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Savannas of Asia: evidence for antiquity, biogeography, and an uncertain future

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Abstract

The savannas of Asia remain locally unrecognized as distinctive ecosystems, and continue to be viewed as degraded forests or seasonally dry tropical forests. These colonial-era legacies are problematic because they fail to recognize the unique diversity of Asian savannas and the critical roles of fire and herbivory in maintaining ecosystem health and diversity. In this review we show that: the paleo-historical evidence suggests that the savannas of Asia have existed for at least 1 million years, long before widespread landscape modification by humans; savanna regions across Asia have levels of C_4 grass endemism and diversity that are consistent with area-based expectations for non-Asian savannas; there are at least three distinct Asian savanna communities, namely deciduous broadleaf savannas, deciduous fine-leafed and spiny savannas and evergreen pine savannas, with distinct functional ecologies consistent with fire- and herbivory-driven community assembly. Via an analysis of savanna climate domains on other continents we map the potential extant of savannas across Asia. We find that the climates of African savannas provide the closest analogues for those of Asian deciduous savannas, but that Asian pine savannas occur in climates different to any of the savannas in the southern hemisphere. Finally, we review major threats to the persistence of savannas in Asia, including the mismanagement of fire and herbivory, alien woody encroachment, afforestation policies, and future climate uncertainty associated with the changing Asian monsoon. Research agendas that target these issues are urgently needed to manage and conserve these ecosystems.

Key words: Asian savannas, diversity, endemism, fire, functional traits, herbivory, tropical dry forest, paleo-history

1. Savannas in Asia: original or man-made?

There is a long-running debate about whether Asia has natural savannas or whether Asia's savannas are derived from forests as the result of long-term management by humans [1–3]. Both biogeography and history have contributed to widespread misperceptions about Asian savannas. Most people visualise savannas as vast open grassy landscapes with sparsely scattered trees. This iconic vegetation physiognomy is common in Africa where most savannas occur in areas that receive less than 700 mm of rainfall per year [4]. In reality, earth's savannas range from grasslands with scattered trees to densely tree-covered woodlands, typically along a gradient of increasing rainfall, with the defining characteristic being that the tree canopy is not closed and the understorey is grassy [4–7]. Tropical Asia is dominated by monsoonal climates with mean annual rainfall > 700 mm. Consequently, Asian savannas support dense and tall woodlands, the physiognomies of which superficially resemble forests rather than the open grassy landscapes that occur widely across Africa.

The history of vegetation classification in the Asian tropics, which is closely tied to its socio-political history, has contributed to a forest-centric legacy in the nomenclature and understanding of Asian vegetation. Formal classifications of the vegetation of South and Southeast Asia originated in the colonial era [8,9], when colonial foresters trained in European forestry traditions were tasked with describing vegetation, generally from the perspective of timber and other extractive uses [2]. As a consequence, most vegetation types with some degree of tree cover in them were described as forests [10,11]. Since then, savannas with their open tree canopies have been viewed as degraded forests resulting from human use and management [10,12]. This forest-centric perception was further reinforced by the savannas of Asia occurring in lowland areas where savannas have been used and managed by humans for thousands of years [13,14]. Finally, in many of the regions where Asia's savannas occur, forests and savannas occur as a mosaic of alternate states within a landscape [5,6,15]. Together, the above factors have culminated in an entrenched ideology of Asian savannas as "degraded forests" [10–12,16–18].

Tropical savannas can be defined as mixed tree-grass systems where the herbaceous layer is usually dominated by C_4 grasses that utilize the C_4 photosynthetic pathway to fix carbon, while trees utilize the ancestral C_3 pathway, although there are exceptions such as parts of the South American cerrado where the herbaceous layer is dominated by C_3 grasses [1,2,4,7]. Several lines of evidence suggest that savannas were present in Asia before human arrival and were likely more extensive under past climates. These include fossil evidence for C_4 grasses and mammalian herbivores, climates similar to that of other savannas, functional diversity that reflects selection under fire or mammalian herbivory, high diversity of C_4 grasses and the presence of endemic species with life histories adapted to savanna environments. We review evidence for each of these and describe the major savanna formations of tropical and sub-tropical Asia. Subsequently, we explore the potential climate domain and geographic extent of savannas in Asia by using the climate domains of savannas in Africa, Australia and South America to predict their distribution. Finally, we provide an overview of the threats facing savannas in Asia.

2. The antiquity of savannas in Asia

Fossil and molecular evidence presented below suggest that savannas across Asia, and the savanna-adapted species associated with them, mostly existed before 1 million years ago (hereafter Ma), placing their existence prior to human modifications of the landscape, which began with the widespread use of fire by modern humans (Homo sapiens) at about 0.12 Ma [19], and before Homo erectus is thought to have used fire for cooking at 0.77 Ma [20,21].

C_4 grassy vegetation became established in different parts of Asia at quite different times [22–24]. The history of Asian savannas is therefore best understood by considering different regions separately. The three regions we consider here are (Fig. S1, Supplementary Materials): South Asia, equivalent to the Indian Subcontinent; East Asia, composed of Southeast and South-central China and Hainan Island; and Southeast Asia, composed of the continental region of Indochina and oceanic region of Malesia. These regions are separated by the Tibetan plateau, the Andaman Sea, the forest belt along the border between India and Myanmar, and montane forests along the southern border of China.

In South Asia, evidence from Himalayan Siwalik sediments suggests that C_4 vegetation and C_4 diets were established by about 16-14 Ma [22], but C_4 grasses became the dominant vegetation type in the late Miocene (9.3 – 6.5 Ma) as indicated by evidence from palynofloras [25], and from δ^{13} C values in tooth enamel and fossil soils [26–28]. Values of δ^{13} C in carbonate rocks from Kudankulum, south India, suggest that C_4 vegetation had extended across all South Asia by the late Miocene [29]. Late Pleistocene values of δ^{13} C in soil organic matter from the Gangetic plain suggest that the ratio of C_3 to C_4 plants has increased and decreased in response to glacial cycles, but has remained predominantly C_4 throughout that period [30].

Within East Asia, savannas are presently only recognised in the deep dry valleys of Yunnan and Sichuan provinces in southwest China, but C_4 grassy vegetation also occurs in Northern China [Chinese Academy of Sciences, 31]. Historically, savannas may have been more widely distributed across East Asia. Fossil evidence suggests that C_4 diets first appear in China about 18 Ma, although extensive C_4 vegetation, based on paleosol carbonate $\delta^{13}C$ is only recorded from 9-7 Ma [22]. The age of savannas appears to be related both to the global aridification beginning in the Eocene, which created drier environments in northeast China, and the uplift of the Tibetan plateau, which either created or intensified the monsoonal climate in southwestern China at a later date. In northern and eastern China, the switch to C_4 diets occurred in the mid to late Miocene [22], when gazelles also appeared in the fossil record [32] and herbaceous pollen was widely distributed across northern and eastern China [33]. By contrast, evidence collected on $\delta^{13}C$ in fossil teeth and soil carbonate nodules [34], leaf and pollen records from dry valleys in Yunnan [35], and molecular data of an endemic savanna tree species [36], all suggest that the transition to savanna in southwest China took place in the late Pliocene – early Pleistocene (4.2-1.2 Ma).

The present extent of savanna in Southeast Asia is probably far smaller than that during past glacial maxima [23,37]. Today savanna physiognomies in Southeast Asia are found in three main areas: Indochina; east Java and the Lesser Sunda Islands north-east of Australia; and the northwest Philippines (Luzon and Mindoro) and scattered parts of Wallacea [38]. These areas are all separated by forests and sea, and today grassland-dependent ruminant species, including bovids (Bos javanicus, Bubalus mindorensis) and several cervids (species in the genera Panolia, Rusa, Hyelaphus) are restricted to these isolated savanna patches and islands across Malesia [39]. These modern disjunct distributions suggest that extant savanna communities were connected during past glaciations when sea levels were low and most areas of Sundaland and parts of Wallacea were connected by land or separated by narrow water straights [23,24,37]. Pollen and megafauna fossil records suggest that Southeast

Asia was humid throughout the Miocene and drying began at the end of the Pliocene [23,24,40,41]. Extant savanna fauna and flora likely developed from the late Pliocene to the present as Sundaland was connected for multiple extended periods during the Pliocene and Pleistocene. Fossil and pollen evidence suggest that by the Middle Pleistocene (< 0.78 Ma) savannas may have existed from Myanmar through to Java [23,41]. Recent molecular phylogenies estimate that grass-dependent cervids and bovines diversified in Asia after the start of the Pliocene, and that the species which are today isolated on islands across Southeast Asia diverged during the Pleistocene [42,43], possibly more than 1 Ma.

3. Asian savannas: formations and environmental drivers

Worldwide understanding of savannas suggests that they may be driven by water limitation or disturbances such as fire or herbivory, leading to distinctive savanna communities that each contain unique species and functional diversity [44–49]. Based on descriptions of extant vegetation across Asia, we have identified three major savanna types, where grasses form the dominant component of the herbaceous layer under open tree canopies, and which are associated with different tree lineages (Table 1, Fig. S1). Below we briefly describe each savanna type and review data on plant functional traits that suggest whether they are mediated by drought, fire or herbivory.

3.1. Deciduous broadleaf savannas

Tall tropical deciduous broadleaf savannas range from tall deciduous dipterocarp savannas (dominated by 6 Shorea and Dipterocarpus species [50]), to teak savannas (dominated by Tectona species), and mixed deciduous savannas (numerous genera including Anogeissus, Lannea, Hardwickia, Lagerstroemia, Pterocarpus, Tectona, Terminalia, Vitex). These occur across all three regions (East, Southeast and South

Asia) [3,50–52] where 700 mm < MAP < 2100 mm MAP [52–55]. A fourth formation dominated by Eucalyptus alba is restricted to the Lesser Sunda Island group to the north-east of Australia [56].

Several lines of evidence suggest that the deciduous broadleaf savannas are maintained by fire. In these communities composition is mostly dominated by the fire-adapted C_4 lineage Andropogoneae (Heteropogon, Themeda, Cymbopogon, Dichanthium, Bothriochloa) [50,52,57–59]. In eastern Indochina, the grass layer of these savannas are dominated by the herbaceous bamboo genus Vietnamosasa [60], a C_3 grass [61], which resprouts and flowers following fire. Deciduous broadleaf savannas can support frequent fire, although annual fire is probably only due to human management of these landscapes [62]. Ground fires are most common [60,62] although crown fires may occur where taller, upright bamboos can carry fire up to the canopy [60]. The characteristic tree species show functional traits typical of adaptation to fire including thick bark [60], sub-cutaneous meristems, and tuberous roots [63]. Woody species rapidly resprout from subterranean stems following fire (personal observation). Saplings are able to tolerate annual low intensity fires but they may be destroyed by high intensity fires [60], and it has been suggested that deciduous dipterocarp savannas convert to semi-evergreen forests where fire has been suppressed (Ashton [3] citing Sarayudh Bunyavejchewin). However we found no evidence that this has been tested experimentally.

3.2. Fine-leafed and spiny savannas

In western and central South Asia, and much smaller areas of Southeast Asia (Central valley of Myanmar, east Java and the Lesser Sunda Islands) and in the dry interior valleys of China, fine-leafed and spiny savannas occur in areas that have rainfall 400 mm < MAP < 1000 mm [54]. These communities are usually dominated by deciduous tree species of lower stature and smaller leaf size than found in the deciduous broadleaf savannas, and numerous species have spines (locally dominant genera include Boswellia, Capparis, Acacia, Dichrostachys, Ziziphus and Catunaregum) [52,55,56,64,65]. Two environmental drivers seem most important for the structure of fine-leafed and spiny savannas. Firstly, growing-season water stress and aridity select for smaller leaves and lower-statured plants, consistent with observations from other low-rainfall savannas [47]. In addition, the herbaceous community shows increased representation of grasses from the lineage Chloridoideae, but these rarely become dominant [66,64] as they do in arid parts of Africa, Australia and America [67,68]. For the most part, dominant genera are still from the lineage Andropogoneae. Possibly this is because MAP rarely falls lower than 500 mm in Asia (small areas in South Asia), whereas large areas of African and Australian savannas are found where MAP < 500 mm [54]. Secondly, high soil fertility in these areas [69] increases the quality and palatability of plants for mammalian herbivores, such that herbivores may be the major disturbance agents in these savannas rather than fire. Numerous species in these savannas possess spines or have bushy forms known to reduce the rates of herbivory by large mammalian herbivores [70]. It is possible that these areas possess the greatest diversity of large mammals in Asia in much the same way as has been observed in Africa [71,72]..

3.3. Pine savannas

Pine savannas have a patchy distribution across the three regions in Asia, but Pinus species (P. kesiya, P. merkusii, P. roxburghii, P. yunannensis) are shared across these patches [3,50,55], which suggests that they were once more widely spread and connected [3,24]. They are usually found at higher altitude than Broadleaf deciduous savannas [55,73], reflecting a tolerance for cooler conditions. Asian pine savannas appear to be maintained by fire [74]. Where fire is rare or suppressed, pine savannas are often invaded by forest species (notably Quercus) [75] and convert to closed canopy forest over time. The pine species are found over a huge rainfall range of 900 mm < MAP < 3200 mm [54; www.gbif.org, accessed 27 March 2016], and are often associated with low nutrient soils, similar to pine savannas in North America [76,77]. This physiognomic similarity may indicate that Asian pine savannas persist where growth rates are slow due to soil nutrient limitation and fire occurs regularly [77]. The herbaceous layer is dominated by fire-adapted Andropogoneae grasses (Cymbopogon, Eulalia, Imperata, Themeda) [74]. Juveniles of some Pinus species develop a grassy stage, where they produce multiple lateral meristems with long photosynthetic needles and keep their apical buds close to the ground. Lateral meristems are embedded in the stem cortex, allowing them to survive fires and increase photosynthetic surface [74]. In this way juveniles store carbohydrate reserves in their roots that can support subsequent stem elevation above fire heights [46,78]. Adult pine trees have thick bark that protect them from low intensity fires, which increases in thickness as a response to increased fire frequency [74]. Asian savanna pine species can survive high intensity fires, sloughing bark where it has been badly damaged by fire and reconnecting cambium to heal the exposed scar [74]. Nevertheless at high fire frequencies, adult pine trees become sparse [73].

The full extent of pine savannas in Asia may be dramatically under-described in East Asia: the hills of southwest China are draped in Pinus yunnanensis and P. kesiya ‘forest’, where fire has been suppressed as a result of government policy [79,80]. The species are closely related [81] and recent evidence suggests that fire may have been an intricate part of these systems: P. yunnanensis in Yunnan develops grassy stage juveniles where it has been burnt, climate models predict that the region should be fire-prone [79], and a study on regeneration in P. yunnanensis savannas subjected to wildfire indicate that >90% of native trees and shrubs recovered after fires, many resprouting from underground bud banks, and that P. yunannensis is itself serotinous [82].

4. Endemism in Asian savannas

Endemic plants and animals with life-histories characteristic of savannas are found across the three savanna regions of Asia. Here we provide some examples for different life forms as available from the literature. Where possible we link these to the three savanna types identified above.

Endemism of C_4 grasses in the Asian regions (Fig. S2, Supplementary Materials), as estimated using the GrassBase database [83] combined with a database of C_3/ C_4 pathways for grass taxa [61], indicates substantial diversity of endemic C_4 taxa (Fig. S2; details in Table S1 in Supplementary Materials). Total C_4 endemism for each region as a function of total grass diversity in each region is similar to estimates for other regions with large savannas around the world (Fig. S2a, Table S1), except for East Asia, where the level of C_4 endemism is much lower. In all regions endemic diversity of Andropogoneae far exceeds Chloridoideae (Table S1), possibly reflecting the far greater extent of humid than semi-arid savannas in Asia. Presently we are not able to link these data to the three identified savanna types.

A recent analysis of the floristics of dry tropical regions across the world [84] suggests that some of the woody floras of savannas in Asia have assembled by local evolution of lineages from other biomes within Asia. These include the six fire-adapted deciduous dipterocarp species that characterize dry Dipterocarp savannas [50,85], fire-adapted pine species that distinguish Asian Pine savannas [74,75] and Tectona [86]. There are likely substantially more species in the deciduous broadleaf savannas [e.g. 64] which possess adaptations to fire. However, presently there is insufficient data to confirm that these species disappear under closed forest conditions, as there are no long-term fire-exclusion experiments in Asia. Some species in the fine-leafed and spiny savannas may be restricted to Asia (e.g. Acacia leucophloea) but many characteristic species extend beyond Asia (e.g. Dichrostachys cinerea, Ziziphus mauritiana, Acacia nilotica).

Several ruminant mammals are endemic to savannas in Asia (distribution maps from IUCN red list of threatened species http://maps.iucnredlist.org). Several Antilopinae (Antilope cervicapra, Gazella bennettii), Bovinae (Boselaphus tragocamelus) and Cervidae (Rusa timorensis) are associated with fine-leafed and spiny savannas in South and Southeast Asia. Several Bovini (Bos javanica, Tetracerus quadricornus) and cervidae (Panolia eldii) in South and Southeast Asia are associated with deciduous broadleaf savannas. Additionally at least one species utilises both fine-leafed and spiny savannas and deciduous broadleaf savannas (Axis axis). In the Philippines (Southeast Asia) Cervidae (Rusa alfredi) and Bovinae (Bubalis mindorensis) are grazers [87] that can be found in C_4 Imperata and Sorghum grasslands.

Several bird species that are typically grassland-associated are also endemic across Asia. These include buttonquails (Turnix spp.) with endemics in the Philippines, associated with pine savannas (T. worcesteri, T. ocellatus), and one species in the Lesser Sunda Islands, associated with lowland fine-leafed and spiny savannas (T. everetti,); two bustard species associated with open savannas with

Panicoid grasses in South and Southeast Asia (Houbaropsis bengalensis; Sypheotides indicus); three species of francolins (Francolinus francolins, F. pictus and F. pondicerianus) and two courser species (Cursorius coromandelius, Rhinoptilus bitorquatus) associated with fine-leafed and spiny savannas in South Asia [88]. Two iconic species of South and Southeast Asia, the Indian and Green peafowls (Pavo spp) prefer deciduous broadleaf savannas to forests [89].

5. Herb species richness in Asian savannas

Herb diversity is poorly documented throughout Asian savannas and is in need of systematic research. Nevertheless evidence at multiple scales suggests that Asian savannas house significant herbaceous diversity. In a deciduous broadleaf savanna of South Asia, Sankaran [90] recorded 278 species within grassy communities across a 1000 km^2 nature reserve. In a fine-leafed and spiny savanna in South Asia, Singh et al. [91] report that Poaceae was the most diverse group in the understorey with 110 species. In a Pine savanna in Southeast Asia, Eiadthong (Wichan Eiadthong, unpublished data, Kasertsart University) recorded 105 herbaceous species in a single 50 x 50 m plot.

At larger scales, species richness of C_4 grasses in the Asian regions as estimated using the GrassBase database combined with a database of C_3/ C_4 pathways for grass taxa [61,83], indicates that total C_4 diversity in each Asian region as a function of land surface is comparable to values in other major savanna and grassland regions (Fig. S2b; Table S1 Supplementary Materials). In a similar vein to endemism, diversity of Andropogoneae species is substantially greater than for Chloridoideae.

6. Defining the potential climatic envelope of Asian savannas

Vegetation mapping of the savannas of Asia is sparse and inconsistent [2]. As a first step towards identifying the geographic extent of Asian savannas, we mapped their potential climatic envelope within Asia, based on the climate envelopes occupied by Africa, South American and Australian savannas. At present, there is insufficient data from Asian savannas to effectively define their climatic domains based on field observations. Savannas on different continents have different floristic compositions with different associations with rainfall, fire and herbivory [7,92,93]. Hence, while globally savannas are structurally similar, their geographic distributions with respect to climate differ [7], and we should expect Asian savannas to be no different. Consequently, we mapped the potential extent of Asian savannas based on climatic domains of African, Australian and South American savannas separately to gauge the most likely geographic distribution of Asian savannas.

We first delimited the extent of savanna versus non-savanna habitats in Africa, Australia and South America based on previous work (Fig. S3a, see Appendix I for full details of the methods) [4, 94]. We then used stochastic gradient boosting [94–97] to statistically assess the distribution of savannas on each continent based on climate, elevation and edaphic parameters. The predictor variables in the models included mean annual temperature (MAT), annual temperature range (TAR), mean temperature of the driest quarter (TDQ), mean annual precipitation (MAP), precipitation of the driest month (PDM), precipitation seasonality (PS), potential evapotranspiration (PET), soil N content (Soil N), soil clay content (% clay) and elevation. We then used these models to predict the potential distribution of savannas in Asia based on the climatic envelopes occupied by savannas on each of these different continents.

Our models recreated the observed distribution of savannas in Africa with a high degree of accuracy (92.2% of savanna pixels correctly classified)), and to a lesser extent, those of South America (72.5% correctly classified),) and Australia (68.2% correctly classified; see Fig. S3 a,b). There are several potential reasons for the observed differences in model performance across continents. First, baseline vegetation maps used to build the models could have differed in their underlying accuracy, with savanna distributions more accurately depicted in vegetation maps of Africa than Australia or South America. Second, environmental and edaphic parameters not considered in our models (e.g. seasonal flooding, soil drainage, acidity, availability of exchangeable bases, aluminum concentrations) might be important determinants of savanna distributions in South America and Australia [7,92,93,98,99]. Finally, savannas in South America and Australia extend into much wetter regions than in Africa, with some South American savannas receiving as much as 750 mm more rainfall annually than Africa's wettest savannas [92]. In these wetter sites, fires are well recognized to play a critical role in extending savanna distributions by maintaining the savanna state under climatic conditions that would otherwise support forests [5,6].

We subsequently used the models developed for each of these continents to predict the potential distribution of savannas in Asia. Our results suggest that Asia supports larger areas with climates that are analogous to those occupied by African savannas than either Australian or South American savannas (Fig. 1). The African model identified large sections of Asia with very high (>0.9; ~1.1×10^6 km^2) or high (0.75 – 0.9; ~0.9×10^6 km^2) probabilities of supporting savannas, including the central Indian plateau, parts of western India and the drier tracts of Southeast Asia in Myanmar and Thailand (Fig. 1a). In contrast, the predicted extent of savannas in Asia that are analogous to Australian and South American savannas is much lower. Based on the Australian model, 0.3 x 10^6 km^2 and 0.6 x 10^6 km^2 of the Asian continent were identified as potentially supporting savannas with very high (>0.9) or high (0.75 – 0.9) probabilities (Fig. 1b), while in the case of the South American model these were 0.1 x 10^6 km^2 and 0.2 x 10^6 km^2, respectively (Fig. 1c).

Interestingly, the predicted occurrence of Asian savannas based on the climate envelopes of Africa, Australia or South America capture different savanna types in Asia. Areas identified with a high probability of supporting savannas based on the African model, but not by the Australian or South American models, include the fine-leaved spiny savannas of western India and the southern Deccan plateau (see [10,100], Fig. 1a; Figs 2a, b for images). In contrast, the areas identified by Australian and South American models correspond largely to the deciduous broadleaf savannas of the central Indian landscape ([10,100], Fig. 1b & c, Fig 2a for image). The Australian model additionally identifies the Terrai grassland and savanna habitats [101] of the Himalayan foothills (Fig. 1b). Only the African model weakly captures the East Asian savanna formations in Yunnan, China, and the savannas in Luzon, the Philippines (Fig 1a, images in Fig 2a,b). Surprisingly, all three models only weakly capture the location of savannas in the Lesser Sunda Islands, but make different predictions about their locations. It is intriguing that while some of these savannas are dominated by Australian tree taxa, others are dominated by African and Asian tree taxa [3,56]. Importantly, none of the models were able to predict the extensive Pine savannas in the Himalayas, China, Sumatra and the Philippines [3], suggesting that these savannas may occupy a unique climate space that is not found in Africa, Australia or South America. Possibly this is because they occupy higher elevations and cooler climates than any of the southern continent savannas and are analogous to pine savannas in North America [77], which are also underlain by C_4 grasses [102]. Thus, as is the case for the southern continents, the climatic space of Asian savannas is different from other continents [7].

Although our models provide us with a first approximation of the potential distribution and extent of savannas in Asia, they are conspicuous in their lack of fire and herbivory as predictors of savanna distribution. Inclusion of such top-down effects in future models will undoubtedly provide us with a more refined understanding of savanna distributions in Asia. Given that the vast majority of savanna habitats in Asia have already been converted or otherwise modified by humans [100,103], there is an urgent need for identifying and mapping Asian savannas, both potential and extant, not only for their effective management but also for a more nuanced picture of tropical savannas globally.

7. Uncertain futures for savannas in Asia

The lack of recognition of Asian savannas as unique ecosystems distinct from forests, and the common misperception of savannas as degraded forests pose significant conservation and management challenges. These include inappropriate fire and herbivore management resulting from a lack of understanding of the functional roles of these disturbances in these ecosystems, land-use conversions to agriculture and tree plantations, severe invasions by exotic woody species and uncertain trajectories under changing climatic regimes.

Beginning in the colonial period, official policy on protected area management in South Asia was to strictly suppress fire and livestock grazing [11,86]. For example, the Indian Forest Act of 1927 (http://envfor.nic.in/legis/forest/forest4.html) officially deemed the wilful setting of fire in protected areas as a punishable crime. Many such policies remain official to this day, contrary to scientific consensus that fire and herbivory are key ecological processes that maintain ecosystem health and diversity in savannas [77,104,105]. In practice, the implementation of such policies varies widely across Asia. In China, official government policies of strict fire prevention in conservation areas and public lands have been implemented, at least since the 1980s [79,80]. In contrast, departments charged with the stewardship of protected areas in other South and Southeast Asian countries often have limited resources, and fire suppression can be erratic [86].

In the Dipterocarp savannas of Thailand, fire suppression resulted in litter build-up and exceptionally intense fires in years when they did occur, with unusually high tree mortalities [11]. In the central and northern Indian mixed deciduous savannas, it was widely recognized by the early 1900s that both teak (Tectona grandis) and sal (Shorea robusta) seedlings were not recruiting in areas with sustained fire suppression [86]. At the other extreme, Saha and Howe [106] found that annual, low intensity fires in a deciduous savanna in Central India resulted in a very restricted set of tree species being able to regenerate, and predicted large declines in tree diversity in these communities in the coming century. Thus, neither fire exclusion nor very frequent burning is desirable. Similarly, policy-driven exclusion of large bodied grazing cattle from a southern Indian deciduous broadleaf savanna released tall-grass species of low nutrient quality from their control, allowing them to dominate the understorey, in turn suppressing populations of small-bodied wild herbivores for which these tall grasses are unpalatable [107]. In sharp contrast to Africa, where the role of herbivores in driving community and ecosystem dynamics has been extensively studied, current knowledge of the functional roles of herbivores in Asian savannas is woefully inadequate [108]. Both long-term herbivore and fire exclusion studies are almost non-existent in Asia. Likewise, studies documenting vegetation responses using experimental burns, which have been invaluable for understanding the role of fires in savannas and grasslands elsewhere, are rare in Asia. Unfortunately, they are likely to remain so because of government policies of fire suppression in countries like India and China [79,80,86].

As is true for savannas elsewhere, Asian savannas are heavily threatened by land-use changes including conversion to agriculture and tree plantations. Of particular concern, government driven afforestation initiatives in the context of emerging programs for carbon sequestration are a major threat to mixed tree-grass biomes globally [109–111]. For example, the Green India mission (http://www.envfor.nic.in/major-initiatives/national-mission-green-india-gim) aims "to increase and improve tree cover on 10 million hectares of forest and non-forest lands" in the subcontinent. A key challenge in this context will be to distinguish derived savannas via forest degradation (and therefore appropriate for reforestation) from ancient savannas that should be conserved for their unique biodiversity, particularly in their herbaceous layers and the herbivore communities that they support [1,15,111,112]. This will require identification of indicator tree, grass and herbaceous species, or combinations of these, that are diagnostic of derived versus ancient savannas across these regions [111,112].

Another major threat to Asia's savannas arises from invasions by exotic plant species that have transformed the physiognomies of these landscapes. Drier tracts of fine-leafed spiny savannas in both South Asia and Southeast Asia have been heavily invaded by Prosopis juliflora which transforms open tree-grass landscapes into woody thickets, often with extensive bare ground [113–116]. In the more mesic tracts of deciduous broadleaf savannas, dense invasions of the woody shrub Lantana camara, have replaced the C_4 grass understorey [117–119], with potential consequences for the fire and nutrient dynamics, and herbivore and prey communities of these systems. The causes for these invasions include tree seeding for fuelwood, overgrazing and suppression of native fire regimes [117–119]. Today, these widespread invasions appear irreversible in many South Asian savannas and may well represent fundamental state shifts in these ecosystems. Research that elucidates how these invasions have transformed the functional ecology of these ecosystems, including the balance of woody and herbaceous components, responses to fire and herbivory, carbon and water dynamics, and how these may respond under anticipated climatic changes in the future is urgently needed.

Analyses of long-term precipitation records for Asia show that the South Asian summer monsoon is undergoing a directional shift, with a trend towards more intense rain events and longer dry periods between rain events during the monsoon season [120,121]. Shifts in patterns of water availability during the monsoon, along with predicted changes in the total rainfall, seasonality and spatial variability of rainfall [122–124] will likely have large impacts on the structure and dynamics of Asian savannas over the coming decades. A recent analysis for South Asia finds that for an ensemble of projected climate scenarios, the savannas of the Indian subcontinent will likely show large losses in their geographical extent, as the drier areas they now occupy are replaced by higher rainfall regimes[125]. Likewise, climate models predict increasing rainfall over East Asia (IPCC 2013 report, http://www.ipcc.ch/report/ar5/wg1/), with the potential to shift these savannas towards densely wooded states from where they may transition to forest ecosystems. Future research that considers the interactive effects of rainfall and temperature changes with changes in fire and herbivore regimes and human use will be critical for forecasting the dynamics of Asian systems. Further, experimental studies that explore changes in recruitment and growth responses of dominant trees of the different savanna types to simulated changes in temperature, precipitation and nutrient regimes will provide critical insights into the potential trajectories of these savannas over the coming century.

Author contributions

JR and KWT are equal first authors on this manuscript. DNR and MS performed the analysis and modelling of climatic envelopes of Asian savannas. JR, KWT and MS wrote the manuscript, with inputs from DNR.

Competing Interests

The authors declare no competing interests.

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Appendices

Supplementary Information: Figures S1, S2, S3, Tables S1, S2, S3, and an appendix on methods used in the stochastic gradient boosting analyses of the climate domains of Asian savannas.

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Figures and Tables

Table 1 Dominant savanna formations in Asia. Location, composition and evidence for functional traits related to tolerance of fire, herbivory or drought. Cells with "No data" indicate areas where information is lacking about Asian savanna types.

Figure 1 Predicted distributions of savannas in Asia based on the climate envelope for a) Africa, b) Australia, and c) South America. The results suggest that Asia supports larger areas with climates that are similar to those occupied by African savannas than either Australian or South American savannas. The numbers shown are known field locations of different Asian savannas. Images corresponding to these numbers are shown in Figures 2a and 2b.

Figure 2a Images of different Asian savannas with numbers on the images corresponding to the numbered geographic locations shown in Figure 1. 1. Fine-leafed and spiny Acacia savanna in Gujarat, western India. 2. Broadleaf Anogeissus-Terminalia savanna in Mudumalai, southern India 3. Broadleaf Anogeissus savanna in Nagarjuna-Sagar in south-eastern India. 4. Broadleaf Dipterocarp savanna in Pa Hin Ngam, Thailand and 5. Broadleaf Dipterocarp savanna underlain by the deciduous bamboo Vietnamosasa spp. in Mondulkiri, Cambodia. Photo Credits: Jayashree Ratnam, Edmund February, Mahesh Sankaran, Komsant Inroung (http://lifexdiscovery.blogspot.in), Kyle Tomlinson.

Figure 2b Images of different Asian savannas with numbers on the images corresponding to the numbered geographic locations shown in Figure 1. 6. Mixed broadleaf savanna in Yuanjiang Valley savanna, Yunnan, China, 7. Pine savanna (Pinus kesiya) on Mt Ugo, The Philippines 8. Eucalypt savanna (Eucalyptus alba) on Mount Curi, East Timor, The Lesser Sunda islands 9. Fine-leafed and spiny Acacia savanna on Mount Manatuto, East Timor, The Lesser Sunda islands 10. Fine-leafed and spiny savanna in Sariska, central India and 11. **Pine** savanna in the Himalayan foothills in Dehradun, north India. Photo Credits: Kyle Tomlinson, Don Franklin, Jayashree Ratnam, Mahesh Sankaran, Anne Jimenez (Wikimedia Commons).

Figure 1

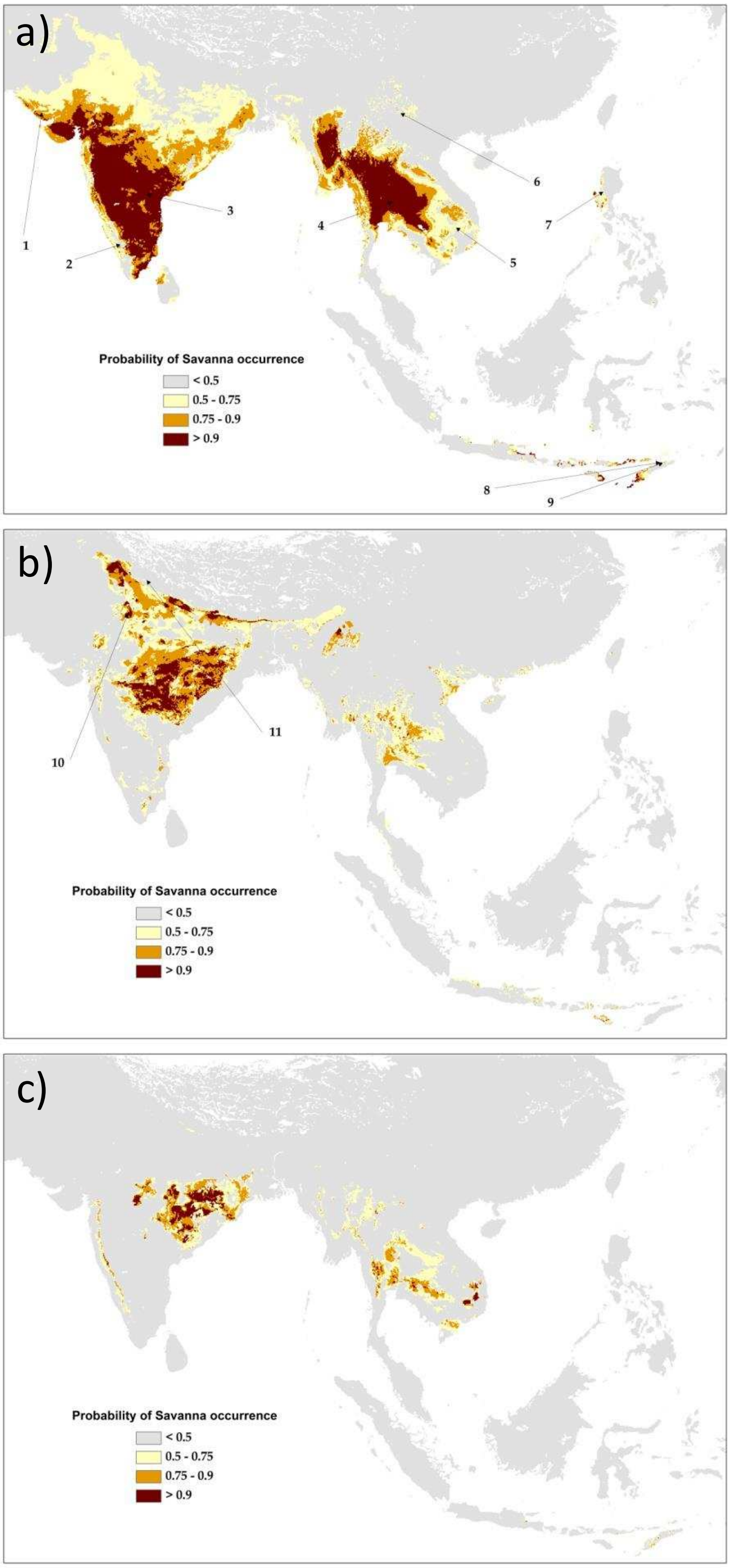
a)
1
2
3
4
5
6
7
8
9
Probability of Savanna occurrence
< 0.5
0.5 - 0.75
0.75 - 0.9
> 0.9
b)
10
11
Probability of Savanna occurrence
< 0.5
0.5 - 0.75
0.75 - 0.9
> 0.9
c)
Probability of Savanna occurrence
< 0.5
0.5 - 0.75
0.75 - 0.9
> 0.9

Figure 2a

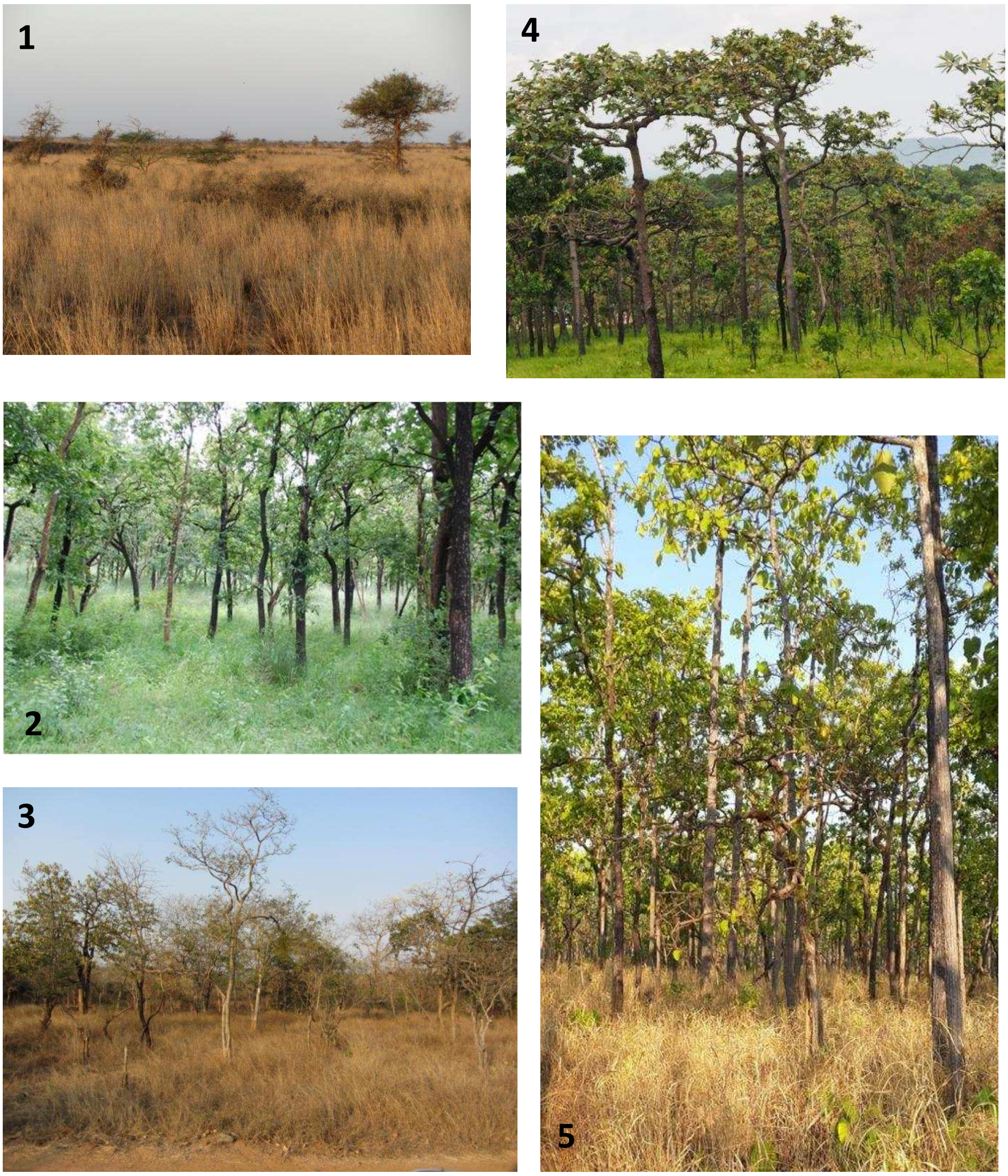

Figure 2b

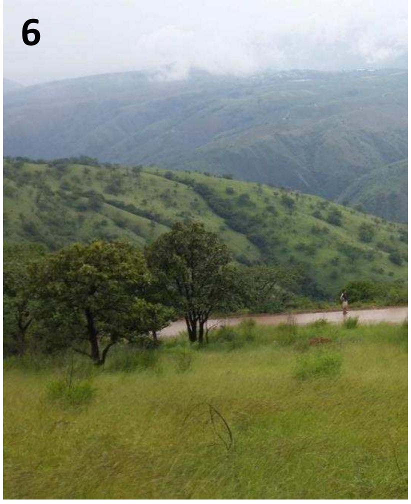
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Table 1 Dominant savanna types in Asia. Location, composition and evidence for functional traits related to fire, herbivory or drought

	Deciduous broadleaf savanna			Fine-leafed and spiny savanna	Pine savanna
Formations	Dipterocarp savanna	Mixed savanna §	Eucalypt savanna §		
Locations in Asia §§	South, Southeast	South, Southeast, East	Southeast (Lesser Sunda Islands)	South, Southeast, East	South, Southeast, East?
Dominant tree clades	Dipterocarpaceae	Anacardiaceae, Combretaceae, Lamiaceae, Lythraceae Fabaceae (Deteriae, Caesalpinioideae)	Myrtaceae	Fabaceae (Mimosoideae) Rhamnaceae, Rubiaceae, Capparaceae, Burseraceae	Pinaceae Fagaceae
Dominant grass clades	Andropogoneae	Andropogoneae	Andropogoneae	Andropogoneae, Chloridoideae	Andropogoneae
Diverse non-Poaceae herb clades	No data	Fabaceae, Asteraceae, Euphorbiaceae	No data	Fabaceae, Malvaceae, Euphorbiaceae	Cyperaceae, Fabaceae, Xyridaceae, Eriocaulaceae
Functional traits for fire	Thickened bark Sub-cutaneous meristems Belowground storage	Thickened bark Sub-cutaneous meristems	No data	No data	Thickened bark Sub-cutaneous meristems Grass-stage juveniles Belowground storage Underground bud banks
Functional traits for herbivory	Spiny plants along river drainage lines	No data	No data	Spiny plants abundant Mammal-dispersed fruits	No data
Functional traits for drought	Deciduous	Deciduous	Deciduous	Small leaves, Deciduous	No data
References	[50,64,85]	[50,52,55,59] K. W. Tomlinson unpublished data		[38,52,56–58,66]	[50,55,73,74,82] W. Eiadthong, unpublished data

§Density of tree cover increases with rainfall. §§ Images of savannas from these regions can be viewed in Figs 2a,b.