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Savanna plant communities in the wetter parts of the Indonesian archipelago

Sutomo · Eddie van Etten

Abstract Savanna occurs in specific locations throughout the Indonesian archipelago, including some high rainfall regions. Little is known about its defining characteristics, such as structure, composition or diversity, and what these characteristics reveal about the origin and age of these savannas. At four locations in eastern Java (Baluran National Park & Alas Purwo National Park), Bali (Bali Barat National Park) and Lombok (Rinjani National Park), we used plots to record the abundance and cover of plant species and to measure local environmental parameters. MODIS burned-area product and field observations were used to obtain information on recent fires. We compared each savanna in terms of dominant species, species diversity and species richness. We also used ANOSIM to analyse the variation in community composition and canonical correspondence analysis to explore relationships between floristic and measured environmental factors. Our results showed there were distinct gradients in elevation (along with related climatic factors such as temperature and precipitation) and fire regime linked to floristic composition across the savannas of Java, Bali and Lombok Islands. Each savanna was characterized by a different set of woody and grass species, with invasive alien species, such as *Acacia nilotica* (syn. *Vachellia nilotica*)*, Lantana camara* and *Chromolaena odorata,* being particularly important in differentiating between savannas. Characteristics of the Baluran savanna suggest that this ecosystem may be of considerable age, whereas the other savannas are likely to be maintained by regular fire. This study is the first study to describe more thoroughly the savanna plant community in the wetter parts of Indonesian archipelago and should serve as a valuable foundation for further studies on the Indonesian savannas and those of other parts of Southeast Asia.

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Introduction

The remarkably diverse tropical forest communities of Indonesia have been widely recognized for their importance to the world's biodiversity and ecosystem services (Dossa et al. 2013; Blackie et al. 2014; Boedhihartono 2017). The structural and floristic

variation of these Indonesian tropical forests have been extensively studied and related to variation in temperature, precipitation, seasonality of rainfall, edaphic conditions, topography, natural and anthropogenic disturbance, elevation, climate change, and invasive alien species (Harger 1995; van der Kaars and Dam 1997; Brearley et al. 2004; Widyatmoko and Burgman 2006; Sutomo et al. 2015). However, little is known about the savanna communities of Indonesia, and indeed right across Southeast Asia, despite such communities being common across this region (Ratnam et al. 2016). Savannas are tropical grass-dominated ecosystems with sparse to mid-dense woody plants, but throughout much of Indonesia, such vegetation would, based on climate alone, be expected to be forest (Bond and Keeley 2005; Scogings and Sankaran 2020).

Savanna in Indonesia is found in specific locations across the archipelago over a wide range of climate and soils (Whitten et al. 1996; Monk et al. 2000). The most well-known and studied savannas occur on the islands of East Nusa Tenggara (Indonesian: Nusa Tenggara Timur; NTT) in the driest eastern parts of the archipelago which have pronounced seasonal rainfall, such as West Timor, Sumba and Flores (Monk et al. 2000; Fisher et al. 2006; Russell-Smith and Edwards 2006; Tacconi and Ruchiat 2006). Species composition of savanna in NTT was studied by Auffenberg (1981) and he described them in terms of dominant woody species. *Borassus flabellifer* (Arecaceae/Palmae) dominated the tree layer of the savanna on Komodo Island, Rinca Island and the coast of Flores Island up to an elevation of about 400 m a.s.l. *Ziziphus mauritiana* was the dominant savanna tree growing from sea level to 500 m a.s.l. Other types of savanna are also commonly found in the eastern part of Indonesia (based on major tree species), namely *Eucalyptus* savanna in Timor and *Casuarina* savanna in Sumba and Timor (Goltenboth et al. 2006). However, detailed information on the occurrence and features of savanna in the wetter regions of Indonesia with less strongly seasonal rainfall, such as Java, Bali and Lombok, is scarce. Whitten et al. (1996) mention the existence of savanna in Baluran, East Java and Bali Barat in Bali; however, they did not describe them thoroughly.

Savanna ecosystems in Southeast Asia have long been regarded as anthropogenic, being derived from tropical forests and maintained via ongoing human manipulation, primarily clearing, grazing and/or burning (Stott 1990; Solbrig et al. 1996; Ratnam et al. 2011). This view has certainly been widely reported for Indonesian savannas (Whitten et al. 1996; Goltenboth et al. 2006). However, a recent review by Ratnam et al. (2016) questions this assumption and points to antiquity of some Southeast Asian savannas. Evidence for this comes from: (1) fossil history and phylogenetic data showing existence of savanna species of plants and animals in the region before humans; (2) dominance by species with adaptations to withstand repeated fire and/or grazing; and (3) climatic consistencies with savannas of other continents.

In this paper, we compare and contrast the vegetation characteristics of four savannas in the wetter part of the Indonesian archipelago (Java – Bali – Lombok) to address two important questions: (1) what environmental factors are linked to, and therefore may be driving, differences in floristic composition across these savannas; and (2) what do these vegetation features tell us about the origin, maintenance and age of these savannas? Given the wide geographic spread of study sites, we hypothesized that floristic gradients across these savannas would be primarily linked to elevation, precipitation and related micro-climatic differences, with disturbance type and frequency being of secondary importance.

Methods

Study sites

The study was conducted in four Indonesian savannas on Java, Lombok and Bali Islands. These were selected based on all the well-known localities of savanna ecosystems in this region as reported in the literature (Whitten et al. 1996). Two savannas were located in East Java (Baluran National Park and Alas Purwo National Park), one in Bali (Bali Barat National Park) and one in Lombok (Rinjani National Park; Fig. 1). Other savannas reported in the literature were visited but not studied here, as they were no longer savanna (e.g. Pangandaran Nature Reserve in West Java, now largely converted to secondary forest). Typical fire regimes and climate for each savanna studied are described in Table 1. In all of these savannas, the soils are of volcanic origin but differ in age.

Fig. 1 Locations of the four studied national parks across Java, Bali and Lombok Islands, Indonesia. The savanna vegetation in each park was sampled for this study
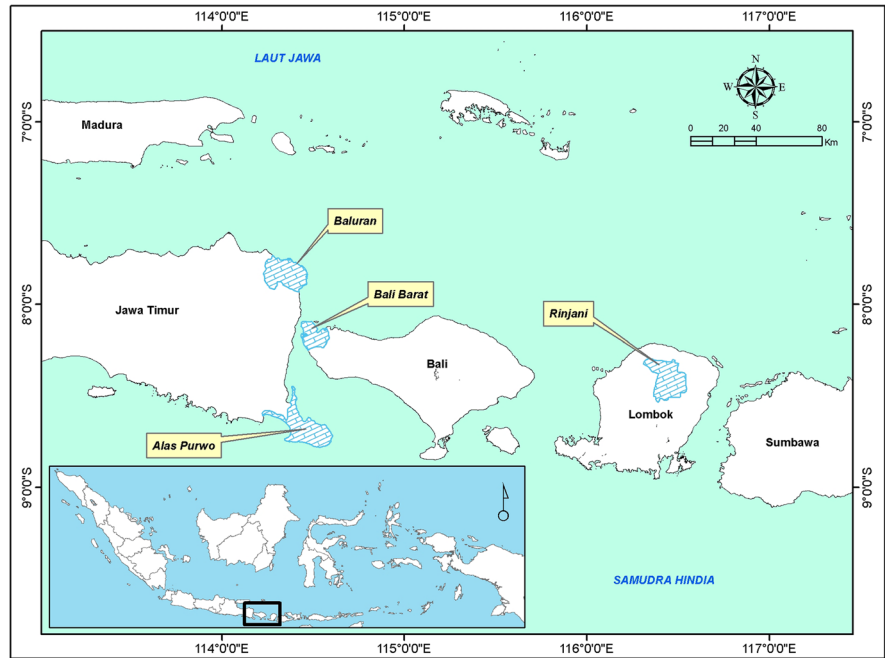

Table 1 Typical fire regime, average precipitation and average temperature for the four study savannas.

Savanna site	Fire frequency (per decade)	Time since last fire	Average Precipitation [mm / year]	Average Temperature [°C]
Alas Purwo National Park	1	~10 years	1,079–1,554	26–29
Rinjani National Park	2	~6 years	2,000	23–30
Bali Barat National Park	1	~10 years	972–1,550	27–29
Baluran National Park	4	~4 years	900–1,600	27–37

Field sampling

Field sampling of vegetation follows standard plot-based approaches commonly used in floristic description and analysis (Kent 2011) and as applied to similar vegetation in the region (e.g. Brearley et al. 2004; Dossa et al. 2013). Between September to November 2014 (dry season), sampling plots (50×50 m) were randomly positioned at ten sites in each of the four savanna areas (Java, Bali and Lombok Islands; 40 study sites in total); they were spaced at least 200 m apart to reduce likelihood of spatial auto-correlation. Inside each of the 50×50-m plots, we randomly placed four nested subplots of 5×5 m. Within the 50×50-m plot we identified and measured the cover, height and width of all woody species (trees and

shrubs), and recorded the position of all tree species ≥ 10-cm stem diameter at 1.3 m (DBH). In the smaller nested subplots we identified all groundcover species (grasses, ferns and forbs) and estimated their cover (Hardjosuwarno, 1990); average cover across the four subplots was then calculated for each groundcover species. Plant identification was primarily done using the resources of the *Hortus Botanicus Baliensis*, Bali Botanical Garden, but also the Flora Malesiana (http://floramalesiana.org), PROSEA (Plant Resources of South East Asia; http://proseanet.org) and the Bioportal at Naturalis Biodiversity Centre, the Netherlands (http://bioportal.naturalis.nl). Nomenclature follows the Plant List (http://www.theplantlist.org) maintained by the Royal Botanic Gardens, Kew and Missouri Botanical Garden. We also recorded

local environmental data for every plot, at a similar time of day (morning): soil pH and moisture (using portable meters made by Hanna Instruments), local microclimate (light intensity, air temperature, relative humidity, wind velocity and heat stress index, using Lutron light and weather meters) and topography (elevation and slope using a Garmin GPS device and a clinometer). The plot locations were cross-checked with fire-scar maps produced using the MODIS (moderate resolution imaging spectroradiometer) burned-area product (Roy et al. 2008; Sutomo and van Etten 2018) for the years 2000 to 2013 to obtain information on time since fire and fire frequency for each plot. Typical fire regime data for the savanna areas (Table 1) were generalizations based on these fire maps for each location, complemented by interviews with park rangers and field observations.

Data analysis

The importance value index or IVI (Kent 2011) was calculated for each species at each site and then averaged to understand the floristic dominance and plant community composition in each savanna. Species richness and the Shannon–Wiener species diversity and evenness indices (Magurran 2004) were also calculated for each site using the total number of species found within the 50×50-m plot (including the 5×5-m nested subplots). For the diversity and evenness indices, the relative abundance was based on species cover. Differences in mean values of vegetation parameters between savannas were tested for significance using ANOVA and Tukey's b post-hoc tests in SPSS (v.23, IBM Corp., New York, USA). The species cover data at each site were square-root transformed prior to constructing a resemblance matrix based on the Bray–Curtis similarity measure (Clarke 1993). A non-metric multidimensional scaling (NMDS) ordination diagram was first generated based on the resemblance matrix. The compositional differences between savannas were then tested for significance using one-way ANOSIM (analysis of similarity; Clarke 1993). SIMPER (similarity percentage) analysis was then used to explore the relative contribution of individual species to the total dissimilarity among the savannas. These multivariate analyses were performed using PRIMER (version 6.0., PRIMER-E Ltd, Plymouth, UK). Correlations

between floristic and local environmental gradients were explored using the BEST (Bio-Env+Stepwise) method (Clarke and Ainsworth 1993) in PRIMER, as well as canonical correspondence analysis (CCA) using CANOCO (version 5, Microcomputer Power, Ithaca, New York).

Results

Structure and dominant species

We discovered as many as 43 plant species within 26 families across the four savannas, including one fern, seven grass or grass-like plants, and two forbs (a full list of species, habit and their typical habitats are presented in Appendix 1). Each savanna has structural characteristics and dominant species that differentiate it from the others (Table 2). For instance, Alas Purwo is dominated by the grass *Arundinella setosa*, the small shrub *Desmodium laxiflorum* (Fabaceae) and the invasive alien species (IAS) *Chromolaena odorata* (Asteraceae) in the groundcover layer whereas the tree layer is dominated by *Flacourtia rukam* (Salicaceae). At Rinjani, the groundcover layer is dominated by the grass *Imperata cylindrica* and the fern *Gleichenia microphylla* whereas the tree layer is mainly composed of *Engelhardia spicata* (Juglandaceae). The ground layer of Bali Barat is also dominated by the Poaceae family (*Calamagrostis australis*), whilst the tree layer mainly consists of *Borassus flabellifer* (Arecaceae). In Baluran, the groundcover layer is characterized by *Desmodium laxiflorum* (Fabaceae), seedlings of *Azadirachta indica* (Meliaceae) and two grasses, *Polytrias indica* and *Dichanthium caricosum,* whereas the tree layer mainly consists of species such as *Ziziphus mauritiana* (Rhamnaceae) and the IAS *Acacia nilotica* (syn. *Vachellia nilotica*; Fabaceae). The presence of invasive alien species is notable in most of the savannas (Appendix 1) and strongly influences their overall structure and composition. Bali Barat and Alas Purwo face similar problems from the obnoxious invasive alien species *Chromolaena odorata*, while at Baluran, *A. nilotica* occurs widely in both the ground (i.e. seedlings and small saplings) and tree layers (Table 2).

Table 2 Importance value index (IVI) and cover [%] for the dominant and common groundcovers and tree species (IVI score greater than 10) from each savanna sampled. Asterisks indicate likely exotic species (see Appendix 1).

Species	Family	IVI	Cover [%]
Groundcover/understorey layer			
Alas Purwo savanna			
Arundinella setosa	Poaceae	93.6	65.9
Desmodium laxiflorum	Fabaceae	42.1	19.8
*Chromolaena odorata**	Asteraceae	30.1	5.9
Cyperus brevifolius	Cyperaceae	10.8	5.3
Flacourtia rukam (seedling)	Salicaceae	10.4	2.1
Mt Rinjani savanna			
Imperata cylindrica	Poaceae	48.3	27.2
Gleichenia microphylla	Gleicheniaceae	21.8	5.2
Melastoma polyanthum	Melastomataceae	14.9	4.3
Bali Barat savanna			
Calamagrostis australis	Poaceae	100	78.4
*Lantana camara**	Verbenaceae	21.2	3.6
*Chromolaena odorata**	Asteraceae	18.5	3.5
Borassus flabellifer (saplings)	Arecaceae	15.2	2.7
Baluran savanna			
Azadirachta indica	Meliaceae	61.4	39.2
Desmodium laxiflorum	Fabaceae	47.7	36.6
Polytrias indica	Poaceae	29.7	7.6
Dichanthium caricosum	Poaceae	19.7	8.6
*Acacia nilotica**(seedlings)	Fabaceae	13.7	2.6
Tree Layer			
Alas Purwo savanna			
Flacourtia rukam	Salicaceae	79.1	50.6
Streblus asper	Moraceae	60.5	38.3
Mt Rinjani savanna			
Engelhardia spicata	Juglandaceae	183.9	35.3
Ficus septica	Moraceae	35.5	6.7
Laportea stimulans	Urticaceae	20.7	6.7
Bali Barat savanna			
Borassus flabellifer	Arecaceae	75.1	38.2
Bridelia stipularis	Phyllanthaceae	50.4	29.4
Albizia chinensis	Fabaceae	25.2	14.7
Baluran savanna			
Ziziphus mauritiana	Rhamnaceae	161.7	42.9
*Azadirachta indica**	Meliaceae	94.7	41.8
*Acacia nilotica**	Fabaceae	43.5	14.3

Table 3 Differences in mean species diversity, species richness and evenness (per 400 m^2) between savannas. Different superscript letters (a, b, c) after mean values ($\pm$SD) indicate significant differences between savannas as assessed with Tukey's b test.

Savanna	Shannon–Wiener species diversity	Species richness	Species evenness
Alas Purwo	0.61 ($\pm$0.30)[a]	2.60 ($\pm$0.52)[a]	0.61 ($\pm$0.27)[b]
Rinjani	1.07 ($\pm$0.45)[b]	4.20 ($\pm$1.87)[b]	0.64 ($\pm$0.23)[ab]
Bali Barat	0.72 ($\pm$0.25)[c]	5.00 ($\pm$1.05)[b]	0.43 ($\pm$0.11)[a]
Baluran	0.74 ($\pm$0.40)[c]	3.10 ($\pm$1.20)[ab]	0.83 ($\pm$0.09)[c]

Diversity measures

There are significant differences between the savannas in terms of mean Shannon–Wiener species diversity and species richness (Table 3). Rinjani has the highest mean species diversity compared to the others, while Alas Purwo has the lowest. There are no differences in species diversity between Baluran and Bali Barat. Significant differences were detected in the mean species richness of savannas, namely between Alas Purwo and Baluran, and between Rinjani and Bali Barat (Table 3). Bali Barat has the highest species richness compared to other savannas, whilst Alas Purwo is lowest in terms of species richness, as well as species diversity. In terms of species evenness, Baluran has the highest evenness score whereas Bali Barat has the lowest (Table 3).

Differences in community composition

The global test of analysis of similarity (ANOSIM) showed there were significant differences in species composition between the savanna sites (Global $R = 0.94$; $P < 0.001$) based on all species (both native and alien). The savannas were also floristically different from each other in terms of native plant species (Global $R = 0.64$; $P < 0.001$). There is also clear separation of savanna sites in the ordination (Fig. 2). Baluran savanna had the lowest value of average similarity (48.1%), indicating it had the greatest variation in floristic composition between the plots. The reverse is true for Alas Purwo (Fig. 2). SIMPER analysis showed that twenty-two species were primarily responsible for the dissimilarity between the sites (Table 4). From all six combinations of pairwise

Fig. 2 Result from NMDS ordination (square root transformation, Bray–Curtis similarity) of vegetation data in four savannas in Indonesia. ANOSIM Global R statistic = 0.94 ($P < 0.001$). Average similarity within each savanna: Baluran – 48.1; Alas Purwo – 64.7; Bali Barat – 55.12; Rinjani – 50.03
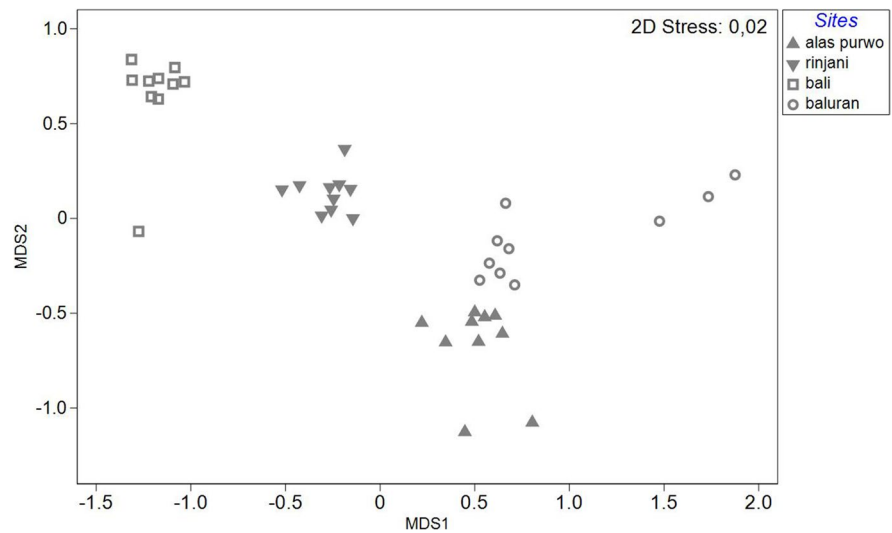

Table 4 SIMPER analysis results showing percentage (%) contributions of species to average Bray–Curtis dissimilarities between pairs of savanna areas. Abbreviations refer to the Baluran (BA), Alas Purwo (AP), Bali (BB) and Rinjani (GR) National Parks.

Savanna sites comparison							
Species	Family	AP & GR	AP & BB	GR & BB	AP & BA	GR & BA	BB & BA
Average dissimilarity [%]		98.6	95.4	98.5	85.4	98.7	99.9
Acacia nilotica	Fabaceae	–	–	–	2.83	2.81	2.29
Albizia chinensis	Fabaceae	–	1.23	1.33	–	–	1.35
Antidesma bunius	Euphorbiaceae	–	2.88	–	–	–	3.14
Borassus flabellifer	Arecaceae	–	5.44	5.84	–	–	5.94
Bridelia stipularis	Phyllanthaceae	–	3.22	3.43	–	–	3.49
Chromolaena odorata	Asteraceae	–	5.33	4.09	–	–	4.17
Desmodium laxiflorum	Fabaceae	12.95	11.89	–	10.63	11.27	9.47
Calamagrostis australis	Poaceae	–	26.22	28.12	–	–	28.63
Engelhardia spicata	Juglandaceae	3.49	–	3.31	–	4.11	–
Flacourtia rukam	Salicaceae	2.33	2.07	–	2.78	–	–
Gleichenia microphylla	Gleicheniaceae	7.3	–	6.95	–	8.47	–
Imperata cylindrica	Poaceae	20.35	–	19.36	–	23.67	–
Lantana camara	Asteraceae	–	4.73	–	–	–	5.17
Melastoma polyanthum	Melastomataceae	4.92	–	4.66	–	5.82	–
Ocimum tenuiflorum	Lamiaceae	3.05	–	2.92	–	3.49	–
Passiflora foetida	Passifloraceae	–	–	–	5.49	–	4.45
Polytrias indica	Poaceae	–	–	–	11.87	5.45	9.62
Streblus asper	Moraceae	–	1.13	–	1.54	–	–
Thespesia lampas	Malvaceae	–	–	–	6.03	5.95	4.88

comparisons of savanna areas, eleven species were important in at least three pairwise comparisons (*Acacia nilotica, Albizia chinensis, Borassus flabellifer, Chromolaena odorata, Engelhardia* spicata, *Flacourtia rukam, Gleichenia microphylla, Imperata cylindrica, Melastoma polyanthum, Polytrias indica, Thespesia lampas*), and six species (*Antidesma bunius, Calamagrostis australis, Lantana camara,*

Ocimum tenuiflorum, *Passiflora foetida*, *Streblus asper*) occurred in two savanna pairwise comparisons. The species that contributed the most to the dissimilarities among almost all pairs of savanna areas was *Desmodium laxiflorum* (Table 4). This species was present in all three savanna sites (Baluran, Alas Purwo and Rinjani), but not in the Bali Barat savanna.

Savanna community composition correlation with physical-environmental factors

Canonical correspondence analysis (CCA; Fig. 3) shows that Rinjani (GR) in Lombok floristically separates from the other savannas along elevation and associated climatic gradients whereas Baluran (BA) is clearly separated from other savannas by differences in fire regime (higher frequency and less time since last fire), but also by slope to a lesser degree. According to the BEST (Bio-Env) analysis, elevation and precipitation are the two environmental factors with the highest correlation to species composition
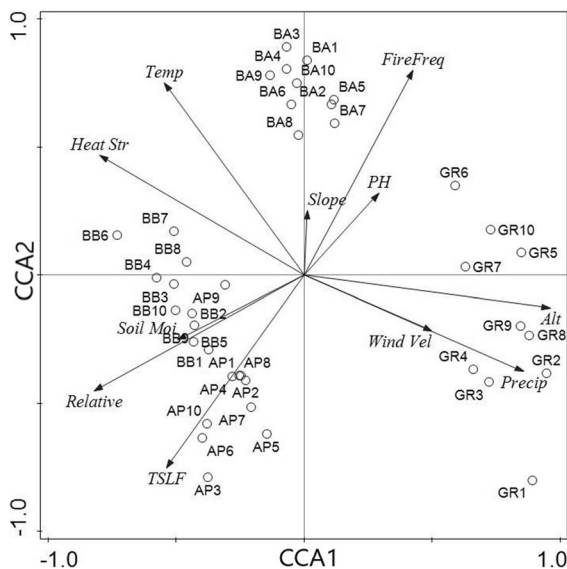

Fig. 3 Results of canonical correspondence analysis (CCA) showing a biplot of sample sites and environmental variables. Temp – air temperature; Heat Str – heat stress index; Relative – relative humidity; Precip – precipitation; Alt –altitude (elevation); Ph – soil pH; Slope – slope Wind vel – wind velocity; Soil moist – soil moisture; FireFreq – fire frequency; TSLF – time since last fire. Baluran NP (BA), Alas Purwo NP (AP), Bali NP (BB) and Rinjani NP (GR). Together, CCA1 and CCA2 explain 63.2% of the total variation in the floristic-environment relationship

across all four of sampled savannas (BEST Global test sample statistic Rho = 0.6; $P < 0.001$).

Discussion

In this study we have characterized the tropical savanna plant communities of the wetter regions of Indonesia distributed across three main Islands, namely Java, Bali and Lombok, and their relationships with the physical environment. We found each of the four savanna ecosystems were distinctive in terms of species composition, ecological traits of dominant species, physical environment and physiognomy. We confirmed our main hypothesis that climate and elevation are likely to be the main drivers for savanna plant community differences. However, fire also potentially plays an important role, as we found variation in fire regime was correlated with gradients in floristic composition between the savannas. We also recognize that fire and climatic variables were derived from coarsely mapped data and, consequently, varied little between plots within each savanna. Therefore, the environmental gradients recognized are more likely to explain floristic dissimilarities between savannas, and more work is required to characterize floristic–environment relationships within discrete areas of savanna (i.e. at the landscape scale).

Savanna sites have a defining feature of dominant groundcover, especially grasses and forbs, with sparse tree cover (Frost et al. 1986). All four savanna sites in our study also showed this structure; however, each one of them is characterized by different combinations of tree species. Bali Barat is characterized by the palm species (*Borassus flabellifer*) as the tree layer. The same species also characterized the savanna in the drier part of the Indonesian archipelago, such as in Kupang, Timor Island in East Nusa Tenggara (Monk et al. 2000). Species of the same genus (*Borassus aethiopum*) also characterize the humid Lamto savanna of the Cote d'Ivoire in West Africa (Barot et al. 1999), and indeed palm savannas are known in Venezuela (Holbrook and Putz 1996), Namibia (Konstant et al. 1995), as well as islands such as Madagascar and Mauritius (Safford 1997). In Baluran National Park (but not in area sampled), near Bama Beach, one species of palm (*Corypha utan*) is known to occur in savanna. These palms in

Bali Barat, Kupang and Baluran occur in lowland areas, especially near to the coast. In any given situation, plant co-occurrence and abundance may be determined largely by resource availability, heterogeneity of the abiotic environment, and microhabitat specialization. Some palms appear to be adapted to specific edaphic conditions, especially those related to soil drainage and depth (Widyatmoko and Burgman 2006).

In the Baluran savanna, common species in the tree layer included *Ziziphus mauritiana*, *Azadirachta indica* and *Acacia nilotica*. The same species has been reported from the drier eastern parts of Indonesia, such as Komodo, Rinca and Flores Islands, East Nusa Tenggara, from sea level up to 500 m a.s.l.. *Ziziphus mauritiana* also occurs in savanna areas of India (Pandey and Singh 1991). The same genus (*Ziziphus*) is common to many savannas of Africa, Arabia and South/Southeast Asia (Hess et al. 1996, Ratnam et al. 2016). In fact, of the four savannas studied, Baluran features typical savanna-type tree species showing adaptations to herbivory (thorns) and drought (small leaves, open architecture) and suggest it may be a relatively old savanna (*sensu* Ratnam et al. 2016). Even the invasive tree species *Acacia nilotica* and *Azadirachta indica* are typical savanna species (Radford et al. 2001; Dhileepan 2009: Swaine et al. 1992). It is not clear if *Z. mauritiana* (Indian jujube) is exotic or native to Baluran as the species is widely cultivated across Asia (for food and medical products), as well as having an uncertain origin and much disputed taxonomy (Islam and Simmons 2006; Janick and Paull 2008). Other evidence of the relative antiquity of the Baluran savanna are the dominance of C_4 grasses, the open vegetation structure and persistence of native forbs, as well as the continued presence of indigenous grazing ungulates (e.g. *Bos javanicus*). The savanna here occurs in a rain shadow of Mt Baluran and appears to have lower and more strongly seasonal rainfall compared with the other savannas studied.

In terms of groundcover, our savannas share similar common species with those found in other savannas of Southeast Asia, especially in Thailand, where species such as *Imperata cylindrica, Lantana camara* and *Chromolaena odorata* are all commonplace (Kurz 1876; Kodandapani 2013; Ratnam et al. 2016; Sutomo et al. 2021). C_4 grasses (mostly from the Andropogoneae clade) dominate

our savannas, as expected for savannas in general, although *Calamagrostis australis*, which is widespread in the Bali Barat savanna, appears to be a C_3 grass based on studies of other species in the genus (Osborne et al. 2014; Appendix 1). Another species which prominently contributes to the compositional similarities between our savannas is the tropical herbaceous legume *Desmodium laxiflorum. Desmodium* spp. are native to tropical Southeast Asia and Pacific Islands (Lenne 1981; Woomer et al. 1988) and are known to occur in higher rainfall savannas where they can survive fire and are known to be a palatable species to grazing animals. Although the species is absent in the Bali Barat savanna, it is present in the other savannas studied. *Desmodium* perhaps requires regular ground disturbance, such as fires, to persist, something which has been largely excluded as part of the management implemented at Bali Barat National Park in recent times.

Although there are some species in common across the savannas, there is very high floristic dissimilarity between them, especially in the tree layer, but also amongst the ground-layer dominants (Table 2). At the family level they are more similar, with certain families common to most of them (e.g. Fabaceae). There are several possible explanatory factors for the dissimilarity at species level, namely geographic, geologic and climatic barriers, as well as management including the use of fire. Baluran in East Java and Bali Barat in Bali, for example, are both national parks and are relatively close to each other (~ 60 km), but they are separated by sea (the Bali Strait) and are climatically different with Baluran having lower and more strongly seasonal precipitation and higher temperatures. This leads to more fire-prone vegetation at Baluran, which also is regularly prescribed to control the domination of woody plant, particularly the invasive alien species *Acacia nilotica* in the savanna. By contrast, fire is now suppressed in Bali Barat and the savanna is shifting to dry forest or secondary regrowth (Sutomo and van Etten 2021). Also, there were many invasive woody plants and climbing plants in the Bali Barat savanna, which is likely to reflect its proximity to human settlements and activity. Similarly, domination by many invasive alien species at Alas Purwo, especially by *Chromolaena odorata*, was recorded (Appendix 1). Both Bali Barat and Alas Purwo savannas are in danger of being transformed into a

forest structure due to lack of fires and prevalence of invasive species.

Globally, savannas in high rainfall areas typically have some woody vegetation and, in the absence of fire, tend to develop high tree cover that would outcompete and suppress grasses species, thereby disabling further fires and facilitating the transition to a forested ecosystem (Rosleine and Suzuki 2013; Staver et al. 2011, Aleman et al. 2020). Thus, regular fire is important to establish grass-tree coexistence in these areas (Sankaran et al.; Bond and Keeley 2005). Sumardja and Kartawinata (1977) described savanna in Pangandaran Peninsula, West Java and reported that some savanna sites had been abandoned around 1957. These areas have not been experienced any fire since then; subsequently, they have become young secondary forests dominated by *Decaspermum fruticosum*. By contrast, woody vegetation is mostly in low abundance in savannas of drier sites, whereas grasses are by far the dominant component. Semi-arid savannas have resource limitations (mostly competition for water) and lower biomass/fuels, and, therefore, fire is perhaps less influential for grass-tree coexistence in this type of savanna (Staver et al. 2011). On the island of Java, especially in East Java, recolonization (primary succession) after lava flow and volcanic eruptions is initially dominated by grasses which may then be maintained by regular fire over long periods. Therefore, in this region of Java, which is subject to a more pronounced dry season (less rain and longer period of dry season) than central and western parts of the island, fire is believed to be the major factor that created and then maintained savannas (van Steenis 1972).

Rinjani on the island of Lombok is also very distinct. This savanna is located at higher elevations on the slopes of the volcano Mt Rinjani and has been maintained in savanna form presumably since the early stages of primary succession after the last major eruption and lava flows in the area of study (Sutomo et al. 2021). The influence of soil depth or the depth of the volcanic deposits plays an important role in the succession, as observed in the Mt Merapi primary succession on Java Island (Sutomo 2013). Once grasses recolonized and dominated the area, only small amounts of tree species have developed, perhaps due to high competition for resources with grasses, unsuitable microclimate and/or the role of regular fire which maintains the grass domination (the fire frequency being intermediate between that of Baluran and the other savannas studied; Sutomo et al. 2021). The dominant grass here (*Imperata cylindrica*) is known for its fire tolerance and is considered a fire-climax species across Southeast Asia (MacDonald 2004). Although the Rinjani savanna studied is not currently shifting to a forest state, of the woody species found in our plots at Rinjani, almost all of them are forest pioneer/edge specialists (Appendix 1), many currently occurring only as seedlings or saplings. This suggests invasion from nearby gallery forests in nearby drainage lines and the potential for conversion to forests in the absence of future fires over a long period. However, the clumps of trees and small forest patches which establish in crevices and drainage lines are likely promoted by the extra moisture and conducive microclimate conditions which encourage dense woody vegetation (Murphy and Bowman 2012). In such landscapes, forests are often constrained to geomorphology/topographic conditions that protected it from fire (Russell-Smith et al. 2012).

Tropical savannas generally have high alpha (local-scale) plant species diversity, particularly when compared with temperate grasslands and dry tropical woodlands (Solbrig et al. 1996). High diversity in savannas, for instance, occurs in the Brazilian Cerrado (Furley 1999). However, savanna diversity can be reduced due to several reasons, such as invasion of exotic species, fire exclusion, herbivore introduction or exclusion, or physical removal of trees and shrubs (Furley 1999, Solbrig et al. 1996). In our study, average species diversity is in the low range for savannas (Magurran 1988). Low species diversity is also found in other Asian savannas, such as in India (Pandey and Singh 1991). In Indonesia, such low diversity is known to occur in the wet-climate savanna at Pangandaran, West Java (Rosleine and Suzuki 2013). This relative paucity of species in these savannas is perhaps due to extensive invasion of exotic species and/or fire exclusion. At Pangandaran, savanna abandonment without recurring fire has resulted in overdominance of *Decaspermum* sp. div. (Myrtaceae), which in turn has resulted in a decline in species diversity (Rosleine and Suzuki 2013). Low species evenness may also be the result of the dominance of certain exotic species (both woody and non-woody) in the savannas we studied (i.e. *Acacia nilotica* in Baluran savanna, *Lantana camara* in Bali Barat and

Chromolaena odorata in Alas Purwo). In their study in Baluran, Caesariantika et al. (2011) found that *Acacia nilotica* invasion had significant effect on species diversity in Baluran savanna, with values of (Shannon–Wiener) species diversity in the range of 0.46 to 1.34. In our study, we found broadly similar mean Shannon–Wiener species diversity of 0.74 at Baluran. In Baluran, *Acacia nilotica*, a woody IAS, is fire-tolerant when mature and unpalatable due to considerable thorns (Djufri 2004, FAO 2014). This poses an increased threat of expansion of *Acacia nilotica* stands in Baluran savanna even with regular fire and high grazing pressure. Evidence of recent expansion of the *A. nilotica* stand in the Bekol savanna at Baluran is outlined in Sutomo et al. (2016). Fire exclusion at Bali Barat and Alas Purwo may also play a role in the relatively low species diversity of these savannas. Although we sampled our savannas in the dry season, many annual and other short-lived species were still able to be identified as remnants of the flowers and/or leaves were still present on at least some plants. However, we accept that we are likely to have under-estimated plant diversity, especially of annual forbs and geophytes, compared to sampling in the late wet season. It is also possible that some of the more sparsely distributed ground layer species may have been missed due to the subsampling employed.

In conclusion, this study is the first to thoroughly describe savanna plant communities in the wetter parts of the Indonesian archipelago. We have shown that differences in elevation (along with related climatic factors such as temperature and precipitation), as well as differences in fire regime and types of colonizing invasive species, are likely drivers of the distinct floristic differences recorded between the savannas we studied across Java, Bali and Lombok Islands. Therefore, invasive weed management should be considered by these national parks authorities as it is likely to increase native species diversity. Lack of prescribed fire and a range of invasive species threaten to convert savanna at Bali Barat and Alas Purwo into secondary forests or shrubland. The presence of forest pioneer/edge species within the savanna at Rinjani suggests successional change from grassland to forest may occur in the absence of future fires, although the roles of soil, topography and microclimate in maintaining grass dominance are also significant (Sutomo et al. 2021). Compared to the others studied, the savanna in Baluran National Park has characteristics

of being relatively old and persistent (Ratnam et al. 2016), rather than one being created and maintained via human conversion of forests. It is recommended that further studies be conducted, including isotopic characterization of soils and organic matter, and manipulative experiments involving fire and grazing as treatments, to more firmly establish the dynamics and age of the savannas studied.

Declaration

Conflict of interest We confirm that there is no conflict of interest among authors of this paper.

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