

Variation in the composition and diversity of ground-layer herbs and shrubs in unburnt and burnt landscapes

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Abstract: Forest fires pose an important threat to tropical rain-forest biodiversity. In the present study, we assessed ground layer (herb and shrub) communities in six differentially disturbed landscape plots in East Kalimantan, Indonesia, including primary and logged forest and once-, twice- and frequently-burnt forest. Overall, we recorded 175 species of herbs and shrubs; richness was highest in twice-burnt forest and lowest in logged forest. Vegetation and topographical variables including the percentage of the plot burnt and tree abundance were significant predictors of variation in composition. The main compositional gradient showed a clear distinction between subplots in unburnt versus burnt forest. A subset of subplots in burnt forest, however, clustered together with subplots from unburnt forest. These plots were located in a network of relatively unscathed forest along floodplains that persisted in the burnt-forest matrix. Small plant species associated with unburnt forest included several species of Dryopteridaceae, Marantaceae and Rubiaceae. Species associated with once- and twice-burnt forest included *Mikania scandens* (Compositae), *Microlepia speluncae* (Dennstaedtiaceae), *Nephrolepis* cf. *biserrata* (Nephrolepidaceae), *Lygodium microphyllum* (Schizaeaceae) and *Hornstedtia* cf. *reticulata* (Zingiberaceae). The frequently-burnt landscape plot was characterized by a high cover of the grass species *Imperata cylindrica* and the invasive exotic shrub *Chromolaena odorata*. Importantly, these species and other exotics had also invaded the once- and twice-burnt forest and represent a potential threat to forest recovery.

Key Words: Borneo, community composition, forest fires, Indonesia, ordination

INTRODUCTION

Tropical deforestation results from a complex interplay of social, political, ecological and climatological interactions in which fires play a key role (Cochrane 2003). Although forest flora and fauna tend to recover following forest fires (Cleary & Genner 2006, Cleary & Priadjati 2005), the importance of fire is not so much the incidence, but rather the frequency. Fires are much more frequent today than in the past with intervals of less than 15 y at present compared to hundreds or thousands of years in the past (Cochrane & Schultze 1998, Cochrane *et al.* 1999). This increase in the frequency of forest fires has been related to increased ignition sources as human population density has increased and people move into previously inaccessible forest areas (Laurance 1998, Laurance *et al.* 2001, Nepstad *et al.* 2001, Peres

2001). In addition to this, moist tropical forests in Indonesia and elsewhere have been subjected to severe droughts during intense El Niño Southern Oscillation (ENSO) events (Cochrane 2003, Siebert *et al.* 2001).

El Niño Southern Oscillation (ENSO) events occur irregularly but typically once every 3–6 y. The occurrence of severe ENSO events has had major implications for ecosystem functioning and biodiversity in deserts, tropical rain forests and marine systems (Cleary *et al.* 2006a, Holmgren *et al.* 2001). With respect to tropical rain forests, ENSO events can cause extended periods of drought and promote forest fires. Using charcoal records, Haberle & Ledru (2001) showed a strong relationship between the occurrence of fires in Latin America and South-East Asia and ENSO events during the past 16 000 y. Recent ENSO-related fires, however, seem to be much more severe than their historic counterparts as ENSO events themselves have become more intense (Tudhope *et al.* 2001). The most destructive ENSO fires in human history were recorded in 1997–1998, when over

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20 million ha were burnt in South-East Asia and Latin America and 5.2 million ha in the Indonesian province of East Kalimantan alone (Cochrane 2003, Siegert *et al.* 2001). These fires surpassed the previous record of 1982–1983 where 3.5 million ha were burnt in East Kalimantan alone (Goldammer *et al.* 1996). These fires affected logged and secondary forests and an estimated 0.8 million ha of primary forest.

In the moist tropics, forest fires are often merely a thin, slowly creeping ribbon of flames a few decimetres high (Cochrane & Schulze 1998) and previously deemed not to be particularly harmful until it was shown that they are able to kill numerous trees (Cochrane & Schulze 1999, Peres 1999) and affect extensive areas of forest (Nepstad *et al.* 1999). The fires themselves are also the starting point in a series of destructive processes and positive feedback loops that can culminate in extensive deforestation if left unchecked (Cochrane *et al.* 1999). For example, burning itself makes a forest more susceptible to subsequent burning as the canopy is opened up and woody debris accumulates as a source of future kindling. The loss of vegetation cover also promotes climatological change and the promotion of future droughts by reducing evaporation, increasing radiation and inhibiting rainfall (Berbet & Costa 2003, Durieux *et al.* 2003, Laurance 1998, Shukla *et al.* 1990). Burning also leads to increased logging pressure and land conversion as farmers take the opportunity to expand their land holdings (Curran *et al.* 2004, Kartawinata *et al.* 1989, Laurance 1998, van Nieuwstadt *et al.* 2001). The unpredictable occurrence of fires also discourages farmers from investing in environmentally benign forest agricultural systems that may not yield the desired return on investments should they burn (Nepstad *et al.* 2001). Instead slash-and-burn agriculture is practiced, which further increases the probability of forest loss. Finally, invasive and often exotic species can invade burnt forests and promote future fires as a means of competing with the native forest plant species (Chapin *et al.* 2000, Otsamo *et al.* 1995).

Numerous studies have focused on the impact of disturbance on tree composition in tropical rain-forest settings. There is, however, a paucity of studies examining the distribution and response of smaller plants to large-scale perturbations such as logging and forest fires (Vieira *et al.* 2015). Forest fires in particular should have a major impact on the herb and shrub community by opening up the forest canopy. Frequent burn events, however, may lead to the demise of shade-tolerant forest herbs that require a moist habitat without direct sun exposure (Marschall & Proctor 2004). In the present study, our main hypothesis was to test if disturbance including logging and (multiple) burn events have affected the richness and composition of the herb and shrub layer of forests in East Kalimantan, Indonesia. A secondary hypothesis was to test if there was a significant association between

the composition of the herb and shrub community and environmental variables related to tree and liana structure, previous burn events and topography.

MATERIALS AND METHODS

Study area

Sampling took place in the Balikpapan-Samarinda region of East Kalimantan, Indonesia from January to October 2000. The Balikpapan-Samarinda region of East Kalimantan mainly consisted of small remnant patches of unburnt forest and a few larger isolates following the 1982–1983 and 1997–1998 ENSO burn events. The larger isolates included a 3500-ha unburnt forest isolate in the Sungai Wain protected forest and a 108 000 ha unburnt isolate in the foothills of Mount Meratus. Despite severe species loss immediately after the fires (Cleary & Grill 2004), the burnt forests have shown vigorous regrowth and steadily increasing biodiversity as plants and animals recolonized fire-affected forest (Cleary & Genner 2006, Cleary & Priadjati 2005, Cleary *et al.* 2006b, Dennis *et al.* 2001, Siegert *et al.* 2001).

In order to test the previously mentioned hypotheses, six 450-ha landscape plots of differentially disturbed forest were selected prior to sampling. These included two relatively pristine landscape plots (P1 and P2), one in the large unburnt forest isolate (108 000 ha; P1) and one in the small (3500-ha; P2) unburnt forest isolate, a logged-landscape plot (L1) in the large unburnt forest isolate (108 000 ha), a once-burnt landscape plot (B1) adjacent to the small (3500-ha) unburnt forest isolate, a twice-burnt landscape plot (B2) and a frequently-burnt, largely grassland landscape plot (B3); 16–40 10 × 20-m subplots were randomly allocated to each landscape plot using grid cells on maps. All landscape plots were located within a 5.2 million-ha area of East Kalimantan in the Balikpapan-Samarinda region that was predominantly undisturbed forest prior to the severe 1982–1983 and 1997–1998 ENSO events. After these events the area was turned into a mosaic of burnt and regenerating forest with smaller and larger unburnt isolates (Siegert *et al.* 2001). B3 was located in a predominantly grassland area, with patches of degraded forest, that has been affected by slash-and-burn agriculture since the 1970s. See Appendix 1 and Cleary (2003) and Cleary *et al.* (2004) for a more detailed description of the sampling design and plot layout.

In the large unburnt isolate, rocks from the Middle-late Miocene and Early Miocene dominated the geology, largely consisting of tertiary sedimentary rocks. Alternating layers of sandstone, claystone, mudstone and siltstone dominated the lithology, but there were only slight differences in soil characteristics. Deep clay-rich

soils dominated the area, predominantly ultisols, but also some inceptisols (van Bremen *et al.* 1990). Only soils over Miocene sandstone had different soil characteristics, but these spodosols were very rare (less than 3% of area). Most differences in soil chemistry were limited to the topsoil and were due to slight mineralogical differences in parent material and vegetation. Overall the logged-forest landscape plot had a slightly more fertile A horizon than primary forest. The topography was very heterogeneous; steeply dissected hills and hillocks (150–500 m asl) with short, steep slopes and narrow crests and valley floors dominated the area (van Bremen *et al.* 1990). In the small unburnt isolate and the surrounding burnt-forest matrix, the topography was characterized by gentle to steep hills intersected by many small rivers. The soil type comprised mainly Alisols, very deep, acid and infertile soils with a high fraction of loam and clay (van Bremen *et al.* 1990). Rainfall in the region is about 2472 mm per year and relatively aseasonal. Note that the unburnt primary forest in the small unburnt isolate and the surrounding burnt-forest mosaic were considered to be very similar with respect to their pre-fire vegetation, soil type and rainfall (Van Nieuwstadt *et al.* 2001).

It is important to note that the burnt forest was not uniformly burnt but had networks of remnant unburnt forest that traversed the burnt vegetation. These networks made up an estimated 10.6% (B1) and 8.1% (B2) respectively of the total area in each landscape (Eichhorn 2006) and were primarily found along the floodplain. Vegetation in these remnants was visually similar to unburnt forest (pers obs. DFRC and KAOE). The frequently-burnt landscape plot also had areas of forest along streams that primarily consisted of pioneer tree species.

Field sampling

All landscape plots were sampled from January to October 2000. Plant (i.e. herb and shrub) species were sampled in small 2 × 2-m subplots nested within larger 10 × 20-m subplots demarcated with ironwood poles. Subplots were located in the field with compass and clinometer and georeferenced with a handheld GPS device (Garmin 12XL; Garmin Ltd, Lenexa, Kansas). In the larger subplots, all trees and climbers higher than 1.3 m and greater than 1 cm diameter at breast height (dbh) were counted, dbh measured and height visually estimated (Cleary 2017, Eichhorn 2006, Slik & Eichhorn 2003). In each subplot, altitude was recorded and slope/inclination was measured with a clinometer. In the smaller 2 × 2-m subplots the percentage cover of herbs and shrubs, i.e. monocot herbs, dicot herbs, ferns, herbaceous climbers, sedges, grasses and shrubs were visually estimated and samples collected for further identification. Field assistants assisted with estimation and

sample collection. Collected samples were identified to (morpho-)species by K.A.O. Eichhorn. Collected samples have been stored at the Wanariset, Samboja Herbarium and at the Naturalis Biodiversity Center Herbarium in the Netherlands.

Analyses

Vegetation and topographical structure (e.g. tree abundance, liana abundance and inclination per subplot) and plant species data matrices (species × subplot) were imported into R (<https://cran.r-project.org>) using the `read.table()` function. Rarefied species richness was assessed per landscape plot with the `specaccum()` function in the `vegan` package using 999 permutations and random subsampling of subplots without replacement (<http://CRAN.R-project.org/package=vegan>). In addition to identifying each recorded plant to a (morpho-)species, the growth form was also recorded as fern, grass, dicot herb, monocot herb, climber, sedge or shrub. Mean values (based on subplot values) of these growth forms are presented per landscape in the Results section.

Given that similarity measures have been shown to be sensitive to sparse samples (Clarke *et al.* 2006), we removed all samples with less than 5% cover when comparing composition among landscapes. Both vegetation structure and species data matrices were $\log_e(x + 1)$ transformed. A vegetation structure distance matrix was subsequently constructed using the Euclidean distance and a herb and shrub composition distance matrix using the Bray–Curtis index with the `vegdist()` function in the `vegan` package in R (<http://CRAN.R-project.org/package=vegan>). The Bray–Curtis index is one of the most frequently applied (dis)similarity indices used in ecology (Cleary 2003, de Voogd *et al.* 2006, Legendre & Gallagher 2001). Variation in herb and shrub species composition among landscapes was assessed with principal coordinates analysis (PCO) using the `cmdscale()` function in R with the Bray–Curtis distance matrix as input. Weighted average scores were computed for species on the first two PCO axes using the `wascores()` function in the `vegan` package. Using the `envfit()` function, we also tested for significant relationships between vegetation and topographical variables, namely, the percentage of the plot burnt (Fire), altitude (Alti), inclination (Incl), total basal area (trees and liana combined; Bas.tot), tree basal area (Bas.tr), mean tree diameter (Dia.tr), maximum tree diameter (Dia.mx.tr), tree density (Ab.tr) and liana density (Ab.li) and the PCO ordination of herb and shrub composition using 999 permutations; all other arguments in the function were left as default. Detailed descriptions of the functions used here can be found in R (e.g. `?cmdscale`) and online in reference manuals (<http://cran.r-project.org/web/packages/vegan/index.html>).

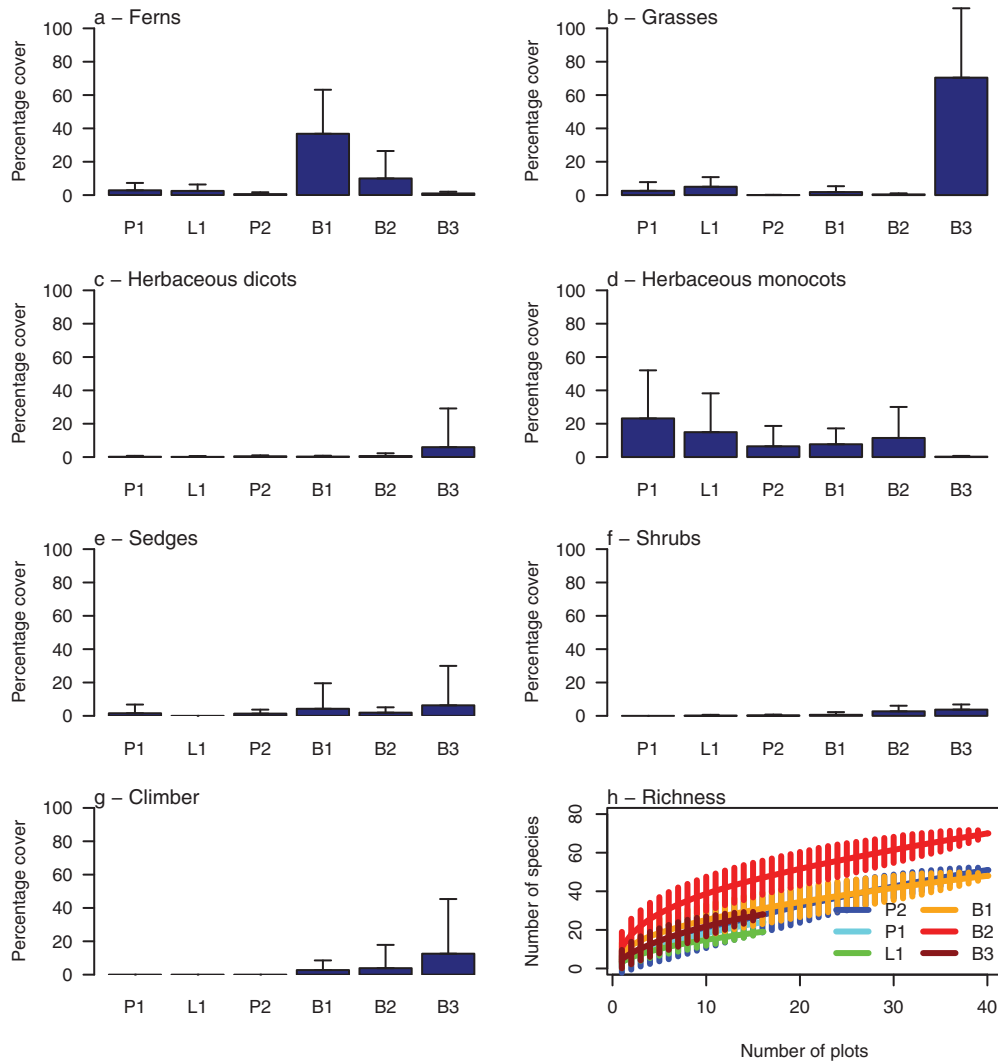


Figure 1. Mean percentage cover (error bars represent a single standard deviation) of ferns (a), grasses (b), monocot herbs (c), dicot herbs (d), sedges (e), shrubs (f) and herbaceous climbers (g) in primary forest in the large (P1) and small (P2) unburnt isolates, logged forest (L1) in the large unburnt isolate, once-burnt forest (B1), twice-burnt forest (B2) and the frequently-burnt landscape plot (B3) in East Kalimantan, Indonesia. (h) Total herb and shrub species richness.

RESULTS

Vegetation cover differed strongly among different landscape plots with a clear effect of burning (Figure 1). Ferns were present but had relatively low cover in unburnt forest, but were an important cover in once- and twice-burnt forest. In the frequently-burnt landscape plot, however, ferns were only a minor component of the plant community. Dicot herbs and grasses in contrast were the major cover in the frequently-burnt landscape. Monocot herbs were important components of the plant community in all landscape plots except the frequently-burnt landscape plot. Both shrub and herbaceous climber cover increased in burnt forest with the highest mean cover in the frequently-burnt landscape plot. There was,

however, pronounced variation in the cover of the various plant (i.e. herb and shrub) components within landscape plots. Plant cover per subplot, for example, varied from 2% to 93% in primary forest in the large unburnt isolate, 0–92% in logged forest and 80–100% in the frequently-burnt landscape plot.

Burning also had an effect on landscape-scale richness, which was highest in twice-burnt forest and lowest in logged forest with relatively little difference between both primary landscape plots, once-burnt forest and the frequently-burnt-landscape plot. Overall, we recorded 175 herb and shrub (morpho)species. Plant (i.e. herb and shrub species) richness ($n = 15$ plots) varied from 18.4 ± 0.69 in logged forest to 23.1 ± 0.78 in primary forest in the large unburnt isolate, 26.6 ± 4.60 in primary forest in

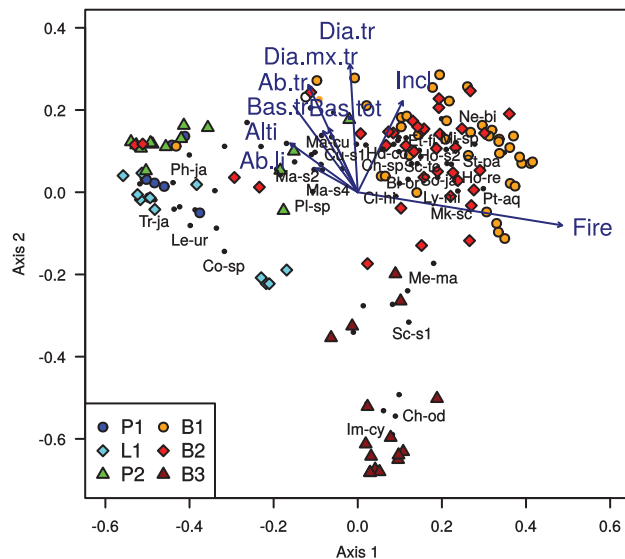


Figure 2. Variation in the composition of herbs and shrubs showing the first two axes of the PCO analysis. Large symbols and codes refer to subplots in primary forest in the large (P1) and small (P2) unburnt isolates, logged forest (L1) in the large unburnt isolate, once-burnt forest (B1), twice-burnt forest (B2) and the frequently-burnt landscape plot (B3) sampled in East Kalimantan, Indonesia. Black codes refer to loadings for selected species; for species codes see Table 1. Abbreviations of vegetation and topography variables (indicated by blue arrows) are: percentage of the plot burnt (Fire), altitude (Alti), inclination (Incl), total basal area (trees and liana combined; Bas.tot), tree basal area (Bas.tr), mean tree diameter (Dia.tr), maximum tree diameter (Dia.mx.tr), tree density (Ab.tr) and liana density (Ab.li).

the small unburnt isolate, 27.1 ± 1.11 in the frequently-burnt landscape, 30.2 ± 4.11 in once-burnt forest and 45.8 ± 4.48 in twice-burnt forest (Figure 1).

Herb composition was primarily structured by burning (Figure 2). Significant variables associated with variation along the first two PCO axes included fire ($r^2 = 0.763$, $P < 0.001$), altitude ($r^2 = 0.122$, $P < 0.001$), inclination ($r^2 = 0.188$, $P < 0.001$), total basal area ($r^2 = 0.091$, $P = 0.005$), tree basal area ($r^2 = 0.090$, $P = 0.005$), tree diameter ($r^2 = 0.312$, $P < 0.001$), maximum tree diameter ($r^2 = 0.265$, $P < 0.001$), tree abundance ($r^2 = 0.282$, $P < 0.001$) and liana abundance ($r^2 = 0.098$, $P = 0.005$). The first axis separated burnt from unburnt forest. There was considerable overlap between subplots from once- and twice-burnt forest, but no overlap between these subplots and subplots from the frequently-burnt landscape plot. There was pronounced overlap among subplots from different unburnt landscape plots and a small subset of subplots from once- and twice-burnt landscape plots that clustered together with subplots from unburnt forest. Axis 2 mainly separated subplots in the frequently-burnt landscape plot from subplots of the other burnt- and unburnt-forest-landscape plots.

Species mainly associated with once- and twice-burnt forest included the ferns *Pteridium aquilinum*

subsp. *caudatum*, *Nephrolepis biserrata*, *Blechnum orientale*, *Stenochlaena palustris* and *Microlepia speluncae* and the monocot herbs *Hornstedtia* cf. *reticulata*, *Hornstedtia* sp. 2, *Cheilocostus speciosus*, *Curculigo* sp. 1, *Amomum* sp. 18 and the shrub *Solanum jamaicense*. Species associated with unburnt forest included the monocot herb *Phrynium jagorianum*, the fern *Trichomanes javanica* and the grass *Leptaspis urceolata*. Species associated with the frequently-burnt landscape plot included the grass *Imperata cylindrica* and the shrub *Chromolaena odorata*. A small subset of subplots in the frequently-burnt landscape plot had relatively high cover of shrubs and sedges including *Melastoma malabathricum* and *Scleria* sp. 1.

The most frequently encountered species included *Phrynium jagorianum* that was recorded in all landscape plots except the frequently-burnt landscape plot, *Nephrolepis biserrata*, *Microlepia speluncae*, *Pteridium aquilinum* subsp. *caudatum*, *Hornstedtia* sp. 2 and *Blechnum orientale* mainly found in once- and twice-burnt forest, *Mapania cuspidata*, *Hedyotis congesta* and *Scleria terrestris* mainly found in the primary-forest-landscape plot in the small unburnt isolate, once- and twice-burnt forest and *Leptaspis urceolata* mainly found in the primary- and logged-landscape plots in the large forest isolate (Table 1). *Costus* sp. was only found in logged forest and *Etilingera fimbriobracteata* was only found in twice-burnt forest. Species found in once- and twice-burnt forest and the frequently-burnt landscape plot included *Nephrolepis biserrata*, *Lygodium microphyllum*, *Stenochlaena palustris*, *Imperata cylindrica*, *Mikania scandens*, *Clidemia hirta*, *Melastoma malabathricum*, *Blechnum orientale*, *Solanum jamaicense*, *Chromolaena odorata* and *Scleria* sp. 1.

DISCUSSION

Plant species richness was similar among both primary-forest-landscape plots, once-burnt forest and the frequently-burnt landscape plot. Logged forest, however, had lower richness than proximate primary forest and the highest overall richness was recorded in twice-burnt forest. Logging appeared to adversely affect richness by the loss of rare forest herbs that may have been affected by the logging-induced modification to the forest microclimate. This effect also appeared to hold in burnt versus proximate primary forest, but richness between primary and once-burnt forest was similar due to the colonization of burnt forest by species that had apparently colonized the burnt forest from proximate degraded grassland or secondary forest.

The very high richness of twice-burnt forest is interesting in that this forest type consisted of plants associated with unburnt forest and those associated with the degraded frequently-burnt landscape plot. A number of species were also, however, only recorded in this forest

Table 1. Family, species, growth form and abundance of the most frequently encountered species of herbs and shrubs in primary forest in the large (P1) and small (P2) unburnt isolates, logged forest (L1) in the large unburnt isolate, once-burnt forest (B1), twice-burnt forest (B2) and the frequently-burnt-landscape plot (B3) in East Kalimantan, Indonesia. The numbers refer to the number of subplots in which the species in question was encountered. Form refers to the growth form whereby HerMon refers to monocot herb and HerDic to dicot herb.

Family	Species	Code	Form	Sum	L1	P1	P2	B1	B2	B3
Marantaceae	<i>Phrynium jagorianum</i> K. Koch	Ph-ja	HerMon	96	9	14	22	24	27	0
Nephrolepidaceae	<i>Nephrolepis biserrata</i> (Sw.) Schott	Ne-bi	Fern	74	0	1	1	39	32	1
Dennstaedtiaceae	<i>Microlepia speluncae</i> (L.)	Mi-sp	Fern	63	0	0	2	32	29	0
Lygodiaceae	<i>Lygodium microphyllum</i> (Cav.) R.Br.	Ly-mi	Fern	57	0	0	1	22	29	5
Blechnaceae	<i>Stenochlaena palustris</i> (Burm. f.) Bedd.	St-pa	Fern	54	0	0	1	28	24	1
Zingiberaceae	<i>Hornstedtia</i> cf. <i>reticulata</i>	Ho-re	HerMon	48	0	1	6	21	20	0
Cyperaceae	<i>Mapania cuspidata</i> (Miq.) Uittien	Ma-cu	Sedge	48	0	0	22	10	16	0
Gramineae	<i>Imperata cylindrica</i> (L.) P. Beauv.	Im-cy	Grass	41	0	0	0	19	9	13
Rubiaceae	<i>Hedyotis congesta</i> R. Brown ex G. Don	Hd-co	HerDic	38	0	1	16	11	10	0
Asteraceae	<i>Mikania scandens</i> B.L.Rob.	Mk-sc	Climber	37	0	0	0	18	16	3
Hypolepidaceae	<i>Pteridium aquilinum</i> subsp. <i>caudatum</i> (L.)	Pt-aq	Fern	31	0	0	0	22	8	1
Melastomataceae	<i>Clidemia hirta</i> (L.) D. Don	Cl-hi	Shrub	29	1	0	0	0	27	1
Melastomataceae	<i>Melastoma malabathricum</i> L.	Me-ma	Shrub	26	0	0	0	3	14	9
Zingiberaceae	<i>Hornstedtia</i> sp. 2	Ho-s2	HerMon	22	0	0	0	4	18	0
Blechnaceae	<i>Blechnum orientale</i> L.	Bl-or	Fern	20	0	0	0	6	12	2
Gramineae	<i>Leptaspis urceolata</i> (Roxb.) R.Br.	Le-ur	Grass	20	11	8	1	0	0	0
Zingiberaceae	<i>Plagiostachys</i> sp.	Pl-sp	HerMon	20	3	4	1	1	11	0
Solanaceae	<i>Solanum jamaicense</i> P. Mill.	So-ja	Shrub	20	0	0	0	0	19	1
Cyperaceae	<i>Scleria terrestris</i> (L.) Fassett	Sc-te	Sedge	19	0	0	6	7	6	0
Zingiberaceae	<i>Cheilocostus speciosus</i> (J.Konig) C.Specht	Ch-sp	HerMon	18	0	0	0	0	18	0
Asteraceae	<i>Chromolaena odorata</i> (L.) R.M.King & H.Rob.	Ch-od	Shrub	16	0	0	0	0	3	13
Hypoxidaceae	<i>Curculigo</i> sp. 1	Cu-s1	HerMon	13	0	0	3	2	8	0
Cyperaceae	<i>Mapania</i> sp. 2	Ma-s2	Sedge	13	0	0	3	5	5	0
Cyperaceae	<i>Mapania</i> sp. 4	Ma-s4	Sedge	13	0	0	3	6	4	0
Hymenophyllaceae	<i>Trichomanes javanica</i> Bl.	Tr-ja	Fern	13	6	5	2	0	0	0
Cyperaceae	<i>Scleria</i> sp. 1	Sc-s1	Sedge	10	0	0	0	0	6	4
Zingiberaceae	<i>Costus</i> sp.	Co-sp	HerMon	6	6	0	0	0	0	0
Zingiberaceae	<i>Elettaria</i> sp. 32	El-32	HerMon	6	0	1	2	2	1	0
Zingiberaceae	<i>Etilingera fimbriobracteata</i> (K.Schum.) R.M.Sm.	Et-fi	HerMon	6	0	0	0	0	6	0
Schyzeaceae	<i>Lygodium circimatum</i> (Burm. f.) Bedd.	Ly-ci	Fern	6	0	0	0	1	5	0
Rubiaceae	<i>Lasianthus oblongatus</i> Merr.	La-ob	Shrub	5	0	0	4	0	1	0
Davalliaceae	<i>Leucostegia pallida</i> (Mett. ex Kuhn) Copel.	Le-pa	Fern	5	2	3	0	0	0	0
Zingiberaceae	Zingiberaceae sp. 2a	Zn-2a	HerMon	5	3	2	0	0	0	0
Zingiberaceae	Zingiberaceae sp. 45	Zn-45	HerMon	5	0	0	0	0	5	0
Zingiberaceae	<i>Alpinia galanga</i> (L.) Willd.	Al-ga	HerMon	4	0	0	0	0	0	4
Zingiberaceae	<i>Ammomum</i> sp. 18	Am-18	HerMon	4	0	0	0	1	3	0
Zingiberaceae	<i>Elettaria</i> sp. 17	El-17	HerMon	54	0	0	0	0	4	0
Zingiberaceae	<i>Etilingera</i> sp. 3	Et-s3	HerMon	4	0	0	3	1	0	0
Rubiaceae	<i>Geophila</i> sp. 3	Ge-s3	Shrub	4	0	0	2	2	0	0
Lygodiaceae	<i>Lygodium salicifolium</i> C. Presl	Ly-sa	Fern	4	0	0	1	0	1	2
Melastomataceae	<i>Melastoma</i> sp. 1	Me-s1	Shrub	4	0	0	0	4	0	0
Marantaceae	<i>Phrynium</i> sp. 2	Ph-s2	HerMon	4	0	0	1	1	2	0
Gramineae	<i>Saccharum spontaneum</i> L.	Sa-sp	Grass	4	1	0	0	0	2	1
Selaginellaceae	<i>Selaginella</i> sp. 1	Se-s1	Club	4	0	0	1	1	2	0
Aspidiaceae	<i>Tectaria</i> sp. 2a	Te-s2a	Fern	4	3	1	0	0	0	0
Aristolochiaceae	<i>Thotea</i> sp. 1	Th-s1	HerDic	4	0	0	2	1	1	0
Zingiberaceae	Zingiberaceae sp. 3a	Zn-3a	HerMon	4	2	2	0	0	0	0

type suggesting that it provides a unique habitat to a number of herb species, particularly members of the ginger family, Zingiberaceae.

Compositionally, there was a clear distinction between unburnt and burnt forest on the one hand and between burnt and unburnt forest versus the frequently-burnt landscape plot on the other. Structurally, this culminated in the dominance of grass, dicot herbs, shrubs and

herbaceous climbers in the frequently-burnt landscape plot along with the almost complete disappearance of monocot herbs and ferns. Ferns were most abundant in the once- and twice-burnt forest. Once- and twice-burnt forest landscape plots were also characterized by the presence of shrubs and climbers that were relatively abundant in the frequently-burnt landscape plot, but largely absent from unburnt forest. This indicates an influx of these

widespread and often exotic plants into the burnt forest matrix from surrounding, severely disturbed areas of grassland and secondary scrub habitat. In contrast, many species found in burnt forest were largely restricted to remnant areas of forest along the floodplains of burnt forest. These low-lying areas were least affected by the previous burn events and contained vegetation similar to that found in unburnt forest. Slik & Eichhorn (2003) previously stressed the importance of these floodplains in preserving tree diversity in burnt-forest landscapes. In twice-burnt forest, the unburnt forest network along floodplains covered less than 10% of the area, but housed the majority of all species recorded and numerous rare species were restricted to it (Slik & Eichhorn 2003).

The monocot herb *Phrynium jagorianum* (Marantaceae) was the most abundant herb in terms of occurrence and percentage cover in unburnt forest and was also relatively common in once- and twice-burnt forest but completely absent from the frequently-burnt landscape plot. It was particularly abundant in temporarily flooded areas of the forest where it often formed a continuous layer. It was much less prevalent in areas that were never waterlogged or that were permanently flooded. In the burnt forest, it apparently recovered from the fires by resprouting from rhizomes that survived in the ground. Other species of Marantaceae were much less abundant and were mainly restricted to floodplains.

The sedge *Mapania cuspidata* (Cyperaceae) was also relatively common in the unburnt primary forest landscape plot in the small unburnt isolate (P2), but not recorded in logged or primary forest in the large unburnt isolate, where the sedge *Mapania palustris* was recorded. Both *Phrynium jagorianum* and *Mapania cuspidata* were also found along unburnt floodplains of the burnt forests. Unidentified species that were also rather common in these floodplain areas included the genera *Curculigo* (Hypoxidaceae) and *Alocasia* (Araceae). Importantly, this floodplain network was still present in twice-burnt forest, 18 y after the initial fires of 1982–1983 and mainly consisted of non-pioneer tree species and herb species such as *Phrynium jagorianum* and *Mapania cuspidata* that were absent in the burnt-forest matrix itself. This demonstrates the persistence of the network and its ability to withstand recurrent fires. Not only is this network a refuge for non-pioneer tree and herb species, but it also probably functions as a dispersal network for animals, enabling them to recolonize the burnt forest (Cleary & Genner 2006). Tropical riparian forests are believed to have functioned as persistent forest refuges during Pleistocene dry periods and subsequently to have served as loci enabling the reconversion of the surrounding savanna into forest (Meave *et al.* 1991). The unburnt-forest network may well serve a similar function in an environment where fire has become a more frequent

phenomenon in tropical forest landscapes and should be a focus of conservation concern.

Other herb species found in unburnt forest included the herbaceous dicot *Hedyotis congesta* (Rubiaceae) and the sedge *Scleria terrestris* (Cyperaceae) that were more often present in canopy gaps and were also common in burnt forest. Overall, monocot herbs were clearly the most abundant plant type in unburnt forest, while monocot herbs and herbaceous ferns were both abundant in terms of cover in burnt forests. Dicot herbs encountered included *Thottea grandiflora* (Aristolochiaceae) and *Labisia pumila* (Myrsinaceae), which were mainly present in the forest understorey and *Spermacoce* sp. and *Vernonia cinerea* in the frequently-burnt landscape plot. With the exception of *Hedyotis congesta*, dicot herbs were a rare component in all forest landscapes but were somewhat more common in the frequently-burnt landscape plot.

Ferns, grasses and sedges were markedly less abundant in twice-burnt than once-burnt forest. All of these growth forms appear to have been affected by the dense canopy of saplings that developed in twice-burnt forest and mainly consisted of rapidly growing pioneer trees belonging to the genera *Macaranga*, *Mallotus* and *Homolanthus* among others (Slik & Eichhorn 2003). In contrast to the above, monocot herbs were more abundant in twice-burnt forest, mainly due to a high cover of Zingiberaceae. The species *Cheilocostus speciosus* was abundant in the twice-burnt forest but was not recorded in the other landscape plots including the frequently-burnt landscape plot. Although unlogged and logged forest did appear to differ in terms of composition, this difference was much less pronounced than that between unburnt and burnt forest. In a study of the impact of logging on Amazonian herbs, there was no impact of logging on herb diversity or composition although the area of logging roads and skid trails did appear to influence composition (Costa & Magnusson 2002). Of the other monocot herb genera, *Etilingera* and *Hornstedtia* were particularly abundant in the once- and twice-burnt-landscape plots, while species of *Elettaria* and *Plagiostachys* were more common in unburnt-landscape plots.

Grasses were rare in primary forest in the small unburnt isolate and twice-burnt forest, moderately abundant in primary and logged forest in the large unburnt isolate and once-burnt forest and the dominant cover in the frequently-burnt landscape plot where *Imperata cylindrica* covered an estimated 65% of the area. The most common grass species in unburnt forest was *Leptaspis urceolata*, which was not recorded in burnt-forest-landscape plots. Sedges were most abundant in once-burnt forest and the frequently-burnt-landscape plot, mainly due to a high cover of *Scleria* spp. (Cyperaceae).

Ferns were clearly most abundant in the once-burnt forest where they were the dominant cover. This was

mainly due to three species: *Pteridium aquilinum* subsp. *caudatum*, *Microlepia speluncae* (Dennstaedtiaceae) and *Nephrolepis biserrata* (Nephrolepidaceae). Two other ferns were also often present in the burnt landscape plots but were never dominant: *Pteris tripartita* (Pteridaceae) and *Blechnum orientale* (Blechnaceae). Ferns belonging to the genus *Pteridium* in particular now cover an immense area of fire-degraded forest across the globe (Gallegos *et al.* 2015). Previous studies have suggested that these ferns (and grasses such as *Imperata cylindrica*) inhibit forest regeneration and promote future fires (Aide & Cavelier 1994, Holl 2002, Holl *et al.* 2000). The accumulated dry, dead fronds, for example, of *Pteridium* species are highly inflammable. *Pteridium* spp. also possess traits such as a large and persistent rhizome system and dense frond canopy that enable them to out-compete other species. Interestingly the dense frond canopy may also provide conditions that facilitate the reestablishment of shade-tolerant climax tree species (Gallegos *et al.* 2015). *Pteridium* spp. have, furthermore, been shown to rapidly colonize degraded forest and to be highly resilient, quickly returning after new burn events (Ramírez-Trejo *et al.* 2010). It is, therefore, interesting that *Pteridium aquilinum* subsp. *caudatum* in our study only managed to dominate once-burned forest, but was largely absent from twice-burned forest and the frequently-burnt-landscape plot.

The most striking difference between the once- and twice-burnt landscape plots was the dominance of ferns in the former and the high densities of pioneer trees in the latter (Slik & Eichhorn 2003). In the twice-burnt forest, ferns apparently suffered from shading under the dense low canopy of pioneer trees as most ferns were present but largely dying off. The prevalence of pioneer trees in twice-burnt forest would appear to reflect the densities of pioneer tree seeds in the soil seed bank before the 1998 fires due to the previous 1982–83 fires. As pioneer species typically have a well-developed soil seed bank (Garwood 1989, Swaine & Whitmore 1988), many more tree seeds may have been present in the topsoil of the twice-burnt forest, that is before the second burn. Similarly, post-clearing regeneration is generally better developed when a site has previously been occupied by successional vegetation rather than old-growth forest (Guariguata & Ostertag 2001). This explanation implies that even a third fire will not lead to permanent deforestation, since tree seeds in the topsoil were most abundant at this site. Thus far, recurrent fires have not led to permanent deforestation and it seems unlikely that subsequent fires will change this very soon, but this may change if fires increase in frequency (Cochrane & Schultze 1998, Cochrane *et al.* 1999).

Ferns in general were only a relatively minor component of the frequently-burnt-landscape plot. The marked difference in fern abundance among burnt-landscape

plots is probably related to their specific burn history. In previously unburnt forests, there are relatively few pioneer trees and thus relatively few pioneer seeds in the seed bank. When these forests burn for the first time, this leaves large areas of bare ground available for ferns to colonize and expand thus explaining the relatively high fern cover in once-burnt forest. In previously burnt forests in contrast, pioneer seeds form an abundant component of the seed bank and quickly germinate and occupy the available bare ground thus pre-empting the bare ground before ferns, which are strongly light-dependent, have had a chance to effectively colonize it. In contrast to the two previous examples, the frequently-burnt-landscape plot does not really represent a pioneer situation. The frequency of the fires has instead shifted the landscape from a forest to a grassland dynamic. Ferns are typically pioneer species that are able to use their very small propagules to colonize suitable habitat over a very large area. They are, however, poor competitors with grass species that are prevalent in the frequently-burnt-landscape plot. These grass species are able to rapidly colonize the burnt area due to the large reserves in their seeds and root system before the ferns have had a chance to establish themselves.

Other ferns were rare or absent in all landscapes and only a few of them could be reliably identified to the species level: *Trichomanes javanica* (Hymenophyllaceae), *Taenitis blechnoides* (Pteridaceae), *Pleocnemia irregularis* (Dryopteridaceae) and *Pityrogramma calomelanos* (Pteridaceae). *Pityrogramma calomelanos* was very abundant along roadsides in the Wanariset area (K.A.O. Eichhorn, pers. obs.), but rare in the forest itself and was also recorded in the frequently-burnt-landscape plot. Other species-rich genera encountered that warrant further study were *Diplazium* (Dryopteridaceae), *Tectaria* (Dryopteridaceae) and the clubmoss *Selaginella* (Selaginellaceae).

Shrubs and to a lesser extent herbaceous climbers were on average more abundant in twice-burnt than once-burnt forest. This was mainly due to the abundance of invasive species such as *Chromolaena odorata*, *Clidemia hirta* (Melastomataceae) and *Solanum jamaicense* (Solanaceae). Other shrubs encountered mainly belonged to genera of Rubiaceae, namely, *Ixora*, *Lasianthus* and *Psychotria*. The first two genera consisted of species that were mainly restricted to unburnt forest, while *Psychotria viridiflora* was most abundant in the burnt forests. *Chromolaena odorata*, *Clidemia hirta* and *Solanum jamaicense* are all exotics and *Chromolaena odorata* and *Clidemia hirta* have a growth form almost intermediate between herbs and shrubs. These species were also all encountered in the frequently-burnt-landscape plot. *Solanum jamaicense* is a shrub, native to the neotropics, that has been reported to displace native shrubs and impede animal movement due to its dense and intertwining prickly stems (Diaz *et al.* 2008). *Clidemia hirta* is native to Central and

South America, is now present in Africa and Asia and is also a problematic species in Hawaii (Schulten *et al.* 2014).

Chromolaena odorata together with *Imperata cylindrica* formed the dominant cover in the frequently-burnt landscape plot and both were present in 13 of 16 subplots. *Chromolaena odorata* is native to North America but has invaded numerous areas of the globe including Africa, Asia and Australia and appears to be rapidly spreading (Yu *et al.* 2016). It has also established widespread monocultures in high biodiversity areas of Africa and Asia. It has already been reported to have adversely affected native species, reduced agricultural productivity and caused general economic losses due to it forming dense thickets where it shades out other vegetation (Yu *et al.* 2016). *Imperata cylindrica* in turn colonizes land degraded by frequent forest fires and has established itself as a highly problematic, weedy species on all continents except Antarctica. The species also competes with other plants by extracting moisture from the soil and produces allelopathic chemicals in its rhizomes (Bryson *et al.* 2010). Once established the dense *I. cylindrica* thatch promotes intense fire that kills off other above-ground vegetation leaving *I. cylindrica* to regenerate from its dense subterranean rhizomes. This frequent burning leads to nitrogen and carbon losses and the erosion of agricultural productivity (Chapin *et al.* 2000, Otsamo *et al.* 1995) making it one of the most problematic of weedy species (Estrada & Flory 2015, MacDonald 2004).

The fact that these species appear to be established in the frequently-burnt-landscape plot and have invaded burnt forest is certainly cause for concern, particularly because they can increase the probability of future fires occurring. Under a frequent-burn regime, newly established pioneer trees are often burnt before seed reproduction can begin leading to successive stands of pioneer trees having a more open structure with the open spaces filling up with fire-promoting species such as *I. cylindrica*. Recurrent fires then have a much higher intensity, destroying remnant climax species that survived the initial fires and even affecting the low-lying unburnt forest remnants (Cochrane & Schultze 1998, Cochrane *et al.* 1999, Goldammer 1999). Mechanisms used by climax trees to regenerate following fires such as resprouting are also lost as this capacity is lost at high fire frequencies (Van Nieuwstadt *et al.* 2001). The resultant permanent deforestation that is the end phase of this process will result in a depauperate grass-dominated landscape similar to the frequently-burnt-landscape plot in this study with impoverished plant and animal communities largely consisting of widespread and generalist species in addition to exotics such as *Chromolaena odorata* and *Clidemia hirta* (Cleary 2016). Importantly, the riparian forest network was also prevalent in the frequently-burnt-landscape plot, but this had been

severely degraded to areas of stunted pioneer trees and shrubs along streams.

In summary, we conclude that previous burn events appear to have had an important impact on the composition of herbs and shrubs in the forests of East Kalimantan. Although richness was similar or higher in burnt forests than unburnt forest, this was largely due to invasion of the burnt forest by widespread and often exotic species that were recorded in the frequently-burnt-landscape plot. Numerous species of herbs associated with unburnt forest were, however, recorded along the floodplains of burnt forest. Preserving these floodplains from further disturbance should be a conservation priority. The twice-burnt-forest-landscape plot additionally had the highest overall recorded richness and contained numerous species not recorded elsewhere. Burnt forest should not, therefore, be seen as unimportant for conserving forest diversity and measures should be taken to avoid future burn events.

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Appendix 1. Table of subplots sampled in the present study. The columns show longitude and latitude in decimal degrees, Landscape (landscape plot), Mosaic (burnt, small unburnt isolate and large unburnt isolate), Fire (percentage of subplot burnt), altitude (metres above sea level) and inclination (slope of plot in degrees) of all subplots sampled in East Kalimantan, Indonesia.

Plot	Longitude	Latitude	Landscape	Mosaic	Fire	Altitude	Inclination
Ka01	116.9439	-1.0552	Frequently-burnt	Burnt	100	34	3
Ka02	116.9430	-1.0606	Frequently-burnt	Burnt	100	41	4
Ka03	116.9443	-1.0606	Frequently-burnt	Burnt	100	31	6
Ka04	116.9475	-1.0552	Frequently-burnt	Burnt	100	24	4
Ka05	116.9488	-1.0539	Frequently-burnt	Burnt	100	23	2
Ka06	116.9520	-1.0557	Frequently-burnt	Burnt	100	26	5
Ka07	116.9565	-1.0552	Frequently-burnt	Burnt	100	25	2
Ka08	116.9556	-1.0593	Frequently-burnt	Burnt	100	26	2
Ka09	116.9560	-1.0520	Frequently-burnt	Burnt	100	24	1
Ka10	116.9587	-1.0539	Frequently-burnt	Burnt	100	31	4
Ka11	116.9583	-1.0606	Frequently-burnt	Burnt	100	27	2
Ka12	116.9605	-1.0566	Frequently-burnt	Burnt	100	49	9
Ka13	116.9605	-1.0597	Frequently-burnt	Burnt	100	28	2
Ka14	116.9610	-1.0511	Frequently-burnt	Burnt	100	34	4
Ka15	116.9650	-1.0552	Frequently-burnt	Burnt	100	42	5
Ka16	116.9443	-1.0530	Frequently-burnt	Burnt	100	35	6
MI16	116.3423	-0.9496	Logged	Large	0	173	12
MI17	116.3414	-0.9551	Logged	Large	0	161	6
MI18	116.3427	-0.9551	Logged	Large	0	167	9
MI19	116.3459	-0.9496	Logged	Large	0	199	4
MI20	116.3472	-0.9483	Logged	Large	0	188	5
MI21	116.3504	-0.9501	Logged	Large	0	219	6
MI22	116.3549	-0.9496	Logged	Large	0	235	11
MI23	116.3540	-0.9537	Logged	Large	0	170	10
MI24	116.3544	-0.9465	Logged	Large	0	236	10
MI25	116.3571	-0.9483	Logged	Large	0	200	17
MI26	116.3567	-0.9551	Logged	Large	0	159	12
MI27	116.3589	-0.9510	Logged	Large	0	161	2
MI28	116.3589	-0.9542	Logged	Large	0	146	3
MI29	116.3594	-0.9456	Logged	Large	0	200	8
MI30	116.3634	-0.9496	Logged	Large	0	157	3
MI31	116.3418	-0.9474	Logged	Large	0	175	4
Mp01	116.3248	-0.9664	Primary-large	Large	0	195	10
Mp02	116.3194	-0.9655	Primary-large	Large	0	197	8
Mp03	116.3194	-0.9668	Primary-large	Large	0	180	11
Mp04	116.3248	-0.9700	Primary-large	Large	0	182	7
Mp05	116.3261	-0.9713	Primary-large	Large	0	161	8
Mp06	116.3243	-0.9745	Primary-large	Large	0	181	7
Mp07	116.3248	-0.9790	Primary-large	Large	0	201	10
Mp08	116.3207	-0.9781	Primary-large	Large	0	227	6
Mp09	116.3279	-0.9786	Primary-large	Large	0	166	20
Mp10	116.3261	-0.9813	Primary-large	Large	0	163	1
Mp11	116.3194	-0.9808	Primary-large	Large	0	202	8
Mp12	116.3234	-0.9831	Primary-large	Large	0	171	14
Mp13	116.3203	-0.9831	Primary-large	Large	0	207	7
Mp14	116.3288	-0.9835	Primary-large	Large	0	165	5
Mp15	116.3248	-0.9876	Primary-large	Large	0	196	8
Mp32	116.3270	-0.9659	Primary-large	Large	0	230	11
U102	116.8144	-1.1013	Once-burnt	Burnt	100	70	6
U126	116.8125	-1.0976	Once-burnt	Burnt	100	62	14
U140	116.8124	-1.0960	Once-burnt	Burnt	45	64	0
U141	116.8105	-1.0981	Once-burnt	Burnt	100	102	21
U142	116.8087	-1.0999	Once-burnt	Burnt	86	69	6
U143	116.8078	-1.0990	Once-burnt	Burnt	100	81	18
U144	116.8073	-1.0986	Once-burnt	Burnt	100	82	27
U145	116.8064	-1.1004	Once-burnt	Burnt	100	88	7
U146	116.8033	-1.0986	Once-burnt	Burnt	100	93	16
U147	116.8091	-1.0963	Once-burnt	Burnt	100	87	8
U148	116.8073	-1.0949	Once-burnt	Burnt	0	57	0
U149	116.8109	-1.0927	Once-burnt	Burnt	100	70	6

Appendix 1. Continued

Plot	Longitude	Latitude	Landscape	Mosaic	Fire	Altitude	Inclination
U150	116.8069	-1.0927	Once-burnt	Burnt	100	102	24
U151	116.8091	-1.0918	Once-burnt	Burnt	100	76	8
U152	116.8073	-1.0913	Once-burnt	Burnt	100	96	21
U153	116.8091	-1.0904	Once-burnt	Burnt	100	75	10
U154	116.8087	-1.0872	Once-burnt	Burnt	100	73	15
U155	116.8060	-1.0868	Once-burnt	Burnt	100	106	9
U156	116.8055	-1.0877	Once-burnt	Burnt	16	82	1
U157	116.8046	-1.0886	Once-burnt	Burnt	100	106	20
U158	116.8046	-1.0891	Once-burnt	Burnt	100	118	12
U159	116.8037	-1.0900	Once-burnt	Burnt	100	96	11
U160	116.8046	-1.0868	Once-burnt	Burnt	100	109	8
U161	116.8073	-1.0850	Once-burnt	Burnt	22	104	4
U162	116.8046	-1.0827	Once-burnt	Burnt	100	95	34
U163	116.8037	-1.0823	Once-burnt	Burnt	100	88	5
U164	116.8046	-1.0800	Once-burnt	Burnt	100	112	10
U165	116.8123	-1.0881	Once-burnt	Burnt	100	85	16
U166	116.8136	-1.0881	Once-burnt	Burnt	100	78	7
U167	116.8145	-1.0891	Once-burnt	Burnt	100	88	21
U168	116.8150	-1.0872	Once-burnt	Burnt	100	89	5
U169	116.8132	-1.0854	Once-burnt	Burnt	100	117	7
U170	116.8141	-1.0854	Once-burnt	Burnt	100	107	7
U171	116.8132	-1.0832	Once-burnt	Burnt	100	102	9
U172	116.8150	-1.0827	Once-burnt	Burnt	94	75	4
U173	116.8100	-1.0832	Once-burnt	Burnt	89	79	17
U174	116.8127	-1.0786	Once-burnt	Burnt	100	115	4
U175	116.8141	-1.0791	Once-burnt	Burnt	100	88	8
U176	116.8087	-1.0786	Once-burnt	Burnt	100	124	9
U177	116.8145	-1.0755	Once-burnt	Burnt	100	112	14
U178	116.8142	-1.0987	Once-burnt	Burnt	100	67	15
U180	116.8142	-1.0993	Once-burnt	Burnt	100	75	15
Up01	116.8168	-1.1070	Primary-small	Small	0	50	2
Up05	116.8149	-1.1069	Primary-small	Small	0	55	4
Up15	116.8163	-1.1051	Primary-small	Small	0	51	1
Up41	116.8187	-1.1053	Primary-small	Small	0	42	5
Up42	116.8205	-1.1035	Primary-small	Small	0	49	24
Up43	116.8214	-1.1044	Primary-small	Small	0	74	14
Up44	116.8218	-1.1049	Primary-small	Small	0	87	20
Up45	116.8227	-1.1031	Primary-small	Small	0	73	19
Up46	116.8259	-1.1049	Primary-small	Small	0	101	16
Up47	116.8200	-1.1071	Primary-small	Small	0	53	10
Up48	116.8218	-1.1085	Primary-small	Small	0	52	10
Up49	116.8182	-1.1108	Primary-small	Small	0	45	6
Up50	116.8223	-1.1108	Primary-small	Small	0	82	20
Up51	116.8200	-1.1117	Primary-small	Small	0	55	22
Up52	116.8218	-1.1121	Primary-small	Small	0	75	8
Up53	116.8200	-1.1130	Primary-small	Small	0	84	4
Up54	116.8205	-1.1162	Primary-small	Small	0	53	26
Up55	116.8232	-1.1166	Primary-small	Small	0	58	13
Up56	116.8236	-1.1157	Primary-small	Small	0	60	9
Up57	116.8245	-1.1148	Primary-small	Small	0	59	20
Up58	116.8245	-1.1144	Primary-small	Small	0	75	9
Up59	116.8254	-1.1135	Primary-small	Small	0	68	13
Up60	116.8245	-1.1166	Primary-small	Small	0	43	1
Up61	116.8218	-1.1184	Primary-small	Small	0	76	10
Up62	116.8245	-1.1207	Primary-small	Small	0	48	13
Up63	116.8254	-1.1212	Primary-small	Small	0	38	23
Up64	116.8245	-1.1234	Primary-small	Small	0	48	13
Up65	116.8169	-1.1153	Primary-small	Small	0	40	17
Up66	116.8155	-1.1153	Primary-small	Small	0	53	24
Up67	116.8146	-1.1144	Primary-small	Small	0	34	18
Up68	116.8142	-1.1162	Primary-small	Small	0	53	23
Up69	116.8160	-1.1180	Primary-small	Small	0	91	8

Appendix 1. Continued

Plot	Longitude	Latitude	Landscape	Mosaic	Fire	Altitude	Inclination
Up70	116.8151	-1.1180	Primary-small	Small	0	87	11
Up71	116.8160	-1.1203	Primary-small	Small	0	52	9
Up72	116.8142	-1.1207	Primary-small	Small	0	64	8
Up73	116.8191	-1.1203	Primary-small	Small	0	77	16
Up74	116.8164	-1.1248	Primary-small	Small	0	63	8
Up75	116.8151	-1.1243	Primary-small	Small	0	81	12
Up76	116.8205	-1.1248	Primary-small	Small	0	35	5
Up77	116.8146	-1.1279	Primary-small	Small	0	46	11
Up78	116.8160	-1.1049	Primary-small	Small	0	52	7
Up80	116.8160	-1.1054	Primary-small	Small	0	52	3
W001	116.9652	-0.9899	Twice-burnt	Burnt	100	41	5
W003	116.9454	-0.9890	Twice-burnt	Burnt	0	66	4
W007	116.9400	-0.9994	Twice-burnt	Burnt	90	38	6
W008	116.9732	-0.9931	Twice-burnt	Burnt	100	28	4
W201	116.9428	-0.9962	Twice-burnt	Burnt	100	71	14
W207	116.9426	-0.9937	Twice-burnt	Burnt	100	83	28
W232	116.9467	-0.9936	Twice-burnt	Burnt	70	48	28
W241	116.9638	-0.9931	Twice-burnt	Burnt	100	78	13
W242	116.9652	-0.9945	Twice-burnt	Burnt	100	33	19
W243	116.9643	-0.9954	Twice-burnt	Burnt	100	56	14
W244	116.9638	-0.9958	Twice-burnt	Burnt	100	68	8
W245	116.9656	-0.9967	Twice-burnt	Burnt	96	39	3
W246	116.9638	-0.9999	Twice-burnt	Burnt	0	45	8
W247	116.9616	-0.9940	Twice-burnt	Burnt	100	80	25
W248	116.9602	-0.9958	Twice-burnt	Burnt	100	53	12
W249	116.9580	-0.9922	Twice-burnt	Burnt	100	76	9
W250	116.9580	-0.9963	Twice-burnt	Burnt	0	32	0
W251	116.9571	-0.9940	Twice-burnt	Burnt	100	58	11
W252	116.9566	-0.9958	Twice-burnt	Burnt	100	46	17
W253	116.9557	-0.9940	Twice-burnt	Burnt	100	52	28
W254	116.9526	-0.9945	Twice-burnt	Burnt	100	57	16
W255	116.9521	-0.9972	Twice-burnt	Burnt	100	42	18
W256	116.9530	-0.9976	Twice-burnt	Burnt	100	35	10
W257	116.9539	-0.9985	Twice-burnt	Burnt	82	33	11
W258	116.9544	-0.9985	Twice-burnt	Burnt	74	41	22
W259	116.9553	-0.9994	Twice-burnt	Burnt	100	41	20
W260	116.9521	-0.9985	Twice-burnt	Burnt	100	33	7
W261	116.9503	-0.9958	Twice-burnt	Burnt	100	52	20
W262	116.9481	-0.9985	Twice-burnt	Burnt	100	48	9
W263	116.9476	-0.9994	Twice-burnt	Burnt	100	58	22
W264	116.9454	-0.9985	Twice-burnt	Burnt	58	37	0
W265	116.9535	-0.9909	Twice-burnt	Burnt	96	55	12
W266	116.9535	-0.9895	Twice-burnt	Burnt	100	59	15
W267	116.9544	-0.9886	Twice-burnt	Burnt	100	89	4
W268	116.9526	-0.9881	Twice-burnt	Burnt	100	64	16
W269	116.9508	-0.9899	Twice-burnt	Burnt	100	69	29
W270	116.9508	-0.9890	Twice-burnt	Burnt	100	58	4
W271	116.9485	-0.9899	Twice-burnt	Burnt	100	110	8
W272	116.9481	-0.9881	Twice-burnt	Burnt	100	71	22
W273	116.9485	-0.9931	Twice-burnt	Burnt	100	49	20
W274	116.9607	-0.9895	Twice-burnt	Burnt	100	63	13
W275	116.9616	-0.9904	Twice-burnt	Burnt	100	66	10
W276	116.9620	-0.9895	Twice-burnt	Burnt	100	65	12
W277	116.9409	-0.9886	Twice-burnt	Burnt	91	37	23