A limited seed bank in both natural and degraded tropical peat swamp forest: the implications for restoration

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SUMMARY

Carbon-rich tropical peat swamp forests (PSFs) are being degraded at an alarming rate. In response to national and global agendas, landscape-scale PSF restoration is underway, although supporting knowledge of PSF ecosystem restoration ecology remains limited. Seed banks are usually an important source of natural regeneration and crucial in post-degradation forest recovery, even in the humid tropics where reduced seed dormancy leads to typically smaller seed banks than in temperate regions. It has been assumed that PSF degradation reduces the seed bank, limiting natural regeneration, but this has not previously been investigated explicitly. This study of PSF in Central Kalimantan explored seed bank prevalence and regenerative capacity across five forest zones (FZs): degraded, open canopy disturbed, edge, closed canopy disturbed and natural. Numbers and species of seeds and seedlings were recorded from surface peat samples collected from each FZ over one year. Seed density, averaged across FZs, was 41 seeds m^{-2}; total species number was 11; and seedling density was 16.0–73.6 m^{-2} depending on FZ. These values were much lower than for other forests in this region. There was little difference in seed bank size between natural and degraded FZs, and only the forest edge showed higher than expected seed bank regenerative capability. Overall, our results suggest that seed banks are not of high importance in tropical PSF regeneration, either before or after degradation. These findings are discussed from the perspective of successional traits in different species and their relevance to ecosystem restoration.

KEY WORDS: dormancy, germination, Indonesia, natural regeneration, PSF, seed dispersal, succession

INTRODUCTION

Soil seed banks (stores of dormant seeds within the soil which have arrived by falling from the parent tree or by dispersal) build up over time in most ecosystems (Saatkamp *et al.* 2014). In some examples, such as temperate forests or savannahs, the seed bank acts as a crucial source of seedlings for recolonisation (Bakker *et al.* 1996). In humid tropical environments, there are fewer seeds adapted for dormancy and most ecosystems have short-lived seed banks (Janzen & Vázquez-Yanes 1991, Corlett 2009). This may be due to the seedlings requiring moist conditions to survive, so although dormancy is advantageous in seasonally dry environments, immediate germination is optimal in year-round humid conditions (Blakesley *et al.* 2002, Corlett 2009).

Following tropical forest degradation, seed banks can act as important sources of new seedlings for re-colonisation (Bakker *et al.* 1996, FORRU 2008, Daïnou *et al.* 2011, Saatkamp *et al.* 2014). After disturbance, however, seed banks may become damaged, and if new seed banks are not built up from nearby trees or through dispersal, this source of seedlings may be lost (Janzen & Vázquez-Yanes 1991, Aide & Cavalier 1994). In degraded areas the seed bank volume can be the same as, or higher than, in comparable natural forest but with different composition, namely a higher proportion of herbs, shrubs and grasses, leading to further complications in the restoration process due to the absence of woody species (Janzen & Vázquez-Yanes 1991, Bakker *et al.* 1996, Brearley *et al.* 2004, Daïnou *et al.* 2011, Madawala *et al.* 2016).

Indonesia hosts one of the world's largest areas of intact tropical peat swamp forest (PSF), covering an estimated 200,000 km^2 (Page *et al.* 2011). However, Southeast Asia's PSF is being degraded at a rapid rate: between 1985 and 2006 about 47 % (121,000 km^2) was degraded, *i.e.* logged, burned, drained or converted to agricultural use (Hooijer *et al.* 2006, 2010) and in 2010 only 4 % of the PSF in Sumatra and Kalimantan was judged still to be in pristine condition, with 37 % classified as degraded forest (Miettinen & Liew 2010).

Tropical PSFs are peatlands and, thus, vast reservoirs of carbon, storing 57 Gt of carbon in Indonesia alone, which amounts to 74 % of the country's total forest soil carbon pool (Page *et al.* 2011). Upon degradation, largely through fires, logging and drainage (Page *et al.* 2009), they become sources of atmospheric carbon emissions. In 1997, 0.81–2.57 Gt of carbon were released to the atmosphere as a result of peatland fires in Indonesia, equivalent to 13–40 % of the global carbon emissions from fossil fuels for that year (Page *et al.* 2002). Furthermore, Indonesia's PSF provides other important environmental services, such as biodiversity support (Posa *et al.* 2011) and hydrological regulation (Wösten *et al.* 2006, 2008).

The net result of tropical PSF degradation is that species-diverse forest is replaced by a variety of less biodiverse secondary communities (Blackham *et al.* 2014, Kostermans 1958, Wyatt-Smith 1959, Whitmore 1984, Appanah *et al*. 1989, Bruenig 1990, Ibrahim 1996, Simbolon 2002, van Eijk *et al*. 2009). Following low-level disturbance, forest re-growth will occur, but after more severe and/or regular disturbance, the re-establishment of woody species is retarded, whilst at extreme levels of degradation (in terms of both severity and frequency), woody vegetation is indefinitely replaced by sedges and ferns (Hoscilo *et al.* 2011). In addition to a reduction in biodiversity, PSF degradation also leads to the loss of most, if not all, ecosystem services including carbon storage, faunal and floral biodiversity and hydrological regulation (Posa *et al.* 2011, Page *et al.* 2009) plus high emissions of greenhouse gases (GHGs) to the atmosphere (Hooijer *et al.* 2006, 2010, Miettinen *et al.* 2016).

Forest and peatland ecosystem restoration could be amongst the most cost-efficient measures for reducing regional CO_2 emissions (Spracklen *et al.* 2008, van Noordwijk *et al.* 2008). For this reason, the Indonesian Government is collaborating with non-government organisations to initiate large-scale restoration programmes on Indonesia's degraded tropical peatlands (van Noordwijk *et al.* 2008, KFCP 2014) as well as with the Australian Government's Centre for International Agricultural Research (ACIAR) to establish the new (2017) project "Improving community fire management and peatland restoration in Indonesia". Furthermore, in 2016 Indonesia's President Joko Widowo established the Peatland Restoration Agency, which is tasked with the rewetting of two million hectares of degraded, drained peatland within four years. Therefore, land and ecosystem management approaches to assist the restoration of PSF are of considerable contemporary interest, both in Indonesia and elsewhere.

Effective restoration actions require intimate knowledge of ecosystem processes (Aide *et al.* 2000), but the study of PSF ecology has really developed only over the last 30 years (Rieley & Page 2005) with, at present, little of that knowledge being applied to ecosystem restoration (Page *et al.* 2009, Graham *et al.* 2017). Degraded PSF has been shown to have poor regeneration capabilities, with post-disturbance succession often following retrogressive pathways, driven in particular by frequent fire, loss of hydrological integrity and wet-season flooding (Page *et al.* 2009, Hoscilo *et al.* 2011, Blackham *et al.* 2014). More scientific studies are required to understand the barriers to PSF regeneration and the effects of external influences on degraded tropical peatland landscapes.

Restoration ecology is the science upon which the practice of ecological restoration is based. One aspect explores the barriers to regeneration that exist at individual sites and examines the methods that can be used to overcome these barriers (Aide *et al.* 2000, Holl 2012) as well as how they can be incorporated into the design and implementation of restoration action plans (RAPs) (SER 2004; Tongway & Ludwig 2011, 2012). The regeneration barriers and appropriate RAP for a specific site will be unique: they will reflect the site's natural history and its disturbance history (Holl *et al.* 2000, Curran *et al.* 2012). Investigation of regeneration barriers usually involves the comparison of at least one ecological factor between the degraded area and a 'reference site' - an adjacent area where the ecosystem remains undegraded (SER 2004). Significant differences highlight the regeneration barriers.

To date there are no published studies of the soil (surface peat) seed bank in tropical PSF under natural conditions. One study considered the soil seed bank in a fire-degraded peatland area in Central Kalimantan (Indonesia) and found that only one wind-dispersed species (*Combretocarpus rotundatus*) emerged post-fire, leading to the assumption that fire had destroyed the seed bank (Simbolon 2002). Other authors have also suggested that disturbance leads to loss of the PSF seed bank (Giesen 2004, Rieley & Page 2005, Blackham *et al.* 2014). This interpretation should be treated with caution, however, as it is widely accepted that forest ecosystems in wetter environments (such as the humid tropics) display a strong tendency towards short seed dormancy and, consequently, have smaller soil seed banks than the forests of other climatic zones (Janzen & Vázquez-Yanes 1991, Bakker *et al.* 1996, Corlett 2009). In these situations, seed dispersal becomes the most important mechanism for seedling recruitment (*ibid.*)

In light of these knowledge gaps, this study aimed to directly compare seed bank volume, diversity and regenerative capabilities between an area of degraded PSF and an adjacent area of relatively undisturbed PSF.

STUDY AREA

The study took place in the PSF of the Natural Laboratory of Peat Swamp Forest (NLPSF) (02º 18' S, 113º 50' E, 30 m a.s.l.), located on the Sebangau peat dome in Central Kalimantan, Indonesia. The site is located in the northern part of the Sungai (= River) Sebangau catchment and forms part of the 5,000 km^2 of PSF that covers the interfluve of the Sebangau and Katingan Rivers (Figure 1). The mixed PSF where our data collection took place was

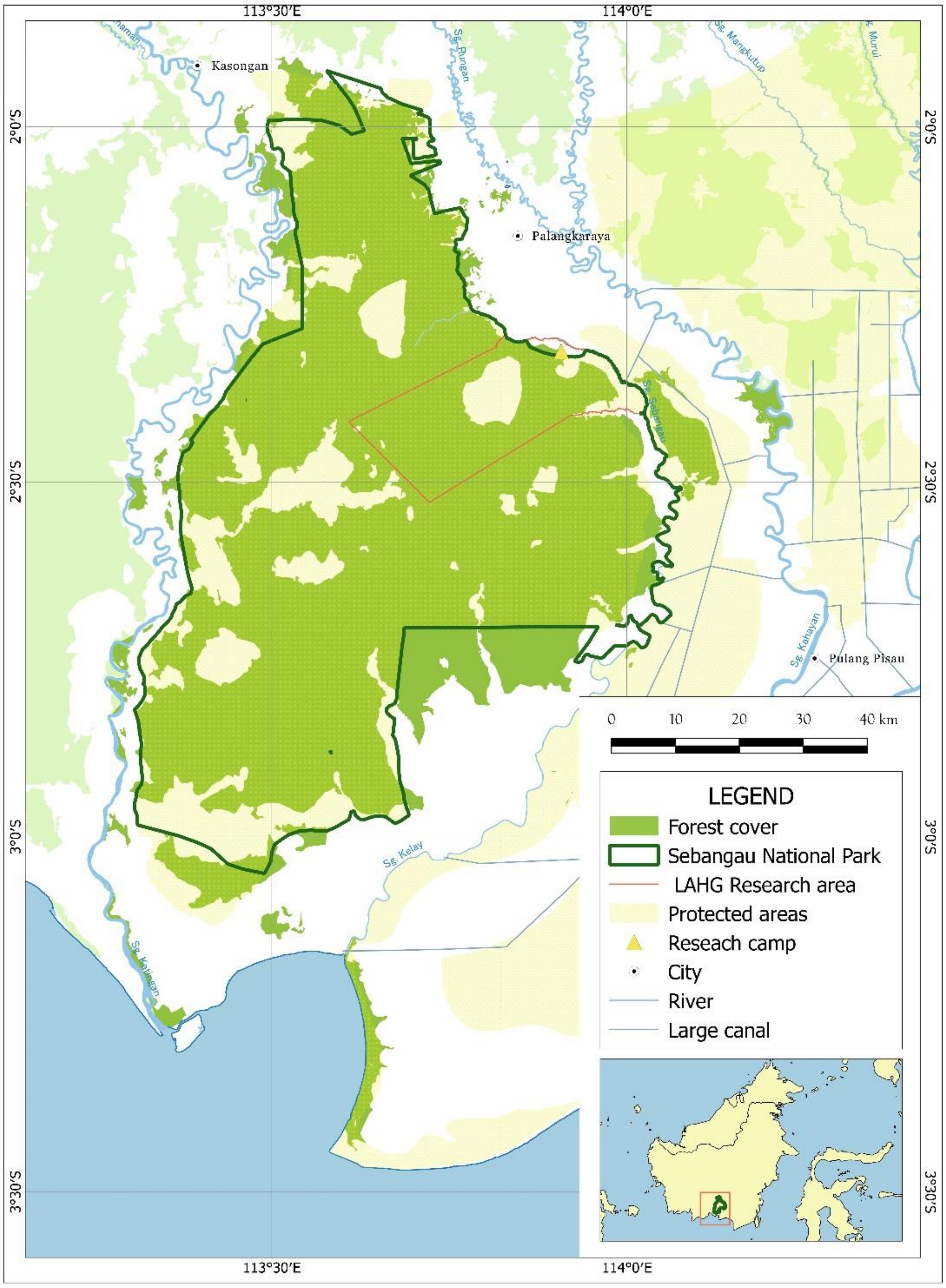

Figure 1. Location map. The seed bank samples were collected slightly to the west of the research camp (yellow triangle), within the NLPSF study site area or LAHG research area (red line), shown in relation to the island of Borneo (inset). Image courtesy of B. Ripoll Capilla.

previously continuous and undisturbed, but concessional logging, illegal logging and fires during recent years have resulted in some areas becoming degraded (Rieley & Page 2005). The climate is humid tropical, with a mean maximum temperature of 28.9 ºC, a mean minimum temperature of 22.0 ºC and an annual rainfall of 2912 mm yr^{-1} (2003–2007 average), with a wet season from October/November through to May/June (Harrison 2009).

METHODS

Five forest zones (FZs) were defined: 'Degraded Forest' (DF, 200 m outside the forest); 'Open-Canopy' disturbed forest (OC, 50 m outside the forest); 'Forest Edge' (FE); 'Closed-Canopy' disturbed forest (CC, 50 m inside the forest); and 'Natural Forest' (NF, 800 m inside the forest) which was relatively undisturbed and where regeneration was operating naturally (regarded as the reference site). In each FZ, one 600 m transect running parallel to the forest edge was established (Figure 2). A detailed description of vegetation in the five forest zones is provided in the Appendix.

In order to assess the seed bank in each FZ, five surface peat samples were taken at stratified random locations along each transect (Duncan 2006), during the months of September and December 2007, and March and June 2008. Each sample was 12.5 cm square and 5 cm deep (Zimmerman *et al.* 2000). In most seed bank studies, leaf litter is removed from the soil surface before the sample is taken. In PSF, the point of transition from litter to peat is unclear, especially as roots come right up to and even above the surface of the litter. Therefore, still-intact dry leaves were removed from the ground surface but any litter below this was taken as part of the sample. The peat samples were extracted by slicing the peat, including roots, to the required size using a sharp knife. The samples were transferred, on the day of sampling, to a seedling nursery which attempted to provide natural forest conditions (*i.e.* shade, water, protection from direct rainfall) and immediately spread out on germination trays to a thickness of 1 cm (Duncan 2006). The number of visible seeds in each sample, and their species if known (if not, morphospecies was used), was recorded. Thereafter,

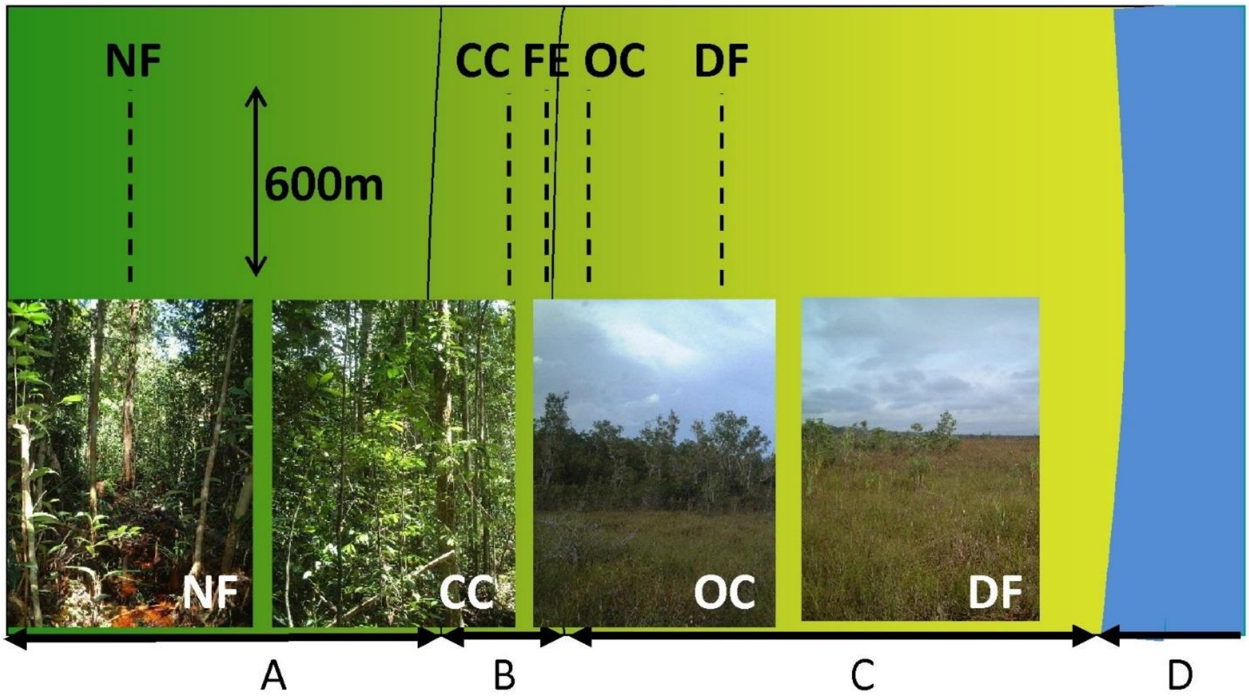

Figure 2. Schematic diagram of the forest study site. The transects are shown as dashed lines, each 600 m long. Transects were positioned parallel to the forest edge in different forest zones: degraded forest (DF), 200 m outside the forest; open-canopy disturbed forest (OC), 50 m outside the forest; forest edge (FE); closed-canopy disturbed forest (CC), 50 m inside the forest; and natural forest (NF in the forested area A), 1 km inside the undisturbed peat swamp forest. The area of degraded sedge swamp (C) was previously riverine forest which was logged and burned decades before this study. The area of transitional forest (B) may be receding farther from the river (D) due to edge effect pressures.

germination and survival of 'seedlings' was recorded at monthly intervals over a six-month period (Zimmerman *et al.* 2000). Some new plants came from very small seeds (with the usual roots and shoots) and were defined as germinated seedlings, whilst others grew from the cut roots and were defined as root sprouts.

Data were analysed first for seasonal effect within each FZ, averaged across the five replicates. If no seasonal effect (*i.e.* wet *versus* dry season) was observed, the data were averaged over the year for each FZ and then compared to the reference FZ (the NF transect). Where the data were normally distributed and the variance homogenous, ANOVA was used (repeated measures in the case of seasonal variation); otherwise, a Friedman repeat measures test was used for seasonal variation and a Mann Whitney U test for comparisons between FZs. All statistical analyses were carried out in SPSS.

RESULTS

Over a one-year period, the cumulative number of seeds collected across all FZs was 64, or 16 seeds at each 3-monthly collection on average, with an average of 3.2 seeds *per* transect or 0.64 seeds *per* peat sample *per* 3-month period, equal to a density of 41 seeds m^{-2}. Using the Freidman test, no effect of season on seed abundance was observed in any of the FZs. Therefore, the total number of seeds found in each FZ was averaged for each season and across the year (Table 1). Whilst FE had the greatest density of seeds overall (80.0 seeds m^{-2}), it was not significantly different from NF (38.4 seeds m^{-2}) due to high variation across both forest zone samples. Indeed, none of the FZs had significantly more or less seeds than NF.

No seasonal effect on the number of seed species found in the peat samples was observed using the Friedman test (Table 1). Therefore, the number of species found was averaged across replicates with regard to FZ and analysed for the year using ANOVA, which showed no significant difference from NF for any of the FZs (Table 1). The highest number of species was found in CC, with an average of 0.4 species *per* sample, or five species during the whole year. In total, eleven species were found across all samples from all FZs. Of these, five were classified by morphospecies and the remaining six were identified to genus or species. All six were tree species, of which four were relatively large-seeded, five animal-dispersed and one wind-dispersed. Seeds of *Combretocarpus rotundatus* and *Tristaniopsis* sp. were found in all disturbed FZs but were absent from NF (Table 2).

Of the seeds recorded during processing of the peat samples, only *Combretocarpus rotundatus* germinated. The new plants that appeared originated either by germination of very small seeds (indistinguishable and inseparable from wet peat) or by sprouting from roots cut during the peat collection process. Using the Friedman test, no seasonal variation was detected in the total numbers of new plants that appeared (from seeds or sprouting roots) during the six-month period in the nursery. Therefore, the numbers of seedlings that germinated from seed in the disturbed FZs were averaged within each season, and for the year, for each FZ, then

Table 1. The average annual number of seeds *per* m^2 and species *per* averaged sample. As noted in the text, no seasonal effects were detected throughout, and no significant differences from the baseline natural forest (NF) were found in any of the disturbed forest zones. See text for details of the statistical tests used.

Forest Zone	Seed density			Number of seed species		
	m^{-2} yr^{-1}	p-value for seasonal effect	p-value for comparison with NF	*per* averaged sample yr^{-1}	p-value for seasonal effect	p-value for comparison with NF
DF	19.2	0.558	0.494	0.15	0.663	0.524
OC	32.0	0.663	0.856	0.15	0.663	0.524
FE	80.0	0.124	0.639	0.25	0.112	0.771
CC	35.2	0.458	0.909	0.4	0.234	0.659
NF	38.4	0.318	-	0.25	0.231	-

Table 2. Characteristics of the six tree species identified in the seed bank samples.

Family	Species	Dispersal	Relative seed size	Successional type	Seed found in degraded FZ?	Germinated ?
Anacardiaceae	*Campnosperma squamatum*	animal	large	early–mid	no	no
Anisophyllaceae	*Combretocarpus rotundatus*	wind	small	pioneer	yes	yes
Lauraceae	*Litsea angulata*	animal	large	mid–late	no	no
Myrtaceae	*Tristaniopsis* sp.	animal	small	early	yes	no
Phyllanthaceae	*Glochidion rubrum*	animal	large	early–mid	no	no
Sapindaceae	*Nephelium lappaceum*	animal	large	mid–late	no	no

Table 3. Numbers of new plants that germinated from seeds and sprouted from roots, the average percentage survival of germinated seedlings and sprouting roots, and the annual total number of seedling and sprout species, for each FZ. Significance at the 0.05 level is denoted with an asterisk (*); see text for details of the statistical tests used.

Forest Zone	Seedlings germinated				Sprouting roots		Species		
	m^{-2} yr^{-1}	p-value for seasonal effect	p-value for comparison with NF	Survival (%)	m^{-2} yr^{-1}	Survival (%)	Total	p-value for seasonal effect	p-value for comparison with NF
DF	19.2	0.910	0.740	33	0	-	3	0.809	0.608
OC	16	0.287	1.000	50	9.6	25	6	0.236	0.347
FE	73.6	0.555	*0.020	62	25.6	50	8	0.238	*0.040
CC	35.2	0.806	0.108	59	12.8	34	3	0.926	0.273
NF	16	0.144	-	25	3.2	0	3	0.287	-

compared with the results for NF using ANOVA (Table 3). Only FE had significantly more germinations (73.6 seedlings m^{-2} $year^{-1}$) than NF (16 seedlings m^{-2} $year^{-1}$). Sample size was not large enough to run a statistical analysis for the number of germinations from sprouting roots, but FE again had a higher mean productivity in terms of regeneration, with 25.6 sprouting roots m^{-2} $year^{-1}$ compared to 3.2 seedlings m^{-2} $year^{-1}$ in NF.

Both the average percentage survival of germinated seedlings (still alive at the end of the six-month recording period) and the percentage survival of sprouting roots were highest for FE (Table 3), although the dataset was not large enough to run a statistical analysis.

Nine morphospecies were identified amongst the new plants originating from either seeds or roots. Of these, only one was identified with any certainty (as *Combretocarpus rotundatus*). There was no seasonal variation in the species abundance of seedlings or sprouts (Freidman test; Table 3). Therefore, the number of species found in each FZ was averaged for the whole year and compared to NF using ANOVA (Table 3). This analysis showed that only FE had a significantly greater number of seedling/sprout species (total 8) than NF (total 3).

DISCUSSION

Tropical forests generally have smaller seed banks than temperate forests (where 500 seeds m^{-2} is typical and up to 5000 seeds m^{-2} common; Bakker *et al.* 1996). Seed bank densities in the tropical rainforests of Southeast Asia also commonly reach hundreds of seeds *per* m^2 (Table 4). In this study, the average seed bank density (41 seeds m^{-2}) in surface peat samples collected across the five FZs was lower than other documented seed bank densities for tropical rainforest ecosystems in this region (Table 4).

The number of seeds identified from the soil samples did not include seeds smaller than were easily visible to the human eye. In other studies it is suggested that, for analysis of seed density, soil samples should be sieved or submerged to separate seeds from the soil (Bakker *et al.* 1996). These methods were not practical here because it was not possible to sieve the peat samples in the same way as mineral soils; and when the peat samples were submerged, fragments of organic matter floated alongside small seeds. As a result, the values for total species numbers and seed density may be under-estimates. Rather than considering seed density directly, some previous studies have based seed density values on the number of seedlings emerging from soil samples in germination trials (*e.g.* Tekle &

Table 4. Comparison of seed densities and number of species found in the seed banks of Southeast Asian rainforest study sites. PSF = peat swamp forest, LER = Tropical lowland evergreen rainforest, R = Tropical rainforest, LR = Tropical lowland rainforest. Adapted from Brearley *et al.* (2004) and Tang *et al.* (2006).

Site	Forest type	Forest quality	Seeds (m^{-2})	No. spp.	Reference
Sebangau, Central Kalimantan, Indonesia	PSF	combined	41 (seed density)	11	this study
Sebangau, Central Kalimantan, Indonesia	PSF	disturbed	74 (seedling density)	8	this study
Sebangau, Central Kalimantan, Indonesia	PSF	primary	16 (seedling density)	3	this study
Barito Ulu, Central Kalimantan, Indonesia	LER	primary	175	25	Brearley *et al.* (2004)
Barito Ulu, Central Kalimantan, Indonesia	LER	disturbed	573	24	Brearley *et al.* (2004)
Chiang Mai, Thailand (Site No.2)	R	primary	128	24	Cheke *et al.* (1979)
Gogol Valley, Papua New Guinea	R	primary	398	-	Saulei & Swaine (1988)
Gogol Valley, Papua New Guinea	R	disturbed	757	-	Saulei & Swaine (1988)
Lungmanis, Sabah, Malaysia	R	primary	58	29	Liew (1973)
Pasoh, Malaysia	LR	primary	131	30	Putz & Appanah (1987)
Bukit Timah, Malaysia	LR	-	1000	-	Metcalfe & Turner (1998)

Bekele 2000, Tang *et al.* 2006). The seedling emergence data in our study were comparable to those for seed density (16–73.6 seedlings m^{-2} depending on FZ), which supports our conclusion that this ecosystem does indeed have an overall low seed bank despite our restrictions on the use of more samples *per* transect) was selected for consistency with other studies in this field (see Methods). Given that we now know the seed bank of tropical PSF is limited, a larger sample size is advised for future studies.

The number of seed bank species at Sebangau was also lower than in other studies (Table 4); all other studies have recorded more than 20 species, whereas just eleven were found in this study. Of these, the six which were identified to species were all trees, with four being relatively large-seeded.

Large-seeded tropical tree species are commonly recalcitrant (*i.e*. have little or no dormancy before germinating), and thus form only a transient portion of the seed bank (Thompson 1992, Bakker *et al.* 1996, Corlett 2009). The very limited dormancy of PSF tree seeds in their natural environment should be taken into consideration when collecting and storing seed for use in seedling nurseries.

The two small-seeded species are found in the three most disturbed FZs (DF, OC and FE). *Combretocarpus rotundatus* is wind-dispersed and *Tristaniopsis* sp. has a small dehiscent fruit with very small seeds. Both are commonly found along the forest edge and in degraded areas, and are adapted to disturbance and high light levels - *i.e*., they are pioneer secondary succession species (Wibisono *et al*. 2005, Giesen & van der Meer 2009). Such species might typically be expected to occur in the seed bank, given that pioneer species often support a longer seed dormancy to ‘sit out’ unfavourable conditions (Janzen & Vázquez-Yanes 1991, Corlett 2009). Therefore, these two species may represent an important element for natural regeneration and restoration in this area (also noted in Blackham *et al.* 2014).

Of the two small-seeded species, only *Combretocarpus rotundatus* went on to germinate in the seedling study. Seedlings of other species emerged from very small seeds that could not be separated from the peat. This supports the results of other studies, which found that seed banks of tropical rain forests in Southeast Asia were largely composed of small-seeded pioneer and secondary succession species (Metcalfe & Turner 1998, Metcalfe *et al.*1998, Brearley *et al.* 2004), although the seedling density of this study was much lower (assuming that germination in the nursery was the same as it would be *in situ* on the forest floor). FE was the only FZ to have significantly greater numbers of seedling morphospecies than NF. However, the overall numbers of morphospecies (eight for FE, three for NF) are still much lower than those observed in other studies in this region. The FE zone also appears to have the highest regenerative capacity overall, in that it had the greatest number of rootlets and the greatest percentage survival of both seedlings and sprouting roots.

While other studies note a seasonal effect in seed banks linked to the phenology of the surrounding forest (Bakker *et al.* 1996, Grombone-Guaratini & Rodrigues 2002, Tang *et al.* 2006, Madawala *et al.* 2016), we observed no seasonal effect for seed and seedling densities or for species composition. The reason may be that Bornean PSF is known to support continuous, year-round fruiting across a range of species (Cannon *et al.* 2007a, 2007b; Harrison *et al.* 2013). The lack of seasonality means that future studies to assess the seed bank in surface peat samples could potentially be carried out over a short period and at any time of year. The limitation to studying seed banks over short periods is that some species may undergo mast fruiting, and thus not be represented in a seed bank that has a short dormancy. This could only be explored through a long-term study.

Because separating small seeds from the peat was problematic, the initial seed density indicates the number of large (classically recalcitrant) seeds that are found within this PSF, whilst the seed density ascertained indirectly from seedling germination indicates the number of small seeds (normally with longer dormancy), which are typical of the pioneer secondary successor group (Thompson 1992, Corlett 2009). Regarding the first group, a small bank of large seeds was observed, as might be expected given that these are mainly of tree species adapted to the wet environment of tropical PSF, and trees from moist conditions tend to have shorter (if any) dormancy (Blakesley *et al.* 2002, Corlett 2009). However, the seed density ascertained from the seedling germination study was similarly low, indicating that PSF lacks an effective or productive seed bank. This may be due to the extremely moist environment resulting in PSF trees evolving rapid germination to avoid decomposition, even for those species that are adapted as pioneers or secondary successors (Blakesley *et al.* 2002, Corlett 2009). Some studies have noted that seed banks actually increase in degraded, disturbed or secondary forest compared to natural forest (Saulei & Swain 1988, Brearley *et al.* 2004), due to the increased numbers of pioneer and secondary succession species associated with these environments that tend to display greater seed dormancy (Saatkamp *et al.* 2014). Other studies have described a reduction in the seed bank in degraded forest areas, linking this to reduced seed input or damage to the seed bank (*e.g.* Aide & Cavalier 1994, Zimmerman *et al.* 2000). As the site used in this study had been degraded for a long time, assessment of the seed bank soon after disturbance might have yielded different findings; although, given the short-lived nature of most tropical seed banks, it can probably be assumed that the seed bank contains only newly arrived seeds rather than those remaining from a time prior to forest disturbance (Aide & Cavalier 1994). However, if this small seed bank, which is relatively unchanged from DF through to NF, is representative of PSF generally, seed banks may not be lost during degradation as previously thought (Giesen 2004, Rieley & Page 2005, Blackham *et al.* 2014). Instead, it may be that a large and (by inference) effective seed bank was never actually in operation. In other words, this appears to be the natural state of the ecosystem, and thus not a factor that is likely to hinder PSF regeneration. This shifts the emphasis for promotion of new seedling recruitment to seed dispersal, either by animals or through water transport (Bakker *et al.* 1996, Holl *et al.* 2000). The implication is that seed dispersal is extremely important for forest regeneration post-disturbance, indicating a probable need for enhancement planting of PSF tree species in degraded areas.

The second important finding from this study is the significantly higher seed bank regeneration activity observed for FE, compared to all other FZs, in terms of both seedling density and species composition. It might be hypothesised that seed banks are unnecessary in intact PSF, which is continually wet and has year-round fruiting. Equally, the degraded environment outside the forest bears so little resemblance to that of a natural forest gap that any seed bank would fail. The only location where a seed bank is both necessary and sufficiently protected is, therefore, the forest edge. Although the seed bank here is very small compared that in other forest types of the region, its presence nevertheless provides an important indication that regeneration by this route is occurring at the forest edge. The regenerative capabilities of the forest edge might also be harnessed in restoration and reforestation projects.

Finally, it was observed that seedlings emerged not only from the small seeds in the seed bank, but also from fine root hairs that were cut during collection of the soil samples. This has not been noted in other studies. Whilst we were unable to identify the species of sprouting roots, it suggests an interesting new avenue for tropical PSF restoration, in that there was a high propensity for root matter to sprout even without the addition of hormone rooting powder. This could potentially be utilised for vegetative propogation in reforestation work, but requires further study.

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Appendix: Summary of vegetation characteristics for the five forest zones (FZs).

FZ	Species diversity and composition	Forest dynamics	Forest structure	Productivity	Comment
DF	Low number of tree, sapling and seedling species. Low species variety with high species dominance.	Very low tree density, very low sapling density and low seedling density, with very low basal area and biomass.	Reduced canopy height and low canopy cover.	Very low litterfall production.	Highly disturbed, showing little sign of regeneration.
OC	Low number of tree, sapling and seedling species. Low species variety with high species dominance.	Very low tree density, low sapling density and high seedling density, with very low basal area and biomass.	Reduced canopy height and low canopy cover.	Low litterfall production.	Disturbed but showing some signs of regeneration.
FE	Moderate number of tree and sapling species, but high number of seedling species. Low to moderate species dominance and variety.	Moderate tree density, high sapling density and very high seedling density, with low basal area and biomass.	High canopy cover, but reduced canopy height.	High litterfall production.	Disturbed and showing signs of high regeneration.
CC	High number of tree, sapling and seedling species. Low species dominance with much variety.	High tree density, moderate sapling density and high seedling density, with high basal area and biomass.	High canopy height and canopy cover.	High litterfall production.	Similar to natural forest but with some disturbance.
NF	High number of tree and sapling species, fewer seedling species. Low species dominance with much variety.	High tree density, moderate sapling density and low seedling density, with high basal area and biomass.	High canopy height and canopy cover.	High litterfall production.	Normal forest.