crandall, R. M., Y. M. Chew, J. M. Fill, J. K. Kreye, J. M. Varner, and L. N. Kobziar. 2024. "Pine Trees Structure Plant Biodiversity Patterns in Savannas." *Ecology and Evolution* 14, no. 7: e70021.

Dexter, K. G., B. Smart, C. Baldauf, et al. 2015. "Floristics and Biogeography of Vegetation in Seasonally Dry Tropical Regions."

International Forestry Review 17, no. 2: 10–32. https://doi.org/10.1505/146554815815834859.

Diaz-Toribio, M. H., S. Carr, and F. E. Putz. 2020. "Pine Savanna Plant Community Disassembly After Fire Suppression." *Journal of Vegetation Science* 31, no. 2: 245–254.

Dunning, L. T., A. L. Liabot, J. K. Olofsson, et al. 2017. "The Recent and Rapid Spread of *Themeda triandra*." *Botany Letters* 164, no. 4: 327–337. https://doi.org/10.1080/23818107.2017.1391120.

Edwards, E. J., C. P. Osborne, C. A. E. Strömberg, et al. 2010. "The Origins of C4 Grasslands: Integrating Evolutionary and Ecosystem Science." *Science* 328, no. 5978: 587–591. https://doi.org/10.1126/science.1177216.

Fick, S. E., and R. J. Hijmans. 2017. "WorldClim 2: New 1-km Spatial Resolution Climate Surfaces for Global Land Areas." *International Journal of Climatology* 37, no. 12: 4302–4315.

Gopalakrishna, T., S. W. Rifai, J. Ratnam, I. Oliveras Menor, N. Stevens, and Y. Malhi. 2024. "The Distribution and Drivers of Tree Cover in Savannas and Forests Across India." *Communications Earth & Environment* 5, no. 1: 399. https://doi.org/10.1038/s43247-024-01568-4.

Haevermans, T., B. L. Nguyen, J. Gurgand, A. Haevermans, S. Dransfield, and M. H. Diep. 2013. "Clearing Up Vietnamosasa (Poaceae, Bambusoideae): Typification and Nomenclature of a Distinctive Paleotropical Bamboo Genus." *Phytotaxa* 137, no. 1: 57–60. https://doi.org/10.11646/phytotaxa.137.1.7.

Hubbell, S. P. 2013. "Tropical Rain Forest Conservation and the Twin Challenges of Diversity and Rarity." *Ecology and Evolution* 3, no. 10: 3263–3274.

Joshi, A. A., M. Sankaran, and J. Ratnam. 2018. "'Foresting' the Grassland: Historical Management Legacies in Forest-Grassland Mosaics in Southern India, and Lessons for the Conservation of Tropical Grassy Biomes." *Biological Conservation* 224: 144–152. https://doi.org/10.1016/j.biocon.2018.05.029.

Kellman, M., and K. Miyanishi. 1982. "Forest Seedling Establishment in Neotropical Savannas: Observations and Experiments in the Mountain Pine Ridge Savanna, Belize." *Journal of Biogeography* 9, no. 3: 193–206. https://doi.org/10.2307/2844663.

Khaing, T. T., B. O. Pasion, R. S. Lapuz, and K. W. Tomlinson. 2019. "Determinants of Composition, Diversity and Structure in a Seasonally Dry Forest in Myanmar." *Global Ecology and Conservation* 19: e00669. https://doi.org/10.1016/j.gecco.2019.e00669.

Kumar, D., M. Pfeiffer, C. Gaillard, L. Langan, C. Martens, and S. Scheiter. 2020. "Misinterpretation of Asian Savannas as Degraded Forest Can Mislead Management and Conservation Policy Under Climate Change." *Biological Conservation* 241, no. 108: 293. https://doi.org/10.1016/j.biocon.2019.108293.

Kumar, D., M. Pfeiffer, C. Gaillard, L. Langan, and S. Scheiter. 2021. "Climate Change and Elevated CO_2 Favor Forest Over Savanna Under Different Future Scenarios in South Asia." *Biogeosciences* 18, no. 9: 2957–2979. https://doi.org/10.5194/bg-18-2957-2021.

Kurniawan, H., and D. Yuniati. 2015. "Carbon Sink Potency in Three Types of Savanna in Nusa Tenggara Timur." *Jurnal Penelitian Kehutanan Wallacea* 4, no. 1: 51–62.

Lannes, L. S., M. M. Bustamante, P. J. Edwards, and H. Olde Venterink. 2016. "Native and Alien Herbaceous Plants in the Brazilian Cerrado Are (Co-) Limited by Different Nutrients." *Plant and Soil* 400, no. 1: 231–243.

Larsson, J. 2022. "eulerr: Area-Proportional Euler and Venn Diagrams with Ellipses." R package version 7.0.0.

Lehmann, C. E. R., T. M. Anderson, M. Sankaran, et al. 2014. "Savanna Vegetation-Fire-Climate Relationships Differ Among Continents." *Science (New York, N.Y.)* 343, no. 6170: 548–552. https://doi.org/10.1126/science.1247355.

Lehmann, C. E. R., S. A. Archibald, W. A. Hoffmann, and W. J. Bond. 2011. "Deciphering the Distribution of the Savanna Biome." *New Phytologist* 191, no. 1: 197–209. https://doi.org/10.1111/j.1469-8137.2011.03689.x.

Li, C., Y. Cai, L. Xiao, et al. 2021. "Rhizome Extension Characteristics, Structure and Carbon Storage Relationships With Culms in a 10-Year Moso Bamboo Reforestation Period." *Forest Ecology and Management* 498, no. 119: 556. https://doi.org/10.1016/j.foreco.2021.119556.

Marage, D., and J. C. Gégout. 2009. "Importance of Soil Nutrients in the Distribution of Forest Communities on a Large Geographical Scale." *Global Ecology and Biogeography* 18, no. 1: 88–97.

McGlone, M. S., G. L. Perry, G. J. Houliston, and H. E. Connor. 2014. "Fire, Grazing and the Evolution of New Zealand Grasses." *New Zealand Journal of Ecology* 38, no. 1: 1–11. https://www.jstor.org/stable/24060818.

Michelakis, D., N. Stuart, G. Lopez, V. Linares, and I. H. Woodhouse. 2014. "Local-Scale Mapping of Biomass in Tropical Lowland Pine Savannas Using ALOS PALSAR." *Forests* 5, no. 9: 2377–2399.

Middleton, D. J., K. Armstrong, Y. Baba, et al. 2019. "Progress on Southeast Asia's Flora Projects." *Gardens' Bulletin Singapore* 71, no. 2: 267–319. https://doi.org/10.26492/gbs71(2)0.2019-02.

Mistry, J. 2000. "World Savannas: Ecology and Human Use." https://www.routledge.com/World-Savannas-Ecology-and-Human-Use/Mistry-Beradi/p/book/9780582356597.

Nerlekar, A. N., A. R. Chorghe, J. V. Dalavi, et al. 2022. "Exponential Rise in the Discovery of Endemic Plants Underscores the Need to Conserve the Indian Savannas." *Biotropica* 54, no. 2: 405–417. https://doi.org/10.1111/btp.13062.

Nguyen, T. T., and P. J. Baker. 2016. "Structure and Composition of Deciduous Dipterocarp Forest in Central Vietnam: Patterns of Species Dominance and Regeneration Failure." *Plant Ecology and Diversity* 9, no. 5–6: 589–601. https://doi.org/10.1080/17550874.2016.1210261.

Nguyen, T. T., B. P. Murphy, and P. J. Baker. 2019. "The Existence of a Fire-Mediated Tree-Recruitment Bottleneck in an Asian Savanna." *Journal of Biogeography* 46, no. 4: 745–756. https://doi.org/10.1111/jbi.13518.

Noss, R. F., W. J. Platt, B. A. Sorrie, et al. 2015. "How Global Biodiversity Hotspots May Go Unrecognized: Lessons From the North American Coastal Plain." *Diversity and Distributions* 21, no. 2: 236–244. https://doi.org/10.1111/ddi.12278.

Oksanen, J., F. G. Blanchet, M. Friendly, et al. 2020. "vegan: Community Ecology Package." R package version 2. 5–7. https://CRAN.R-project.org/package=vegan.

Osborne, C. P. 2008. "Atmosphere, Ecology and Evolution: What Drove the Miocene Expansion of C4 Grasslands?" *Journal of Ecology* 96, no. 1: 35–45. https://doi.org/10.1111/j.1365-2745.2007.01323.x.

Ott, J. P., J. Klimešová, and D. C. Hartnett. 2019. "The Ecology and Significance of Below-Ground Bud Banks in Plants." *Annals of Botany* 123, no. 7: 1099–1118. https://doi.org/10.1093/aob/mcz051.

Packalen, P., J. Strunk, M. Maltamo, and M. Myllymäki. 2023. "Circular or Square Plots in ALS-Based Forest Inventories—Does It Matter?" *Forestry* 96, no. 1: 49–61.

Pausas, J. G., and S. Paula. 2020. "Grasses and Fire." *New Phytologist* 226, no. 4: 957–959. https://www.jstor.org/stable/26914597.

Pellegrini, A. F. 2016. "Nutrient Limitation in Tropical Savannas Across Multiple Scales and Mechanisms." *Ecology* 97, no. 2: 313–324. https://doi.org/10.1890/15-0869.1.

Phengvichith, V., and J. B. Hacker. 2024. IGC Proceedings (1985–2023), 7. "Diversity and Sustainability of the Pek Savannas of the Lao PDR." https://uknowledge.uky.edu/igc/1997/session1/7.

Pilon, N. A. L., G. Durigan, J. Rickenback, et al. 2021. "Shade Alters Savanna Grass Layer Structure and Function Along a Gradient of Canopy Cover." *Journal of Vegetation Science* 32, no. 1: e12959. https://doi.org/10.1111/jvs.12959.

Platt, W. J., D. P. Ellair, J. M. Huffman, S. E. Potts, and B. Beckage. 2016. "Pyrogenic Fuels Produced by Savanna Trees Can Engineer Humid Savannas." *Ecological Monographs* 86, no. 3: 352–372.

Pletcher, E., C. Staver, and N. B. Schwartz. 2022. "The Environmental Drivers of Tree Cover and Forest–Savanna Mosaics in Southeast Asia." *Ecography* 2022, no. 8: e06280. https://doi.org/10.1111/ecog.06280.

Pongthornpruek, S., S. Pampasit, N. Sriprang, P. Nabheerong, and K. Promtep. 2013. "Heavy Metal Accumulation in Soil and Some Fern Species at Phu Soi Dao National Park, Phitsanulok Province, Thailand, NU." *International Journal of Science* 5, no. 2: 151–164. https://www.semanticscholar.org/paper/Heavy-Metal-Accumulation-in-Soil-and-Some-Fern-at-Pongthornpruek-Pampasit/1d5f8bf6d7cead35a3faf04790b276e4048c7ae6.

POWO. 2022. *Plants of the World Online*. Facilitated by the Royal Botanic Gardens, Kew. https://powo.science.kew.org.

Ratnam, J., W. J. Bond, R. J. Fensham, et al. 2011. "When Is a 'Forest' a Savanna, and Why Does It Matter?" *Global Ecology and Biogeography* 20, no. 5: 653–660. https://doi.org/10.1111/j.1466-8238.2010.00634.x.

Ratnam, J., C. Sheth, and M. Sankaran. 2019. "African and Asian Savannas: Comparisons of Vegetation Composition and Drivers of Vegetation Structure and Function." In *Savanna Woody Plants and Large Herbivores*, 25–49. John Wiley & Sons. https://doi.org/10.1002/9781119081111.ch2.

Ratnam, J., K. W. Tomlinson, D. N. Rasquinha, and M. Sankaran. 2016. "Savannahs of Asia: Antiquity, Biogeography, and an Uncertain Future." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 371, no. 1703: 20150305. https://doi.org/10.1098/rstb.2015.0305.

Rawat, G. S., and B. S. Adhikari. 2015. "Ecology and Management of Grassland Habitats in India." *ENVIS Bulletin: Wildlife & Protected Areas* 17: 1–240.

Ripley, B., V. Visser, P.-A. Christin, S. Archibald, T. Martin, and C. Osborne. 2015. "Fire Ecology of C3 and C4 Grasses Depends on Evolutionary History and Frequency of Burning but Not Photosynthetic Type." *Ecology* 96, no. 10: 2679–2691. https://doi.org/10.1890/14-1495.1.

Sankaran, M. 2009. "Diversity Patterns in Savanna Grassland Communities: Implications for Conservation Strategies in a Biodiversity Hotspot." *Biodiversity and Conservation* 18, no. 4: 1099–1115. https://doi.org/10.1007/s10531-008-9519-9.

Sankaran, M., and J. Ratnam. 2013. "African and Asian Savannas, Volume 1." In *Encyclopedia of Biodiversity*, 2nd ed., 58–74. Elsevier Press.

Schwartz, N., J. S. Powers, L. K. Werden, et al. 2025. "Seeing the Savanna Through the Trees: Vegetation Structure, Composition and Function Along a Forest-Savanna Boundary in Cambodia." *Biotropica* 57, no. 1: e70000. https://doi.org/10.1111/btp.70000.

Simpson, K. J., S. Archibald, and C. P. Osborne. 2022. "Savanna Fire Regimes Depend on Grass Trait Diversity." *Trends in Ecology & Evolution* 37, no. 9: 749–758.

Snyman, H. A., L. J. Ingram, and K. P. Kirkman. 2013. "*Themeda triandra*: A Keystone Grass Species." *African Journal of Range & Forage Science* 30, no. 3: 99–125.

Solofondranohatra, C. L., M. S. Vorontsova, R. A. Dewhirst, et al. 2021. "Shade Alters the Growth and Architecture of Tropical Grasses by Reducing Root Biomass." *Biotropica* 53, no. 4: 1052–1062. https://doi.org/10.1111/btp.12943.

Solofondranohatra, C. L., M. S. Vorontsova, J. Hackel, et al. 2018. "Grass Functional Traits Differentiate Forest and Savanna in the Madagascar Central Highlands." *Frontiers in Ecology and Evolution* 6: 184. https://doi.org/10.3389/fevo.2018.00184.

Solofondranohatra, C. L., M. S. Vorontsova, G. P. Hempson, et al. 2020. "Fire and Grazing Determined Grasslands of Central Madagascar Represent Ancient Assemblages." *Proceedings of the Royal Society B* 287, no. 1927: 20,200,598. https://doi.org/10.1098/rspb.2020.0598.

Souza, A., C. Z. Sandrin, M. F. A. Calió, S. T. Meirelles, V. R. Pivello, and R. C. L. Figueiredo-Ribeiro. 2010. "Seasonal Variation of Soluble Carbohydrates and Starch in *Echinolaena inflexa*, a Native Grass Species from the Brazilian Savanna, and in the Invasive Grass *Melinis minutiflora*." *Brazilian Journal of Biology* 70: 395–404.

Staver, A. C., J. O. Abraham, G. P. Hempson, A. T. Karp, and J. T. Faith. 2021. "The Past, Present, and Future of Herbivore Impacts on Savanna Vegetation." *Journal of Ecology* 109, no. 8: 2804–2822.

Stott, P. 1984. "The Savanna Forests of Mainland Southeast Asia: An Ecological Survey." *Progress in Physical Geography: Earth and Environment* 8, no. 3: 315–335. https://doi.org/10.1177/030913338400800301.

Stott, P. 1990. "Stability and Stress in the Savanna Forests of Mainland South-East Asia." *Journal of Biogeography* 17, no. 4/5: 373–383. https://doi.org/10.2307/2845366.

Sutomo, S., I. D. P. Darma, and R. Iryadi. 2020. "The Dissimilarity in Plant Species Composition of Savanna Ecosystem Along the Elevation Gradient on Flores Island, East Nusa Tenggara, Indonesia." *Biodiversitas Journal of Biological Diversity* 21, no. 2: 492–496. https://doi.org/10.13057/biodiv/d210209.

Sutomo, S., and E. van Etten. 2021. "Savanna Plant Communities in the Wetter Parts of the Indonesian Archipelago." *Folia Geobotanica* 56, no. 4: 193–204. https://doi.org/10.1007/s12224-021-09401-y.

Thakur, D., and Z. Münzbergová. 2022. "Rhizome Trait Scaling Relationships Are Modulated by Growth Conditions and Are Linked to Plant Fitness." *Annals of Botany* 129, no. 5: 529–540. https://doi.org/10.1093/aob/mcac023.

Thompson, J. P. 2012. "*Sacciolepis indica* (glen Woodgrass)." CABI Compendium 116,837 [online]. https://doi.org/10.1079/cabicompendium.116837.

Tornorsam, M., T. T. Nguyen, A. Poortinga, et al. 2024. "Managing South-East Asia's Savannas: Challenges and Holistic Approaches Through Community-Based Fire Management." *International Journal of Wildland Fire* 33, no. 12: WF24098.

Veeravinantanakul, A., P. Kanjanapayont, A. Sangsompong, N. Hasebe, and P. Charusiri. 2018. "Structure of Phu Phan Range in the Khorat Plateau: Its Apatite Fission Track Ages and Geological Syntheses." *Bulletin of Earth Sciences of Thailand* 10, no. 1: 8–16.

Vorontsova, M. S., G. Besnard, F. Forest, et al. 2016. "Madagascar's Grasses and Grasslands: Anthropogenic or Natural?" *Proceedings of the Royal Society B: Biological Sciences* 283, no. 1823: 20152262.

Wieczorkowski, J. D., C. E. Lehmann, S. Archibald, et al. 2024. "Fire Facilitates Ground Layer Plant Diversity in a Miombo Ecosystem." *Annals of Botany* 133, no. 5–6: 743–756. https://doi.org/10.1093/aob/mcae035.

Wong, K. M. 2004. *Bamboo the Amazing Grass: A Guide to the Diversity and Study of Bamboos in Southeast Asia*. International Plant Genetic Resources Institute; University of Malaya. https://cgspace.cgiar.org/handle/10568/104354.

Zhao, S., C. Peng, H. Jiang, D. Tian, X. Lei, and X. Zhou. 2006. "Land Use Change in Asia and the Ecological Consequences." *Ecological Research* 21, no. 6: 890–896. https://doi.org/10.1007/s11284-006-0048-2.

Zhou, Y., T. W. Boutton, and X. B. Wu. 2018. "Soil C: N: P Stoichiometry Responds to Vegetation Change From Grassland to Woodland." *Biogeochemistry* 140, no. 3: 341–357.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Environmental data for sites in each savanna type of (a) mean annual precipitation, (b) precipitation seasonality, (c) annual mean temperature and (d) annual temperature range. Bioclimatic data were extracted using site geolocations from WorldClim 2.1 at a 2.5 min resolution (Fick and Hijmans 2017). **Figure S2:** (a) Species accumulation curves for all grass species, and (b) for all grass species identified to genus, calculated with specaccum function in the package "vegan" v2.5-7 (Oksanen et al. 2020) which infer species accumulation curves using the random method, which adds sites in a random order, for 100 permutations. **Table S1:** Site characteristics including location information and breakdown of dominant tree species recorded at each site. **Table S2:** Most common grass species recorded in the savanna types, their tribes, functional traits and distributions. **Table S3:** Each savanna type is characterized by a unique grass community based on pairwise analyses of grass species composition (presence–absence) using a PERMANOVA in "vegan" v2.5-7 (Oksanen et al. 2020) using the 'jaccard' distance which is based on presence-absence data, with savanna type as the dependent variable based on a reduced dataset where all singletons and doubletons are excluded, and where unknown grasses are included or excluded. Homogeneity of multivariate dispersion was tested using "betadisper" function. **Table S4:** Ecosystem-specific grasses, tribe, and subfamily.