

1-5-2023

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[10.3390/f14010106](https://doi.org/10.3390/f14010106)

Sutomo, van Etten, E. J. (2023). Fire impacts and dynamics of seasonally dry tropical forest of East Java, Indonesia. *Forests*, 14(1), Article 106. <https://doi.org/10.3390/f14010106>

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Article

Fire Impacts and Dynamics of Seasonally Dry Tropical Forest of East Java, Indonesia

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Abstract: (1) Background: Seasonally dry tropical forests (SDTFs) are globally important ecosystems which receive less research attention compared to tropical rainforests but are equally under serious threat. The objectives of this paper are to characterize the vegetation structure, diversity and composition of SDTF of Baluran National Park, East Java, Indonesia, and to assess the impact of burning this SDTF and its post-fire recovery. (2) Methods: In the field, we measured floristic composition and dominance at sites with different fire histories in both SDTF and adjacent savannas of Baluran. Remote sensing image analysis was also employed using the MODIS burn area product and various thematic maps. (3) Results: SDTF at Baluran has moderately high tree cover, is less diverse in species than rainforest, and has a prominent vegetative response to fire, especially in the tree layer. The immediate post-fire period in SDTF featured lower densities of tree seedlings and saplings, more grasses and herbs, and lower species richness than older unburned forest. Species composition varied with fire age and vegetation type, with relatively rapid recovery with time since fire evident, although there was some convergence of long-unburned savanna and SDTF sites in terms of floristics. (4) Conclusions: The SDTF of Baluran recovers after fire principally via resprouting but also via seedling regeneration, with structural attributes returning more quickly (<10 years) than floristic composition (>10 years). We did not find consistent evidence of ecosystem transitions between SDTF and savanna despite a small number of long-unburned savanna sites having floristic similarities to dry forest (particularly in terms of characteristic tree species), and we identify the need for more study to determine the degree and mechanisms of forest–savanna transitions in the region, with a future research agenda outlined. Relatively large areas of savanna–dry forest transitions demonstrated from remote sensing analyses were primarily attributed to spread of *Acacia nilotica* (an alien invasive small tree or shrub) into long-unburned savanna, and its decline in areas where the species is being successfully controlled via burning and cutting. Knowledge of such ecological shifting is important for the ecosystem management, especially in terms of their usage by large mammals.

Keywords: seasonally dry tropical forest; savanna; fire; state-transition model; Indonesia



Citation: Sutomo; van Etten, E.J.B. Fire Impacts and Dynamics of Seasonally Dry Tropical Forest of East Java, Indonesia. *Forests* **2023**, *14*, 106. <https://doi.org/10.3390/f14010106>

Academic Editor: Wil De Jong

Received: 28 September 2022

Revised: 20 December 2022

Accepted: 22 December 2022

Published: 5 January 2023



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1. Introduction

Seasonally dry tropical forests (SDTF) are an important global biome which have received far less research attention compared to tropical rainforests [1,2] despite their conservation status being more endangered than rainforest in some regions [3,4]. Although SDTFs are typically less diverse than tropical rainforests, they still harbour a wide variety of wildlife such as monkeys, deer, large cats, rodents and ground-dwelling birds. SDTFs—which are also known as tropical deciduous forests, monsoon forests or tropical dry forests—are forests of tropical regions that endure a prolonged dry season followed by a pronounced short period of high rainfall [2,5]. Such forests have a variety of deciduous tree and shrub species, which shed their leaves during the dry season and grow them again early during the following wet season [3–6]. Although there has been considerable debate regarding the

terminology and context of this forest [2,3], in this paper, we use the term seasonally dry tropical forest (SDTF).

Miles et al. [1] presented a global distribution map of SDTF based on MODIS vegetation continuous fields (VCF) and estimated about 1,048,700 km² of dry tropical forest remained worldwide in 2005 (about half of which occurred in South America) and that only 3 percent of this land was protected in conservation reserves. The MODIS data showed that only about 3.8 percent of the world's SDTFs are in Australia and Southeast Asia [1] where they are at risk from human disturbance [7–10]. Numerous studies have demonstrated that SDTFs are under serious threat in several regions of the world, with key threatening processes being clearing for agriculture and other land uses, invasive plants, unsustainable grazing practices, climate change, and fire, often acting synergistically [1–3,7,10,11]. Fires are considered a serious threatening process in SDTF as they are a major modifier of this ecosystem with many fire-sensitive species known [2], whereas others argue too-frequent fire is the main threat, given that at least some plants are adapted to withstand or regenerate after fire [10]. Overall, it is clear we know little about the impact of fire on SDTFs, both broadly and for specific regions [10,12–14].

One of the natural mechanisms of dry forest regeneration, especially after fire, is through vegetative means, such as resprouting (regrowth from dormant vegetative buds, typically under the bark or underground) [14]. Widespread resprouting gives rise to more resilient biomes able to cope with severe disturbance regimes (such as regular and/or intense fire) [15]. Further plant adaptations to fire include protection of stem tissue by thick bark and fire-stimulated seed germination [14,16]. In contrast, fire sensitive ecosystems generally have non-adapted plants readily killed by fire (low resistance), as well as limited post-fire recovery (low resilience) [17].

Although mostly confined to the neotropics [2], SDTFs are also widespread in sub-Saharan Africa and South Asia, but are relatively uncommon in Southeast Asia and Pacific regions, with the exception of the Indochina, the Sundas and northern Australia [3,10]. In Indonesia, SDTF occurs in several locations, but are found predominantly in the eastern parts of the archipelago. Miles et al. [1] only recognized SDTF on the Lesser Sunda Islands of the Eastern Indonesia Province (Indonesian: Nusa Tenggara Timur, or NTT). Studies are lacking for SDTF in Indonesia, especially when considering the relatively large areas of SDTF present in NTT, many of which are adjacent or proximate to savanna [18–21]. In addition to NTT, one of the locations in Indonesia where SDTF and savannas co-occur is Baluran National Park (BNP), East Java. Lowland dry forest in BNP covers an area of c.1500 ha. These forests are located in areas adjacent to savanna, teak forest, and small patches (c.2 ha) of dense rainforest. Various animals including large nocturnal cats and other carnivores, such as the Javan leopard *Panthera pardus melas*, use these forests to gather food during the cooler night-time conditions, which helps them to conserve water. The combination of extensive areas of both savanna and SDTF in BNP plays a significant role in supporting its diversity of plants and big mammals, including herbivores such as the banteng (*Bos javanicus*), which is categorized as endangered on the IUCN Red List [22–24]. The banteng is an endemic bovine species of Southeast Asia and only seven populations with approximately 50 individuals each are known to remain in its native range [25].

In many places, SDTFs tend to be bordered by or are mixed (in a landscape mosaic) with savanna ecosystems [7,8]. Savannas are also widespread ecosystems of seasonal wet–dry tropics consisting of low to no tree cover, but with dense grassy understories (of predominantly C4 grasses) which are typically maintained via regular fire [9]. The dynamic nature of many SDTF–savanna ecotones have led many to hypothesize they can exist as alternative stable states where they co-occur, each being maintained by positive feedbacks [8]. For example, savanna can be promoted and maintained by regular fire which reduces woody plants and enhance grasses which, in turn, promotes further fire, whereas SDTFs are typically maintained by fire exclusion with increasing shading by trees suppressing grass cover (and thereby fuel loads and fire likelihood) [8–10]. Transitions

from SDTF to savanna (and vice versa) are possible but typically are predicated by a change in fire regime (or other disturbances).

There is still considerable debate regarding the origins of much savanna [18], especially in Southeast Asia [26]. Key unresolved questions include: (1) are these savannas human-derived forms of SDTFs and other tropical forests, or are they formed by more natural processes; and (2) are they recently converted through fire or are they older systems which reflect soil/microclimate distinctions, with fire a secondary force? Research in Brazil, Africa and Australia has shown that regardless of their origins, most savanna is maintained by fire, and will typically convert to woody-dominated vegetation in the absence of fire [8,18,27–30]. Some researchers view savannas, especially those in higher rainfall zones, as originally deriving from dry forests/monsoon forests that are maintained via frequent burning [18,31–33]. For Indonesia, information on the effects of various disturbances to forest, and relationships between forest fire regimes and the savanna community, is currently inadequate [32]. Research into the origins of savannas in Indonesia, especially in more mesic savannas such as Baluran in eastern Java, is therefore needed.

Ecosystems cannot be managed without adequate knowledge and understanding of what factors drive their formation and maintain their condition and features. As little is known about the SDTF of Baluran, Indonesia, research into the key plant species and the effects of fire of them, including post-fire recovery, are vital to achieving this understanding. Therefore, the main objectives of this paper are to: (i) characterize the structure and composition of SDTF in Baluran National Park, East Java, Indonesia; (ii) to explore the impact of fire on these vegetation attributes; and (iii) assess the means and strength of SDTF recovery following burning. Intermixing and coexistence of SDTF and savannas occur at Baluran, as they clearly do in many tropical regions, for example in Mexico and the Brazilian Cerrado [34,35]. Savannas and SDTF are often seen to form mosaics, and a small distinction in factors such as soil, topography, disturbance type/history, and/or microclimate, can resolve whether savanna or dry forest will arise in a particular area [7,8,17,36]. Due to this repeatedly close link shown between the two ecosystems, it is valuable to consider the status of SDTF in conjunction with that of savannas. Therefore, another aspect of this paper is to critically evaluate the evidence for ecological transitions between SDTF and savanna in this area. This is the first study in this region that explores potential links between the SDTF of Baluran National Park and its savanna ecosystem, which also is a significant feature of the national park and one of the reasons it is protected.

2. Materials and Methods

2.1. Study Area

The study was conducted in Baluran National Park (BNP), located in the Situbondo Regency, East Java Province, Indonesia (Figure A1). The park is bordered by the Madura Strait to the north and Bali Strait to the east. It covers an area of about 25,000 ha located between 7°29'10" and 7°55'55" S and 114°29'20" and 114°39'10" E, and features the single volcanic cone of Baluran Mountain with a summit of 1247 m [23,37]. Baluran has monsoonal climate affected by dry easterly winds, particular in the dry season. Precipitation in BNP ranges from 900–1600 mm/year with an average nine months of no or low rainfall (generally April to November). Highest rainfall usually occurs in December up to February. Baluran Mountain provides a rain shadow so that rainfall is lower and more seasonal than other parts of East Java [24].

2.2. Field Data Collection

Field data was collected in Baluran National Park during January (wet season) and August 2015 (dry season). The recent fire history of the study area was first acquired from various sources of unpublished reports, interviews with park managers and rangers, and from the MODIS burned area product data for the previous 15 years (2000–2014 inclusive). For investigating the structure and composition of SDTF, sampling was conducted in lowland SDTF on the southern side of Mt. Baluran (Figure A1). This area was chosen

because of the large areas of continuous forest with easy access. Based on the fire history data, sampling was conducted in SDTF which was either: (i) recently burned SDTF (last burned between 1 to 3 years prior to study); (ii) approximately 10 years since last fire; and (iii) long-unburned SDTF (no evidence of fires for at least 14 years). Within disjunct forest patches of each fire-age class, a plot 50×50 m (0.25 ha) in size was randomly placed to sample species composition and abundance of tree and groundcover layers. In total there were 22 plots established, with at least 5 in each of the three fire-age classes. Within each plot, each plant species was identified, and the height and diameter of all mature trees (with bole dbh ≥ 20 cm), pole trees (pole dbh 10–20 cm), and saplings (dbh 2–10 cm) were recorded. The numbers of understorey plants and tree seedlings were also counted. Plant identification was assisted by taxonomists at the Bali Botanical Garden, and published Floras of the region [32,38,39], and then names were updated to reflect “World Flora Online (WFO)” (www.worldfloraonline.org, accessed on 30 September 2022). One exception is that we preferred the genus name *Acacia* (rather than *Vachellia*) [24].

We sampled fuel loads by collecting all ground-level biomass/leaf litter (all living and dead plant material <0.5 cm in diameter) in small 1×1 m quadrats within each plot. These samples were dried in oven at 95°C for 48 h and then weighed to measure dry weight. In the recently burned SDTF plots, we also recorded which species re-sprouted after fire, the number of mature plants resprouting, and whether these were resprouting basally (shoots emerging from or below ground level) or above the ground.

2.3. Data Analyses

To characterise the floristics and determine the most dominant species in each layer of SDTF (trees, poles, saplings and groundcover), we calculated the importance value index (IVI) of each species in these layers. The IVI in our study was calculated by the sum of the relative density, basal area, and frequency [40], each expressed as a percentage of the total across all sites, although for groundcover only relative density and frequency were summed.

To explore effects of fire within SDTF, we compared species diversity and composition across the three fire-age groups (recently burned, ~ 10 years since burning and long-unburned). Mean species richness (number of species per plot) and mean Shannon–Weiner diversity index [40] were compared between the three fire-age groups using one-way ANOVA. The species composition of sites was firstly compared visually using ordination analysis, specifically non-metric multidimensional scaling (NMDS) on the site \times site dissimilarity matrix (based on the Bray–Curtis measure) in the PRIMER v6 software [41]. This was performed separately for tree species and understorey species. ANOSIM (analysis of similarity) and SIMPER (similarity percentage) analyses were then used to explore the floristic differences and relative contribution of individual species to dissimilarity among fire-age classes also performed using PRIMER v6. Tree species responses to fire (resprout, basal and above ground) were graphed in Excel, as were fuel loads against time since last fire and sizeclass distribution for each fire-age group (recently burned, ~ 10 y.o., and long-unburned). These size class distributions for each fire-age group were then compared using the chi-square test of independence.

To evaluate evidence of transitions between savanna and SDTF, we combined our SDTF plot data with other data collected in nearby savanna and other patches of SDTF as part of a larger study in BNP [42]. Altogether, we had data from 11 sites of relatively long-unburned savanna (>10 years of fire absence), 11 sites of relatively unburned SDTF (also >10 years of fire absence), 12 recently burned SDTF (fire in last 1–2 years) and 10 of recently burned savanna which were burned at least twice in the last 6 years. All sites were consistently sampled with species cover and abundance being measured in plots of 50×50 m in size. Soil samples were also collected from several of these plots and taken to the soil laboratory at Udayana University, Bali, for analysis of pH, soil organic matter and nitrogen. Square-root transformation of plant species cover data was used to construct resemblance matrices based on the Bray–Curtis similarity index. These matrices

formed the basis for NMDS (with time since fire as overlay vector) and cluster analysis to compare species composition of the savanna with the SDTF (each with two distinct fire classes, long-unburned and recently burned). SIMPER (similarity percentage) analysis was then used to explore the relative contribution of individual species to dissimilarity among savanna and SDTF plots. These multivariate analyses were carried out within the PRIMER v.6 package [41].

Further evaluation of evidence for savanna-SDTF transitions were conducted by remote sensing analysis using the standard overlay method of the following data: MODIS burned area product 2000–2013 downloaded from the website <http://modis.gsfc.nasa.gov/> (accessed on 23 June 2018); land type map for the years 2000 and 2013 for BNP obtained from the park management office (this is a map of the main ecosystem types for management purposes—it is derived based on field observations combined with aerial photo interpretation), and 2013 Google Earth images. MODIS burn area data was overlaid with the BNP land type map. From this analysis we extracted information on which locations were burned in the range period of 2000–2013 in BNP. We also calculated the area burned, and the average peak time of the year when fires occurred. To check whether there is a change in vegetation (savanna to SDTF, or vice versa) we overlaid the BNP land type map (for year 2000; Figure 1) with the current (2013) BNP land type map and the MODIS fire mapping (2000–2013). This remote sensing analysis was carried out using ARC-GIS v.10.1.

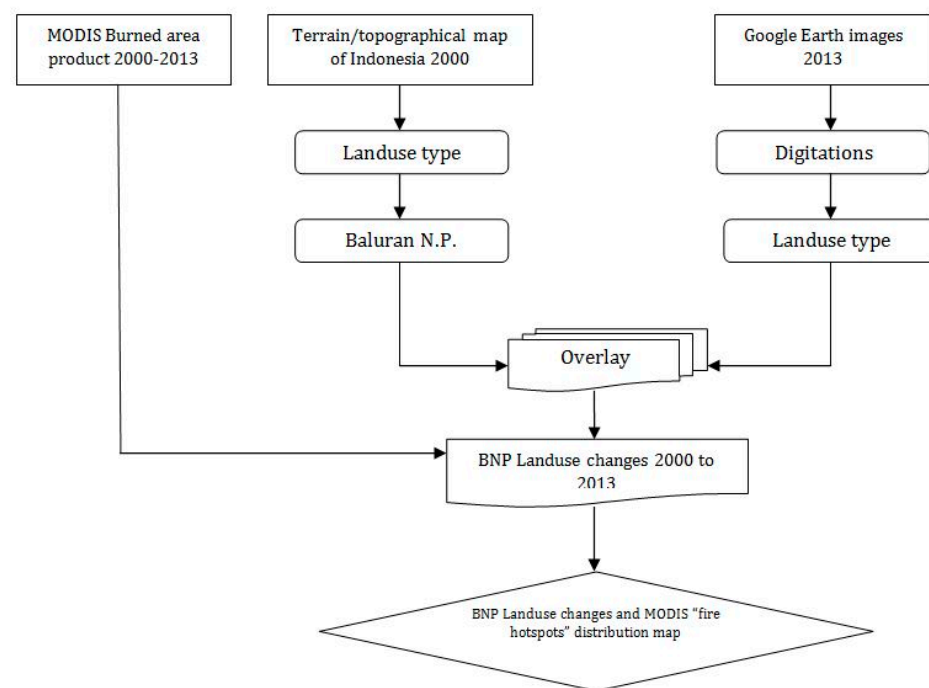


Figure 1. Flowchart of remote sensing works for detecting land-type change in relation to fire occurrence in Baluran National Park.

3. Results

3.1. Structure and Composition of SDTF

A total of 22 tree species in 19 genera and 13 families were recorded in the SDTF. In the mature tree stratum, there were eight species (in eight families) with IVI greater than 10 (Table 1). The highest tree IVI (75.14) belonged to *Glochidion zeylanicum* (syn. *G. sumatranum*; Phyllanthaceae), followed by *Premna oblongata* (Lamiaceae; 51.4). Similarly, in the young tree (poles) stratum, there were eight species (but in seven families) with *Streblus asper* (Moraceae) having the highest IVI (72.96) and *Acronychia trifoliata* (Rutaceae) the lowest (11.65). In the sapling strata, ten species belonging to seven families have IVIs of greater than 10, all being same species as found in the tree strata, with *G. Zeylanicum* being the

highest (55.39) and *Tamarindus indica* (Fabaceae) the lowest (12.94). Notable in this stratum is the appearance of exotic invasive species *Acacia nilotica* (syn. *Vachellia nilotica*) with an IVI about half that of the *G. zeylanicum*. Groundcover strata comprises some 49 species of which 5 species in three families having IVI > 10, ranging from *Brachiaria ramosa* (Poaceae) with the highest IVI (22.8), to *Cosmos caudatus* (Asteraceae, annual herb) with the lowest (10.32).

Table 1. Species with highest IVI (importance value index) for mature trees, young trees ('poles'), saplings, and groundcover strata in lowland SDTF at Baluran National Park.

Species/Stratum	Family	Habit	Importance Value Index
Mature tree (dbh \geq 20 cm)			
<i>Glochidion zeylanicum</i>	Phyllanthaceae	Tree	75.14
<i>Premna tomentosa</i>	Lamiaceae	Tree	51.35
<i>Schoutenia ovata</i>	Tiliaceae	Tree	28.76
<i>Tamarindus indica</i>	Fabaceae	Tree	25.34
<i>Schleichera oleosa</i>	Sapindaceae	Tree	25.25
<i>Flacourtia rukam</i>	Salicaceae	Tree	15.73
<i>Streblus asper</i>	Moraceae	Tree	14.65
Poles (dbh 10–20 cm)			
<i>Streblus asper</i>	Moraceae	Tree	72.96
<i>Capparis sepiaria</i>	Capparaceae	Tree/Shrub	57.30
<i>Schoutenia ovata</i>	Tiliaceae	Tree	44.89
<i>Glochidion zeylanicum</i>	Phyllanthaceae	Tree	43.92
<i>Antidesma bunius</i>	Phyllanthaceae	Tree	34.21
<i>Premna tomentosa</i>	Lamiaceae	Tree	13.43
<i>Kleinhovia hospita</i>	Malvaceae	Tree	12.21
<i>Acronychia trifoliata</i>	Rutaceae	Tree	11.65
Saplings (height > 1.5 m and dbh < 10 cm)			
<i>Glochidion zeylanicum</i>	Phyllanthaceae	Tree	55.39
<i>Capparis sepiaria</i>	Capparaceae	Tree/Shrub	48.94
<i>Schoutenia ovata</i>	Tiliaceae	Tree	42.14
<i>Streblus asper</i>	Moraceae	Tree	28.41
<i>Acacia nilotica</i>	Fabaceae	Small Tree	25.38
<i>Antidesma bunius</i>	Phyllanthaceae	Tree	23.04
<i>Kleinhovia hospita</i>	Malvaceae	Tree	20.05
<i>Abutilon indicum</i>	Malvaceae	Small shrub	15.72
<i>Hibiscus panduriformis</i>	Malvaceae	Shrub	13.46
<i>Tamarindus indica</i>	Fabaceae	Tree	12.94
Ground cover			
<i>Brachiaria ramosa</i>	Poaceae	Perennial Grass	22.80
<i>Chionachne punctata</i>	Poaceae	Perennial Grass	22.25
<i>Mimosa invisa</i> *	Mimosaceae	Herb	18.64
<i>Oplismenus burmannii</i>	Poaceae	Annual Grass	12.80
<i>Cosmos caudatus</i> *	Asteraceae	Annual Herb	10.32

* refers to exotic (non-native) species.

3.2. Comparison of SDTF Fire-Age Classes

Mean tree species richness per (0.25 ha) plot varied significantly between fire-age classes ($F = 10.2$, $p = 0.0010$), with long-unburned sites having more tree species (mean of 5.4 species per plot) compared to recently burned and ~10-year-old sites (mean of 2.9 and 2.8 species, respectively). Understory species richness did not vary between fire-age classes ($F = 1.26$; $p = 0.31$) with an overall average of 5.1 species per plot. There was no difference in Shannon–Wiener species diversity between fire-age classes ($F = 0.53$; $p = 0.43$). This

diversity index ranged from 0.6 to 1.9 across sites (and averaged 1.4) which demonstrates low to moderate species diversity levels at the plot level.

Structurally, tree density averaged 39 ha⁻¹ (mature and pole trees combined) and was broadly similar between the SDTF fire-age classes in (Figure 2). Most trees were 10–30 cm in bole diameter, with relatively fewer large trees >30 cm in diameter (generally eight trees ha⁻¹, with long-unburned sites having slightly higher densities of these presumably older trees). Density of seedlings (<2 cm stem diameter and <1 m in height) and saplings (2–10 cm stem diameter) were, however, several times lower in recently burned plots compared to plots not burned for some 10 or more years (Figure 2). Despite this, a chi-square test of independence showed that the frequency distribution (of plants in each size class) was not significantly different between the fire-age groups ($\chi^2 = 14.7$; $df = 12$; $p = 0.26$).

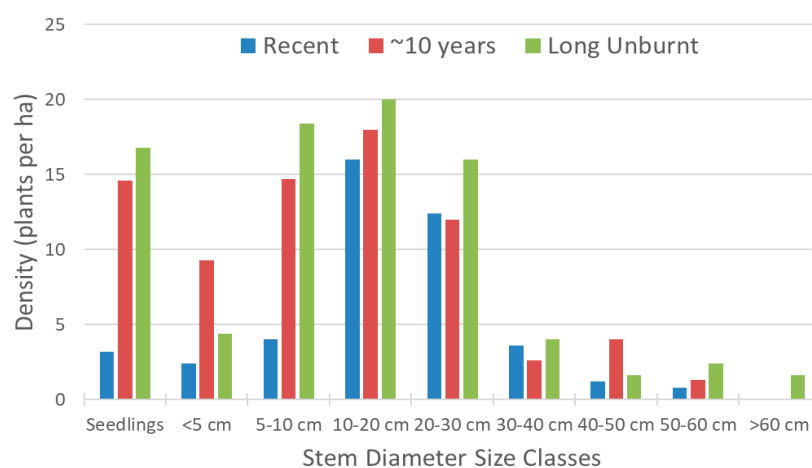


Figure 2. Size class distribution of trees showing plant density (per ha) for each diameter size class as well as seedlings (<2 cm diameter) for the three fire-age groups.

Overall, non-metric multidimensional scaling (NMDS) based on the Bray–Curtis similarity between vegetation plots showed a clear separation between the three SDTF fire-age groups (recently burned, ~10 years since last burned and long-unburned) (Figure 3). There were significant differences in species composition between fire-age groups with a global ANOSIM R value of 0.4 (for tree species) and 0.6 (for groundcover species) ($p < 0.1\%$). Results of the similarity percentage analysis (SIMPER) showed which species were most important in differentiating between the fire-age classes (Table 2). For the groundcover stratum, *Chionachne punctata* (grass) was the most important species for discriminating between recently burned and ~10-year-old sites, followed by *Oplismenus burmannii* (grass), *B. ramosa* (grass), and *Mimosa invisa* (small shrub/climber, Fabaceae), which were all higher in recently burned sites. For tree strata, *Premna tomentosa* was the most important species differentiating 10-year-old plots from the recently burned dry forests, followed by *G. zeylanicum* and *Schoutenia ovata*. There were no tree species which consistently discriminated (i.e., dissimilarity/SD > 2) between ‘10 years’ and ‘recent fire’. For the groundcover stratum, although *Cosmos caudatus* was the most important species differentiating the three fire-age classes (Table 2). For tree strata, there were six species that differentiated the between ~10 year and long-unburned dry forests (Table 2) with *F. rukam* being the most important species as well as highly consistent. Five tree species mostly differentiated recently burned and long-unburned SDTF, with *P. tomentosa* being the most important differentiating species, although the most consistent species was *F. rukam* (Table 2).

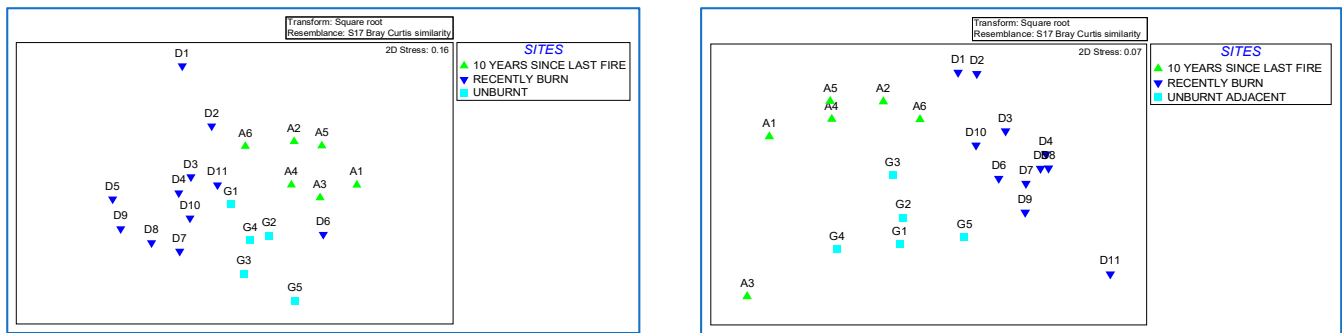


Figure 3. Two-dimensional NMDS ordinations of sampled sites (~10 years since last burned, recently burned, and unburned) based on Bray–Curtis similarity (with square-root transformation). (**Left side**): NMDS graph based on tree species composition. Global R ANOSIM = 0.4. (**Right side**): NMDS graph based on groundcover species. Global R ANOSIM = 0.6.

Table 2. Similarity Percentage (SIMPER) analysis results showing (i) species percentage contribution to the dissimilarity between the three dry forests groups (recently burned, ~10 years since last burned, and long unburned); and (ii) ratio of average dissimilarity to SD (standard deviation) with larger values indicating that not only does that species contribute much to the dissimilarity between dry forests but that it also does so consistently in comparisons with all samples in the three dry forests.

Species	Diss/SD			Contrib%		
	10 Years vs. Recent	10 Years vs. Unburned	Recent vs. Unburned	10 Years vs. Recent	10 Years vs. Unburned	Recent vs. Unburned
Groundcover						
<i>Brachiaria ramosa</i>	1.27	-	-	10.03	-	-
<i>Cosmos caudatus</i>	-	1.7	1.8	-	16.36	12.83
<i>Oplismenus burmannii</i>	1.43	1.35	-	11.2	11.97	-
<i>Chionachne punctata</i>	1.44	-	1.52	12.63	-	10.41
<i>Mimosa invisa</i>	0.88	0.58	0.98	8.32	3.51	8.03
Trees						
<i>Flacourtia rukam</i>	-	1.85	1.81	-	13.45	14.58
<i>Glochidion zeylanicum</i>	1.44	1.30	1.25	21.03	9.31	10.03
<i>Premna tomentosa</i>	1.4	1.07	1.45	21.28	7.5	44.11
<i>Schleichera oleosa</i>	-	0.92	0.93	-	13.94	15.04
<i>Schoutenia ovata</i>	0.82	0.89	1.04	11.35	9.17	9.67
<i>Streblus asper</i>	-	0.69	-	-	9.37	-

Fine fuel loads in the dry forests were low (mostly less than 1 t/ha) but broadly increased with time since last fire (Pearson correlation: $r = 0.58$; Figure 4). Two types of resprouting trees were found in recently burned plots: basal and above-ground, with more individuals showing above-ground resprouting than basal resprouting (Figure 5). Tree species recorded as resprouting after recent fire were *P. tomentosa*, *G. zeylanicum*, *Schoutenia ovata*, *F. rukam*, *Acacia nilotica*, *Microcos tomentosa*, *Bauhinia* sp., and *Acacia tomentosa* (Figure 6). *P. tomentosa* had the highest number of individuals resprouting after fire, whereas the lowest was *A. tomentosa* (Figure 6). Three members of the Fabaceae family showed resprouting ability (*Acacia* and *Bauhinia*), including the exotic invasive species *Acacia nilotica*. In terms of resprouting percentage, *A. tomentosa*, *Bauhinia* sp., *F. rukam*, and *M. tomentosa* have the highest percentage of resprouting individuals (all >95%), followed by *G. zeylanicum* (91%), *P. tomentosa* (77%), *A. nilotica* (75%) and, the lowest, *S. ovata* (57%) (Figure 7). In all, 74% of individual trees assessed across all plots were observed to resprout following the recent burns, with no resprouting response noted in a number of common tree species, including *Tamarindus indica* and *Streblus asper*. Tree seedlings were relatively

uncommon across all fire-age classes. The most common tree seedlings found in recently burned plots were: *A. nilotica* (average density of 0.74 m^{-2}), other (unidentified) *Acacia* species (0.12 m^{-2}), *T. indica* (0.09 m^{-2}), *F. rukam* (0.07 m^{-2}), *Azadirachta excelsa* (0.02 m^{-2}), *Flacourtia indica* (0.02 m^{-2}) and *Toona sureni* (0.01 m^{-2}).

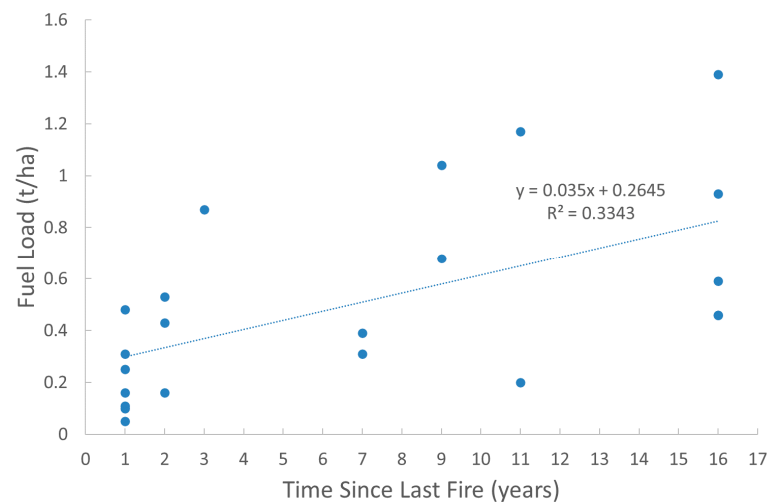


Figure 4. Relationship between fine fuel load and time since last fire, including linear regression line, in SDTF of Baluran National Park.

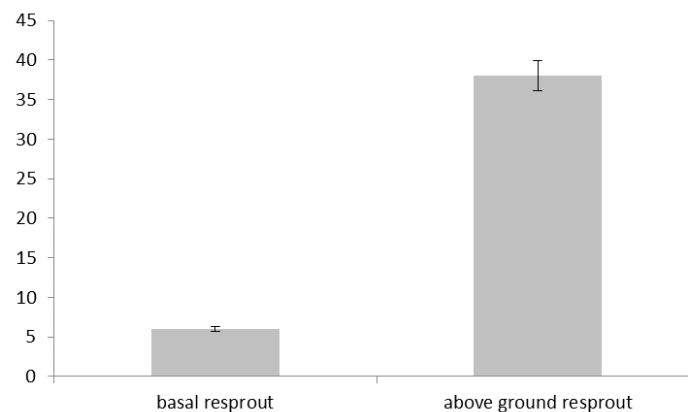


Figure 5. Histogram showing number of trees resprouting (per plot) in recently burned SDTF sites for the two types of resprouting in Baluran National Park.

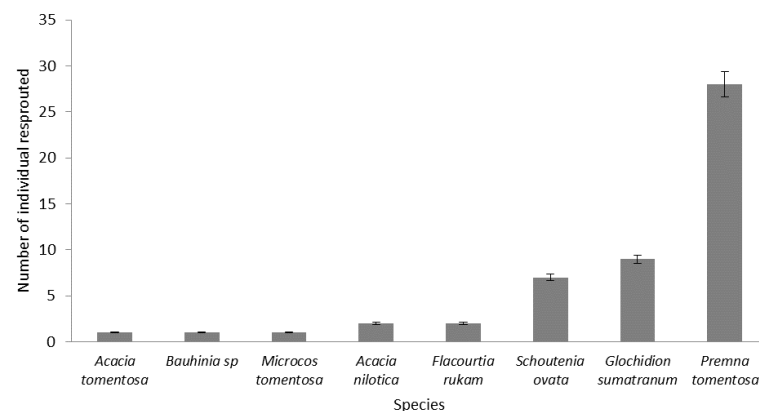


Figure 6. Histogram illustrating the number of individual trees of selected species that were observed resprouting (per plot) following recent fires in Baluran National Park's SDTF areas.

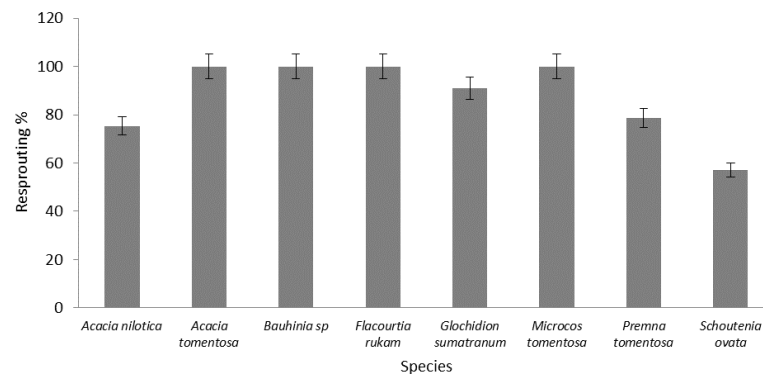


Figure 7. Histogram showing the percentage of individual trees resprouting for the major resprouting species following recent fires in SDTFs of Baluran National Park.

3.3. Evidence for SDTF–Savanna Transitions

Overall, the non-metric multidimensional scaling (NMDS) ordination result shows the plant communities are moderately distinct (Global R ANOSIM = 0.53, $p < 0.1\%$). There is separation of burned and unburned sites along the vertical axis, and of dry forest and savanna sites along the horizontal axis. However, quite a few of the recently burned SDTF sites are placed intermediately between burned savanna and long-unburned SDTF. Also, a small number of the long-unburned savannas are grouped with or are positioned close to long-unburned savanna (Figure 8). Site age (time since fire, in years) had high correlation with species composition ($\rho = 0.702$; $p = 0.001$; Figure 8). Older SDTF and savanna sites (SDTF long unburned and savanna long unburned) tend to cluster to the left-hand side of the ordination which is aligned with the time since fire (Spearman) correlation vector (Figure 8).

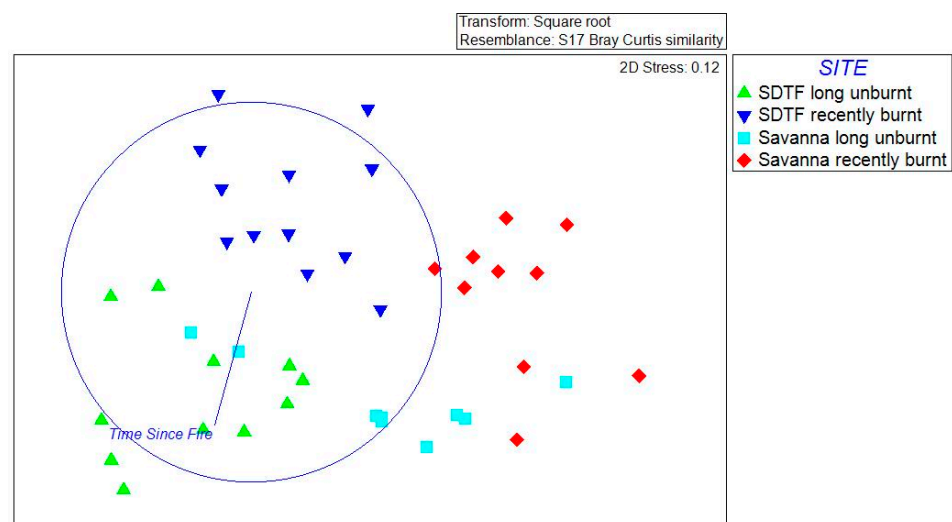


Figure 8. NMDS ordination for SDTFs and savannas sites with different time-since-last-fire class in Baluran National Park. Global R ANOSIM = 0.53, $p < 0.1\%$. The Spearman correlation of time since fire has also been included as a vector displaying the direction and influence on distribution of sites. Spearman correlation value on MDS axis 2 is 0.702.

Cluster analysis revealed three (out of ten) of the long-unburned savanna sites grouped with long-unburned SDTF. Conversely, two long-unburned SDTF sites grouped with the long-unburned savanna (Figure 9). A pairwise test of the two groups showed they were not different, with a relatively low R value of 0.35 ($p > 0.1\%$). SIMPER analysis result showed ten tree species mostly contributed to the differentiation between SDTF and savanna (Table 3). *Erythrina euodiphylla* and *F. rukam* were species that contributed the

most (12.66% and 11.25%, respectively). *E. euodiphylla* and *F. rukam* were both present in the two groups but with different relative abundance. *E. euodiphylla* was more abundant in SDTF whereas *F. rukam* was more abundant in the long-unburned savanna. In total, there were seven tree species that were present in both groups. There was only one species that was absent in SDTF and only present in the long-unburned savanna, namely *Acacia leucophloea*. Conversely, there were five species that were absent in the savanna and only occurred in SDTF (Table 3). Species normally found in SDTF in Baluran National Park, such as walikukun (*S. ovata*), rukem (*F. rukam*) and asam jawa (*Tamarindus indica*), were also found in the long-unburned savanna site. Distinct boundaries (narrow ecotones) were observed in the field between savannas and adjacent SDTF and soil analyses did not reveal major edaphic differences across this boundary (Table 4).

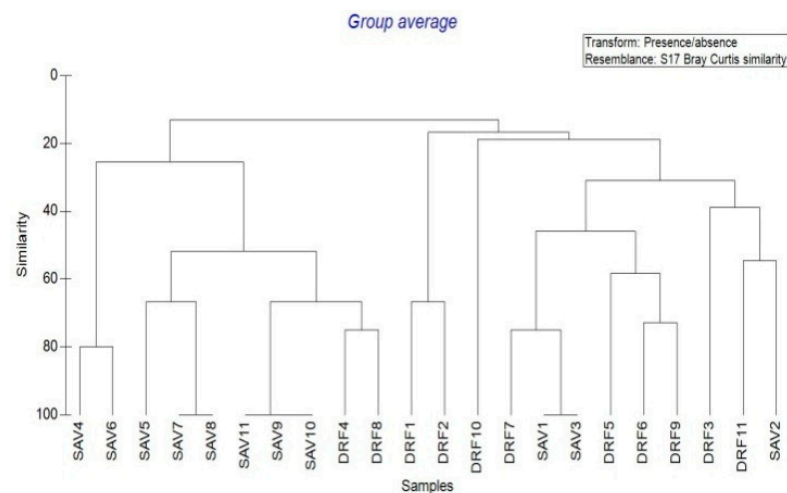


Figure 9. Dendrogram cluster analysis of community composition in long-unburned savanna (SAV) and unburned SDTF (DRF), Baluran National Park. $R = 0.35$, $p < 0.1\%$.

Table 3. SIMPER analysis results showing percentage (%) contribution of species to average Bray–Curtis dissimilarities in all pairs of sites. Only those species with a contribution to average dissimilarity of $>5\%$ are included. Species in bold refers to species that are commonly found in SDTF of Java [43].

Species	SDTF	Unburned Savanna	Contrib%	Cum.%
	Av. Abund	Av. Abund		
<i>Erythrina euodiphylla</i>	1.87	0.47	21.15	21.15
<i>Flacourtia rukam</i>	0.33	1.28	11.25	32.4
<i>Hibiscuspanduriformis</i>	0.82	0	8.71	41.11
<i>Schoutenia ovata</i>	2.55	2.46	8.54	49.65
<i>Schleichera oleosa</i>	0.47	0.67	8.26	57.91
<i>Grewia eriocarpa</i>	0.67	0	7.79	65.7
<i>Acacia leucophloea</i>	0	0.67	6.51	72.2
<i>Capparis sepiaria</i>	0.33	0.33	5.15	77.35
<i>Tamarindus indica</i>	0.33	0.33	4.92	82.27
<i>Glochidionzeylanicum</i>	0.33	0	3.81	86.08
<i>Cordia bantamensis</i>	0.33	0	3.56	89.63
<i>Helicteres isora</i>	0.33	0	3.56	93.19

Table 4. Soil sample analysis results for savanna and SDTF in Baluran National Park. Values represent means for each vegetation type (with no significant differences found, $p > 0.10$).

Vegetation	Soil	pH	C%	N%
Savanna	Volcanic	6.74 Neutral	3.51 High	0.23 Medium
SDTF	Volcanic	6.65 Neutral	4.39 High	0.27 Medium

Transitions from savanna to dry forest in Baluran National Park based on land type mapping (using remote sensing) are shown in Figure 10. As much as 280 ha of the savanna shifted to dry forest in the 14-year period 2000–2013. Most of the shifted area experienced little or no fires (at least as detected by MODIS) during the same period. Conversely, woody-plant-dominated vegetation with frequent fires were observed to have also shifted to savanna during the similar period (Figure 10). There were 1711 fire “hotspots” detected in Baluran National Park across this period. Fire detection was higher in the dry months of June, July, August and September, with August being the month in which usually fires were detected the most.

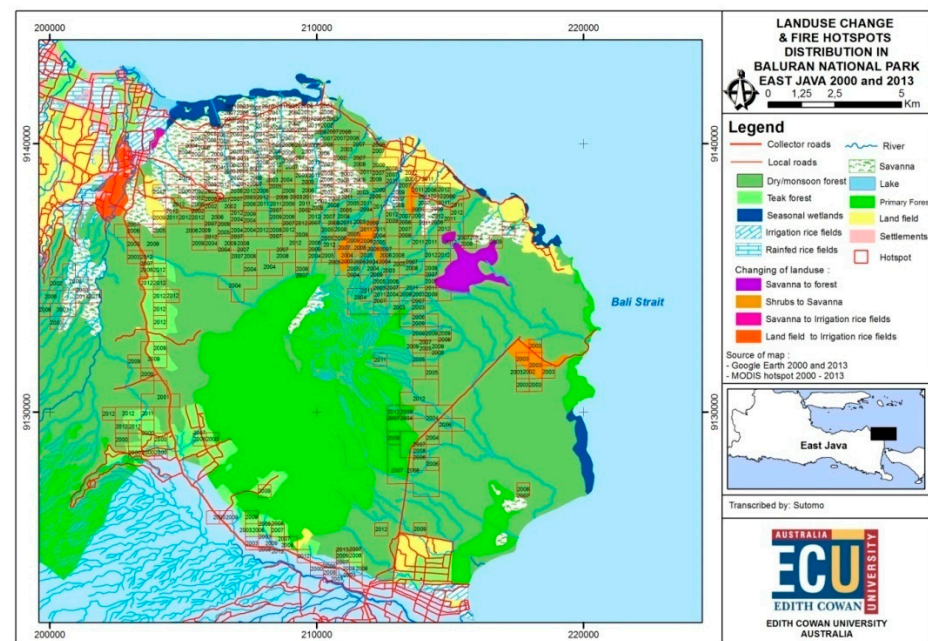


Figure 10. Land-type changes in Baluran National Park and MODIS fire hotspot distribution for years 2000–2013. Note the change in savanna to dry forest (marked in purple coloured area) covers an area of 280.4 ha.

4. Discussion

4.1. Characteristics of SDTF at Baluran

Seasonally dry tropical forest (SDTF) in Baluran National Park (BNP) has high tree cover as expected for forest, but lower species diversity than wet tropical (rain) forest. This is supported by field measurements across dry forests with different time since last fire in Baluran National Park. SDTF in Baluran National Park comprise of up to four strata: trees, poles (young trees), saplings, and sparse groundcover consisting of dicot herbs and grasses. The tree stratum is characterized by *P. tomentosa*, *F. rukam*, *S. ovata* and *T. indica* (the latter originally from Africa but now naturalized in Indonesia), in line with vegetation descriptions by Whitten et al. [43]. A notable species present in the sapling stratum is the obnoxious exotic invasive species *Acacia nilotica*. *A. nilotica* was first planted inside BNP in the 1960s as fire breaks; however, it has become widespread and is now forming dense

thickets of pure *A. nilotica* especially in the Bekol area of BNP where it was reported to dominate at the boundary between savanna and SDTF [44] and to be rapidly spreading into adjacent savanna [37]. The presence and abundance of this species as saplings and seedlings in SDTF may indicate the species has started to spread deep into the SDTF of Baluran National Park, with fire likely to stimulate germination of this species from the soil seed bank [37]. There have been few reports on the expansion of *A. nilotica* stands into SDTF, unlike the well-studied expansion and or invasion of this species into a savanna or grassland [44–47]. However, Kriticos et al. [48] predicted that under current climatic conditions, SDTFs are at risk of invasion and expansion by *Acacia nilotica* will increase markedly with climate change.

SDTF is not as rich in species when compared to rainforests, but still retains a considerable amount of diversity [2,3]. Shannon–Wiener species diversity measured in our study demonstrated low to moderate species diversity in this type of forest, with a total of 20 tree species (in 19 genera and 13 families) and 49 ground species recorded across the 15 plots (each 0.25 ha). Other studies report higher species diversity in SDTF, such as Gonzales-Rivas et al. [49] in Nicaragua, who found 29 families, 49 genera and 59 species of plants in 2 ha of SDTF. Although Dirzo et al. [2] state there is not enough collated data to compare species diversity of SDTF across different regions of the globe, it appears alpha diversity of neotropical SDTFs are typically much higher than we have found in central Indonesia. However, we mostly sampled early in the wet season, and this may have influenced our results. Also, we found no succulent species in Baluran SDTF which supports the proposition by Pennington et al. [50] that this is one of the major distinctions between Asian and neotropical SDTFs (the latter having many succulent plants). Many of the common tree species we found in SDTF were either widespread tropical forest species occurring throughout Southeast Asia (e.g., *Schoutenia ovata*, *Pterocarpus indicus*) and sometimes also southern Asia (e.g., *Premna tomentosa*, *Flacourtia rukam*, *Glochidion zeylanicum*) [51]. Many of these have medical, cultural or food values, with dispersal and spread believed to have been facilitated, at least in part, by humans [51,52].

In India and Burma, dry forests were the first types of tropical forests to be recognized [51,53]. In fact, the seven main tropical forest types recognized by the most complete classification of Indian forests—first proposed by Champion in 1963 [53] and later revised by Champion and Seth in 1968 [54]—are wet evergreen, semi-evergreen, moist, dry deciduous, thorn, littoral and swamp, and dry evergreen forests. According to their assessment, the dry deciduous forest, which most closely aligns with our studied forest type, has 5–8 months of dry weather each year, a mean annual temperature of 20 to 29 °C, and annual precipitation between 750 and 1400 mm. Our study was conducted in the Baluran National Park (BNP), located in the Situbondo Regency, East Java Province, Indonesia, an area which also has a monsoonal climate affected by relatively dry easterly winds, particularly in the dry season. Precipitation in the BNP ranges from 900–1600 mm/year with an average nine months of no or low rainfall (generally April to November). Highest rainfall usually occurs in December up to February [42–44]. Baluran Mountain provides a rain shadow so that rainfall is lower and more seasonal than other parts of East Java.

4.2. Effect of Fire on SDTF

Comparisons of species diversity, composition and structure across different fire-age classes reveal the short-term impact of fire in SDTF at Baluran through reduced species richness, particularly in the understory where many fire-sensitive species occur, and a loss of tree seedlings and young saplings (<10 cm stem diameter). Other studies of SDTF in Asia have also reported this temporary reduction in younger cohorts of trees [10,55] which is explained by such plants being most susceptible to fire as growing tips are closer to the heat of the fire and stems are yet to develop sufficient bark protection. Our results also point to relatively rapid recovery of these structural attributes via resprouting and regeneration by seed (returning to pre-fire levels within 10 years), which has also been reported in other SDTF following burning [13,55,56].

In the SDTF of BNP, resprouting is a widespread adaptation to withstand the effects of fire, with the majority of its tree species consistently responding by resprouting following fires, with above-ground resprouting being the most common type. Vegetative regeneration is prominent in SDTF, especially for species that regenerate poorly from seed. Other studies of fire impacts and recovery in SDTF also report high levels of tree resprouting [14,57,58], but there remains some conjecture over whether this is a specific adaptation to fire or a typical response of trees to loss of leaf cover, such as occurs during drought or following strong winds [57,59].

Although a key finding of this study is the rapid vegetation recovery following fire in SDTF, questions remain on the effect of repeated fires. Several tree and many understorey species were killed and did not resprout—such fire-sensitive species require germination from seed banks (in soil or above-ground) to persist following fire, which tends to take longer to recover and makes them susceptible to short fire intervals (i.e., before they have opportunity to reach sexual maturity and replenish seed banks; [16]). The ability of species to resprout following defoliation differs with age, size, and fire severity [56,60]. Only some species have the capacity to resprout when they are young, as shown in many leguminous savanna trees [16], which was found for three legume species in this study, including the exotic invasive species *A. nilotica*. Repeated burning can also reduce the capacity of woody plants to resprout as the time available to replenish protected dormant buds may be insufficient [15].

Even though dry forests have species that are either resistant to fire or are advantaged from it, recurrent fires can simplify community species composition of SDTF [12]. In this study, SDTF species composition was found to differ between recently burned plots and those that have not been burned for a significant amount of time, suggesting the short-term effect of fire on the community composition. Grasses and short-lived herbs particularly increased in the first few years after burning, although they did not contribute to a large change in understorey plant cover post fire. This is reflected in our fuel load measurements, which, although increasing with time (without fire), were consistently low (generally less than 1 t/ha). However, fuel loads are likely to vary seasonally in the wet–dry tropics (due to curing of grasses and other herbs, as well as substantial leaf fall, during the dry season [61]), and this was not captured in our sampling. Despite this, fuel and vegetation characteristics point to typically low-intensity and patchy fires in SDTF in Baluran, which is what we observed in the field. However, again, repeated burns with short fire intervals may further favour grasses at the expense of woody plants (particularly younger cohorts) which may over time facilitate more severe fires and more dramatic vegetation changes.

4.3. Evaluating Evidence for Transitions

Savanna and dry forests are often considered as alternative states within a state-and-transition framework [8,9,62,63]. Previous findings and evidence around the globe suggest that many savannas are not in a stable state where climate, fire and soil nutrient stocks are coupled, creating a dynamic coexistence between savanna and forest [33,36,64,65]. This transition can also be influenced by human activity, with derived savanna used to describe those formed and maintained by anthropogenic disturbance such as forest clearing, burning, and/or livestock grazing [31]. Several ecological reviews have concluded that certain savannas are derived from SDTF which have been frequently burned, both in Java [32,43] and elsewhere [33,66].

Our field results do not show strong support for transitions between SDTF and savanna, as long-unburned savanna sites are floristically distinct overall compared to SDTF (both recently burned and unburned). It is important to note, however, that a small number of long-unburned savanna sites grouped floristically with SDTF (with characteristic dry forest species present in savanna) but these tended to be sites positioned closer to forest–savanna ecotones. Further, recently burned forests in our study did not show a distinct floristic transition towards savanna despite the presence of more grasses and other herbs in the understorey. Although the potential remains for such ecosystem transitions, especially

given the broad uniformity of soils across the study area, more study is needed. This future research needs to incorporate long-term monitoring focussed on understanding vegetation responses to repeated burning (rather than single burns, as studied here) given this is a requirement for savanna formation and maintenance [9,36], as well the establishment of permanent plots in areas excluded from fire.

Our land-type mapping based on remote sensing supports relatively large forest–savanna transitions, but closer examination shows this is primarily driven by *A. nilotica* spread or control. Although most of the shifted area (from savanna to dry forest) detected via remote sensing experienced little or no fires during the 2000–2013 period, field observations confirmed this was primarily expansion of the small tree/tall shrub *A. nilotica*, a well-known problematic invasive species of the national park [44]. Conversely, no mapped areas of forest were found to have transformed into savanna over this period, although areas of dense shrubs were shown to have shifted to savanna with frequent fires during the same period (these were areas of dense *A. nilotica* invasion which have been managed/controlled through burning). However, the assessment on the role of fire in this transition is very often complicated by other effects of human-induced disturbances as well as grazing by herbivores [66]. Indeed, from our results, the area of dense shrubland showing signs of transition to savanna, besides experiencing frequent fire, apparently also endures heavy grazing from cattle owned by local people that live nearby. Future studies therefore should also investigate the effects of grazing–fire interactions in both SDTF and savanna (which require grazing exclusion plots or areas).

Sharp vegetation boundaries (also known as narrow ecotones) are well known in areas where forest and savanna co-occur [8,33,36] and indeed this was observed in the field and remotely at Baluran. Such boundaries are dynamic, potentially shifting spatially in response to disturbance regimes operating around this boundary [64–67]. The degree to which such boundaries may shift over time is also controlled by broader environmental controls on vegetation distribution at the landscape scale (particularly edaphic variables). The spatial limits of such forest–savanna transition are not known for our study area, but should be the focus of future studies.

5. Conclusions

In conclusion, SDTF at Baluran in East Java has floristic and structural similarities with those elsewhere in Asia, as well as some key distinctions. Response to fire is mainly via resprouting from woody plants (measured in most but not all common tree species) and less so by seedling regeneration. Overall results show Baluran SDTFs are likely to be resilient to single, low-intensity burning as studied here. Although SDTF and savanna have potential to be alternative ecosystem states, this was not conclusively shown here. Further studies are needed to obtain more evidence of such ecosystem transitions, as well as the controlling factors. Knowledge of this ecological shifting is important as the savanna and SDTF of BNP have significant roles in supporting the diversity of plants and big mammals, including herbivores such as the Banteng (*Bos javanicus*) which is categorized as an endangered species on the IUCN Red List. Therefore, conservation of endemic wildlife would be greatly benefited by their successful habitat management. Additionally, more research is needed to be able to delimit SDTFs properly, understanding their resilience to climate change [68], and response to repeated fires, as well as other disturbances and threats.

Author Contributions: All author contributed equally to this paper. Conceptualization, S. and E.J.B.v.E.; methodology, S. and E.J.B.v.E.; software, S.; fieldwork S.; draft preparation, S.; supervision, E.J.B.v.E.; review and editing, E.J.B.v.E. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: Data will be deposited in the first author’s Research Gate website and will be publicly available online.

Acknowledgments: We thank the Centre for Ecosystem Management and School of Sciences at Edith Cowan University, Indonesian Ministry of Research and Technology, Bali Botanical Garden-Indonesian Institute of Sciences and the Rufford Foundation for their support.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

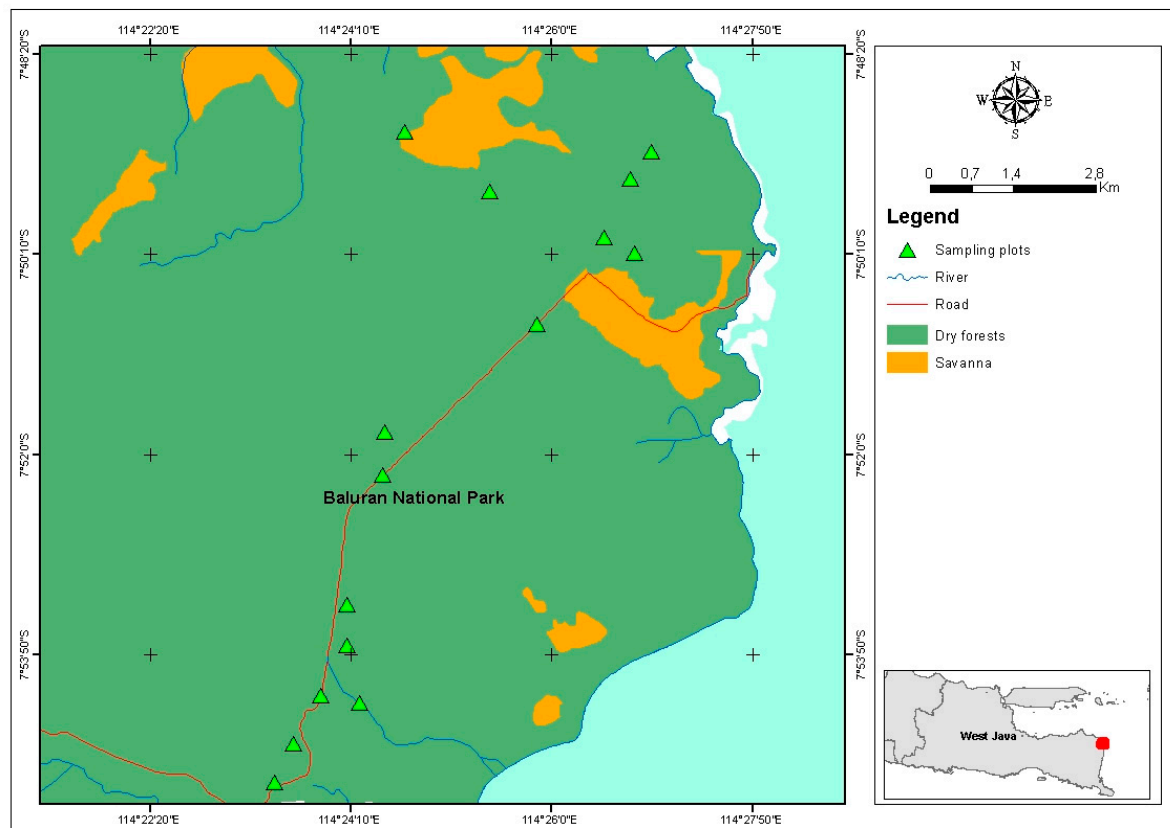


Figure A1. Map of the study site in Baluran National Park.

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