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Sustaining rainforest remnants in plantation landscapes: degree of oil palm stand-induced edge effects on forest microclimate and regeneration

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ECOLOGY

ABSTRACT

Background: Amplified edge effects stemming from land use change interfere with the community dynamics of forests by altering abiotic conditions. However, the impact of oil palm plantation-induced edge effects on forest remnants is still not well-understood. This study investigated the edge influences of an oil palm plantation on adjoining rainforest remnants' microclimates and regeneration, along with variations in the effects imposed by oil palm stands' structural differences. Parallel transects were established perpendicular to the forest border in four forest patches. Distance and magnitude of edge influence (DEI and MEI, respectively) were calculated for each response variable, and PCA and ANOVA tests were used to examine variations among the variables.

Results: DEIs did not extend beyond 60 m, while the number of influenced variables decreased with increasing oil palm stand shade. MEI values were generally low, except for light intensity and seedlings. Significant differences were mostly observed only for variables at the forest fringe, and the reduction in edge influence was most prominent only with a minimum stand height of 8.5 m. Invasive undergrowth species penetrated less into the forest interior with more shade. Tree regeneration, especially of old growth species, was low, and seedlings were dominated by fast-growing trees.

Conclusion: Forest remnants benefit from edge effect-minimizing shade, but by the time this shade has formed, regeneration has already been impacted. Sustaining the ecosystem integrity of forest fragments consequently requires continuous shade from adjacent ecosystems coupled with intervention to boost old growth forest species'regeneration in low-shade areas.

Keywords: Species richness; regeneration; high conservation value; invasive species; climax species

HIGHLIGHTS

Sustaining forest fragments' integrity needs continuous shade from adjacent ecosystems. By the time edge effect-minimizing shade forms, forest regeneration is already impacted. Reductions in edge influences require a minimum oil palm stand height of 8.5 m. Tree regeneration of oil palm plantation-adjacent old growth species is reduced.

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INTRODUCTION

Edge effects stemming from forest fragmentation have been known to reduce forests' structural complexity (Laurance et al., 1998; Tabarelli et al., 2008), trigger morphogenetic tree responses (Shavnin et al., 2020), facilitate the invasion of alien species (Laurance, 2002), and adversely impact flora and fauna diversity and the community dynamics of a forest (e.g., Wilcove and Koh, 2010; Sayer et al., 2012; Luskin et al., 2017; Scriven et al., 2018), in spite of reports indicating that there could be some increase in biodiversity due to the spillover effect (Lucey et al., 2014; Chapman et al., 2019). Some studies have reported that there is a decrease in species richness with proximity to the forest edge and lower canopy closure (Scriven et al., 2018), although one finding by Alignier and Deconchat (2013) suggests that species richness may remain constant, whereas composition changes. In tropical forests, the edge effect can extend up to 300 m into the interior (Laurance et al., 1998).

The adjacency of forest edges to forest-oil palm plantations has been found to result in decreased primary productivity and carbon storage (Ordway and Asner, 2020). Although this industry contributes significantly to the economic growth of developing countries in the tropics (Sayer et al., 2012), its growth is predicated on agricultural expansion at the expense of forests, and palm oil production is considered a primary driver of forest loss and greenhouse gas emissions (Koh and Wilcove, 2008; Carlson et al., 2012). Where the seed source of an alien species is available, the edge effect of fragmented habitats will amplify its proliferation into the forest interior, up to a certain distance, which in turn may hinder or thwart the course of development of a climax community by allowing them to outcompete the old growth species (McDonald and Urban, 2006), including in forests impacted by the expansion of oil palm plantations.

Regeneration in a tropical canopy gap regime is often simplified in a scheme of shade-tolerant versus shade-intolerant species' survival ability (Schupp et al., 1989). However, there are other determining factors related to regeneration, including the arrival and survival of seeds, along with their relative advantage in successfully establishing themselves in a given site (Schupp et al., 1989). Forest remnants are prone to various biotic and abiotic changes brought about by edge effects (Ordway and Asner, 2020), including the so-called "edge-mediated effect" observed by Kupfer and Runkle (2003). It has also been reported that edges in a fragmented forest boost the growth of successional trees, both in size and number, potentially surpassing the original old growth species, due to elevated tree mortality and increased seed input of successional plants from the edges (Laurance et al., 2006). In the case of oil palm plantations, especially when the stands are still young, their air is found to be significantly warmer, and their microclimate more variable, than their forest counterparts, whose leaf area indices are higher (Hardwick et al., 2015). The microclimates of oil palm plantations, in particular, may never reach a level comparable to that of forests (Laurance et al., 2006).

There have been numerous studies dedicated to understanding the edge effects of various types of land clearings and their impacts on fragmented forests (among others, Kupfer and Runkle 2003; Harper et al., 2005; Chapman et al., 2019; Ordway and Asner 2020), and those dealing with the aftermath of the establishment of oil palm plantations (e.g., Koh and Wilcove, 2008; Hardwick et al., 2015; Scriven et al., 2018), and even research on the biodiversity in these plantations (e.g., Rembold et al., 2017; Ashton-Butt et al., 2018; Luke et al., 2019). Little is actually known about the impact of an oil palm plantation's structure on forest environmental conditions in the forest–oil palm plantation interface, even though it has been reported that mature oil palm stands have a better ability to buffer microclimates than their younger counterparts (Luskin and Potts, 2011). This research therefore aimed to fill this gap, by investigating the edge effect resulting from the establishment of oil palm plantations on adjoining rainforest remnants' microclimates and regeneration, along with variations in the effects imposed by oil palm stands' structural differences. We hypothesized that in a site with a corrugated topography like ours, the variation in canopy height and coverage of the oil palm stand plays a determining factor in influencing the depth to which the edge effect penetrates into the neighboring rainforest remnants, and that the influence of the edge effect on the forest's regeneration will vary depending on the former's depth.

MATERIAL AND METHODS

Research Area

Data collection took place in a conservation forest area located in South Solok, West Sumatra, Indonesia, managed by PT Kencana Sawit Indonesia, an Indonesian oil palm plantation company (Figure 1). This forest is part of a high conservation value area set aside by the company for conservation purposes, covering 1,772.01 ha (17.72 km^2) and bordered by the oil palm field, which is aged up to 22 years old. The forest area itself consists of four patches, interspersed within the oil palm plantation, on sites with high elevations that are unsuitable for oil palm cultivation. These patches comprise Tengah 107 Pulau hill (1°28′10″S, 101°31′38″E; 357.60 ha), Lipai 1 hill (1°26′9″S, 101°20′59″E; 267.13 ha), Lipai 2 hill (1°26′1″S, 101°35′17″E; 210.84 ha), and Salo hill (1°29′17″S,101°32′55″; 418.96 ha). Each is similar in history and structure, with dipterocarps (such as *Shorea* spp., *Parashorea* spp., and *Dipterocarpus* spp.) and other climax tree species (such as *Diospyros* spp., *Elaeocarpus* spp., and *Dysoxylum* spp.) dominating in the forest interior and a mixture of fast-growing tree species and shrubs in the outer sections (Permana, 2017). At the time of data collection, the ages of the stands bordering the forest ranged from 9 to 17 years old. While much of the forest area directly borders the plantation, these conservation patches are separated by a road that has been used for transporting harvested oil palm fruits. In the past, around 25 years ago, this initially dipterocarp-dominated forest was partially logged for timber. Before that, local people were known to cut trees from the forest for their subsistence needs. At the time of this research, the area had developed into a mixed secondary forest, in which dipterocarp species from the previous climax community could still be found among newly established pioneer tree species.

Data Collection

Data were collected from the four forest patches during the period of 10–24 January 2020, using a stratified systematic sampling method. Sampling locations were composed of parts of the forest bordering selected oil palm stands. Oil palm stand appearances differed from site to site, so we selected and classified the sampling locations of the forest based on the overall height of the oil palm trees in the bordering stand (*h*) and the canopy width of each tree (*cw*), as opposed to the age of the trees, to ensure uniformity in the measured effects. Because the forest sites were mostly located on elevated terrain compared with the plantation, and due to the corrugated nature of the terrain, oil palm tree height measurements were conducted using the floor of the forest edge as the reference point, as this study aimed to measure the effect of the oil palm shade. For our purposes, the sampling locations were categorized into five classes based on their respective bordering oil palm stand's shade: class 1 (*h* = 1.5 m, *cw* = 5.5–6.5 m), class 2 (*h* = 4.0 m, *cw* = 5.5–6.5 m), class 3 (*h* = 8.5 m, *cw* = 7.0–9.0 m), class 4 (*h* = 10.0 m, *cw* = 8.0–10.0 m), and class 5 (*h* = 12.0 m, *cw* = 8.0–10.0 m). To examine the differences of the edge effect towards the forest interior, several parallel transects were established in each fragment perpendicular to the forest border—which itself was determined as the imaginary line formed by the forest's outermost trees—100 m into theforest interior, with 15 m distances between the transects. The transects were segmented into ten 10 m depth classes, in each of which canopy photographs were taken and seedling data were collected. The number of transects varied depending on the forest terrain's accessibility and the extent of oil palm stand in each category. The aforementioned sampling design used in this study is illustrated in Figure 2. In total, 32 transects amounting to 3,200 m in length were placed, with 10 transects placed in Tengah Pulau hill, 4 in Lipai 1 hill, 10 in Lipai 2 hill, and 8 in Salo hill.

Hemispherical canopy photographs were taken continuously on clear days along the transect line from 1.5 m above ground. A smartphone (Asus ZenFone 3) attached with a 180° fisheye lens was used for photography, while the Gap Light Analysis Mobile App (GLAMA) version 3.0 developed by Tichý (2016) was used to estimate canopy covers based on the photographs. Twenty plots 1 m^2 in size were placed systematically every 10 m on each side of the transect segment to collect tree seedling species and density data. From each plot, air temperature and humidity were recorded using a thermohygrometer, soil temperature and pH using a digital soil meter, and light intensity was measured using a digital lux meter. Identification of plant specimens was conducted at the Laboratory of Plant Systematics, Faculty of Biology, Universitas Gadjah Mada, Indonesia. The classification system and identification of species referred to the Angiosperm Phylogeny Group (APG IV, 2016), whereas nomenclatural validation followed the Plants of the World Online (n.d.) database by Royal Botanic Gardens, Kew.

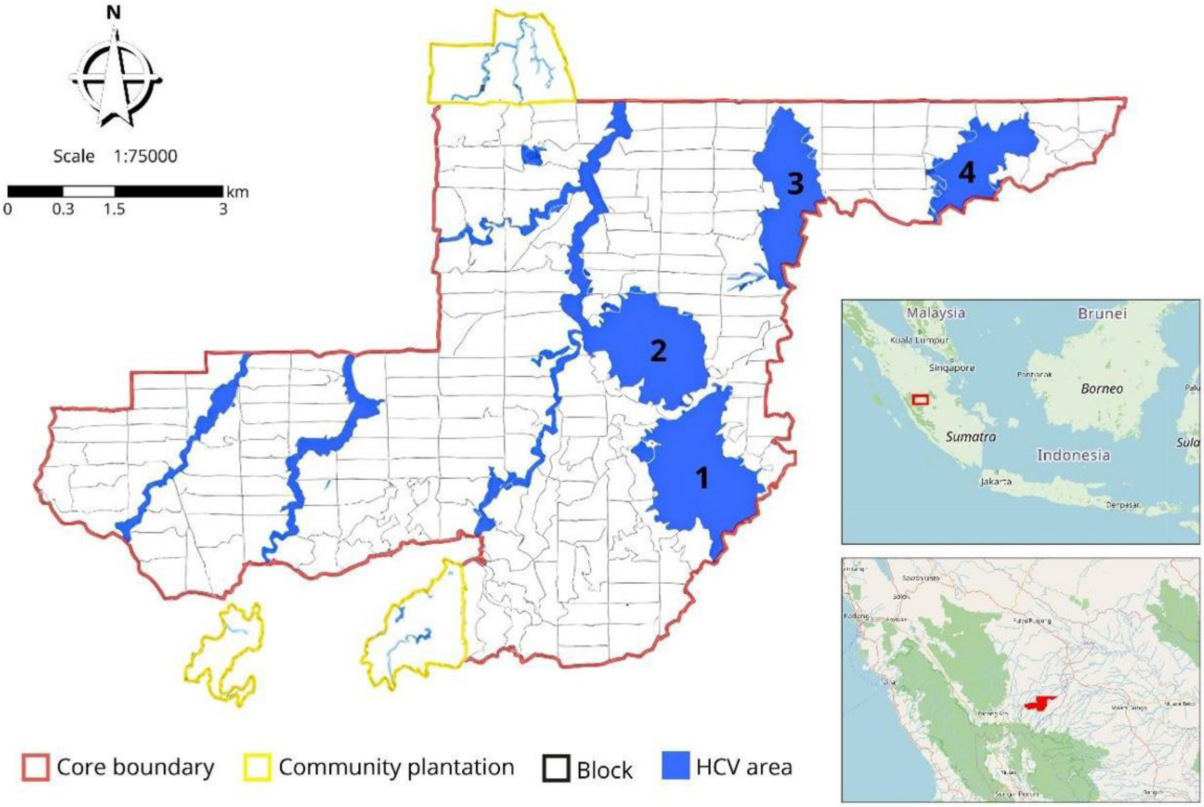

Figure 1. Locations of forest patches (blue shade) in the oil palm plantation area managed by PT Kencana Sawit Indonesia located in West Sumatra, Indonesia (see inset). 1. Salo hill; 2. Tengah Pulau hill; 3. Lipai 1 hill; 4. Lipai 2 hill. (High conservation value area map modified from PT Kencana Sawit Indonesia, 2020; inset maps by OpenStreetMap contributors, 2022).

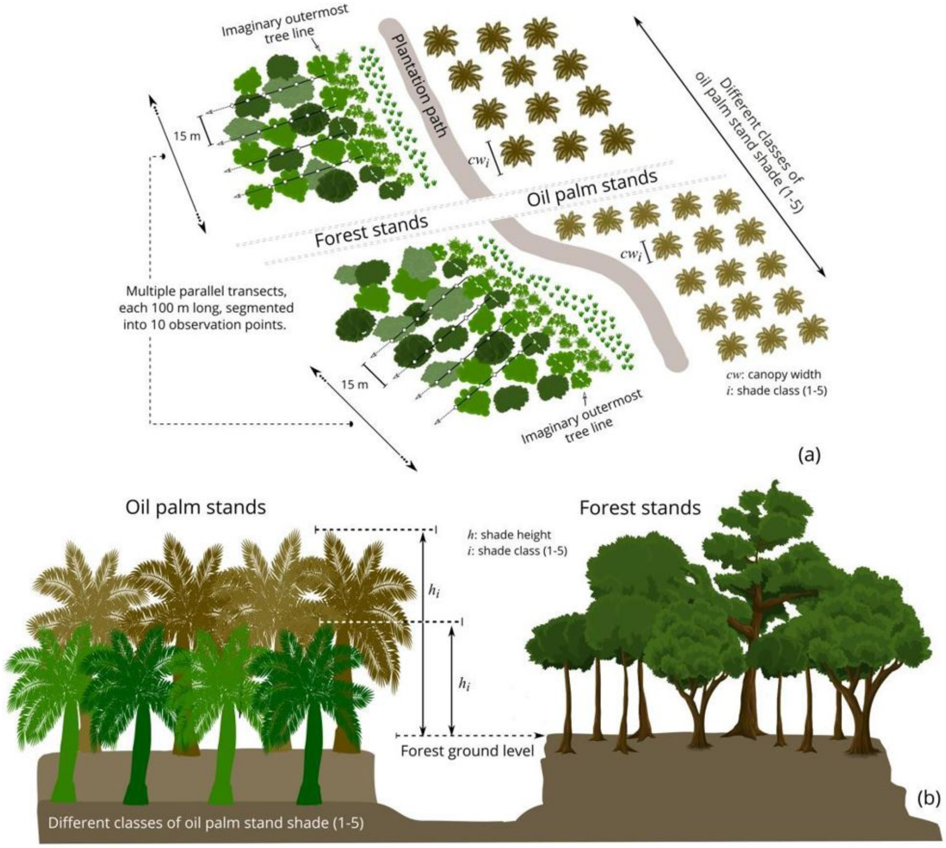

Figure 2. Visualization of the sampling design: (a) stand stratification and transect placement in each forest patch, with an illustration of oil palm canopy width measurement (*cw*), and (b) illustration on the measurement of shade height (*h*), to determine the oil palm stand shade class.

Data Analyses

The strength of edge influence was determined by calculating the magnitude of edge influence (MEI), and the depth to which the edge influence extended by calculating the distance of edge influence (DEI) for each response variable (environmental and biotic) using the randomization test of edge influence (RTEI) developed by Harper and Macdonald (2011). We used RTEI analysis with blocking, wherein data from 80, 90, and 100 m distances were used as references and data from distances of 0–70 m were used as edge data. MEI represents a spectrum of edge influence, and ranges from a very negative (MEI value = –1) to very positive influence (MEI value = 1). The MEI of each stand class was determined to be the distance where the MEI held the highest absolute value. The significance level was set for a two-tailed test at *a* = 0.05. A *p*-value of <0.025 suggested a significant negative edge influence, whereas a *p*-value of >0.975 suggested a significant positive one. The number of permutations were set at 5,000. The DEI for each stand class was determined following Harper and Macdonald's (2011) criteria. Analysis of variance (ANOVA) was performed to test the statistical differences between the environmental and biotic variables taken at different forest depths. Multicollinearity tests were performed through calculations of the variance inflation factor (VIF) for the environmental variables to observe any collinearity between variables. To examine the response of seedling density and species richness to the environmental variables, we conducted multivariate multiple regression tests. Principal component analysis (PCA) was carried out on the environmental factors to determine which of them had the most significant impact on the local environmental variations. The ANOVA tests, regression tests, and PCA were performed using PAST ver. 4.03 (Hammer et al., 2001).

RESULTS

Depth of Edge Influence (DEI) and Magnitude of Edge Influence (MEI)

Multicollinearity tests on the environmental variables resulted in VIF values below 5 (ranging 1.04–3.55), indicating a low correlation among all of the variables. As such, all these variables were used in subsequent analyses. With the exception of class 1, an irregular pattern was found in the edge influence on various environmental variables in each oil palm stand shade class (Figure 3), but the number of environmental variables whose DEIs went beyond the forest edge decreased with the increasing level of shade. In class 1, the edge effect influenced all of the environmental variables equally up to a depth of 10 m, with light intensity and soil and air temperature showing some significances at depths of 50–70 m. In class 2, canopy cover, light intensity, and humidity were significantly influenced by oil palm shade, penetrating into distances of 30, 20, and 40 m, respectively. The edge influence on canopy cover only impacted classes 1 and 2.In class 3, the DEI on light intensity, humidity, and air temperature reached depths of

30, 60, and 40 m, respectively, whereas soil pH, with a DEI of 0 m, showed an anomaly of significance at a depth of 70 m. Only humidity and air temperature were received significantly influenced by from the edge in class 4, with the DEI going as far as 50 m and 10 m, respectively. In class 5, the edge influence was limited to the periphery of the forest at 0 m for all environmental variables, except for light intensity, whose DEI reached up to 50 m. Meanwhile, the edge effect had little impact on the biotic variables (seedling species richness and density), with significant DEIs at 0 m found in classes 1 and 2, only.

In general, the magnitude of edge influence on each environmental variable either decreased or increased significantly from the forest edge to a depth of 10 m, and from then on fluctuated slightly around their median (Figure 4). Except for class 3, the edge effect showed a negative influence on canopy cover, and the effect diminished towards the forest interior. Class 3 showed a similar pattern at 0 m, before jumping to a positive magnitude at a depth of 10–40 m and thereafter returning to conforming with the general pattern. The MEI on canopy cover tended to decrease with the increase in shade class, but the values were slightly low, between −0.17 and 0.03. The pattern of edge influence on light intensity was more erratic, but overall showed a positively high magnitude, between 0.5 and 0.9 at the forest edge, diminishing with depth until 40 m, at which point the classes split off from each other. Class 2 stood out among the classes, showing a sharp decline in MEI with distance that was punctuated by a moderate positive magnitude at 40 m followed by another sharp decline into negative values. The MEI on soil pH was very low, fluctuating between −0.02 and 0.04 with no detectable pattern. Similarly, soil temperature also had low a MEI, between −0.01 and −0.03, with the significant influence occurring at 0 m, except for class 3, whose interior MEIs fluctuated at near-zero values. The general pattern showed a decreasing magnitude of influence with distance from the edge. A low magnitude of negative influence was also observed in the humidity response of the forest, with MEIs between −0.07 and 0.025, and increasing alongside depth and shade class. Except for the MEI value of class 3 at 60m, the edge influence on air temperature showed a decreasing trend with distance, albeit with a very low magnitude of influence (ranging 0.005–0.045). The classes also shared a similar MEI at 0 m, with the exception of class 2.

For the biotic variables, both seedling species richness and density started out with an MEI of −1 for all classes, which then increased with distance to a positive magnitude up to 0.6 before staying within the range of 0 and 0.7. Meanwhile, classes 3 and 5 had the highest MEI on both species richness and density. Classes 1 and 2's values were somewhat similar, but still noticeably lower than those of classes 3 and 5.

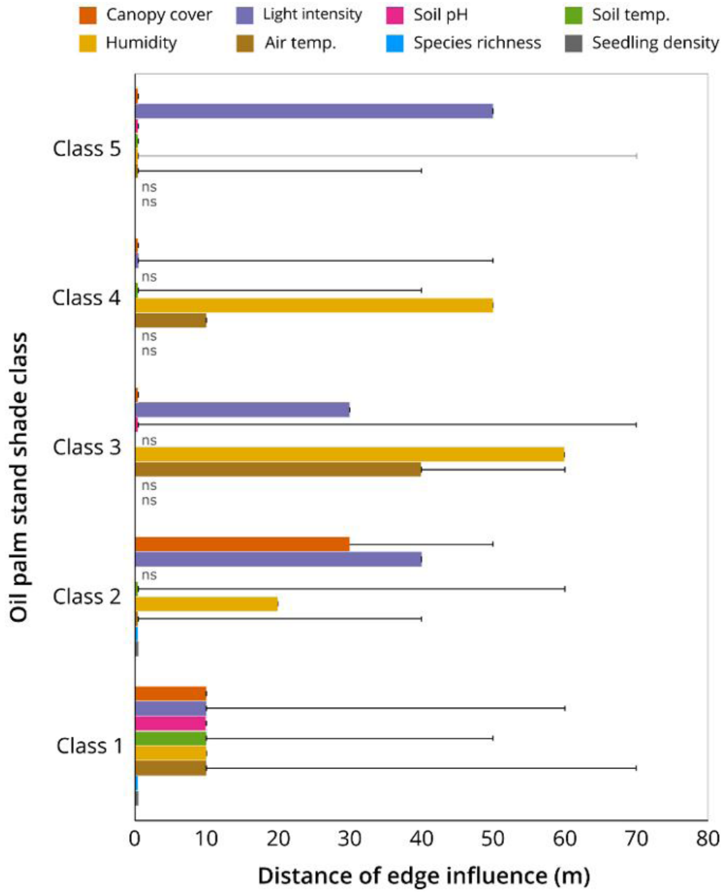

Figure 3. Distance of edge influence (DEI) of various levels of oil palm stand shade on environmental variables of forest patches. Error bars represent the farthest distance into the forest interior, where the DEI *p*-values were significant (p = 0.05, two-tailed). DEIs at 0 m are presented as 0.5 m to make them visible and to differentiate them from those with non- significant values (ns). Class 1: stand height (h) = 1.5 m, canopy width (cw) = 5.5–6.5 m; class 2: h = 4.0 m, cw = 5.5–6.5 m; class 3: h = 8.5 m, cw = 7.0–9.0 m; class 4: h = 10.0 m, cw = 8.0–10.0 m; class 5: h = 12.0 m, cw = 8.0–10.0 m. 40 m.

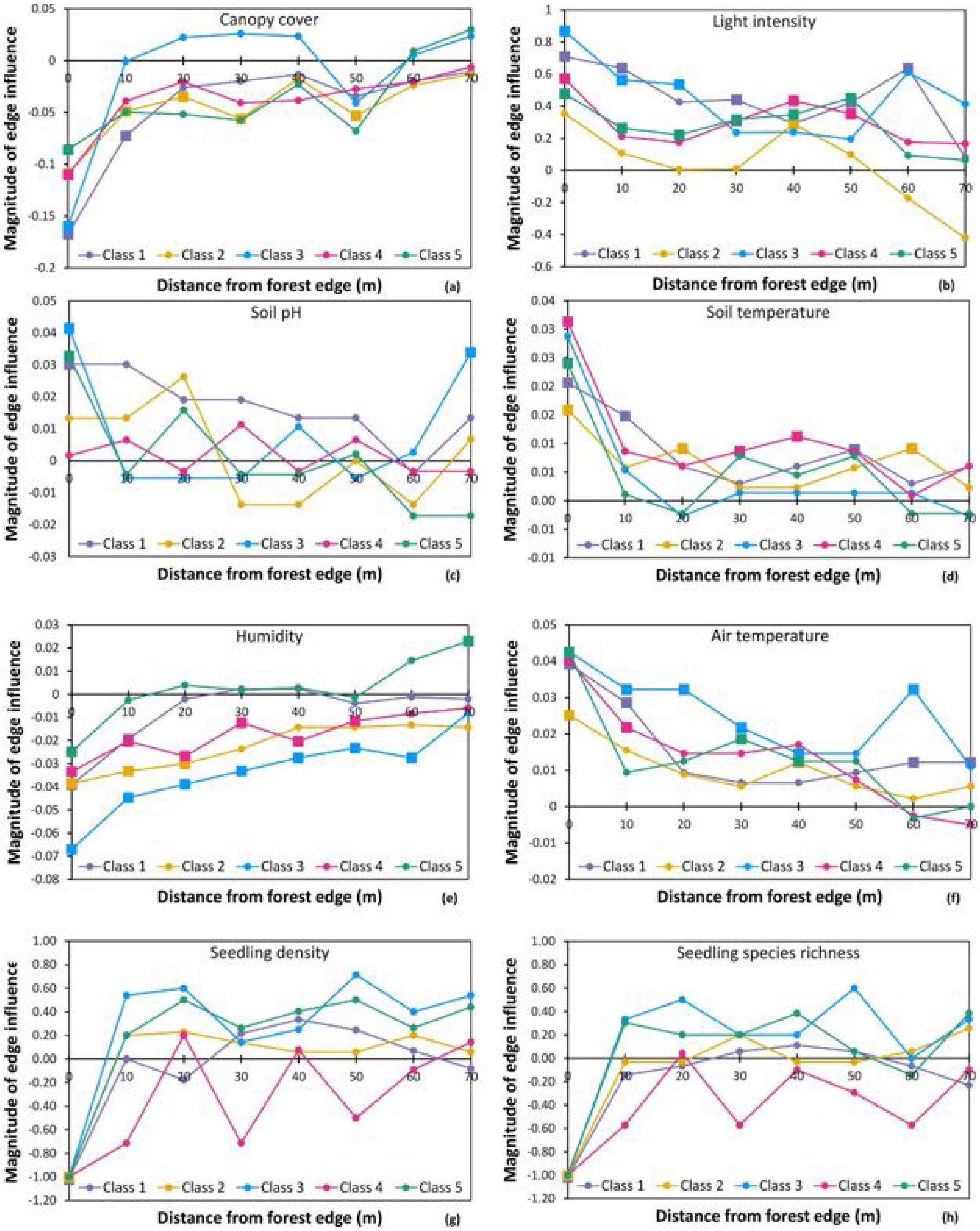

Figure 4. Patterns of magnitude of edge influence (MEI) of various levels of oil palm stand shade on environmental variables of the forest fragments. The depths in which the DEI's *p*- values were significant (*p* = 0.05, two-tailed) are denoted with square markers. Class 1: stand height (*h*) = 1.5 m, canopy width (*cw*) = 5.5–6.5 m; class 2: *h* = 4.0 m, *cw* = 5.5–6.5 m; class 3: *h* = 8.5 m, *cw* = 7.0–9.0 m; class 4: *h* = 10.0 m, *cw* = 8.0–10.0 m; and class 5: *h* = 12.0 m, *cw* = 8.0–10.0 m. (a) canopy cover, (b) light intensity, (c) soil pH, (d) soil temperature, (e) humidity, (f) air temperature, (g) seedling density, (h) seedling species richness.

Patterns of Edge Influence on Environmental and Biotic Variables

Principal component analysis of the environmental variables extracted three significant components explaining 80.2% of the total variation (Table S1). In general, themajority of observation points were found to cluster around the intercept, and appeared to be drawn towards PC1 (Figure 5). Observation points in classes 1 and 2 revealed a similar pattern, where most of the points were located between or near the soil temperature and canopy cover vectors, with a significant number of points drawn towards the light intensity vector (Figure 5a, 5b). Further scrutiny showed that these points originated from observations at the 0 m depth (Figure 5c, 5d). The patterns observed in class 3 deviated from those in classes 1 and 2. Here, the points mainly clumped near soil temperature, with some near the air temperature and pH vectors and several drawn towards the canopy cover vector (Figure 5a, 5b). Class 4 observation points exhibited a similar clustering pattern to those of class 3, but with a larger cluster towards the soil temperature and canopy cover vectors (Figure 5a, 5b). Similar patterns were observed in class 5, where clustering was strongly determined by soil temperature and canopy cover, but with more points grouped near the soil pH and air temperature vectors (Figure 5a, 5b). For both class 4 and class 5, some points scattered around the light intensity vector also came from 0 m depth observations (Figure 5c, 5d). There seemed to be a gradual overall pattern shift in the PCA observation clusters, wherein classes 1 and 2 showed a strong influence from soil temperature and canopy cover, and this influence then shifted towards soil temperature and pH and air temperature in class 3. Classes 4 and 5 retained the influence of soil temperature and canopy cover, while the influence of soil pH and air temperature was even stronger.

Based on separate scrutiny of the observation points in each forest patch depth, there appeared to be no consistent clustering pattern in any shade classes (Figure 5c, 3d). At 0 m, observation points tended to congregate around the light intensity vector for all classes, but the clustering was less strong with increasing stand shade. In class 1, specifically, the influence of light intensity was clearly observable for the 0 m and 10 m depths, while the clusters of observations in the PC1–PC2 axes shifted slightly counterclockwise in accordance with forest depth, and ending with clusters influenced by canopy cover and soil temperature at the farthest distances, indicating a shift in the influence of the other environmental variables. The clustering patterns were not as readily detectable in the other stand shade classes, nor was a consistent pattern found in each depth's observation points for these classes, instead appearing to be pulled out in the directions of the different vectors (Figure 5c, 5d).

ANOVA tests revealed that canopy covers were significantly different between forest depths in shade classes 1–4, but this significance lessened with the increase in stand shade, and became non-significant by class 5 (Table 1). In the Kruskal-Wallis test on the biotic variables, seedlings' species richness and density did not yield significant differences between any depths in all classes (Table 2).

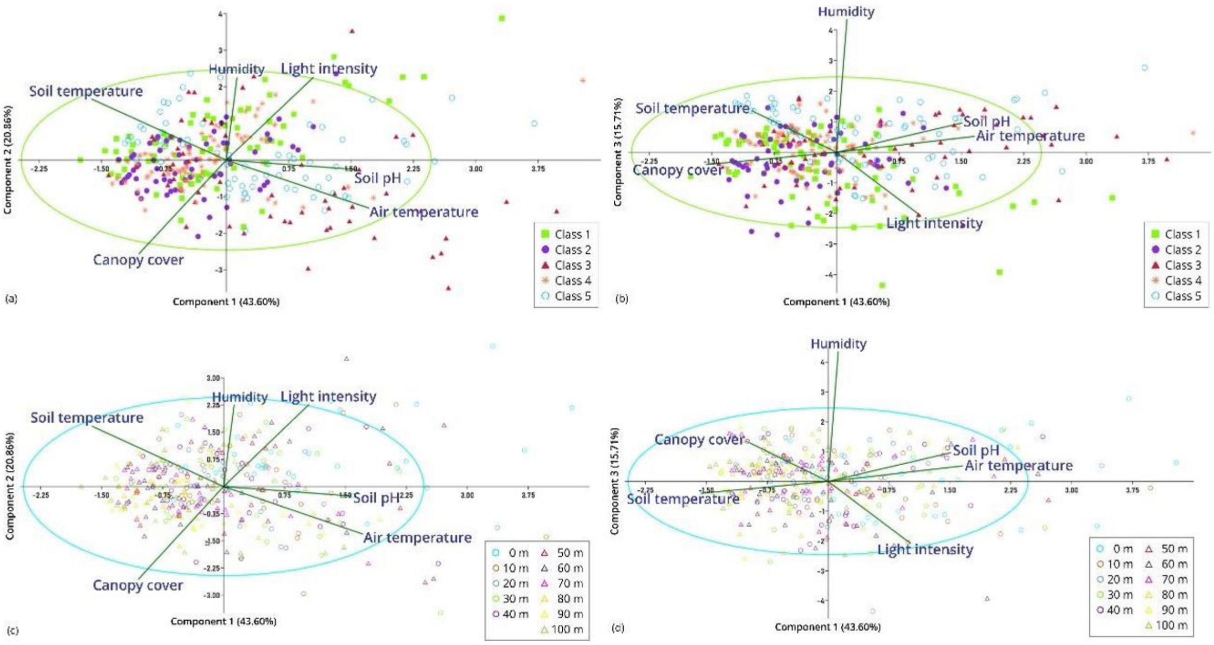

Figure 5. Eigenvalue biplots of principal component analysis (PCA) with a correlation matrix on the environmental variables measured at various depths (distance from the edge) of forest patches in different oil palm stand shade classes. Ellipse covers 95% of the observations. (a) PC1–PC2 biplot, grouped by stand classes; (b) PC1–PC3 biplot, grouped by stand classes; (c) PC1–PC2 biplot, grouped by forest depths; (d) PC1–PC3 biplot, grouped by forest depths.

Table 1. One-way ANOVA test results on the variation of environmental variables at various depths (distance from the edge) of forest patches in each oil palm stand shade class, tested at α = 0.05.

Variable	Mean	SD	*F*	*p*	Tukey's HSD‡
Canopy cover					
Class 1	46.234	12.352	3.544**	0.001	0 to (20–40,60-80, 100) 10 to 100
Class 2	83.727	9.039	2.728**	0.008	0 to (80-100)
Class 3	79.236	12.779	2.721*	0.011	0 to (20–40,70, 90, 100)
Class 4	80.739	10.592	2.229*	0.024	0 to (90–100)
Class 5	77.091	11.027	1.518	0.165	n/a
Light intensity					
Class 1	451.138	598.951	1.902	0.060	n/a
Class 2	288.456	288.852	1.108	0.373	n/a
Class 3	505.704	1147.214	1.499	0.172	n/a
Class 4	262.784	256.413	2.169*	0.029	0 to 100
Class 5	264.039	217.655	1.518	0.165	n/a
Soil pH					
Class 1	6.273	0.418	2.562*	0.011	0 to (80–100)
Class 2	6.189	0.436	0.394	0.942	n/a
Class 3	6.245	0.508	2.218*	0,025	0 to (60.80-100)
Class 4	6.369	0.298	1.042	0.422	n/a
Class 5	6.562	0.500	1.518	0.165	n/a
Soil					
Class 1	24.013	0.573	1.076	0.393	n/a
Class 2	24.288	0.489	1.042	0.422	n/a
Class 3	24.891	1.511	0.333	0.967	n/a
Class 4	24.193	0.895	1.518	0.149	n/a
Class 5	24.955	0.968	0.356	0.960	n/a
Humidity					
Class 1	79.442	5.159	1.017	0.439	n/a
Class 2	80.333	5.551	0.910	0.531	n/a
Class 3	71.273	11.014	0.932	0.514	n/a
Class 4	78.591	4.217	0.784	0.644	n/a
Class 5	77.152	7.072	0.867	0.569	n/a
Air temperature					
Class 1	25.675	1.743	0.987	0.464	n/a
Class 2	25.091	0.972	1.042	0.422	n/a
Class 3	28.018	3.064	0.338	0.966	n/a
Class 4	25.761	1.633	1.622	0.116	n/a
Class 5	26.848	2.136	0.661	0.755	n/a

**, significant at $p = 0.01$; *, significant at $p = 0.05$. ‡ Pairwise depths showing a significant difference on the Tukey's HSD test. n/a, not applicable.

Table 2. Kruskal-Wallis test results on biotic variables between various forest patch depths in each oil palm stand shade class, tested at α = 0.05.

Variable	Mean	SD	*H*	*p*
Seedling species richness				
Class 1	1.026	1.203	10.930	0.268
Class 2	0.894	0.994	13.320	0.123
Class 3	0.655	0.886	10.780	0.199
Class 4	0.295	0.590	4.069	0.666
Class 5	0.576	0.766	10.570	0.200
Seedling density				
Class 1	1.545	2.149	12.480	0.202
Class 2	0.992	1.394	12.140	0.181
Class 3	0.682	1.172	11.280	0.181
Class 4	0.580	1.319	4.156	0.656
Class 5	0.667	1.111	9.897	0.280

Significant variations within the forest depth group and shade class group were observed for all measured environmental variables, with the exception of humidity within the shade class group (Table S2). Seedling species richness showed significant variations within each group, whereas seedling density varied significantly only within the shade class group. Inter-group interactions showed no significant values for all variables measured (Table S2). Seedlings were found in low numbers, ranging from 0.5 to 1.5 individuals per square meter, and this number trended downward with each increasing shade class.

The pattern of tree seedling species richness at various forest depths beyond 0m did not show a strong trend. Richness was relatively congruous across depths, ranging from 14 to 23, with the highest occurring at 20 m and lowest at the fringe and deepest point. In spite of this similarity in richness, species composition actually differed, and species overlap between depths was low, with only 8 species present in at least 50% of the depths (Table S3). The total species richness was noticeably higher in class 1 (43 species), compared with that of the other classes, which ranged from 18 to 22 species. The most ubiquitous species in all depths and classes—*Croton argyratus*, *Bellucia pentamera*, *Neonauclea glabra*, *Ostodes paniculata*, and *Aporosa frutescens*—are all sun-loving and known to be pioneer species in disturbed forests (Slik, n.d.). Old growth forest species were still found sporadically at various depths and classes but, with a few exceptions (e.g., *Diospyros foxworthyi* and *Elaeocarpus* sp.), were conspicuously absent from the forest fringe (Table S3).

DISCUSSION

Patterns of Edge Influence on Forest Patches with Different Stand Shade Levels

A consistent but short-distanced habitat edge influence on all environmental factors was observed in oil palm stand shade class 1. With a canopy height of 1.5 m, this class presumably accorded the forest a negligible amount of protection from the edge effect, and thus its data can be seen as a proxy for the ambient environmental conditions of the forest. The results from class 1 suggest that under the minimum crown shade, the edge effect penetrated up to 10 m into the forest. The irregular pattern of edge influence observed in classes 2 to 5, along with the significant observations at several distances beyond each environmental variable's DEI depths, indicated the involvement of local factors in producing an effect that interfered with the edge effect on the forest's deeper interior. This indication is further supported by the fluctuating nature of edge influence magnitudes along the forest depths. For example, in class 5, all variables had a significant DEI of 0 m (excluding light intensity with a DEI of 50 m), despite it being the most-shaded patch. The role of a terrain's characteristics in influencing the conditions under a forest's canopy has been explored by Kupfer and Runkle (1996). The uneven, elevated terrain of the forests in our study site, a result of them being located on hills, may contribute to the variation in environmental variables in each stand class and patch depth. Nonetheless, the trend of diminishing edge influence can be seen towards the higher class of shade. Canopy cover and light intensity had a stronger magnitude of influence in the lower shade classes, whereas the influence on soil and air quality was more pronounced in the higher shade classes, albeit with relatively low magnitudes.

All six environmental variables played a role-at different levels-in determining variations in the conditions of the forest. The results suggested that each shade class had a different pattern of interactions with the environmental variables, and that each class's corresponding forest patch was subjected to different levels of edge influences as a result. The patterns of observation clusters shifted for each class, as well as the measured DEIs and MEIs, indicating that only the outer part of the forest patches and the lower shade classes received significant influences from the edge. The MEI values and PCA results also suggest that the conditions of the forest interior were shaped by more locally specific circumstances, and the role of the edge influence was minor in this matter. The fact that the measured variables largely did not differ significantly between depths in each class but did between the classes themselves shows that the influence of variations in oil palm stand shading on the forest patches is more significant between the patches than within them. This could clearly be observed in terms of canopy cover, where shade reduced the edge effect on canopy cover along the fringes of the forestpatches (in classes 1–4, significant differences in variations in canopy cover diminished between 0 m and the subsequent depths). Overall, the edge influence for all environmental variables mostly did not go beyond 60 m from the forest outer perimeter, much less than what was found by (Laurance et al., 1998) for a tropical forest.

Edge Effect and Forest Regeneration

No significant differences in seedling species richness and density were observed between any depths in each class, indicating two possibilities: that the edge influence was not strong enough to change the environmental conditions beyond the forest fringe, or was equally strong at all depths, although the latter was not supported by the MEI values. Since the DEI varied between environmental variables and shade classes, it is more plausible that in addition to other local factors playing a more significant role in interior forest regeneration, the edge effect on plan composition had faded with time, as suggested by Kupfer and Runkle (2003). The significant variations in species richness between forest depths in all classes as well as between shade classes provided a stronger indication that despite the weak edge influence on the forest interior, the level of shade from the oil palm stand canopy itself provided enough of an influence to cause significant variation in seedling species richness between forest patches. The number of seedlings along each depth class was not similarly affected, but did vary significantly with shade class. The low number of seedlings in the forest interior, which consisted mainly of shade-tolerant old growth trees and species with a wide light tolerance indicated that the canopy closure in the deeper part of the forest was not affected by the edge effect, or possibly due to a microclimate reset after the edge influence diminished with time.

With regard to seedling species richness and density, a significant DEI was only found in class 1 and class 2 at 0 m, indicating that canopy cover and light intensity were the determining factors on seedings' absence in the area. Forest fragmentation has been known to facilitate the invasion of alien species (Laurance, 2002), and we observed that the fringe area of the forest patches were overrun by dense thickets of ruderal undergrowth species-predominantly the sun-loving Old World forked fern *Dicranopteris linearis* and Indian rhododendron *Melastoma malabathricum*-and thus no tree seedlings were found at the forest edges. Undergrowth prevalence decreased towards the forest interior, and the farthest distance of their occupation was at around 30 m. Despite every class being heavily invaded by various fast-growing shrubs and ferns at their fringe, the fact that only classes 1 and 2 were observed with significant DEIs on the seedling variables suggests that this pattern was not merely shaped by competitive interaction between light-demanding versus shade-tolerant species, but also determined by the level of influence exerted by the edge's environmental conditions (canopy cover and light intensity in this case being the most significant factors).

The edge influence on seedling species richness for different classes approached zero at various interior depths, indicating almost no influence on the variable beyond the forest fringe, where no seedling was found. Seedlings became more scarce with depth. The most dominant species of trees (*Croton argyratus*, *Bellucia pentamera*, and *Elaeocarpus* spp.) also dominated as seedlings in this study, and were encountered across all classes and depths, albeit more frequently at the fringe and less so towards the interior. *Croton argyratus* and *B. pentamera* are both fast-growing, sun-loving tree species commonly found in disturbed dipterocarp forests. Another predominant seedling species, *Neonauclea glabra*, is also known as a native plant typical of disturbed dipterocarp forests. A large-scale floristic convergence caused by aggressive pioneer spreading triggered by elevated light intensity, as suggested by Michalski et al. (2007) and Santos et al. (2008), was not observable in our research area, as the edge-induced microclimatic changes did not reach deep into the forest, so pioneer species' diffusion into the forest interior was significantly hindered, and the normally problematic invasions occurred only at the fringe.

Despite being exposed to amplified edge effects from the establishment of the oil palm plantation, we still found plenty of old growth seedling species scattered throughout the forest interior, particularly those from the dipterocarp family. The susceptibility of a forest plant species to fragmentation rises with an increase in seed size due to the animal-aided nature of these seeds' dispersal (Cramer et al., 2007). However, this may not apply to dipterocarp forests in the tropics, as their large seeds are wind-dispersed. We also found several seedlings of threatened species (based on the

IUCN Red List): *Anisoptera marginata* (vulnerable; Kalima et al., 2019), *Shorea sumatrana* (endangered; Pooma and Newman, 2017), *Shorea balanocarpoides* (endangered; Ashton, 1998), and *Vatica javanica* (critically endangered; Ashton, 1998a, 1998b), all of which are members of the Dipterocarpaceae family, as well as *Swietenia macrophylla* (vulnerable; World Conservation Monitoring Centre, 1998). This suggests that, even with these ecological conditions, the forest patches were nonetheless valuable as a conservation area for various old growth species. The fact, however, that their presence was rather rare—some were found as singletons or doubletons—suggests their regeneration has been hindered. Improvement of their regeneration must therefore be prioritized, as a means of sustaining the intactness of the existing forest and preventing future degradation.

CONCLUSIONS

Forest fragments are widely known to be negatively impacted by edge effects associated with land conversion, but the severity of these effects varies with the purpose of the land clearing. In the case of forest fragments left unconverted during the establishment of an oil palm plantation, the edge effects induced differ with the level of shade provided by the adjoining stand, wherein taller stands result in a reduced edge influence. Our results showed this reduction to become most prominent only with a minimum stand height of 8.5 m. Invasive undergrowth species also penetrated less into the forest interior with more shade. Tree regeneration, however, was low, especially that of old growth species. We also found seedlings to be dominated by three fast-growing trees (*Croton argyratus*, *Bellucia pentamera*, and *Neonauclea glabra*) typical of disturbed dipterocarp forests, and which can potentially outcompete old growth trees with sufficient disturbance. As such, although forest remnants benefit from edge effect-minimizing shade, the regeneration of old growth species will already have been impacted by the time this shade has formed. Ensuring the sustainability of forest fragments' ecosystem integrity consequently necessitates measures that provide these fragments with continuous shade from adjacent ecosystems, along with intervention aimed at boosting old growth forest species' regeneration in areas where shade is low.

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SUPPLEMENTARY TABLES

Table S1. Principal component loadings of the environmental variables from different forest patch depths and oil palm stand shade classes.

Variables	PC 1	PC 2	PC 3
Canopy cover	-0.531	-0.621	0.257
Soil pH	0.789	-0.063	0.182
Humidity	0.065	0.545	0.821
Light intensity	0.531	0.548	-0.392
Soil temperature	-0.819	0.404	-0.076
Air temperature	0.868	-0.318	0.098
Variance explained by components	2.616	1.252	0.943
Percent of total variation explained	43.605	20.858	15.713

Table S2. Two-way ANOVA test results showing the variation between sample means of the different groups of observed environmental variables: forest depths (all classes combined) group, and oil palm stand shade classes group. Tested at α = 0.05.

Variables	F	p-value
Canopy cover		
Forest depths	9.994**	<0.001
Stand shade classes	6.232**	<0.001
Interaction	0.812	0.785
Light intensity		
Forest depths	3.059*	0,017
Stand shade classes	4.669**	<0.001
Interaction	1.177	0.225
Soil pH		
Forest depths	14.800**	<0.001
Stand shade classes	4.480**	<0.001
Interaction	0.259	1.000
Soil temperature		
Forest depths	16.320**	<0.001
Stand shade classes	2.334**	0.012
Interaction	0.211	1.000
Humidity		
Forest depths	7.659**	<0.001
Stand shade classes	1.788	0.062
Interaction	0.76	0.852
Air temperature		
Forest depths	20.690**	<0.001
Stand shade classes	2.997**	0.001
Interaction	0.184	1.000
Seedling sp richness		
Forest depths	2.589**	0.005
Stand shade classes	7.961**	<0.001
Interaction	0.676	0.933
Seedling density		
Forest depths	1.724	0.075
Stand shade classes	5.094**	0.001
Interaction	0.549	0.988

Table S3. Tree seedling species found at various forest patch depths and stand shade classes. (x) denotes species that was present.

Species	Family	Distance from the edge (m)											Shade class					Presence in distances (%)	Presence in classes (%)
		0	10	20	30	40	50	60	70	80	90	100	1	2	3	4	5		
Actephila excelsa	Phyllanthaceae				x								x					10	20
Actinodaphne borneensis	Lauraceae					x	x			x	x		x	x			x	40	60
Aglaia oligophylla	Meliaceae						x		x				x					20	20
Anisoptera marginata	Dipterocarpaceae											x				x		10	20
Annona muricata	Annonaceae			x						x		x	x	x		x		30	60
Aporosa frutescens	Phyllanthaceae		x	x		x	x	x	x		x		x	x	x		x	70	80
Aporosa octandra	Phyllanthaceae		x	x				x					x					30	20
Aporosa sp.	Phyllanthaceae									x			x					10	20
Aquilariasp.	Thymelaeaceae		x						x								x	20	20
Archidendron cf. microcarpum	Fabaceae						x		x			x	x	x		x	x	30	80
Archidendron sp.	Fabaceae						x						x					10	20
Baccaurea javanica	Phyllanthaceae									x						x		10	20
Bellucia pentamera	Melastomataceae		x	x		x	x		x	x	x	x	x	x	x	x	x	80	100
Brucea javanica	Simaroubaceae		x	x		x							x			x		30	40
Buchanania arborescens	Anacardiaceae					x											x	10	20
Callophyllum	Calophyllaceae					x	x								x			20	20
Cananga odorata	Annonaceae								x	x	x				x			30	20
Canarium denticulatum	Burseraceae					x										x		10	20
Cinnamomum burmanni	Lauraceae							x					x					10	20
Cinnamomum heyneanum	Lauraceae			x						x			x				x	20	40
Cinnamomum sp.	Lauraceae			x													x	10	20
Cordia caffra	Boraginaceae			x											x			10	20
Cotylelobium melanoxylon	Dipterocarpaceae										x		x					10	20
Croton argyratus	Euphorbiaceae		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	100	100
Dictyoneura acuminata	Sapindaceae										x			x				10	20
Diospyros cf. cauliflora	Ebenaceae						x							x				10	20
Diospyros foxworthyi	Ebenaceae		x			x	x									x	x	30	40
Dysoxylum acutangulum	Meliaceae											x	x					10	20
Elaeis guineensis	Arecaceae		x		x								x					20	20
Elaeocarpus angustifolius	Elaeocarpaceae			x	x	x					x		x		x		x	40	60
Elaeocarpussp.	Elaeocarpaceae		x			x	x			x			x		x			40	40
Elateriospermum tapos	Euphorbiaceae				x					x			x	x				20	40
Ganophyllum falcatum	Sapindaceae									x							x	10	20
Garcinia parvifolia	Clusiaceae										x		x					10	20
Glochidion sp.	Phyllanthaceae				x												x	10	20
Goniothalamus miquelianus	Annonaceae				x												x	10	20
Gonystylus macrophyllus	Thymelaeaceae						x		x								x	20	20
Hancea eucausta	Euphorbiaceae										x	x	x					20	20

Table S3. (continue) Tree seedling species found at various forest patch depths and stand shade classes. (x) denotes species that was present.

Species	Family	Distance from the edge (m)											Shade class					Presence in distances (%)	Presence in classes (%)
		0	10	20	30	40	50	60	70	80	90	100	1	2	3	4	5		
Huberantha rumphii	Annonaceae			x				x		x	x					x	x	40	40
Jackiopsis ornata	Rubiaceae								x						x			10	20
Lepisanthes tetraphylla	Sapindaceae									x						x		10	20
Litsea firma	Lauraceae			x									x					10	20
Macaranga cf bancana	Euphorbiaceae						x								x			10	20
Mallotus macrostachyus	Euphorbiaceae								x				x					10	20
Mallotus peltatus	Euphorbiaceae			x	x	x		x		x			x	x				50	40
Messua ferrea	Calophyllaceae							x		x			x	x	x			20	60
Neonauclea glabra	Rubiaceae			x	x	x	x		x	x	x	x	x	x		x	x	80	80
Ochanostachys amentacea	Coulaceae		x	x	x			x				x	x		x	x		50	60
Ostodes paniculata	Euphorbiaceae		x	x	x			x	x			x	x			x	x	60	60
Parashoreasp.	Dipterocarpaceae								x	x			x	x				20	40
Pavetta indica	Rubiaceae		x	x	x						x	x	x	x				50	40
Payena sp.	Sapotaceae		x										x					10	20
Pentace sp.	Malvaceae			x									x					10	20
Pimelodendron griffithianum	Euphorbiaceae						x						x					10	20
Pseudoxandra duckei	Annonaceae		x														x	10	20
Psychotria sp. (grandiflora?)	Rubiaceae				x	x		x					x	x				30	40
Rourea minor	Connaraceae								x							x		10	20
Shorea acuminata	Dipterocarpaceae								x						x			10	20
Shorea balanocarpoides	Dipterocarpaceae							x					x					10	20
Shorea cf. multiflora	Dipterocarpaceae								x			x	x				x	20	40
Shorea sumatrana	Dipterocarpaceae							x						x				10	20
Sloanea floribunda	Elaeocarpaceae						x							x				10	20
Sloanea guianensis	Elaeocarpaceae			x				x						x		x		20	40
Swietenia macrophylla	Meliaceae								x							x		10	20
Syzygium cumini	Myrtaceae			x							x				x			20	20
Syzygium jambos	Myrtaceae			x		x				x			x	x		x		30	60
Tectona grandis	Lamiaceae							x					x					10	20
Toona sureni	Meliaceae				x				x							x	x	20	40
Vatica javanica	Dipterocarpaceae								x				x					10	20
Unidentified species 1				x			x								x		x	20	40
Unidentified species 2					x									x				10	20
Unidentified species 3				x		x							x					20	20
Unidentified species 4						x		x			x	x	x	x				40	40
Unidentified species 5					x	x			x		x		x	x	x			40	60
Unidentified species 6					x		x					x			x			30	20
Total number of species		0	14	23	17	18	18	15	20	18	16	14	43	22	18	19	22		