

Microclimate and habitat heterogeneity through the oil palm lifecycle

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Abstract

The rapid expansion of oil palm cultivation and corresponding deforestation has invoked widespread concern for biodiversity in Southeast Asia and throughout the tropics. However, no study explicitly addresses how habitat characteristics change when (1) forest is converted to oil palm, or (2) through the dynamic 25–30-year oil palm lifecycle. These two questions are fundamental to understanding how biodiversity will be impacted by oil palm development.

Our results from a chronosequence study on microclimate and vegetation structure in oil palm plantations surrounding the Pasoh Forest Reserve, Peninsular Malaysia, show dramatic habitat changes when forest is converted to oil palm. However, they also reveal substantial habitat heterogeneity throughout the plantation lifecycle. Oil palm plantations are created by clear-cutting forests and then terracing the land. This reduces the 25 m-tall forest canopy to bare ground with a harsh microclimate. Eight-year-old oil palm plantations had 4 m open-canopies; 22-year-old plantations had 13 m closed-canopies. Old plantations had significantly more buffered microclimates than young plantations. Understory vegetation was twice as tall in young plantations, but leaf litter depth and total epiphyte abundance were double in old plantations. Nonetheless, leaf litter coverage was patchy throughout the oil palm life cycle due to the stacking of all palm fronds. Overall, oil palm plantations were substantially hotter (+2.84 °C) and drier (+0.80 hPa vapor pressure deficit), than forests during diurnal hours. However, there were no nocturnal microclimate differences between forests and plantations. Finally, we describe how the variable retention of old palm trees during crop rotation can retain habitat features and maintain more stable microclimate conditions than clear-cutting senescent plantations. We discuss the implications of habitat changes for biodiversity and introduce three methods to utilize temporal habitat heterogeneity to enhance the quality of the oil palm landscape matrix.

Zusammenfassung

Die rasante Ausbreitung des Ölpalmenanbaus und die damit einhergehende Abholzung hat weithin Besorgnis um die Biodiversität in Südostasien und in den Tropen hervorgerufen. Indessen hat noch keine Studie explizit untersucht, wie sich die Habitateigenschaften ändern, wenn (1) Wald durch Ölpalme ersetzt wird, bzw. (2) welche Änderungen im Laufe des dynamischen 25–30-jährigen Lebenszyklus der Ölpalme eintreten. Beide Fragen sind grundlegend für das Verständnis, wie die Biodiversität durch die Entfaltung der Ölpalme beeinflusst wird.

Unsere Ergebnisse aus einer Zeitreihenuntersuchung zum Mikroklima und zur Vegetationsstruktur in Ölpalmenplantagen in der Umgebung des Pasoh-Waldschutzgebiets (malaiische Halbinsel) zeigen dramatische Habitatänderungen, wenn Wald durch Ölpalme ersetzt wird. Es zeigte sich aber auch eine erhebliche Habitatheterogenität im Laufe des Lebenszyklus der Plantagen. Ölpalmenplantagen entstehen, indem erst Wald gerodet und dann das Land terrassiert wird. Dies reduziert den 25 m hohen Waldbestand zu kahlem Boden. Achtjährige Ölpalmenplantagen hatten eine 4 m hohe, offene Kronenschicht, 22-jährige

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Plantagen wiesen 13 m hohe, geschlossene Kronenschichten auf. In alten Plantagen war das Mikroklima deutlich stärker gepuffert als in jungen Plantagen. Der Unterwuchs war in jungen Plantagen zweimal höher, die Streuschichtdicke und die Epiphytensiedlungsdichte waren in alten Plantagen verdoppelt. Nichtsdestotrotz war die Bodenbedeckung durch Blattstreu in allen Plantagenstadien fleckenhaft, weil die Palmwedel gestapelt werden. Insgesamt waren die Plantagen während des Tages erheblich wärmer (+2.84 °C) und trockener (+0.80 hPa Wasserdampf-sättigungsdefizit) als die Wälder. Allerdings gab es keine Unterschiede zwischen Plantagen und Wald hinsichtlich des nächtlichen Mikroklimas.

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Introduction

Oil palm

Large-scale deforestation for oil palm, *Elaeis guineensis*, within the Southeast Asian “biodiversity hotspot” has emerged as a paramount global conservation issue (Myers et al. 2000; Sodhi, Koh, Brook, & Ng 2004; Koh & Wilcove 2008; Sodhi et al. 2010). Palm oil has recently become the world’s most-consumed vegetable oil, and oil palm plantations have become the largest perennial cropland on earth, their exponential growth partly driven by unparalleled oil yields compared to other crops (Corley 2009; FAO 2009). Oil palm’s rapid expansion has fueled widespread concern over how and where oil palm production is occurring and its impacts on the environment and biodiversity (Curran et al. 2004; Fitzherbert et al. 2008; Koh & Ghazoul 2010).

Ecologists argue that a growing number of studies on diverse taxa demonstrate native biodiversity is undoubtedly negatively impacted when oil palm replaces forests because few native species can persist in oil palm plantations (Fitzherbert et al. 2008; Wilcove & Koh 2010). Meanwhile, the oil palm industry maintains that plantations grow into “forests” that can support high biodiversity (MPOC 2008; RSPO 2008; Butler 2011). Indeed, current research does indicate that oil palm plantations can sustain high abundances and a diverse array of species. However, these species assemblages are distinct from those in natural forests and lack most native species (Danielsen et al. 2009). The magnitude of current oil palm expansion and controversy surrounding its consequences has sent ecologists scrambling to increase research efforts to quantify the biodiversity impacts (Turner, Snaddon, Fayle, & Foster 2008).

Habitat and biodiversity

An essential preliminary step to exploring *in situ* and landscape-level biodiversity responses to oil palm expansion is understanding the biotic and abiotic habitat characteristics that are central to shaping species distributions. Important habitat conditions for native species in plantations include tolerable microclimate conditions, leaf litter depth and

coverage, and the structure, composition and complexity of the herbaceous understory and canopy (Lawton et al. 1998; Tews et al. 2003; Schroth et al. 2004). Minimizing the differences between forest and plantation habitat conditions can increase the ability of native species to live within plantations or to periodically use plantations for foraging or other resources (Brockerhoff, Jactel, Parrotta, Quine, & Sayer 2008). Increasing the permeability of the agricultural matrix with favourable habitat conditions also facilitates native species movement between remaining forest patches, bolstering native species persistence in the landscape (Fischer, Lindenmayer, & Manning 2006).

Habitat features change throughout the plantation life-cycle, such as forage availability and continuity of canopy cover. As oil palm trees grow and gain structural complexity, native species may be more likely to utilize resources or disperse through plantations (Schroth et al. 2004; Brockerhoff et al. 2008). For example, ants, currently the best-studied taxonomic group within oil palm, exhibit marked shifts in diversity and abundance in relation to local habitat features such as microclimate, ground cover, leaf litter, and extent of epiphytes within plantations (Room 1975; Taylor 1977; Dejean, Djieto-Lordon, & Durand 1997; Pfeiffer, Tuck, & Lay 2008; Brühl & Eltz 2010; Turner & Foster 2009; Fayle et al. 2010). However, despite the fundamental role that habitat plays in determining biodiversity, little is currently known about specific habitat differences between oil palm plantations and native forests. Similarly, there is sparse data on habitat variations throughout the plantation lifecycle or at different spatial scales. Understanding how habitats change over time is especially important for oil palm plantations due to their prolonged lifecycles. Moreover, a thorough understanding of spatio-temporal habitat idiosyncrasies is vital to suggesting plantation management practices that are relatively biodiversity-friendly.

Habitat in oil palm plantations

Converting forests to establish oil palm plantations dramatically alters habitat features. It requires clearing all vegetation mechanically and/or with fire, then terracing soil, building roads and drainages, and finally planting exotic oil palm seedlings (Butler 2011). A plantation has a 25–30-year life-cycle with palms beginning to fruit after just 3–5 years



Fig. 1. Major oil palm plantation lifecycle stages relative to forest, shown with stacked palm fronds and understory vegetation. Far left is a young, 8-year-old plantation with an open canopy with a mean canopy height of 4.3 m, the middle shows an 22-year-old plantation with a closed canopy and a mean height of 13.4 m, and the far right shows adjacent forest with mean canopy height of 24.8 m (forest height from Okuda et al., 2003). Initial site preparation including clear-cutting, terracing and planting of oil palm seedlings is not shown.

(Butler, Koh, & Ghazoul 2009). Plantations go through a small tree phase with high solar radiation and wind exposure before the canopy closes (Wilson & Ludlow 1990; Corley & Tinker 2003; Fig. 1). Finally, plantations are rotated by clear-cutting existing palms when yield diminishes and trees become too tall to harvest economically (Butler et al. 2009). Slash is either reduced mechanically, by fire, or leaving it to decompose, the land is then prepared and new oil palm seedlings are replanted (Corley & Tinker 2003). Beyond the lifecycle-related effects on plantation habitat, spatial heterogeneity emerges within the oil palm landscape due to different plantation sizes and shapes. For example, oil palm cultivation ranges from smallholder plots of 1–10 ha to international corporations and government-operated mega-plantations exceeding 10 km² (Corley & Tinker 2003). The size, shape, layout and management of plantations ultimately determine much of the important landscape-scale biological processes such as connectivity, permeability and edge effects (Forman 1995).

Management

Oil palm is continually managed in evenly spaced monocultures without overstorey shade trees, which limits the capacity of characteristic forest habitat features to develop. At the local scale, periodic herbicide applications commonly

maintain easy access to the palms for harvesting and inhibit competition between the palms and other plants (Corley & Tinker 2003). Alternatively, beneficial groundcover such as small ferns or leguminous nitrogen-fixing species may be cultivated to minimize erosion and hold water close to the palms (Corley & Tinker 2003; Koh 2008). Trimmed palm leaves are stacked in large piles beneath the oil palms, which creates a patchy environment of leaf litter. The process of trimming leaves to harvest fruit bunches creates stubs that protrude 10–30 cm upwards from palm trunks. These stubs act as “pots” that collect organic matter where epiphytes then grow. Epiphytes are ubiquitous in oil palm plantations and can support epiphyte-associated species. However, the majority of epiphytes in plantations are exotic species (Danielsen et al. 2009; Fayle et al. 2010).

Objectives

This study’s primary aim was to enumerate the habitat differences between forests and oil palm that affect biodiversity responses to conversion. Next, we sought to describe how habitat conditions in oil palm change over the course of the 25–30-year plantation lifecycle. Finally, due the vast scales which oil palm is grown, we sought to understand how habitat changes at different distances from forests. In order to account for changes due to management, we also compare our results from plantations using herbicides to published results from plantations that cultivate an understory of beneficial plants (Koh 2008).

Methods

Study location

Sampling was conducted from June to August 2010 across oil palm plantations and late-successional lowland dipterocarp forest of the 2450 ha Pasoh Research Forest, Peninsular Malaysia (lat 2°5′N, long 102°18′W; Okuda et al. 2003; Fig. 2). At the landscape scale, the Pasoh Research Forest is bordered on three sides by monocultures of oil palm plantations that extend 4–10 km in each direction and forest on the fourth side (Sun, Chen, Hubbell, Wright, & Noor 2007). All plantation land was clear-cut over 30 years ago, terraced, and planted with oil palm (Naoki, Nur Supardi, Mazlan, Mahdan, & Toshinori 2001). No riparian areas or High Conservation Value Forest (HCVF) were spared and there was no intercropping. In 2010, the majority of area was in its second oil palm rotation while 22-year-old plantations were at the end of their first rotation (Fig. 2). Malaysia’s largest oil palm developer, the Federal Land Development Agency (FELDA), operated the plantations using standard techniques advocated by the Malaysian Palm Oil Board (MPOB 2010). All plantations practiced identical 9 m × 9 m palm spacing in a triangular formation by offsetting every other row. Herbicides

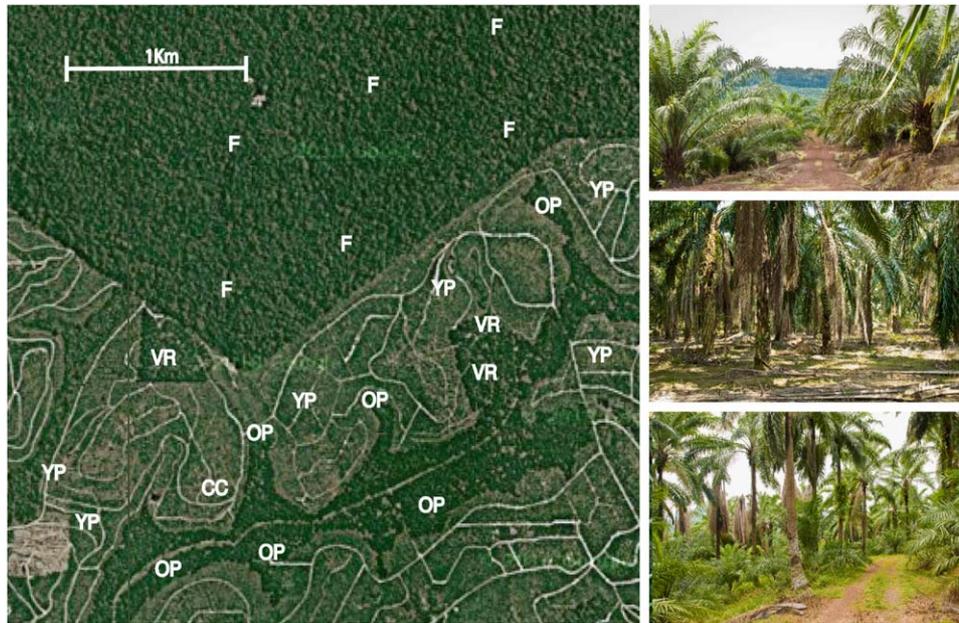


Fig. 2. Map of sampling design. F=Forest, OP=Old Plantation, YP=Young Plantation, VR=Variable Retention Regenerating Plantation, CC=Clear-Cut. Top right photo shows a young plantation at 8 years since planting, the center right photo shows a 22-year-old plantation, and lower right photo shows a plantation being rotated using the “variable retention” method (22-year-old palms have been thinned and a new cohort planted 6 years ago).

were periodically applied in plantations, but no applications occurred for at least 3 months prior to sampling. Ground-cover and epiphytes were otherwise left unmanaged unless they became obstacles to harvesting.

Sampling design

We measured microclimate in: (i) *clear-cut*, as might be found during standard plantation establishment or rotation; (ii) *young plantations*, 8 years since planting, characterized by short palm trunks (<3 m) and an open canopy; (iii) *old plantations*, 22 years since planting, characterized by tall palm trunks and a closed canopy; (iv) “*variable retention*” regeneration, an experimental rotation where every other row of 22-year-old palms was selectively thinned and an understory of new palms was re-planted 6 years prior to the study; and (v) *forest*, mature rainforest including both primary forest and forest selectively logged ~50 years earlier (Okuda et al. 2003). Vegetation was only sampled in young and old plantations. Finally, due to the vastly different scales at which oil palm production is grown, we sampled young and old plantations at both 100 m and 1 km from the forest edge. Within the forest, young plantations, and old plantations, we randomly located 6 sites, three of which were 100 m from the forest-plantation edge and three of which were 1 km from this edge. The three “variable retention” regeneration sites were opportunistically located 100–500 m from forests, and the one bare ground site was located in a 15 m × 15 m clearing at about 500 m from forest (Fig. 2).

Data collection

Temperature and relative humidity were sampled at 10 cm above the ground at 20-min intervals using 15 iButton^R sensors (model DS1923) rotated among all sites for 10 weeks (42,609 total observations collected for both temperature and humidity). The iButton^R sensors took readings accurate to 0.0625 °Celsius and 0.04% relative humidity (Maxim Integrated Products 2009). Sensors were housed in small open microclimate stations to allow for the measurement of ambient conditions while being shielded from direct sunlight and rain. For all analyses, relative humidity was converted to vapor pressure deficit (VPD) using simultaneous temperature readings (World Meteorological Organization 2008). VPD is a more biologically meaningful measure of potential water-stress, with 0 hPa representing the water vapor saturation point for a given temperature and positive values showing drier conditions.

Vegetation structure data was collected in young and old plantations along 12, 50-m transects, but not in forests, variable retention, or clear-cut sites (but see Okuda et al. 2003 for forest description). Canopy height was measured with a telescoping pole, and canopy density was measured by counting the number of separate leaves directly overhead at every metre. Trunk height (m), trunk diameter at breast height (dbh; cm), epiphytes (abundance and size per m²) and the number of palm stubs per m² were measured for closest tree at 5-m intervals along transects, including at the first and last metre (132 observations for each variable). The depth of leaf litter, height of live understory vegetation, or presence of *bare*

ground were measured at every metre point along the 50-m transects (600 observations; the mean vegetation height and leaf litter depth reported excludes zeros). *Percent area covered* represents mean presence of vegetation, leaf litter, or bare ground for all data points.

Epiphytes were quantified by creating vertical plots (1 m × 1 m) at 0.5–1.5 m above the ground on tree trunks yielding 132 plots and 2373 total epiphyte observations. The size of each epiphyte was measured as length from base to the end of the longest leaf, and only epiphytes originating within the vertical plot were counted. Epiphytes were identified into five broad groups: (i) ferns (phylum: *Pteridophyte*); (ii) palms (family: *Arecaceae*); (iii) grasses (family: *Poaceae*); (iv) vines and climbers (distinctive functional group of Angiosperms); and (v) leafy plants (all other Angiosperms). When a vertical plot could not be established, every epiphyte on the palm was counted and then transformed into a per m² value based on trunk surface area.

Statistical analyses

All microclimate analyses used generalized linear mixed models (GLMM) and controlled for the known effect of time of day (blocked by hour; (R-Cran lme4 package). We allowed for random site and day variation. In order to highlight diurnal and nocturnal microclimate differences without washing out daily fluxes, for each site we grouped 6 diurnal hours from midday (12:00 to 18:00) and 6 h following midnight (00:00 to 06:00). These were the two time periods separated by 12 h that showed the greatest statistical difference. Variable retention regeneration and bare ground sites were analyzed separately unless specifically noted. We also used GLMMs to explore differences between each type of plantation (young or old and 100 m or 1 km from forest). Vegetation analyses allowed for random site and tree variation. There were no significant temperature or VPD differences within forests at 100 m and 1 km from plantation edge, which is consistent with results from the Amazon where microclimate edge effects became undetectable at 100 m (Didham & Lawton 1999). Thus, all forest sites were grouped for the remainder of the comparisons with plantation sites.

Finally, to compare our results with results from plantations with understories actively managed for beneficial fern and nitrogen-fixing leguminous species, we ran the same analyses on vegetation data from the oil palm plantations in Malaysian Borneo reported by Koh (2008). We combined all ground vegetation types reported in Koh (2008) together and ran GLMMs for the response variables total abundance of ground vegetation and epiphytes. Fixed effect predictors consisted of plantation age and two covariates (forested area in the landscape and sampling effort, which were the only other significant predictors) and allowed for random variation between each plantation.

Results

Microclimate results

In forests, the mean diurnal temperature was 26.33 °C and the mean VPD remained near the saturation point (0.00 hPa). After controlling for normal diurnal flux in forests, plantation conditions were +2.84 °C hotter and +0.80 hPa drier (Table 1). For comparison, the daily forest microclimate flux was less than +4 °C and +0.20 hPa, so plantations produced large deviations from forest conditions (Fig. 3). There were no nocturnal microclimate differences between forests and any treatments and thus we only report diurnal results for the remainder of analyses.

The microclimate in old plantations showed less deviation from forest conditions than young plantations, being –1.20 °C cooler and +0.19 hPa more humid than young plantations ($p=0.01$ and $p=0.06$, respectively). Spatial effects from the distance from forests had low statistical significance with the most pronounced effect being young plantations +0.22 hPa drier at 1 km from forest than young plantation at 100 m ($p=0.099$). Variable retention sites showed much less deviation from forest conditions than both clear-cut and young plantations (–1.28 hPa more humid and –3.73 °C cooler than clear-cut, both $p<0.01$; –0.30 hPa more humid than young plantations, $p=0.045$). The clear-cut site was substantially hotter and drier than all other sites (Table 1; Fig. 3).

Table 1. Mean microclimate conditions in forest and relative differences (effect size) in plantations. Values show mean changes during the 12:00 to 18:00 time period. In the lower portion of the table, the relative difference of the latter category is shown (e.g. young plantations are +1.20 °C hotter and +0.19 hPa drier than old plantations). Statistical significance between groups indicated by *** for $p<0.01$, ** for $p<0.05$, and * for $p<0.10$.

	Temp (°C)	VPD (hPa)
Forest means	26.33	0.00
Forest vs	Mean Diurnal Plantation Effect Size	
All old and young	+2.84***	+0.80***
Old 100 m	+2.03***	+0.72***
Old 1 km	+2.34***	+0.66***
Young 100 m	+2.97***	+0.80***
Young 1 km	+4.03***	+1.02***
Variable retention	+3.18***	+0.73***
Clear-cut	+6.86***	+2.00***
Within Plantation Differences		
All: Old vs young	+1.20**	+0.19*
All: Near vs. far	+0.72	+0.09
Young: Near vs. far	+0.92	+0.22*
Old: Near vs. far	+0.31	+0.07

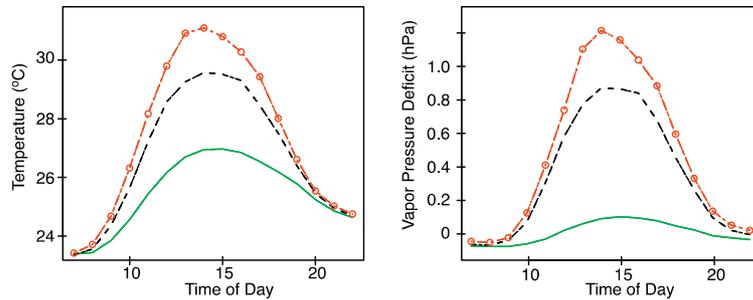
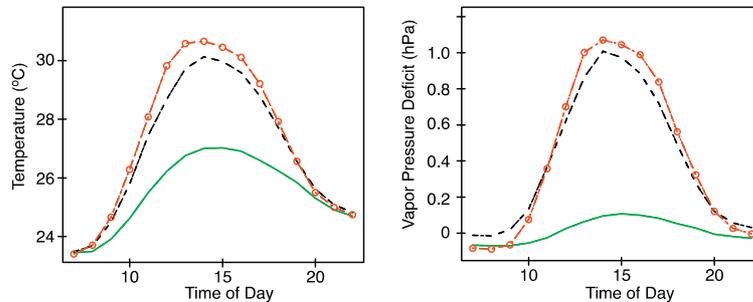
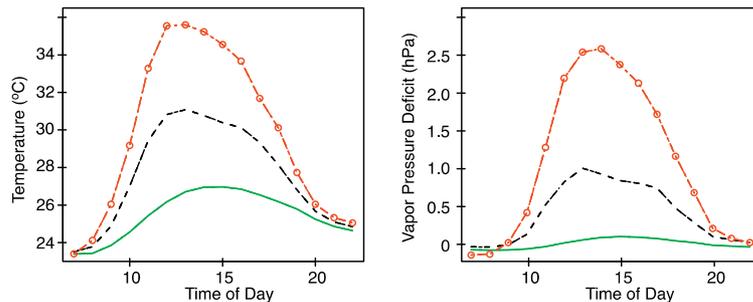
(A) Forest (solid green), old (dashed black), and young plantations (red open circles)**(B)** Forest (solid green), plantations at 100m (dashed black), and 1km (red open circles)**(C)** Forest (solid green), variable retention (dashed black), clear-cut (red open circles)

Fig. 3. Microclimate conditions in forests and different oil palm plantations. Graphs on the left show temperature (degrees Celsius); graphs on right show vapor pressure deficit (hPa). Panel (A) shows young plantations are hotter and drier than old plantations, panel (B) shows plantations further from forests are only slightly hotter and drier, and panel (C) shows clear-cut sites are considerably hotter and drier than the “variable retention” method of rotating plantations. Note the scale changes in (C).

Vegetation results

Leaf litter was twice as deep in old plantations as in young plantations (mean 9.84 cm depth in young plantations compared to 20.61 cm in old plantations), while the live vegetation understory was twice as high in young plantations (mean 11.46 cm in old plantations compared to 21.77 cm in young plantations; Fig. 4). However, the percentage of ground area occupied by bare ground, vegetation, and leaf litter did not vary between old and young plantations. Old plantations had taller trees and increased canopy depth but fewer frond stubs remaining per m^2 on trunks. Distance from forest had no detectable effects on vegetation characteristics.

Epiphyte density in young plantations was twice that in old plantations (mean 12.35 epiphytes m^{-2} compared to

23.50 epiphytes m^{-2} in young plantations), yet total epiphyte abundance was still much greater in old plantations due to vastly greater trunk surface area (Table 2). In old plantations, there was a fourfold decrease in the density of ferns and palms, while grasses were more abundant. Leafy and climbing epiphytes showed no differences between young and old plantations. Overall, ferns dominated the epiphytic community, climbers were the largest and most rare, and grasses were the smallest.

The analysis of the Koh (2008) vegetation data from plantations in Borneo with managed understories showed a similar decreasing trend for epiphyte density with plantation age (1.29% less “epiphyte coverage” per year; $p < 0.05$), yet a positive trend for understory vegetation coverage through time (1.19% more ground coverage per year; $p < 0.05$; see Appendix A).

Palm Structure	Young	Old	
Canopy Top (m)	4.31	13.38	***
Trunk Height (m)	1.31	9.63	***
Canopy Bottom (m)	2.21	8.17	***
Leaves Overhead	2.20	2.76	
Trunk DBH (m)	0.77	0.61	***
Trunk Surface Area (m ²)	3.16	18.49	***
FronD Stubs (per m ²)	30.82	19.42	***
Ground Structure			
Height Live Veg (cm)	21.77	11.46	**
Leaf Litter (cm)	9.84	20.61	**
Bare Ground Coverage	22%	22%	
Live Veg Coverage	46%	45%	
Leaf Litter Coverage	47%	47%	

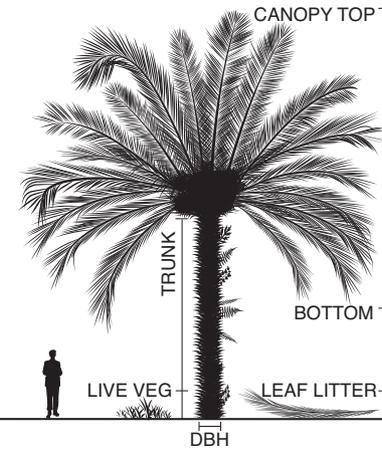


Fig. 4. Vegetation structure of oil palms, ground vegetation and leaf litter in plantations. Young plantations are 8 years since planting, old plantations are 22 years since planting. Statistical significance between old and young plantations indicated by *** for $p < 0.01$, ** for $p < 0.05$, and * for $p < 0.10$.

Discussion

There are complicated and sometimes opposing habitat trends through the oil palm plantation lifecycle. Overall, there is a shift from taller ground vegetation in open young plantations to a more buffered microclimate, increased leaf litter, and a closed-canopy in old plantations (Fig. 5). The diurnal microclimate was dramatically altered during plantation establishment (clear-cut), became increasingly buffered though time as palms grew and the canopy closed, but never regained the stability of forest conditions (Fig. 5). Leaf litter depth increased as plantations aged, but more importantly, the percentage of area covered by leaf litter was always low (47%), with the vast majority neatly stacked into even patchier piles (for comparison, leaf litter coverage is >90% in forests). The understory vegetation height and epiphyte density were greater in young plantations where the open canopy allowed more sunlight to penetrate (Wilson & Ludlow 1990), yet the ground area covered with vegetation remained constant between old and young plantations. We anticipated nocturnal conditions to be colder, windier and drier in plantations due to less standing biomass and less structural complexity to trap and re-radiate heat and moisture

than forests (Siles & Harmand 2009). However, there were no microclimate differences between forests and plantations or between plantation types during the night.

Spatial effects were less pronounced than lifecycle-related changes but suggested young plantations might be drier further from forests ($p = 0.099$; Fig. 3). We anticipated microclimate would be more extreme at 1 km away due to less spillover from forests and greater all-around exposure; however, our results showed only small changes that may require increased sampling to detect with statistical certainty. Similarly, we hypothesized that epiphyte abundance and ground vegetation would decline further from forest source populations, yet there were no detectable spatial effects on any vegetation parameter (but note that species composition was not studied).

Habitat changes and biodiversity

The substantial microclimate differences in all plantations relative to forests confirm ecologists' concern that forest-dependent species will be threatened by oil palm expansion (Fitzherbert et al. 2008). Hot and dry diurnal conditions observed throughout the plantation lifecycle present a

Table 2. Epiphyte density (number of individuals per m² of stem surface), total epiphyte abundance per tree, and mean size of each epiphyte (length from base to tip measured in cm) in 22-year-old and 8-year-old oil palm plantations. Statistical significance between old and young plantations is indicated by *** for $p < 0.01$.

	Epiphyte density (per m ²)		Epiphyte abundance (per plant)		Epiphyte length (per tree)	
	Old	Young	Old	Young	Old	Young
Fern	4.24	14.7***	78.40	46.45***	15.6	12.3
Climber	0.26	0.48	4.81	1.52	107.9	105.7
Leafy	4.09	5.55	75.62	17.54***	14.2	16.2
Grass	3.24	0.02***	59.91	0.06***	7.6	8.8
Palm	0.52	2.76***	9.61	8.72	27.5	15.1
Total	12.35	23.50***	228.35	74.26***	15.5	16.0

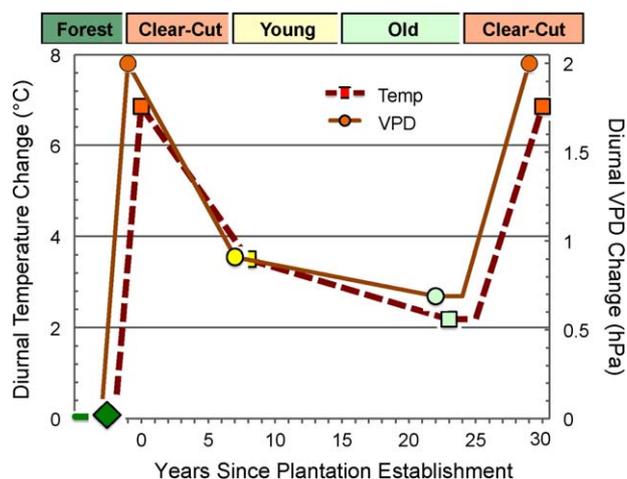


Fig. 5. Diurnal microclimate changes over the oil palm plantation lifecycle relative to forest conditions. Points denote where data was collected, lines between points estimate interim conditions. Forest values are standardized to 0 (no change from natural conditions). Plantations are hotter (+°C) and drier (+hPa) relative to forests. VPD is shown offset 1-year back to differentiate overlapping points. In this scenario, forest is clear-cut in year -2 , oil palm seedlings are planted in year 0, and the senescing plantation is rotated by clear-cutting in years 25–30 (replanting not shown).

microclimatic barrier to sensitive native species that are adapted to moist, buffered rainforest climates (Perfecto and Vandermeer 1996; Porter & Kearney 2009). This effect would be reduced for nocturnal species, as plantation conditions were indistinguishable from forests at night. A species' ability to live or move through plantations will also change through time as plantations grow. For example, the dramatically drier conditions in clear-cut and young plantations could preclude understory herbaceous plants or amphibians that require stable, moist conditions for recolonizing. By contrast, these species may survive later when the plantation canopy closes and microclimate is more buffered. Thus, old plantations with smaller microclimate differences from forests will be relatively more hospitable to native species in this niche dimension. Nonetheless, predicting species-specific impacts requires significantly more research (Jackson, Betancourt, Booth, & Gray 2008; Tewksbury, Huey, & Deutsch 2008).

More ground vegetation in young plantations may attract herbivores to forage (Lawton et al. 1998; Tews et al. 2004). Wahab (2000) similarly showed a decreasing trend in total understory vegetation biomass through the oil palm lifecycle, led by declines in grasses, legumes, and edible dicots (see Appendix A). However, old plantations possess other habitat features including epiphyte abundance, leaf litter depth, increased ferns and non-edible dicots, and a closed canopy that may provide cover and support wildlife movement (see Appendix A, Armbrrecht, Perfecto, & Vandermeer 2004; Hilty, Lidicker, & Merenlender 2006). A closer examination of wildlife usage of large leaf litter piles is warranted, as we opportunistically observed passerine birds, birds of prey,

snakes, monitor lizards, small lizards, rodents, macaques, pigs, a civet, and leopard cats within or on top of piles.

Management implications

Habitat heterogeneity through the plantation lifecycle should be integrated into planning more biodiversity-friendly oil palm landscapes (Pimentel et al. 1992; Tews et al. 2004; Perfecto, Vandermeer, & Wright 2009; Fig. 5). First, reducing patch/field size and creating a patchwork of different-aged plantations can increase the total habitat variety and complementarity in the landscape (Fig. 6, "Increased Heterogeneity"). This also reduces the contiguous size of major disturbances and increases the availability of features through time. Even massive plantations could designate "blocks" for rotation/replanting at different time periods, a widespread biodiversity-friendly tactic used in timber production forests throughout the world, including parts of Southeast Asia (Thang 1987; Smith, Larson, Kelty, & Ashton 1997; van Kuijk, Zagt, & Putz 2009). Furthermore, increasing landscape-scale heterogeneity could have social and economic benefits by more evenly distributing costs, oil production, income, and labor requirements through time. A detailed cost-benefit analysis is warranted.

In addition to creating a patchwork of different aged plantations, planting schedules could be augmented to increase permeability and connectivity between remaining forests. Planting in progressive strips between remaining forests would create a multitude of continuous plantation "corridors" of the same habitat types (Fig. 6, "Increased Connectivity"). Also, special attention to maintain continuous oil palm canopy cover and shade could increase wildlife propensity to traverse between forest patches (Perfecto, Rice, Greenberg, & Van der Voort 1996). These methods could complement, not replace, natural habitat corridors, riparian corridors, and High Conservation Value Forest, to increase the quality of the landscape matrix (Hilty et al. 2006; RSPO 2008).

Clear-cutting old palms to regenerate senescent plantations creates a barren landscape and harsh microclimate (Figs. 3 and 5). This eliminates most *in situ* biodiversity, restarting the process of biodiversity colonization and accumulation within plantations. On the other hand, a "variable retention" method leaves mature palm trees during the initial conversion (usually every-other row), and then converts the rest after 5–10 years when the new crop has started fruiting (Fig. 6, "Variable Retention"). This incurs less severe disturbance and retains a more hospitable microclimate and vegetation structure that native species are more likely to utilize and traverse (Smith et al. 1997; van Kuijk et al. 2009). However, local FELDA managers complain that retained old palms can serve as disease and pest reservoirs, and the Malaysian Palm Oil Board advises against this method, citing disease and efficiency reasons (Corley & Tinker 2003; MPOB 2010). Nonetheless, smallholders often practice variable retention due to logistical, personal, and economic reasons,

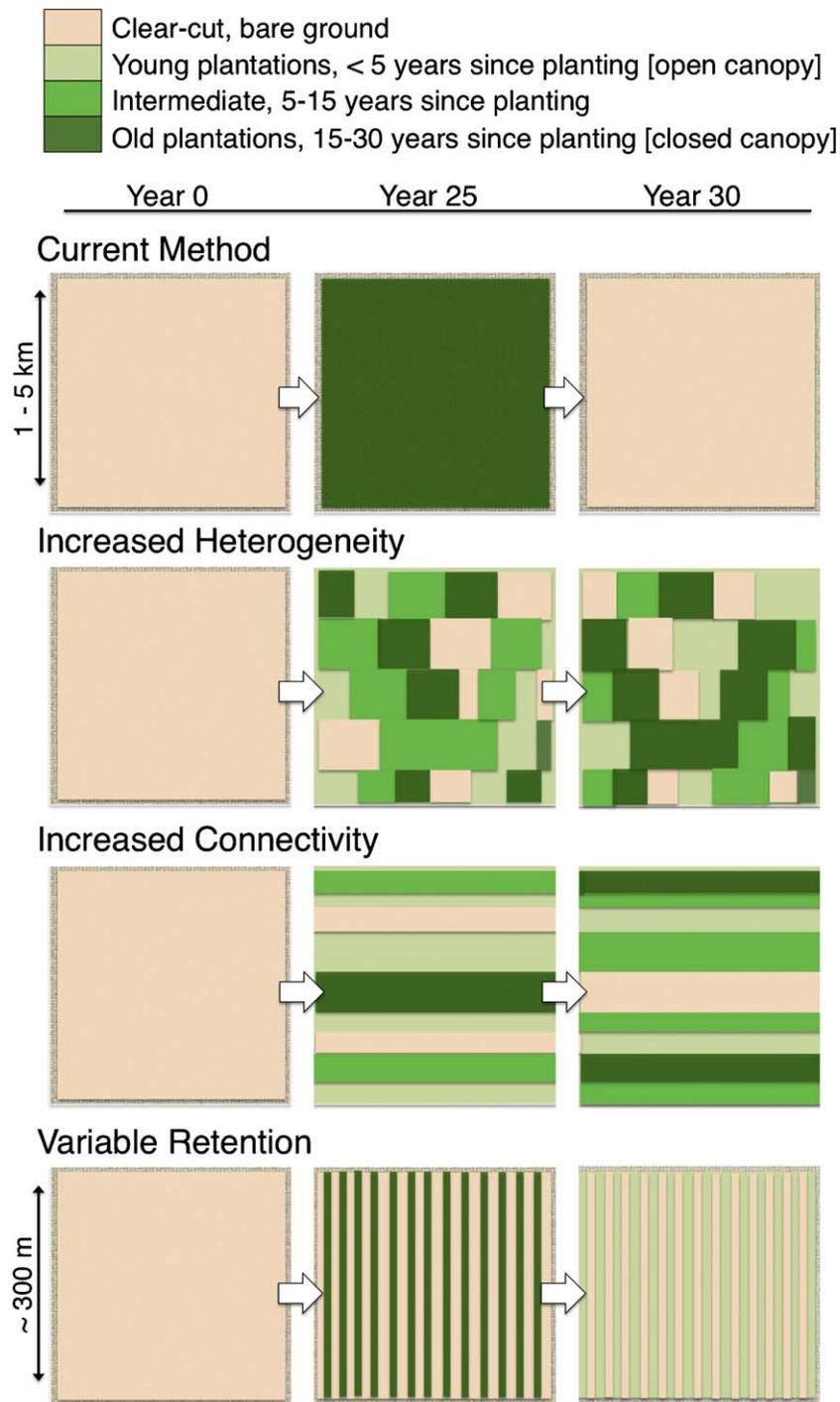


Fig. 6. Conceptual models to increase field and landscape-level plantation habitat heterogeneity. The prevalent “Current Method” is to plant single-aged mega-plantations. This creates large tracts of monotonous habitat and periodic large-scale high-intensity disturbances during clearing and replanting. The “Increased Heterogeneity” scenario shows the same landscape when smaller patches of oil palm are planted at intervals. This creates a patchwork of different fields and reduces the area clear-cut at a given time. The “Increased Connectivity” scenario provides a continuous habitat-type (i.e. a closed canopy) between remaining forests by planting in successive strips. These “corridors” of continuous oil palm habitat can enhance forest species movement through the matrix. The “Variable Retention” of palms during crop rotation reduces the severity of disturbance. First, *every other row* is cleared and replanted after 20–25 years, and then 5–10 years later the remaining rows are replanted. These three methods can be combined and their scale and orientation adapted to realistic situations.

such as maintaining consistent fruit production and revenue streams over the rotational period (FELDA, pers. comm.). The biodiversity responses, yield effects, economics, and disease-related dimensions of variable retention regeneration should be a research priority, as currently available data suggest it may be a relatively easy method to reduce the severity of continued disturbances within plantations.

At the local scale, agricultural land with unmanaged understory can support greater plant diversity, including more weedy species that host additional associated biodiversity (Légère, Stevenson, & Benoit 2005). Our analysis of Koh's (2008) data from managed plantations shows vegetation coverage increasing through time, yet this likely reduces floral diversity (De Chenon & Susanto 2006). Thus, in young plantations where sunlight is abundant, allowing the understory to develop naturally by minimizing herbicide application may promote high floral diversity and abundance (see Appendix A). In old plantations, more research is needed to weigh the relative benefits of floral diversity and total ground vegetation coverage provided by managed understories.

Overall, these management suggestions echo the calls of other ecologists for careful spatial design of oil palm landscapes to minimize impacts on biodiversity (Koh, Levang, & Ghazoul 2009). However, we further this discussion by introducing another layer, the temporal scales associated with the oil palm lifecycle, which can be manipulated at both the field level (variable retention rotations) and landscape level (reduced field size and altering planting/rotation times; Fig. 6). Spatio-temporal landscape design should be integrated with improved management within plantations, and most importantly, traditional conservation efforts (HCVF, riparian corridors, et cetera) to improve the quality of oil palm landscapes for biodiversity.

Conclusion

Oil palm plantations are characterized by continued high-intensity disturbances and habitat features that are strikingly different than those of the forests they often replace. These conditions present a barrier to sensitive rainforest species and oil palm should never be considered a substitute for natural forests. Ongoing conservation efforts should therefore continue to focus on slowing deforestation by limiting oil palm expansion to existing degraded areas, of which there are plenty (Koh & Ghazoul 2010). While oil palm plantations never regain the microclimate or vegetation structure of forests, specific habitat characteristics evolve following different trajectories, creating a heterogeneous habitat through time. Our discussion highlights several potential methods to utilize temporal habitat heterogeneity to create a higher-quality landscape matrix. Specifically, the oil palm matrix may be improved by (1) reducing field sizes and creating a patchwork of different aged plantations, (2) increasing connectivity by maintaining continuous tracts of same-age plantations through the landscape, and (3) mini-

mizing the intensity of continued disturbances by using the variable retention method of rotating senescent plantations instead of clear cutting. These tools should be incorporated into landscape planning to improve the oil palm matrix quality, but cannot replace traditional conservation efforts.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2011.06.004.

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