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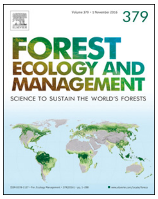

Distance to forest, mammal and bird dispersal drive natural regeneration on degraded tropical peatland

Lahiru S. Wijedasa[a,b,*], Ronald Vernimmen[c], Susan E. Page[d], Dedi Mulyadi[c], Samsul Bahri[e], Agusti Randi[f,g], Theodore A. Evans[h], Lasmito[c], Dolly Priatna[i,j], Rolf M. Jensen[i], Aljosja Hooijer[c]

[a] Department of Biological Sciences, 16, Science Drive 4, Singapore 117558, Singapore
[b] ConservationLinks Pvt Ltd., 100, Commonwealth Crescent, #08-80, Singapore 140100, Singapore
[c] Deltares, P.O. Box 177, Delft 2600 MH, The Netherlands
[d] Centre for Landscape and Climate Research, School of Geography, Geology and the Environment, University of Leicester, LE1 7RH, UK
[e] PT. Tri Pupa Jaya, Sin Mas Forestry, Palembang, Indonesia
[f] Faculty of Forestry, Bogor Agricultural University, Jalan Raya Dramaga, Kampus IPB Dramaga, Bogor 16680, Jawa Barat, Indonesia
[g] Indonesian Forum for Threatened Trees, Jalan Ir. H. Djuanda No. 18, Bogor, Jawa Barat, Indonesia
[h] School of Biological Sciences, University of Western Australia, 6009 Perth, Australia
[i] Asia Pulp and Paper Group, Sinar Mas Land Plaza, Jakarta 10350, Indonesia
[j] Study Program of Environment Management, Postgraduate Program, Pakuan University, Jl. Pakuan Kotak Pos 452, Bogor 16143, Indonesia

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ABSTRACT

Restoration of peat swamp forest (PSF) on degraded Southeast Asian peatlands could reduce global carbon emissions and biodiversity loss. However, multiple ecological barriers are believed to hinder natural regeneration of native trees on degraded peatland and make restoration expensive. We evaluated if natural PSF regeneration occurs and what factors may influence it on eight different land use and land cover (LULC) classes with different types of disturbance, including drainage and fire, in a retired *Acacia crassicarpa* Benth. (*Acacia*) plantation landscape. The study involved 42 plots inside five PSF LULCs – intact, logged, burnt (1997, 2015), remnant and 212 plots at distances up to 2 km from the PSF edge in three *Acacia* plantation LULCs – unharvested, harvested, and burnt. The number of species per plot were similar between intact PSF (25 ± 6 (SD) per 20 m × 10 m plot), logged forest (30 ± 6) and 1997 burnt forest (30 ± 13) but lower in 2015 burnt forest (11 ± 10) and remnant forest (18 ± 11). Regeneration away from the PSF across all degraded LULCs varied from fern dominated areas with no regeneration to clusters with high stem densities. The plantation LULCs, unharvested (94 species) and harvested *Acacia* (71 species), had similar overall species diversity after 3–4 years of regeneration to the intact and logged PSF (90 species). In unharvested *Acacia*, total species diversity, species per plot and stem density decreased with distance from forest edge (1–300 m – 87 species; 9 ± 6 (SD) species per 20 m × 10 m plot; 1,056 stems/ha; 301–500 m – 33; 5 ± 2; 511 and > 500 m – 38; 6 ± 3; 683). In harvested *Acacia*, there was low plot species diversity irrespective of distance from the forest (1–300 m – 51; 4 ± 2; 578; 301–500 m – 17; 4 ± 2; 1,100; > 500 m – 48; 4 ± 2; 780). Factors which may influence regeneration differed between different LULCs, but there was a clear influence of distance from forest edge and dispersal mechanism – i.e. whether a tree was bird or mammal dispersed and the interaction between these two factors. While our study suggests that if not further disturbed by logging, drainage and/or fire, degraded PSF could regenerate naturally to a similar species diversity as intact PSF, the lower levels of natural regeneration further away from the forest may warrant selective planting of species which do not disperse over long distances. More study is needed on the factors facilitating natural regeneration, whether it leads to restoration of PSF ecosystem functioning and the role of *Acacia* as a potential regeneration catalyst.

1. Introduction

Tropical peat swamp forests (PSFs) exist in the equatorial zone where rainfall is consistently high and the land is flat. The resulting slow drainage promotes waterlogged, anaerobic conditions that have allowed swamps to form and the forest litter to be preserved as peat

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* Corresponding author at: ConservationLinks Pvt Ltd., 100, Commonwealth Crescent, #08-80, Singapore 140100, Singapore.
E-mail address: lahirux@gmail.com (L.S. Wijedasa).

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(Anderson, 1964). Despite the stressful environmental conditions of anoxia, acidity and low nutrient availability, the PSFs of Southeast Asia have a relatively high tree species diversity with 1300–1500 plant species (Posa et al., 2011; Giesen et al., 2018). There is typically a zonation of plant communities across the peat dome with taller marginal forest replaced by increasingly smaller stature, lower biomass forest towards the dome centre (Anderson, 1983; Page et al., 1999). On the forest floor, variations in microtopography produce a hummock and hollow system which results in unique plant species distributions on the local scale (Lampela et al., 2016). The naturally high water tables have led to the accumulation of carbon both in above ground forest vegetation and below ground in thick peat layers that, across the tropics, store the equivalent of 10% of total atmospheric carbon (70–130 Gt CO_2 equivalent) (Dargie et al., 2017).

Degradation and agricultural conversion of Southeast Asian PSF releases stored carbon into the atmosphere. Conversion involves: (i) clearing natural vegetation, often with fire, which stops the formation of new peat; (ii) digging of drainage canals, to lower the water table and dry the peat; and (iii) planting of crops. The carbon is released by increased decomposition of the drained peat by microorganisms and by anthropogenic fires that are usually set to clear land for agriculture. Fires set to clear a specific area often spread to other drained areas leading to large burned areas. Resulting emissions are 40–73 t of CO_2 per hectare per year from peat oxidation under agricultural land uses (Drösler et al., 2014) and 0.23–2.57 Gt CO_2 per fire event, particularly during dry El-Niño years. The impact of fire on PSF will depend upon both fire severity and frequency; secondary succession back to forest may follow a low-intensity fire but with increased intensity and frequency, the numbers of regenerating tree species and their density are greatly reduced and at the highest levels of disturbance succession back to forest is inhibited and the vegetation is dominated by ferns and scrub (Page et al., 2009).

By 2015, an estimated 25–45% of the PSF in Southeast Asia had been deforested, drained and converted to oil palm, *Acacia crassicarpa* Benth. for paper pulp, and multiple crops in small holder agriculture, while 18–25% was covered by unmanaged fern and scrub vegetation created by deforestation and regular fires (Miettinen et al., 2017; Wijedasa et al., 2018). Of the remaining PSF in 2010, only 55% was inside protected areas, although even here PSF continues to be lost due to illegal logging, land encroachment and fires spreading in from the surrounding landscape (Miettinen et al., 2013; Wijedasa et al., 2018).

Restoration of ecosystem functioning (involving rewetting and reforesting) of degraded tropical peatlands in Southeast Asia aims to reestablish a self-regulating hydrological system that could stop the ongoing release of carbon from peat oxidation and fires and protect biodiversity (Hooijer et al., 2010; Evans et al., 2017; Wijedasa et al., 2018). In response to extensive forest and peatland fires in 2015, Indonesia committed to restoring 2 million hectares of peatland (Republic of Indonesia, 2016; Wijedasa et al., 2016). Rewetting and revegetation are key to these efforts but previous restoration tree planting attempts have (i) met with limited, small scale, short-term success with only a few tree species able to survive the altered environmental conditions of degraded peatlands (Page et al., 2009; Graham et al., 2017), and (ii) been expensive, with estimated costs of USD 235–1,575 per hectare based on planting density, labour costs and canal blocking for rewetting (Saito et al., 2005; Graham et al., 2017; Lampela et al., 2017; Hansson and Dargusch, 2018).

Cheaper methods are essential if PSF restoration is to be successful at large scale (Holl et al., 2017). The cheapest possible method is natural forest regeneration arising from ecological succession (Zahawi et al., 2013). Natural regeneration is the recovery of the structure, function, and composition of the pre-disturbance forest ecosystem, without human influence (Chazdon and Guariguata, 2016 and references therein). For this to happen, trees need to survive and vegetatively propagate or seeds must reach a degraded site, germinate, survive and grow. Known barriers that limit natural regeneration include: size of the seed bank in the soil; seed dispersal methods; seed germination and survival rates; soil moisture; soil nutrients; competition from the existing plant community; and repeated fires (Graham et al., 2017).

Unlike other Southeast Asian lowland forest types which have low levels of fruiting until a mass-fruiting event, the tree community in PSF produces a steady supply of fruits, reflected in almost double the densities of orangutans in PSF compared to other lowland forest (Russon et al., 2001). The regular fruiting might be an adaptation to the absence of a seed bank in the acidic, waterlogged peat soil (Graham et al., 2017), and yet despite good fruit availability, previous efforts to facilitate forest recovery have met with limited success (Cannon et al., 2007; Harrison et al., 2010). In fragmented and degraded PSF landscapes, many key dispersers (i.e. birds and mammals) avoid open inhospitable vegetation and thus have limited capacity to exploit the constant fruit supply provided by the forest and to disperse seeds into non-forest land covers (Page et al., 2009; Graham and Page, 2012; Blackham et al., 2014; Graham et al., 2017).

Furthermore, seedling establishment in degraded/converted sites may be limited by dense ground cover of ferns and sedges, regular fires, seed predation, and changes in peat soil physical and chemical characteristics, microbial communities and hydrology (Holl et al., 2000; Page et al., 2009; Banjarbaru Forestry Research Unit et al., 2014; Blackham and Corlett, 2015; Graham et al., 2017; Lampela et al., 2018). The altered hydrology of disturbed peatlands results in particularly challenging conditions, with water shortages in the dry season and excess water in the wet season, both of which can limit seedling survival (Wösten et al., 2006; Banjarbaru Forestry Research Unit et al., 2014). For example, in the Berbak peatland, Sumatra, low-diversity fern-, sedge- and shrub-dominated vegetation occurred in areas experiencing regular episodes of drought and flooding, whereas regenerating, small-statured secondary forest was restricted to areas with more intact hydrology (Van Eijk and Leenman, 2004; Wösten et al., 2006; Hoscilo et al., 2011).

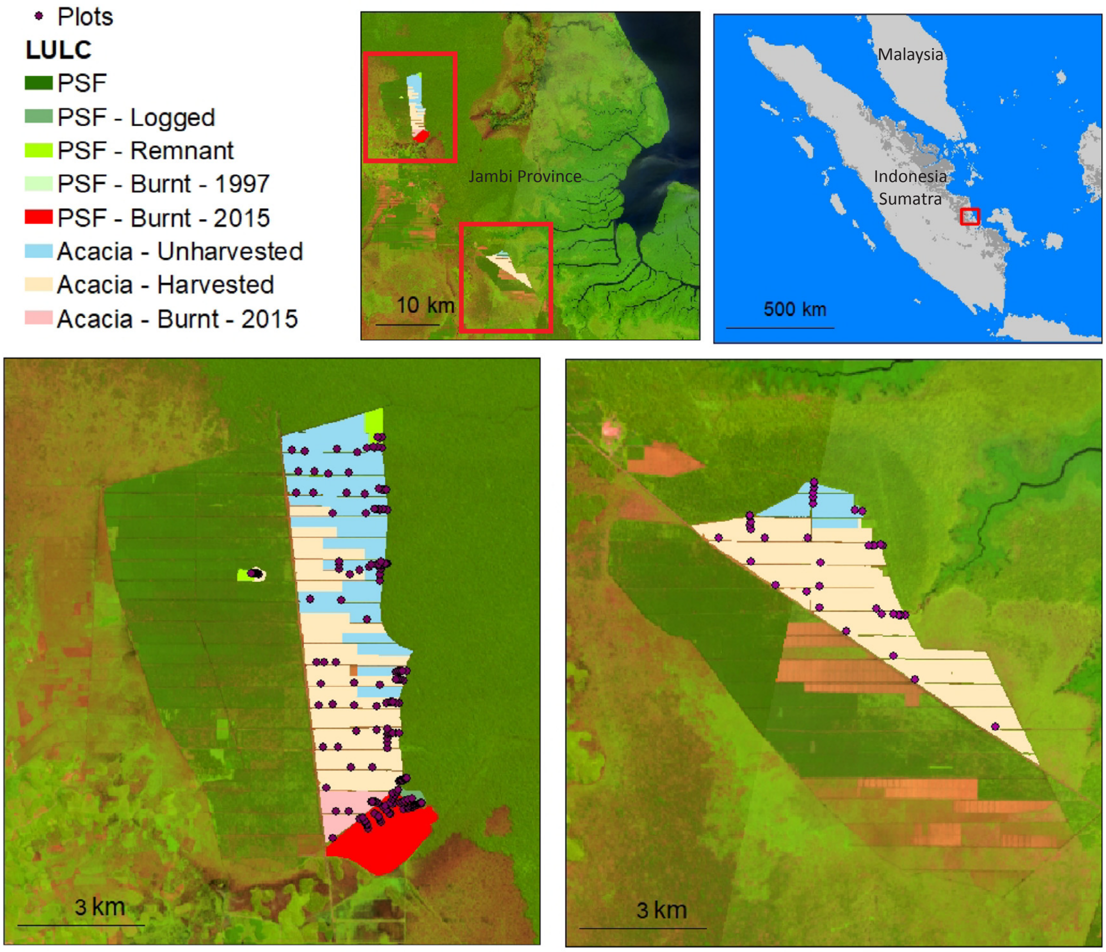
While various limitations to natural regeneration of PSF have been previously identified, we observed PSF recovery occurring across different land uses and land covers (LULCs) in a retired pulp wood landscape in South Sumatra, Indonesia. The aim of this study is to: 1) determine if natural regeneration is occurring on different LULCs with different disturbance histories, and 2) if natural regeneration is found, to understand the factors influencing this process.

2. Materials and methods

2.1. Study region

Sampling was carried out from August to December 2018 in eight different LULCs (Fig. 1 & Table 1) in a retired *Acacia crassicarpa* Benth. (hereafter *Acacia*) pulp wood concession located on peatland in the province of South Sumatra, Indonesia. To protect the Berbak-Sembilang National Park from degradation due to drainage and fires, the company managing the concession decided in 2015 to retire the east side of their plantation to create a reforested and rewetted plantation buffer zone, 2 to 3 km wide that was adjacent to the National Park and the conservation forest.

The retired area consists of two parts that are both adjacent to PSF in the National Park (Fig. 1). The intact PSF (PSF – Intact) adjacent to the area in the north has not been logged and is at a lower elevation than the drained plantation and so is not affected by drainage, while the PSF adjacent to the area in the south has naturally regenerated since an El-Niño related fire in 1997 (PSF – Burnt – 1997). Besides planted *Acacia*, the concession includes patches of remnant forest (PSF – Remnant) surrounded by drained plantation areas. The PSF in the lower part of the North area had been illegally logged (PSF – Logged) prior to the 2015 fire event. Fire in 2015 burnt down some of the logged forest (PSF – Burnt – 2015) and an adjacent area of *Acacia* plantation (Acacia – Burnt – 2015). The *Acacia* crop had been planted for the first time in the



Acacia - Unharvested >300m from PSF - Intact | Acacia - Unharvested 0-300m from PSF - Intact | PSF - Intact

Acacia - Harvested >300m from PSF - Intact | Acacia - Harvested 0-300m from PSF - Intact | PSF – Burnt - 2015

Fig. 1. Location of the study area in Sumatra with land use and land cover (LULC) classes and sampling plots marked out. The photos illustrate the four major LULCs studied – PSF – Intact, PSF – Burnt, and two distances (< 300 m and > 300 m) away from PSF – Intact for Acacia – Unharvested and Acacia – Harvested.

period 2012–2014 following the clearance of PSF and digging of 10 m wide drainage canals with a 500 m spacing and west to east orientation. In addition, a perimeter canal separates the forest from the plantation. Following retirement of the site in 2015, compacted peat dams were constructed in the canals at a 500 m spacing to raise water levels and rewet the site. While dams were not built in the perimeter canal, the canals were silted up with only wet peat with no standing water in the dry season. The plantation area consists of unharvested *Acacia* (*Acacia* – Unharvested) and areas harvested (*Acacia* – Harvested) in 2015 and areas that burnt in 2015 (*Acacia* – Burnt – 2015) (Fig. 1, Table 1).

Table 1
Different LULCs types in the restoration site. Fig. 1 shows the locations of these plots. *Acacia* = *Acacia crassicarpa*; PSF = Peat swamp forest.

LULC	Land use history
PSF – Intact	Peat swamp forest contiguous with the larger PSF extent in the Berbak-Sembilang National Park. The forest has not been logged previously. The forest is also at a lower elevation than the drained plantation, with water flowing into the forest and is thus not affected by drainage. The intact forest is a mix of small treelets, pandans and large trees up to 35 m tall. The microtopography varies from hummocks and hollows with variations in wet and dry areas.
PSF – Logged	Peat swamp forest logged illegally until the 2015 fire event. The logged forest has the same species composition and is structurally similar to the intact forest site, but with the removal of selected species of large trees due to illegal logging. Trees were removed using wooden railways and not canals. The species removed are mostly *Shorea* and *Madhuca*. The smaller treelets and *Pandan* composition is the same as the intact forest.
PSF – Burnt – 1997	Undisturbed peat swamp forest that burnt a single time in the 1997 fire event. The forest was intact prior to burning once in 1997. Vegetation has regenerated over 21 years since the fire. The overall species composition of the forest is similar to intact forest. However, the vegetation structure is dominated by smaller trees with larger trees mostly missing.
PSF – Burnt – 2015	Peat swamp forest burnt a single time in the 2015 fire event. This LULC is a mosaic of clusters of forest regeneration and fern/sedge dominated open areas. Some of the trees in the clusters consist of remnant trees that have survived the fires. The forest was similar to the logged forest prior to the 2015 fires. The site has only burnt once.
PSF – Remnant	Isolated fragments of peat swamp forest surrounded by drainage canals and plantation. Remnant forest has the same species composition as intact and logged forest. However, the larger trees have been removed or fallen over due to drainage canals and *Acacia* planted surrounding the forest.
Acacia – Unharvested	*Accacia crassicarpa* plantation planted for the first time following clearance of intact PSF in 2012 and 2013. The trees in this area are 12–15 m tall and were not harvested prior to retirement of this site. Excavators are used in clearing the forest and to flatten the microtopography prior to planting of *Acacia*, but slight changes in microtopography have developed since the original planting.
Acacia – Harvested	Harvested *Acacia crassicarpa* area. The *Acacia* planted in 2012 following clearance of PSF, was harvested in 2015. Trees are less than 8 m tall. Harvesting is by clear felling and removal using excavators. This results in clearance of all vegetation, including natural regeneration and flattening of any slight changes in microtopography that may have formed after initial planting.
Acacia – Burnt – 2015	Unharvested *Acacia crassicarpa* areas planted in 2012 that burnt once in the 2015 fire event. The remaining trees were not harvested after the fire. Some remnant *Acacia* trees survived the fires and are 12–15 m tall. Regeneration of *Acacia* dominates this site. Microtopography is similar to other unharvested *Acacia sites.*

Acacia is a nitrogen-fixing leguminous tree native to coastal and seasonally flooded riverine areas in Australia and eastern Indonesia (Orwa et al., 2009). Growing this species as a plantation crop on peat requires drainage to lower the water table to at least 70 cm. Harvesting occurs four years after planting and, within the first two years of crop growth, the standard protocol is to manually cut down all regenerating non-*Acacia* species and naturally seeded *Acacia*. Any regeneration of native PSF tree species that we observed during our 2018 survey of the study site could, therefore, be dated to two years post planting of the crop*,* i.e. observed regeneration was between 3 and 4 years old.

2.2. Experimental design

We sampled 254 plots of 20 m × 10 m in eight different LULC classes inside the PSF and at varying distances (up to 2 km; Dist_Forest) away from it (Fig. 1**,** Table 1). Plot locations were selected systematically at different distances away from the perimeter canal separating the forest from the plantation; plots were spaced at least 50 m apart. The orientation of plots was either with the longer edge west to east or north to south, following the alignment of the drainage canal network (Fig. 1). The location of each plot was recorded using a Garmin 65x GPS and used to calculate Dist_Forest to intact or logged PSF of each plot using the Near tool in ArcGIS version 9.2 using the GPS location and the LULC map (Fig. 1).

Within each plot the species and diameter at breast height (DBH) of all trees above 2 cm diameter were recorded. Detailed photographs for taxonomic identification of each species were taken and used to prepare a photographic herbarium for the site. Herbarium specimens were taken and compared to those in Herbarium Bogoriense in Bogor, Java.

To compare between plots, for each plot, we recorded the number of species (NumSpecies), trees per hectare (CountperHa), average DBH of native trees (DBH_Native) and *Acacia* (DBH_Acacia), basal area per hectare of native trees (BA_m2Ha_Native) and of *Acacia* (BA_m2Ha_Acacia). A native tree is defined as one found naturally in PSF and not introduced to the landscape by humans. In the case of trees with multiple stems, diameter of individual stems was used for calculation of basal area which was then summed to give the basal area of the specific tree.

To determine the effect of seed dispersal agents (i.e. whether mammal, bird, water or wind dispersed) on regeneration, we determined the dispersal mechanism for each species from literature and expert knowledge, and then calculated the percentage of trees within each plot for each dispersal category (%Mammal, %Bird, % Wind, %Water). In addition, the percentage of trees which were *Acacia* (%Acacia) was also calculated.

In the plots, we mapped the number of *Pandanus andersonii* and *Hanguana* sp. per hectare (PHperHa) when encountered as these often stem-less species are considered an indicator of good quality PSF or natural regeneration in an advanced stage (personal observation by the first and sixth author in intact PSF throughout Southeast Asia).

2.3. Data analysis

All analyses were carried out in Rstudio v. 1.1.463 statistical package (R Core Team, 2019). Data exploration, and Generalized linear models (GLMs) were carried out and reported based on the outline of Zuur et al. (Zuur et al., 2010; Zuur and Ieno, 2016).

Relationships between variables (Table S1) within specific LULCs and between different LULCs were explored by calculating Pearson correlations (rcorr; cran.r-project.org/web/packages/Hmisc) followed by visualization using a correlation matrix and hierarchical clustering (corrplot; cran.r-project.org/web/packages/corrplot). Highly correlated pairs of variables (≥ ± 0.5) were visually compared using the pairs function in the base R package. When the correlated variables had the same effect on all other variables only one was used in further analyses. However, in the case of percentage of trees with seeds distributed by mammals and birds we found that the correlation differed between different land covers, so we retained these two variables for further analyses.

To visualize relationships between plots and potential factors that may drive differences within and between LULC classes, we carried out a principal component analysis (PCA) and plotted the results as bi-plots (ggbiplot; cran.r-project.org/web/packages/ggbiplot).

The effect of variables and interactions between variables that influenced natural regeneration was analyzed using GLMs with a logit link and Poisson error structure. Response variables were NumSpecies and CountperHa. We used only second-order interactions in the GLMs. The maximal models were created, then stepwise model reduction was carried out using the Akaike Information Criterion (AIC) (Zhang, 2016) in the MASS package (stepAIC; cran.r-project.org/web/packages/

Table 2

Plot statistics on number of native species, number of native trees per hectare (ha) and basal area of native species in different LULC. Also provided the mean number of *Acacia* as well as *Pandanus andersonii* and *Hanguana sp.* (PandHan).

		No. of plots	No. of native species/plot				Native trees/ha				Basal area native trees (m^2/ha)	*Acacia* trees/ha	PandHan trees/ha
LULC	Distance from PSF	n	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	Mean	Mean
PSF – Intact	inside	20	25	6	10	34	2205	988	500	4150	30.2	3	753
PSF – Logged	inside	11	30	6	18	41	3105	610	2400	4450	26.5	0	209
PSF – Remnant	inside	11	18	11	3	37	2168	1,827	150	5800	14.5	0	832
PSF – Burnt – 1997	inside	3	30	13	21	44	2733	1,068	1950	3950	29.9	0	783
PSF – Burnt – 2015	1–300 m	26	10	8	1	26	775	756	0	2600	3.7	10	12
	301–500 m	6	18	15	2	36	2217	1,918	150	4300	10.4	17	8
	> 500 m	12	12	11	1	30	1338	1,309	0	3650	8.3	79	25
	All Distances	44	11	10	1	36	1125	1,205	0	4350	5.9	30	15
Acacia – Unharvested	1–300 m	50	9	6	1	30	1056	673	100	2750	4.4	519	18
	301–500 m	9	6	2	3	9	683	252	250	1050	2.1	583	6
	> 500 m	18	5	3	1	10	511	472	50	2000	2.0	836	3
	All Distances	77	8	5	1	30	885	638	50	2750	3.5	601	13
Acacia – Harvested	1–300 m	45	4	2	1	10	578	648	0	3950	2	427	1
	301–500 m	5	4	2	1	6	1100	1,577	50	3850	2	1,510	0
	> 500 m	29	4	2	1	7	798	905	0	3400	4	816	0
	All Distances	79	4	2	1	10	692	824	0	3950	3	637	0
Acacia – Burnt – 2015	> 500 m	9	2	1	1	3	83	90	0	250	0.21	622	0

MASS). Of the 254 LULCs studied (Table 2), only PSF – burnt – 2015 ($n = 44$), *Acacia* – unharvested ($n = 77$) and *Acacia* – harvested ($n = 79$) had sufficiently large areas to have enough independent replicates (≥30, Table 2) at varying distances away from the forest to model effects on natural regeneration.

3. Results

3.1. Overview of natural regeneration

We recorded 8313 trees representing 154 species in the 254 plots (Tables 2 and S2). Natural regeneration was observed with high overall species diversity (62 – 106; Table S2) in all LULC classes except the unharvested burnt *Acacia* LULC class (6 species).

In the PSF – Burnt – 2015, species regeneration was mostly restricted to species rich (11 ± 10 species), high density patches (1125 trees/ha) occurring at all distances away from the PSF – Intact with these patches surrounded by tree-less fern-dominated vegetation (Table 2 and Fig. 2A). The three plots established in the PSF – Burnt – 1997 had higher numbers of species and stem density (30 ± 13 species, 2,733 trees/ha) to those in PSF – Intact (25 ± 6 species, 2,205 trees/ha) (Table 1).

Within the *Acacia* LULC classes, the highest total and average species diversity per plot (87 total species; 9 ± 6 (SD) species per plot; 1,056 stems/ha) was in the first 300 m from PSF – Intact in the *Acacia* – Unharvested (Table 2, S3 and Fig. 2**C**). In *Acacia* – Unharvested, beyond the first 300 m from the PSF – Intact, the species diversity decreased with increasing distance (301–500 m — 33; 5 ± 2; 511 and > 500 m — 38; 6 ± 3; 683). In *Acacia* – Harvested, there was low plot species diversity but similar stem numbers (1–300 m — 51; 4 ± 2; 578; 301–500 m — 17; 4 ± 2; 1100; > 500 m — 48; 4 ± 2; 780) irrespective of distance from the PSF – Intact (Table 2, S3 and Fig. 2C-D). In both of these *Acacia* land covers, natural regeneration occurred in patches spanning a few square meters. These patches had high species diversity in *Acacia* – Unharvested within 300 m of the PSF – Intact, with taller, more established young trees similar in density to PSF – Intact, but at greater distance from the PSF – Intact these patches had fewer native trees and were in otherwise tree-less, dense fern-dominated vegetation (Fig. 1B & 2B-D).

Species richness and number of trees in the PSF – Intact, PSF – Logged and PSF – Remnant patches were similar, with 18–30 species and 2168–3105 trees/ha (Table 2), but overall structure varied with the loss of big trees in the latter two LULCs as illustrated by the lower basal area (Table 2).

3.2. Relationships between variables and lulcs

Plots corresponding to each LULC class were clustered in the PCA, with overlap between clusters (Fig. 3A). The forest classes that had regenerated following a fire in 1997 clustered with PSF – Intact, PSF – Logged and PSF – Remnant. The other LULC classes, namely *Acacia* – Unharvested, *Acacia* – Harvested, *Acacia* – Burnt – 2015 and PSF – Burnt – 2015, partially overlapped with each other. Dist_Forest did not have an effect on the distribution of plots within each LULC cluster (Fig. 3A). However, a difference in clustering was observed when displaying plots based on the percentage of species with different seed dispersal mechanisms (Fig. 3B-E), with PSF – Intact, PSF – Logged and PSF – Remnant plots containing more trees of species that are dispersed by mammals, birds and water compared with other LULCs (Fig. 3B-E). In both *Acacia* – Unharvested and *Acacia* – Harvested there were two groups of plots – one dominated by mammal and bird dispersed species and the other by species that are wind dispersed, neither of which were affected by Dist_Forest (Fig. 3B-E).

The Pearson correlations and hierarchical clusters of variables studied (e.g. method of dispersal) had different effects on each other and on natural regeneration in the different LULCs (Fig. 4A-D). When we considered the effect of different factors and interactions of factors on natural regeneration using the GLMs we found they were significant when all plots irrespective of LULC were combined and in the PSF – Burnt – 2015. However, fewer factors and interactions were significant ($p > 0.05$) in *Acacia* – Harvested and *Acacia* – Unharvested (Table S4**)**.

Among the different seed dispersal methods, %Mammal, %Bird and %Water all show a decrease with increasing Dist_Forest while %Wind increases with Dist_Forest across all LULC classes, except for the 2015 burnt forest (Fig. 5A-C). In *Acacia* –Unharvested, %Mammal and %Bird decrease faster away from the forest than in *Acacia* – Harvested, while %Wind increases slightly faster with increasing Dist_Forest in *Acacia* – Unharvested compared to *Acacia* – Harvested. In the PSF – Burnt – 2015, natural regeneration occurs in high density patches irrespective of distance away from the PSF – Intact.

Pandanus and *Hanguana* densities in PSF – Intact, PSF – Logged and PSF –Remnant were, with 209 – 832 plants/ha, much higher than in *Acacia* – Unharvested and PSF – Burnt – 2015 at 13 and 15 trees/ha, averaged over all distances, respectively (Table 2).

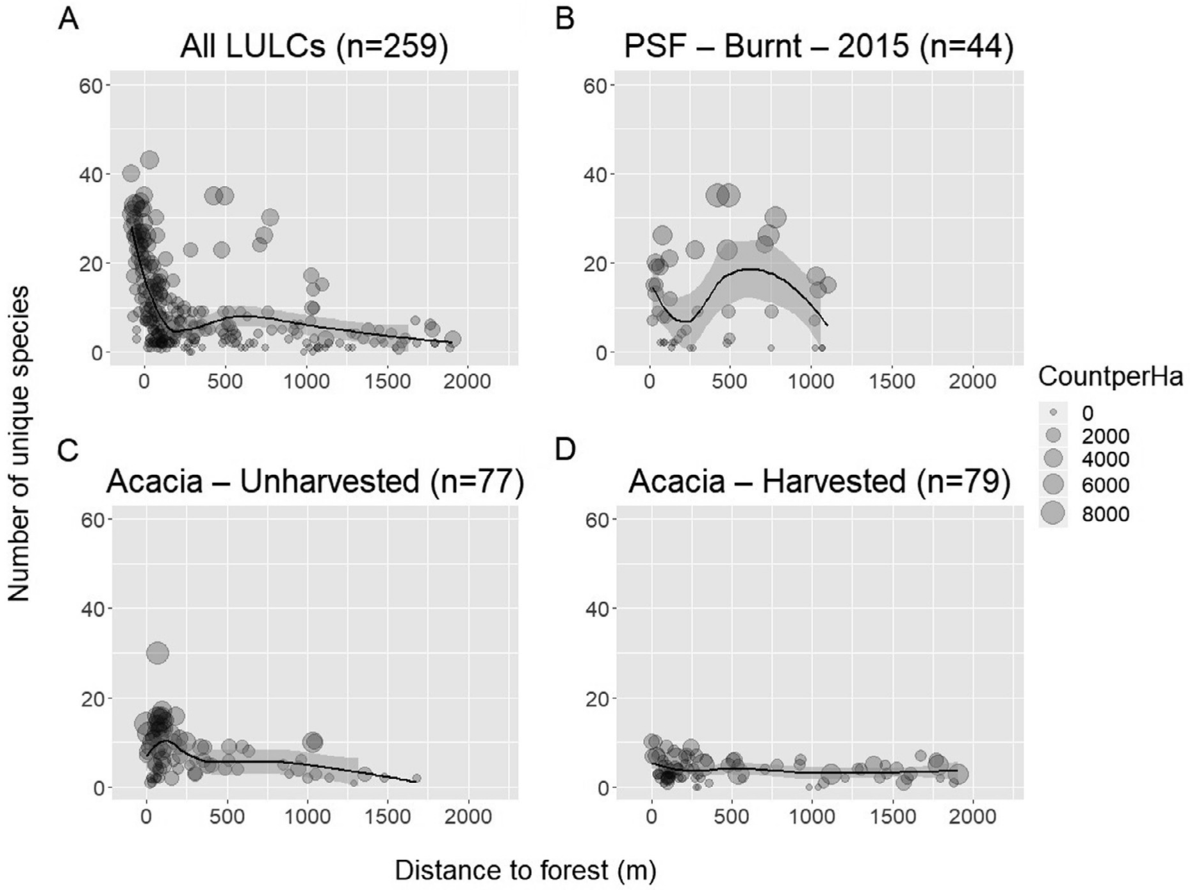


Fig. 2. Number of species found in different LULCs at different distances away from the forest. The bubble sizes are the number of non-*Acacia* trees per hectare (see graphical legend). The curves in each plot are locally weighted regressions with 95% confidence intervals fit using the data. The data points to the left of 0 m in panel (A) shows the plots inside the forest.

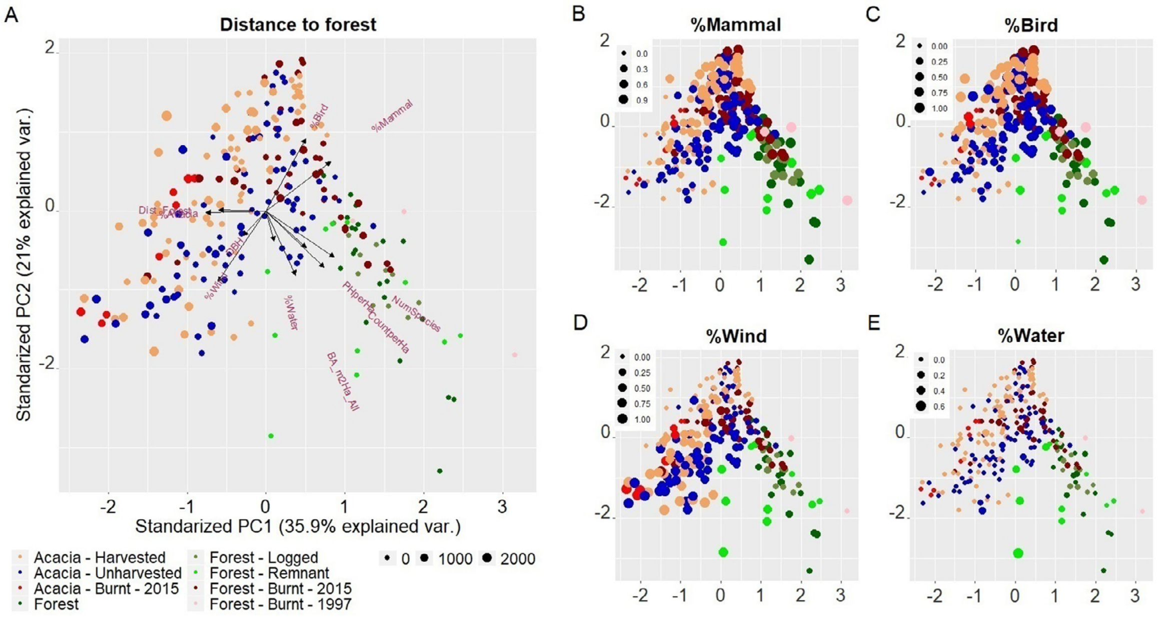


Fig. 3. Principal Component Analysis (PCA) of (A) all plots and (B-E) percentage of trees in each dispersal method (i.e. mammal, bird, wind and water) with increasing point sizes reflecting increasing distance to forest or increasing % of stems belonging to each dispersal type. The legends in the smaller pictures reflect the percentage of stems in each plot that belong that particular dispersal type. The axes of all the plots are the same.

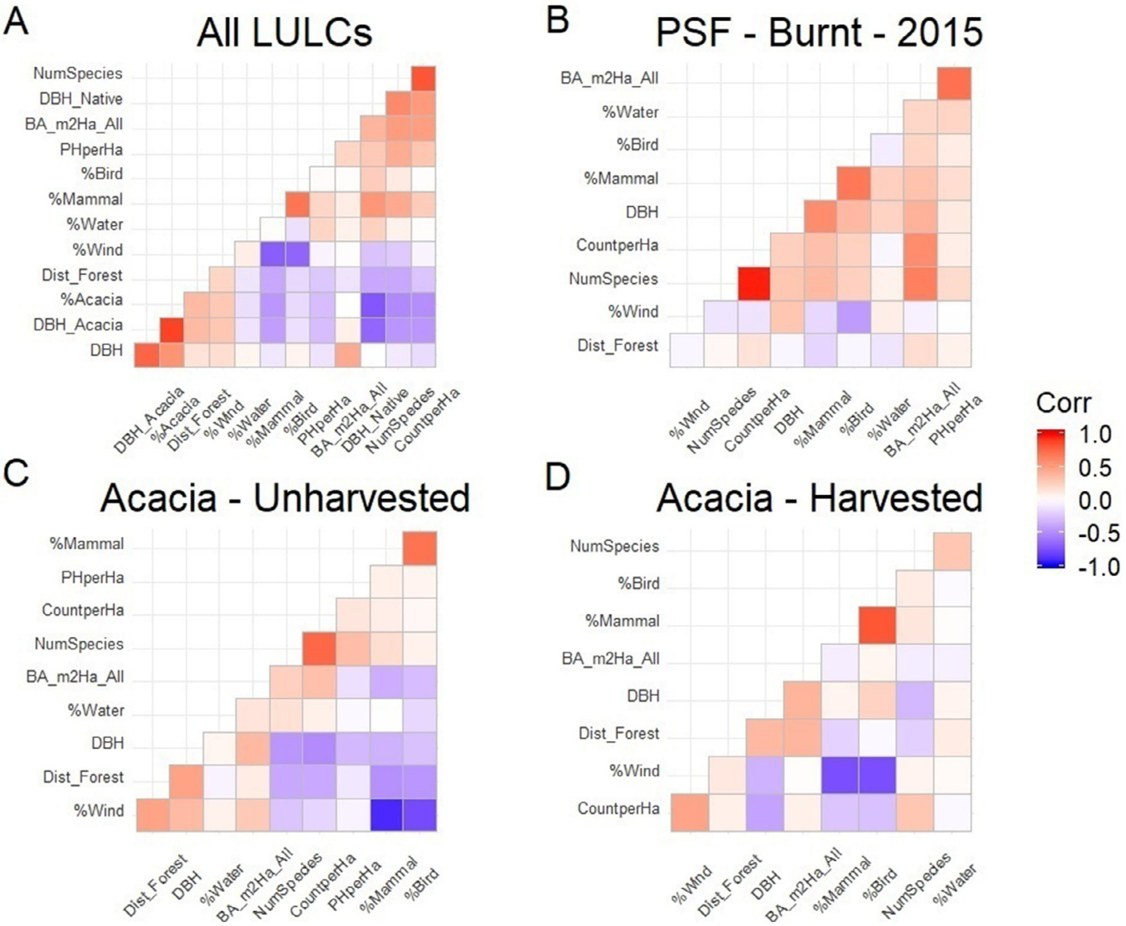


Fig. 4. Correlogram of variables that may affect regeneration. Variables are hierarchically clustered based on correlation coefficients. Autocorrelations are not displayed in the figure.

3.3. *Acacia regeneration and natural regeneration*

In both *Acacia* – Unharvested and *Acacia* – Harvested the %Acacia decreases with increasing %Mammal and %Bird (i.e. natural regeneration) dispersed trees (Fig. 5A-D). Only 3 *Acacia* trees were present in PSF – Intact and *Acacia* was absent in PSF – Logged and PSF – Remnant.

4. Discussion

We found a range of PSF species regenerating on degraded peatlands under different land use histories after pulp wood plantations were retired and partially rewetted (Table 2 & S2, Figs. 1 and 2). The regeneration in the logged and remnant PSF was expected and is similar to that documented in the Giam Siak Kecil peatland in Riau where logged and disturbed forests were found to regenerate over 5–10 years (Gunawan et al., 2012). Regeneration in harvested and unharvested *Acacia* on peatland has not been previously described, but there have been a few previous studies of regeneration in heavily degraded peatland LULCs (deforested, drained, burnt) in Central Kalimantan that had undergone repeated fires and demonstrated limited capacity for unassisted PSF recovery (Graham and Page, 2012; Blackham et al., 2014). Of particular interest in our study is the high species richness and number of trees in tree patches at all distances from the PSF edge in the 2015 burnt forest (up to 36 species), in the 1997 burnt forest (30 ± 13 species, 2733 trees/ha) and in plots within 300 m of the PSF in the unharvested *Acacia* areas (9 ± 6 species) (Table 2). The high numbers is despite the perimeter canal not being dammed, which may have been a barrier to mammal dispersal during the wet season. In the PSF – Burnt – 2015 LULC in particular the patches were a combination of a few remnant trees from the PSF prior to the fire and new recruitment. Hornbills were observed within these patches at all distances, suggesting the role of remnant trees as perches for large seed dispersers that contribute to patch species richness and stem density. These results provide some encouragement that the restoration of degraded peatlands can occur by natural regeneration given time and an appropriate environmental setting. Whilst proximity to PSF was associated with the highest tree species richness and density, the plots located in unharvested *Acacia* more than 300 m away from the forest and in harvested *Acacia* at all distances away from the forest still allowed for the establishment of a number of native species, albeit at a lower species richness (4–6 species per plot; Table 2). In the 2015 burnt forest, there were remnant islands of high tree species diversity, which likely also facilitated regeneration. These results suggest that suitable conditions enabling natural regeneration are present across all the LULCs at this site and that regeneration might be limited mainly by the rate of seed dispersal. Nevertheless, the wider range of biotic and abiotic factors, including *inter alia* competition with ground cover vegetation, presence of mycorrhizal associates, water and nutrient availability, and seasonal fluctuations in groundwater levels that might be influencing the nature and success of natural regeneration do need further study.

4.1. *Factors that affect natural regeneration*

Our results showing a decline in mammal- and bird-dispersal at distances greater than 300 m away from intact forests in all LULC classes suggests that regeneration is likely to be constrained by dispersal limitation (Table 2 and S4). Similar results were found in burnt

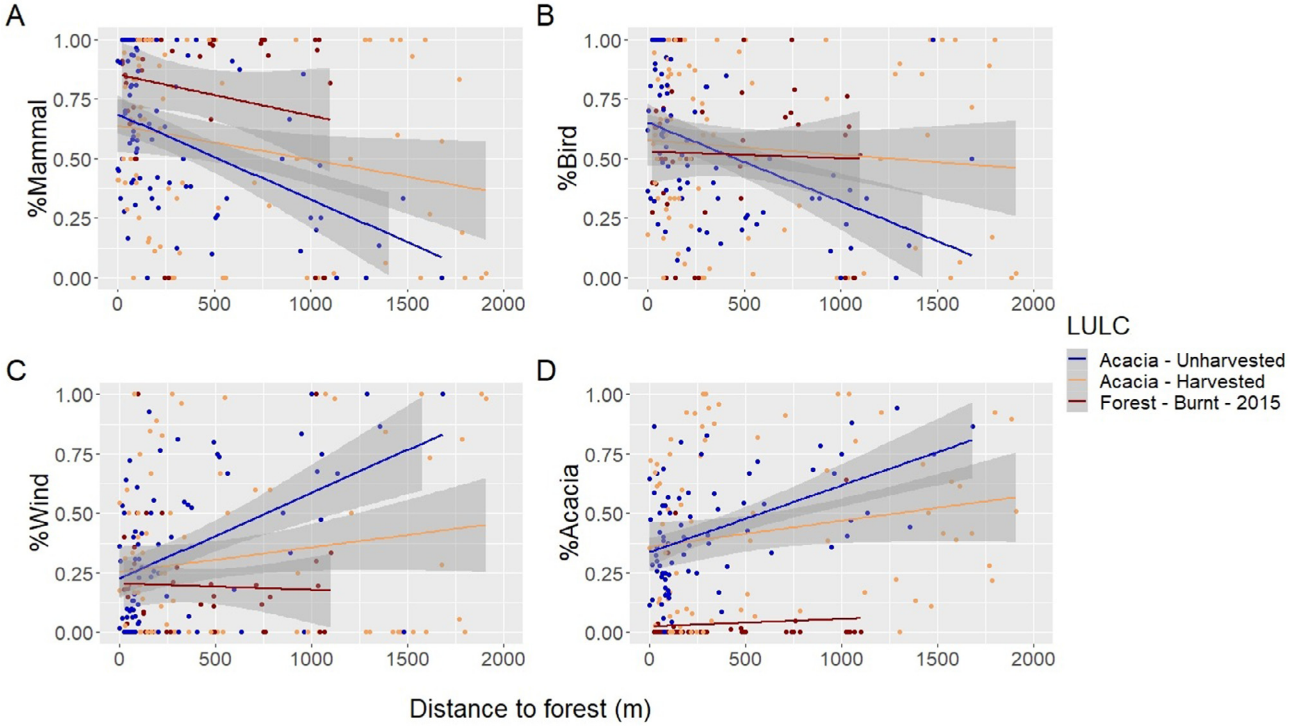


Fig. 5. Proportion of mammal, bird, wind dispersal and *Acacia* versus distance from the forest. Each point represents a plot; lines show linear regressions with 95% confidence intervals. Mammal and bird dispersal dominate near the forest but shows a decreasing trend with distance away from forest while the opposite is true for wind dispersed species. Note the percentage of *Acacia* increases with distance from the forest because of the less natural regeneration.

peatlands in Kalimantan, where forest seed dispersal agents did not venture into open areas which were instead dominated by a few dispersal agents characteristic of open habitats; this barrier to dispersal was reflected in the species composition of the seed rain which was dominated by seeds of pioneer rather than closed forest species (Graham and Page, 2012; Blackham et al., 2014). On the other hand, a higher proportion of wind dispersed plants is present in harvested *Acacia* at all distances and in unharvested *Acacia* more than 300 m from the forest. It would be interesting to see whether and how this pattern changes over time as species rich regeneration within 300 m from the forest starts to mature. In the 2015 burnt forest, the absence of a pattern of decreasing species diversity away from the forest could be attributed to some remnant large trees that survived the fire and to the presence of large, strong flying dispersers such as hornbills, which were observed up to 2 km from the intact PSF during the study.

4.2. Restoration through applied nucleation

The islands of high diversity forest remaining in the 2015 burnt forest are likely to be conducive to promoting both animal dispersal and seed rain and the relatively species diverse regeneration patches that we observed across other LULCs may fulfil a similar role. These results suggest that natural forest recovery could be replicated by planting tree islands at increasing distance from the forest edge, thereby imitating the spatial dynamics of natural nucleation that occur during primary succession (Yarranton and Morrison, 1974). This approach has previously been recommended by (Holl et al., 2017) for restoring large areas of tropical forest in Costa Rica.

The low species density and number of trees beyond 300 m in unharvested *Acacia* and at all distances in harvested areas is similar to the limited forest regeneration reported for the extensive degraded, burnt peatlands in Central Kalimantan (Graham and Page, 2012; Blackham et al., 2014). This again suggests a need to enhance regeneration by establishing tree islands at greater distances from the forest edge. Given the costs involved, assisted regeneration does, however, need careful planning, and should be based on vegetation surveys to determine if natural regeneration is already occurring alongside an assessment of whether the site conditions (biotic and abiotic) are suitable for specific species (Graham et al., 2017). For instance, based on our study, of the 154 native species (i.e. excluding *Acacia*), 111 species were found at distances beyond 300 m from the forest, of which 3 species (*Alstonia angustifolia*, *Macaranga pruinosa*, and *Timonius flavescens*) were found in more than 24 of the 109 plots located over 300 m from the forest (Table S5). These species might naturally reach a restoration site and may not need to be planted. However, in heavily degraded sites far from intact forest, such as sites repeatedly burnt or with a long history of agriculture and where, for example, the peat nutrient status and hydrological regime may be greatly modified, these first colonizing species might be selected for initial plantings as they are likely to be tolerant of more degraded peatland environments. The conditions under which tree planting may enhance natural regeneration should be a priority for further research, as should the edaphic, hydrological and biotic factors that may influence species performance.

4.3. Restoration through catalytic plantations

From the current study, it is not clear what role *Acacia* has played in natural regeneration at the study site. Compared to the harvested *Acacia*, the plots in unharvested areas had a higher diversity of regenerating species, taller saplings and a more diverse habitat matrix which likely provided suitable structure and shelter for dispersal agents. However, these differences may also be because natural regeneration in the unharvested areas had proceeded undisturbed for at least 3–4 years compared to the regeneration in the harvested areas which had occurred over only 2–3 years, commencing on an exposed, bare peat substrate. While we did characterize natural regeneration and factors such as distance to forest and mode of seed dispersal, we were not able to study the exact causes of the higher rates of natural regeneration recorded in certain places (i.e. closer to the forest or in patches within each LULC), and as discussed above the influence of a range of biotic and abiotic factors merits further study.

A related species – *Acacia mangium*, has been used in Indonesia as a catalyst to initiate forest regeneration of mineral soil forests (Kuusipalo et al., 1995), and it is possible that the presence of *Acacia crassicarpa* on degraded peatlands is likewise facilitating natural establishment of other species. By growing rapidly to a height of 15 m and establishing a closed canopy in only four years, *Acacia* alters the microclimate by reducing sunlight and wind, resulting in higher humidity and a higher peat surface moisture content; the otherwise dense growth of ferns is inhibited by shading, while the plantation trees may increase seed dispersal by providing cover for ground dwelling mammals and perches for flying animals. Below ground, *Acacia* fixes nitrogen, restores one part of the peatland hydrological function by transpiring to regulate water tables, and may lead to the recolonization and restoration of peat soil microbial and fungal communities which could be important in facilitating forest regeneration (Graham et al., 2013; Hirano et al., 2014). These above and below ground changes also bring about some limited restoration of the peat surface microtopography, by creating higher and lower areas (close to and at further distance from tree boles) similar to the hummocks and hollows which support distinct vegetation communities found in intact PSF but which are destroyed by agricultural conversion and fire (Lampela et al., 2014, 2016; Freund et al., 2017; Nishimua et al., 2007).

There is, however, a need to further understand the mechanisms driving natural regeneration at our site before our findings, particularly on the potential use of *Acacia* as a potential foundation species for forest regeneration, can be applied more widely to other degraded peatlands. For instance, a potential flip side to the use of non-native species to catalyse ecological restoration is that most such species on mineral soils are fast-growing pioneer trees, such as *Acacia mangium* and *Leucaena leucocephala* which could be invasive (Lugo, 1997; Parotta, 2012). While our site does have a range of different LULCs, it was converted relatively recently (i.e. between 2012 and 2014), and the degradation of the peat soils might not be as severe as at other peatlands that have undergone long term alterations as a result of drainage, agriculture, fires and flooding. Given the potential for considerable inter-site variation, the introduction of *Acacia* as a catalyst species in these already modified peatlands must be done with caution. In addition, whilst *Acacia* spp. may tolerate short-term inundation, they are not tolerant of longer-term waterlogging of the rooting environment (Basak et al., 2015). Thus the use of *Acacia* as an ecological catalyst species is likely to be limited on peatlands that are undergoing rewetting as part of hydrological restoration. This is supported by our results which indicate the almost complete absence of *Acacia crassicarpa* in the intact, logged and remnant PSFs which had a more intact hydrology and higher water tables than the more degraded LULCs.

4.4. Restoration through forest buffer zones

Our study has shown that over distances from the forest of 300 m and possibly up to 500 m, the regeneration of natural PSF may not require tree planting, while beyond 500 m regeneration occurs but might take longer and require the planting of selected species that do not disperse to these distances. With vast areas of peatlands to be restored, a pragmatic approach may be to prioritize restoration to areas within 500 m of existing forests. This will allow natural regeneration to initiate PSF restoration. However, this will require active control of illegal forest access, e.g. for logging and poaching, which could limit the success of dispersal agents in initiating regeneration through seed dispersal. In case the area is drained this will also require rewetting of the buffer zone.

Author contributions

LSW and AH conceived the idea; LSW, RV, AH, TAE and DM designed the study; DM, RA, SB and Lasmito carried out the field work; LSW and RV analysed the data; LSW, RV, AH, TAE, DP, RJ and SEP led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.117868.

References

Anderson, J.A.R., 1964. The structure and development of the peat swamps of Sarawak and Brunei. J. Trop. Geogr. 18, 7–15.

Anderson, J.A.R., 1983. The tropical peat swamps of western Malesia. Mires: swamp, bog, fen and moor: regional studies.

Banjarbaru Forestry Research Unit, FORDA, Graham, L.L.B., 2014. Tropical Peat Swamp Forest Silviculture in Central Kalimantan: A series of five research papers. doi: 10.13140/rg.2.1.1071.9126.

Basak, S.R., Basak, A.C., Rahman, M.A., 2015. Impacts of floods on forest trees and their coping strategies in Bangladesh. Weather Clim. Extrem. 7, 43–48. https://doi.org/10.1016/j.wace.2014.12.002.

Blackham, G.V., Corlett, R.T., 2015. Post-dispersal seed removal by ground-feeding rodents in tropical peatlands, Central Kalimantan, Indonesia. Sci. Rep. 5. https://doi.org/10.1038/srep14152.

Blackham, G.V., Webb, E.L., Corlett, R.T., 2014. Natural regeneration in a degraded tropical peatland, Central Kalimantan, Indonesia: implications for forest restoration. For. Ecol. Manage. 324, 8–15. https://doi.org/10.1016/j.foreco.2014.03.041.

Cannon, C.H., Curran, L.M., Marshall, A.R., Leighton, M., Leighton, M., 2007. Long-term reproductive behaviour of woody plants across seven Bornean forest types in the Gunung Palung National Park (Indonesia): suprannual synchrony, temporal productivity and fruiting diversity. Ecol. Lett. 10, 956–969. https://doi.org/10.1111/j.1461-0248.2007.01089.x.

Chazdon, R.L., Guariguata, M.R., 2016. Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. Biotropica 48, 716–730. https://doi.org/10.1111/btp.12381.

Dargie, G.C., Lewis, S.L., Lawson, I.T., Mitchard, E.T.A., Page, S.E., Bocko, Y.E., Ifo, S.A., 2017. Age, extent and carbon storage of the central Congo Basin peatland complex. Nature 542, 86–90. https://doi.org/10.1038/nature21048.

Drösler, M., Verchot, L.V., Freibauer, A., Pan, G., Evans, C.D., Bourbonniere, R.A., Alm, J.P., Page, S., Agus, F., Hergoualc'h, K., Couwenberg, J., Jauhiainen, J., Sabiham, S., Wang, C., Srivastava, N., Borgeau-Chavez, L., Hooijer, A., Minkkinen, K., French, N., Strand, T., Sirin, A., Mickler, R., Tansey, K., Larkin, N., 2014. Chapter 2: Drained inland organic soils, in: Hiraishi, T., Krug, T., Tanabe, K., Srivastava, N., Jamsranjav, B., Fukuda, M., Troxler, T. (Eds.), 2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands. IPCC, Switzerland, pp. 1–79.

Evans, C.D., Page, S.E., Morrison, R., Artz, R., Wijedasa, L.S., 2017. The potential of responsible peatland management to reduce global soil carbon loss and greenhouse gas emissions, in: Global Symposium on Soil Organic Carbon. Rome, Italy, pp. 21–23.

Freund, C.A., Harsanto, F.A., Purwanto, A., Takahashi, H., Harrison, M.E., 2017. Microtopographic specialization and flexibility in tropical peat swamp forest tree species. Biotropica 1–7. https://doi.org/10.1111/btp.12512.

Giesen, W., Wijedasa, L.S., Page, S.E., 2018. Unique Southeast Asian peat swamp forest habitats have relatively few distinctive plant species. Mires Peat 1–13. https://doi.org/10.19189/MaP.2017.OMB.287.

Graham, L.L.B., Giesen, W., Page, S.E., 2017. A common-sense approach to tropical peat swamp forest restoration in Southeast Asia. Restor. Ecol. 25, 312–321. https://doi.org/10.1111/rec.12465.

Graham, L.L.B., Page, S.E., 2012. Artificial bird perches for the regeneration of degraded tropical peat swamp forest: a restoration tool with limited potential. Restor. Ecol. 20, 631–637. https://doi.org/10.1111/j.1526-100X.2011.00805.x.

Gunawan, H., Kobayashi, S., Mizuno, K., Kono, Y., 2012. Peat swamp forest types and their regeneration in Giam Siak Kecil-Bukit Batu Biosphere Reserve, Riau, East Sumatra, Indonesia. Mires Peat 10, 1–17. doi: 1819-754X.

Hansson, A., Dargusch, P., 2018. An estimate of the financial cost of peatland restoration in Indonesia. Case Stud. Environ. doi: 10.1525/cse.2017.000695.

Harrison, M., Husson, S.J., D'Arcy, L., Morrogh-Bernard, H., Cheyne, S.M., Van Noordwijk, M., van Schaik, C.P., 2010. The Fruiting Phenology of Peat-swamp Forest Tree Species at Sabangau and Tuanan, Central Kalimantan, Indonesia, The Kalimantan Forests and Climate Partnership.

Hirano, T., Kusin, K., Limin, S., Osaki, M., 2014. Evapotranspiration of tropical peat swamp forests. Glob. Change Biol. 1914–1927. https://doi.org/10.1111/gcb.12653.

Holl, K.D., Loik, M.E., Lin, E.H.V., Samuels, I.A., 2000. Tropical Montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. Restor. Ecol. 8, 339–349. https://doi.org/10.1046/j.1526-100x.2000.80049.x.

Holl, K.D., Reid, J.L., Chaves-Fallas, J.M., Oviedo-Brenes, F., Zahawi, R.A., 2017. Local tropical forest restoration strategies affect tree recruitment more strongly than does landscape forest cover. J. Appl. Ecol. 54, 1091–1099. https://doi.org/10.1111/1365-2664.12814.

Hooijer, A., Page, S., Canadell, J.G., Silvius, M., Kwadijk, J., Wösten, H., Jauhiainen, J., 2010. Current and future CO2 emissions from drained peatlands in Southeast Asia. Biogeosciences 7, 1505–1514. https://doi.org/10.5194/bg-7-1505-2010.

Hoscilo, A., Page, S.E., Tansey, K.J., Rieley, J.O., 2011. Effect of repeated fires on land-cover change on peatland in southern Central Kalimantan, Indonesia, from 1973 to 2005. Int. J. Wildland Fire 20, 578–588. https://doi.org/10.1071/WF10029.

Kuusipalo, J., Ådjers, G., Jafarsidik, Y., Otsamo, A., Tuomela, K., Vuokko, R., 1995. Restoration of natural vegetation in degraded *Imperata cylindrica* grassland: understorey development in forest plantations. J. Veg. Sci. 6, 205–210. https://doi.org/10.2307/3236215.

Lampela, M., Jauhiainen, J., Kämäri, I., Koskinen, M., Tanhuanpää, T., Valkeapää, A., Vasander, H., 2016. Ground surface microtopography and vegetation patterns in a tropical peat swamp forest. Catena 139, 127–136. https://doi.org/10.1016/j.catena.2015.12.016.

Lampela, M., Jauhiainen, J., Sarkkola, S., Vasander, H., 2017. Promising native tree species for reforestation of degraded tropical peatlands. For. Ecol. Manage. 394, 52–63. https://doi.org/10.1016/j.foreco.2016.12.004.

Lampela, M., Jauhiainen, J., Sarkkola, S., Vassander, H., 2018. To treat or not to treat? The seedling performance of native tree species for reforestation on degraded tropical peatlands of SE Asia. For. Ecol. Manage. 429, 217–225. https://doi.org/10.1016/j.foreco.2018.06.029.

Lampela, M., Jauhiainen, J., Vasander, H., 2014. Surface peat structure and chemistry in a tropical peat swamp forest. Plant Soil 382, 329–347. https://doi.org/10.1007/s11104-014-2187-5.

Lugo, A.E., 1997. The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. For. Ecol. Manage. 99, 9–19. https://doi.org/10.1016/S0378-1127(97)00191-6.

Miettinen, J., Hooijer, A., Vernimmen, R., Liew, S.C., Page, S.E., 2017. From carbon sink to carbon source: extensive peat oxidation in insular Southeast Asia since 1990. Environ. Res. Lett. 12.

Miettinen, J., Wang, J., Hooijer, A., Liew, S., 2013. Peatland conversion and degradation processes in insular Southeast Asia: a case study in Jambi, Indonesia. Land Degrad. Dev. 24, 334–341. https://doi.org/10.1002/ldr.1130.

Nishimua, T.B., Suzuki, E., Kohyama, T., Tsuyuzaki, S., 2007. Mortality and growth of trees in peat-swamp and heath forests in Central Kalimantan after severe drought. Plant Ecol. 188, 165–177. https://doi.org/10.1007/s11258-006-9154-z.

Orwa, C., Mutua, A., Kindt, R., Jamnadass, R., Anthony, S., 2009. Agroforestree Database: a tree reference and selection guide version 4.0. World Agroforestry Centre, Kenya.

Page, S.E., Rieley, J.O., Shotyk, Ø.W., Weiss, D., 1999. Interdependence of peat and vegetation in a tropical peat swamp forest. In: Changes and Disturbance in Tropical Rainforest in South-East Asia, pp. 161–173.

Page, S., Hosciło, A., Wösten, H., Jauhiainen, J., Silvius, M., Rieley, J., Ritzema, H., Tansey, K., Graham, L., Vasander, H., Limin, S., 2009. Restoration ecology of lowland tropical peatlands in Southeast Asia: current knowledge and future research directions. Ecosystems 12, 888–905. https://doi.org/10.1007/s10021-008-9216-2.

Parotta, J.A., 2012. Restoration and management of degraded tropical forest landscapes. In: Ambasht, R.S., Ambasht, N.K. (Eds.), Modern Trends in Applied Terrestrial Ecology. Springer Science and Business Media.

Posa, M.R.C., Wijedasa, L.S., Corlett, R.T., 2011. Biodiversity and conservation of tropical peat swamp forests. BioScience 61, 49–57. https://doi.org/10.1525/bio.2011.61.1.10.

R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Republic of Indonesia, 2016. First Nationally Determined Contribution.

Russon, A.E., Erman, A., Dennis, R., 2001. The population and distribution of orangutans (Pongo pygmaeus pygmaeus) in and around the Danau Sentarum Wildlife Reserve, West Kalimantan, Indonesia. Biol. Conserv. 97, 21–28. https://doi.org/10.1016/S0006-3207(00)00087-2.

Saito, H., Shibuya, M., Tuah, S.J., Turjaman, M., Takahashi, K., Jamal, Y., Segah, H., Putir, P.E., Limin, S.H., 2005. Initial screening of fast-growing tree species being tolerant of dry tropical peatlands in Central Kalimantan, Indonesia. J. For. Res. 2, 1–10.

Van Eijk, P., Leenman, P.H., 2004. Regeneration of fire degraded peatswamp forest in Berbak National Park and implementation replanting programmes, Water for food & ecosystems programme project on: 'Promoting the river basin and ecosystem approach for sustainable management of SE Asian lowland peatswamp forests.' Alterra, Wageningen, The Netherlands.

Wijedasa, L., Jauhiainen, J., Könönen, M., Lampela, M., Vasander, H., LeBlanc, M.-C., Evers, S., Smith, T.E.L., Yule, C.M., Varkkey, H., Lupascu, M., Parish, F., Singleton, I., Clements, G.R., Aziz, S.A., Harrison, M.E., Cheyne, S., Anshari, G.Z., Meijaard, E., Goldstein, J.E., Waldron, S., Hergoualc'h, K., Dommain, R., Frolking, S., Evans, C.D., Posa, M.R.C., Glaser, P.H., Suryadiputra, N., Lubis, R., Santika, T., Padfield, R., Kurnianto, S., Hadisiswoyo, P., Lim, T.W., Page, S.E., Gauci, V., van der Meer, P.J., Buckland, H., Garnier, F., Samuel, M.K., Choo, L.N.L.K., O'Reilly, P., Warren, M., Suksuwan, S., Sumarga, E., Jain, A., Laurance, W.F., Couwenberg, J., Joosten, H., Vernimmen, R., Hooijer, A., Malins, C., Cochrane, M.A., Perumal, B., Siegert, F., Peh, K.S.-H., Comeau, L.-P., Verchot, L., Harvey, C.F., Cobb, A., Jaafar, Z., Wösten, H., Manuri, S., Müller, M., Giesen, W., Phelps, J., Yong, D.L., Silvius, M., Wedeux, B.M.M., Hoyt, A., Osaki, M., Takashi, H., Takahashi, H., Kohyama, T.S., Haraguchi, A., Nugroho, N.P., Coomes, D.A., Quoi, L.P., Dohong, A., Gunawan, H., Gaveau, D.L.A., Langner, A., Lim, F.K.S., Edwards, D.P., Giam, X., van der Werf, G., Carmenta, R., Verwer, C.C., Gibson, L., Grandois, L., Graham, L.L.B., Regalino, J., Wich, S.A., Rieley, J., Kettridge, N., Brown, C., Pirard, R., Moore, S., Ripoll Capilla, B., Ballhorn, U., Ho, H.C., Hoscilo, A., Lohberger, S., Evans, T.A., Yulianti, N., Blackham, G., Onrizal, Husson, S., Murdiyarso, D., Pangala, S., Cole, L.E.S., Tacconi, L., Segah, H., Tonoto, P., Lee, J.S.H., Schmilewski, G., Wulffraat, S., Putra, E.I., Cattau, M.E., Clymo, R.S., Morrison, R., Mujahid, A., Miettinen, J., Liew, S.C., Valpola, S., Wilson, D., D'Arcy, L., Gerding, M., Sundari, S., Thornton, S.A., Kalisz, B., Chapman, S.J., Su, A.S.M., Basuki, I., Itoh, M., Traeholt, C., Sloan, S., Sayok, A.K., Andersen, R., 2016. Denial of long-term issues with agriculture on tropical peatlands will have devastating consequences. Glob. Change Biol. 23, 977–982. doi: 10.1111/gcb.13516.

Wijedasa, L.S., Sloan, S., Page, S.E., Clements, G.R., Lupascu, M., Evans, T.A., 2018. Carbon emissions from South-East Asian peatlands will increase despite emission-reduction schemes. Glob. Change Biol. 24, 4598–4613. https://doi.org/10.1111/gcb.14340.

Wösten, J.H.M., Van Den Berg, J., Van Eijk, P., Gevers, G.J.M., Giesen, W.B.J.T., Hooijer, A., Idris, A., Leenman, P.H., Rais, D.S., Siderius, C., Silvius, M.J., Suryadiputra, N., Wibisono, I.T., 2006. Interrelationships between hydrology and ecology in fire degraded tropical peat swamp forests. Int. J. Water Resour. Dev. 22, 157–174. https://doi.org/10.1080/07900620500405973.

Yarranton, G.A., Morrison, R.G., 1974. Spatial dynamics of a primary succession: nucleation. J. Ecol. 62, 417. https://doi.org/10.2307/2258988.

Zahawi, R.A., Holl, K.D., Cole, R.J., Reid, J.L., 2013. Testing applied nucleation as a strategy to facilitate tropical forest recovery. J. Appl. Ecol. 50, 88–96. https://doi.org/10.1111/1365-2664.12014.

Zhang, Z., 2016. Variable selection with stepwise and best subset approaches. Ann. Transl. Med. 4https://doi.org/10.21037/atm.2016.03.35. 136–136.

Zuur, A.F., Ieno, E.N., 2016. A protocol for conducting and presenting results of regression-type analyses. Methods Ecol. Evol. 7, 636–645. https://doi.org/10.1111/2041-210X.12577.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems: data exploration. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.