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Research

Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia

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The conversion of natural forest to oil palm plantation is a major current threat to the conservation of biodiversity in South East Asia. Most animal taxa decrease in both species richness and abundance on conversion of forest to oil palm, and there is usually a severe loss of forest species. The extent of loss varies significantly across both different taxa and different microhabitats within the oil palm habitat. The principal driver of this loss in diversity is probably the biological and physical simplification of the habitat, but there is little direct evidence for this. The conservation of forest species requires the preservation of large reserves of intact forest, but we must not lose sight of the importance of conserving biodiversity and ecosystem processes within the oil palm habitat itself. We urgently need to carry out research that will establish whether maintaining diversity supports economically and ecologically important processes. There is some evidence that both landscape and local complexity can have positive impacts on biodiversity in the oil palm habitat. By intelligent manipulation of habitat complexity, it could be possible to enhance not only the number of species that can live in oil palm plantations but also their contribution to the healthy functioning of this exceptionally important and widespread landscape.

Keywords: oil palm; *Elaeis* spp.; biodiversity; ecosystem function; ecosystem service; habitat complexity

1. INTRODUCTION

Agricultural ecosystems have become the dominant landscapes in many areas of the tropics, as they have been—often for centuries—in temperate regions [1,2]. The loss of pristine habitats to agriculture in the tropics is of particular concern, since this is where global biodiversity is concentrated [3]. We argue here for the development of mosaic landscapes that include two vital elements. First, the landscape must contain old-growth forest reserves: these can provide the ecosystem benefit of conserving rare and threatened species [4]. Second, biodiversity must be conserved within the remainder of the landscape to provide potential support to a variety of other ecosystem functions such as pollination, biological control, litter and dung decomposition, maintenance of water quality and environmental awareness. We will chiefly be concerned here with this second element, the crop habitat, since this is a dominant part of the landscape and the part that is continually managed. We concentrate here on arthropods, because they are the animals that play the most important roles in maintaining ecosystem functions [5] and hence are potentially the key players in fostering sustainability in these mosaic landscapes. They also operate at small spatial scales and exist within small niches so that management practices to increase habitat complexity may very readily enhance arthropod biodiversity.

Oil palm, *Elaeis* spp., is of immense global importance and is an excellent model system in which to investigate the relationship between biodiversity and ecosystem services at the landscape level. Oil palm now covers over 14.5 million hectares. Indonesia and Malaysia are the largest producers, and oil palm cultivation is rapidly expanding in areas such as Thailand, Nigeria and Colombia [6]. Palm oil is the most widely used vegetable oil in the world and of huge importance as a biofuel feedstock [7]. Although much has been

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written about oil palm, a recent analysis showed that less than 1 per cent of these publications related to biodiversity [8] and almost nothing at all seeks to relate biodiversity and ecosystem services. In the past three years, although a further approximately 1100 manuscripts have been published on oil palm, only 4 per cent of these have been on biodiversity and conservation, and more than half of *these* manuscripts have been focused on policy and meta-analysis, rather than the provision of field-based data. A further problem is that much of what has been written on environmental issues relating to oil palm is in the grey literature and not accessible to the wider scientific community [9]. A general consensus is emerging that the only way to conserve species of high conservation value in the tropics is by land sparing and the provision of large forest reserves [4,10]. Although this may be true for many forest species, it is nevertheless important to examine critically conservation practices within plantation areas. We therefore advocate an approach that is much broader, both in its taxonomic range and in considering the effects of biodiversity on the whole spectrum of ecosystem functions provided within the oil palm ecosystem. Such an approach is crucial, as biodiversity maintained within plantation areas can still be substantial, and a more biodiversity-friendly environment can help to buffer and provide a foraging resource for species within forest areas [11] and also provide important ecosystem functions and increase productivity within the crop area itself [12]. In addition, the oil palm industry provides direct employment for over half a million people in Malaysia [13], and oil palm plantations are one of the most common landscape types that people see in large parts of the tropics. If a healthy general attitude to conservation is to be maintained, we therefore think it is vital to deal seriously with the issues of biodiversity and ecosystem services within this extensively managed landscape. If the biodiversity regularly visible in forest areas within oil palm plantations is altogether extinguished, then so also may be people's concern for the conservation enterprise as a whole.

In this article, we will present an up-to-date review of the evidence that is available on the extent and nature of biodiversity loss when forest is converted to oil palm; on the causes of this biodiversity loss; and on the implications of this for the functioning of the oil palm environment. We will consider what practical methods might be adopted to mitigate this biodiversity loss and allow a more sustainable development of this vitally important tropical landscape. Our aim is to develop an approach that will look beyond simply conserving forest species to one that also sustains the functioning of the landscape as a whole.

2. BIODIVERSITY LOSS ON THE CONVERSION OF FOREST TO OIL PALM

The majority of taxonomic groups show decreased species richness and overall abundance in plantations when compared with primary forest (figure 1 and table 1). However, there are some exceptions to this, with dung beetles [20], isopods [21], lizards [22] and bats [16] all increasing in abundance, although still decreasing in richness. Only one group, the bees,

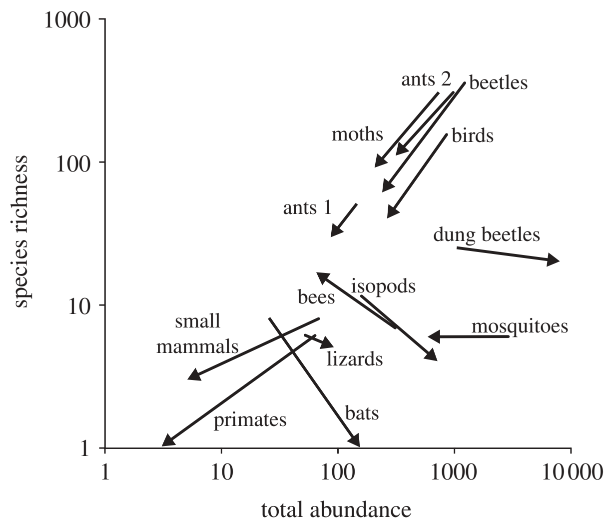

Figure 1. The impacts of converting primary rainforest into an oil palm plantation on the abundance and species richness of different taxa. Arrow tails denote primary forest communities and arrow heads oil palm communities. Where multiple oil palm plantations were surveyed, or multiple techniques were used to sample a single taxon (but where sampling effort was equivalent in both habitats), average values are used. Note that we do not include studies where collection methods differed between habitats or those that do not provide abundance data. Data sources: ants 1 [14]; ants 2 [15]; bats [16]; bees [17]; beetles [18]; birds [19]; dung beetles [20]; isopods [21]; lizards [22]; mosquitoes [23]; moths [24]; primates [16]; small mammals [25].

increases in species richness [17]. These groups carry out important ecosystem functions, such as nutrient cycling, predation and pollination, and so their increase in abundance or species richness might have the potential to buffer ecosystem functioning against changes caused by the losses of other species. All other taxonomic groups surveyed to date (eight studies) are negatively affected in terms of both species richness and abundance by oil palm expansion (figure 1) [10,39–41].

Much of the forest that is converted to oil palm is not primary forest but forests that have already been logged or degraded in a variety of ways or indeed have previously been under another land use such as rubber [34]: this factor is included in table 1. Once-logged forest appears to retain a reasonable proportion of the species present in old-growth forest [42,43], although it is likely that further rounds of logging will be more detrimental [44]. It is therefore not surprising that comparisons of species richness and composition between logged forest and oil palm plantations show a similar pattern to that for old-growth forest, with extensive species losses occurring [10]. Assessments of the biodiversity value of forest fragments are rarer, but show that populations become more genetically isolated [27], and become very similar in terms of species composition to those found in oil palm [4]. The abundant oil palm/forest boundaries that have arisen during this shift in landscape use [45] may provide benefits to some species, such as leopard cats, owing to increased numbers of prey in the plantations [46], although it is unclear how the majority of taxa respond. We urgently need further data on the importance of forest fragments, for example, on steep slopes and as riverine strips, as reservoirs for taxa and as wildlife corridors within the oil palm matrix.

The impacts of habitat conversion may vary between different parts of a habitat. For example, the responses of whole arthropod communities vary between those inhabiting the canopy, those within epiphytes and those found in litter on the ground [26]. The change in ant species richness is also dependent on the microhabitat studied, with epiphytes maintaining a similar number of species in plantations to that found in forest, despite drastic reductions in species richness in the rest of the canopy and the leaf litter. There is, however, almost complete turnover in species composition between forest and plantation fern-dwelling ant communities [15]. These observations show that only a careful and detailed sampling protocol can fully capture the effects of habitat conversion on forest arthropods.

In order to understand the consequences of the conversion of forest to oil palm, we need to know more than just the overall quantitative changes in biodiversity. What kinds of species are we losing and what are their roles in the oil palm landscape? It is clear that many forest species and species of conservation importance are lost during habitat conversion to oil palm. In 17 of the 19 studies where the origin of a species was noted (table 1), there was a loss in either abundance or diversity of specifically forest species.

We know almost nothing at all about the levels of beta diversity of the animals and plants in the oil palm landscape (but see [32,33,47,48]). It would be expected that the increased homogeneity would cause a decrease in beta diversity in plantations. This depends on whether plantation species are a subset of the forest species found locally, or mainly composed of widespread tramp species. So far it appears that they are a mixture of both [15,49]. The manner in which succession of species occurs on oil palm plantations also remains to be discovered. Palms are often allowed to grow for up to 30 years, creating the potential for the development of temporally distinct communities [50].

Plantations are unlikely to support viable populations of species of conservation importance. But it does not follow from this that we should simply abandon attempts to study biodiversity within the oil palm landscape. What matters in plantations is whether there is a functional role for biodiversity and whether we therefore need to focus our research on the causes of diversity loss and the consequences of these losses for ecosystem function.

3. CAUSES OF BIODIVERSITY LOSS

The broad reasons for the loss of animal biodiversity when natural ecosystems are converted to agriculture are clear. The man-made landscape is now drastically simpler, in terms of both its plant diversity and its architectural complexity. This simplification is especially stark if the natural ecosystem is tropical rainforest, the most biodiverse ecosystem on Earth. But can we identify specific factors that are of crucial importance to biodiversity loss when forest is converted to oil palm? If we can, this will assist us in any attempt to minimize impacts on ecosystem function. The postulated causes of reductions in biodiversity on habitat conversion to oil palm are listed in table 2.

The key features of the context of biodiversity loss on conversion of forest to oil palm are captured in figure 2, which shows transects in a lowland dipterocarp forest and an oil palm plantation in Sabah. These features can be grouped into two broad categories (table 2), biological and microclimatic, which, together with direct human impacts, are the major causes of biodiversity loss.

(a) *Biological simplification*

The huge reduction in tree species diversity (table 2) will inevitably lead to a comparable reduction in the diversity of animals that use trees, especially the legions of herbivorous insects: plant biodiversity begets animal biodiversity [59–61]. Not only is diversity reduced at the taxonomic level, but clearly oil palm plantations are architecturally much simpler than forests, with fewer canopy layers, and less diverse elements of, for example, lianas, epiphytes and litter (table 2). Of the 14 studies that discuss the likely causes of changes in diversity of arthropods on conversion to oil palm (table 1), 10 mention changes in habitat suitability and three of these also mention reductions in plant diversity, although there is no supporting quantitative evidence for this.

However, this simplification should not be overstressed. Oil palm estates, even in the areas away from forest fragments and riverine strips, do contain significant structural complexity, particularly if they are compared with other tropical agricultural crops (e.g. soya bean or rice). The palm trees are large and long-lived, and this provides some heterogeneity and time for a complex assemblage of species to be built up [62]. There is a herb layer, which can be of some complexity, and there is the potential for a relatively rich assemblage of epiphytes, which readily gain a foothold on the oil palm trunks. Indeed it is notable that in West Malaysia, half of the epiphyte species of lowland areas have also been recorded from oil palm plantations (table 2).

(b) *Microclimatic effects*

Six of the 10 arthropod studies that mention changes in habitat suitability in table 1 suggest that changes in microclimate underlie the observed changes in arthropod diversity on conversion of forest to oil palm. Because the oil palm canopy is lower, more open and simpler than that of closed-canopy rainforest, the temperature and humidity conditions are more challenging for most organisms. There are two elements to this change: the conditions are more extreme (higher temperatures, lower humidities) and they also vary much more on a daily basis [63,64] (figure 3). It is interesting that the conditions in the oil palm understorey are in general more similar to those in the high canopy of emergent rainforest trees: organisms from this layer of the forest may therefore face fewer problems in colonizing oil palm than those that live in the more extensive forest understorey. Indeed, the single species of the epiphytic bird's nest fern that survives in oil palm plantations appears to be a high-canopy species, with the forest understorey species becoming extinct [57,65].

Table 1. Studies comparing the abundance and diversity of particular taxonomic groups in forest and oil palm plantations, including fragments within plantations. Only those studies that used similar sampling techniques across habitats are included.

group	habitats compared with oil palm	oil palm age (years)	effects of conversion on taxa surveyed	postulated drivers of these effects	study location	source
arthropods						
all arthropods	primary and secondary forest	14–18	decrease in arthropod abundance and biomass across three microhabitats	altered habitat structure and microclimate	Sabah, Malaysia	Turner & Foster [26]
two ant species (*Odontomachus rixosus* and *Pheidole annexus*)	primary forest and forest fragments within plantations. Plantation matrix not surveyed	40[a]	decrease in genetic variability in two ant species in small forest fragments in the oil palm matrix	isolation owing to unsuitability of the oil palm matrix	Sabah, Malaysia	Bickel *et al.* [27]
ants	primary forest	7–20	reduction in species richness, most abundant oil palm ant species are non-forest ones[b]	extreme reduction in leaf-litter volume, unsuitable microclimate	Sabah, Malaysia	Bruhl & Eltz [28]
ants	primary forest	14–18	reduced ant species richness in canopy and leaf litter, but not in ferns, but high turnover in all microhabitats[b]	altered habitat structure and microclimate	Sabah, Malaysia	Fayle *et al.* [15]
ants	mangrove	7	very low species richness in both oil palm and mangrove owing to low sampling intensity[b]	not assessed or discussed	Peninsular Malaysia	Hashim *et al.* [29]
ants	primary forest, rubber and oil plantations, grassland, savannah, urban areas	'very young'	reduction in species richness and equitability, changes in dominance patterns. Twenty-five per cent of species found in both forest and oil palm[b]	lower diversity of herb species and consequently of homopterans, availability of colonists	Papua New Guinea	Room [14]
ants	primary/secondary forest and kola, cashew, coffee and plantain plantations	—	reduction in species richness	availability of nesting sites, reduction in canopy cover	Nigeria	Taylor [30]
bees	primary and secondary forest	52[a]	higher species richness in oil palm than in most forested areas, but lower abundances	changes in the density of large trees, temperature and flowering intensity of trees and shrubs	Peninsular Malaysia and Singapore	Liow *et al.* [17]
beetles	primary and secondary forest and acacia	6–7	reduction in species richness, with a small number of species becoming numerically dominant	reduction in litter volume, plant and tree species richness, sapling density and canopy cover	Sabah, Malaysia	Chung *et al.* [18]
family of beetles (Staphylinidae)	primary and secondary forest and acacia plantation	6–7	decrease in staphylinid species richness and abundance	not assessed or discussed	Sabah, Malaysia	Chung *et al.* [31]
dung beetles	primary and secondary forest and cacao plantation	—	reduction in species richness, but increase in abundance. Most forest species absent or rare in plantations[b]	changes in microclimate and surface cover. Reduction in mammal densities	Ghana	Davis & Philips [20]

(*Continued.*)

Table 1. (*Continued.*)

group	habitats compared with oil palm	oil palm age (years)	effects of conversion on taxa surveyed	postulated drivers of these effects	study location	source
butterflies	primary forest and forest fragments within plantations. Plantation matrix not surveyed	—	larger and less isolated fragments have more species. But smaller fragments (120 ha) can still support species of conservation importance	fragment size and isolation	Sabah, Malaysia	Benedick *et al.* [32]
species of butterfly (*Mycalesis orseis*)	primary forest and forest fragments within plantations. Plantation matrix not surveyed	—	decreased genetic diversity with increasing fragment isolation, but no effect of fragment size	reduced migration between more isolated fragments	Sabah, Malaysia	Benedick *et al.* [33]
butterflies	primary and secondary forest	—	reduction in forest butterfly species richness from both primary and secondary forest[b]	not assessed or discussed	Peninsular Malaysia and Borneo	Koh & Wilcove [34]
moths	primary and secondary forest	5–15	reduction of species richness by 67%, reduction in species evenness	reduction in understorey plant diversity owing to herbicide application	Sabah, Malaysia	Chey [24]
mosquitoes	primary forest	0–2	reduction in abundance, but not in richness of forest species and consequent reduction in risk of malaria transmission[b]	reduction in shaded areas of standing water required for larval survival	Sarawak, Malaysia	Chang *et al.* [23]
terrestrial isopods	primary and secondary forest and fruit orchard	10	reduction in species richness and evenness for some forest sites but not others. Loss of forest species at all sites. Increase in abundance[b]	increase in canopy openness, more fluctuating microclimatic conditions at soil surface	Sabah, Malaysia	Hassall *et al.* [21]
mammals						
primates	primary forest and rubber plantation	—	only one forest primate species remaining in oil palm[b]	not assessed or discussed	Sumatra, Indonesia	Danielsen & Heegaard [16]
squirrels	primary forest and rubber plantation	—	no species in oil palm[b]	not assessed or discussed	Sumatra, Indonesia	Danielsen & Heegaard [16]
tree shrews	primary forest and rubber plantation	—	no species in oil palm[b]	not assessed or discussed	Sumatra, Indonesia	Danielsen & Heegaard [16]
bats	primary forest and rubber plantation	—	reduction in species richness to 13–25% of primary forest, change in community structure[b]	not assessed or discussed	Sumatra, Indonesia	Danielsen & Heegaard [16]
bats	primary and secondary forest and fragments within oil palm (and rubber). Plantation matrix not surveyed	—	fragments >100 ha contribute usefully to landscape-scale bat conservation	differences in roosting requirements	Peninsular Malaysia	Struebig *et al.* [35]
large mammals	secondary forest and scrub	—	only 10% of mammal species found in oil palm, but many more species survive in adjacent forest edges[b]	lack of cover and plant diversity, increased visibility to predators (including humans) and prey, lack of food resources	Sumatra, Indonesia	Maddox *et al.* [11]

(*Continued.*)

Table 1. (*Continued.*)

group	habitats compared with oil palm	oil palm age (years)	effects of conversion on taxa surveyed	postulated drivers of these effects	study location	source
small mammals	primary forest and secondary forest	recent to over 20	reduction in species richness and abundance, plantations of no conservation importance and act as barriers to dispersal[b]	not assessed or discussed	Sabah, Malaysia	Bernard *et al.* [25]
birds						
birds	primary forest and rubber plantation	<20	reduction in species richness and in species of conservation importance, more species in plantations with undergrowth[b]	not assessed or discussed	Thailand	Aratrakorn *et al.* [36]
birds	primary forest and rubber plantation	—	5–10% of forest species remain in oil palm, more generalist species[b]	not assessed or discussed	Sumatra, Indonesia	Danielsen & Heegaard [16]
birds	secondary forest and forest fragments	20–30	drastic reduction in abundance and diversity in fragments within oil palm compared with contiguous forest. Fragments support bird communities more similar to those found in the matrix than to those found in forest[b]	not assessed or discussed	Sabah, Malaysia	Edwards *et al.* [4]
birds	primary forest and rubber plantation	>15	reduction of 80% in forest species richness[b]	reduction in canopy cover	Peninsular Malaysia	Peh *et al.* [19]
birds	secondary forest and acacia plantation	<10	very few forest species in oil palm plantations. Acacia is better for forest bird species[b]	habitat simplification	Sabah, Malaysia	Sheldon *et al.* [37]
reptiles						
lizards	secondary forest, cacao plantation, pasture, home gardens, undisturbed hilltops	—	reduction in species richness, but increase in abundance[b]	reduction in the range of microhabitats available	Dominican Republic	Glor *et al.* [22]
single-celled eukaryotes						
diatoms	unpolluted river versus river polluted with palm oil effluent	—	reduction in diatom species richness and evenness. Reduction in seasonal variation in communities	deterioration in water quality, although no correlations between diatom diversity and water quality parameters	Peninsular Malaysia	Khan [38]

[a]Time since clearing, not the age of the oil palm stand.
[b]Studies showing changes in numbers of *forest* species on conversion to oil palm, rather than changes in overall richness or other parameters.

Table 2. Comparisons of selected environmental variables in primary dipterocarp forest and mature oil palm plantations (Malaysia).

category	rainforest	oil palm
tree species diversity (>10 cm g.b.h., no. of spp.)	587[a]	1
	820[b]	
mean tree density (>10 cm g.b.h., stems ha^{-1})	2248[c]	145[d]
basal area (>10 cm g.b.h., m^2 ha^{-1})	30.7[e]	59.4[d]
epiphytic fern diversity (no. of spp.)	88[f]	44[g]
Asplenium nidus biomass (kg ha^{-1})	886 ± 133[h]	131 ± 37.1[i]
Asplenium nidus abundance (no. ha^{-1})	44 ± 9.2[j]	112 ± 21.3[i]
litter diversity (spp. m^{-2})	11.7 ± 0.7[k]	2.4 ± 0.2[k]
litter abundance (g m^{-2})	437.9 ± 24.4[k]	310.5 ± 29.9[k]
canopy cover	90.2 ± 0.8%[k]	66.9 ± 1.6%[k]
	97.1 ± 0.47%[l]	78.3 ± 2.51%[l]
food resource index	0.82 ± 0.24[m]	1.37 ± 0.20[m]
temperature (°C)	21–33[n]	23–36[o]
	22–30[p]	
	20–28[j]	21–44[i]
humidity (% R.H.)	65–100[n]	48–100[o]
	94–100[p]	
	82–109[j]	38–100[i]

[a]Trees >10 cm g.b.h. in 8 ha, lowland Forest, Danum Valley, Sabah [51].
[b]Trees >10 cm g.b.h. in 50 ha, lowland forest, Pasoh, West Malaysia [52].
[c]Trees >10 cm g.b.h. in 8 ha, lowland Forest, Danum Valley, Sabah [53].
[d]Trees >10 cm g.b.h. in 1 ha of 14–18-year-old oil palm plantation at Sabahmas Estate, Sabah (current data).
[e]Trees >10 cm g.b.h. in lowland forest, Danum Valley Sabah [53].
[f]No. of spp. of epiphytic ferns in lowland rainforest, West Malaysia [54].
[g]No. of spp. of epiphytic ferns in oil palm plantations, West Malaysia [55].
[h]Mean values from 7 ha lowland forest, Danum Valley, Sabah [56].
[i]Age of oil palm 14–18 years. $n = 20$ [26].
[j]Mean ± s.e.m. from 20 transects, lowland forest, Danum Valley, Sabah [57].
[k]For both rainforest and oil palm, $n = 20$ litter samples (4 m^2); age of oil palm 14–18 years [58].
[l]Means ± 95% CI, in lowland forest, Sungei Bantang, West Malaysia, and in 15-year-old oil palm plantations, in Johor, West Malaysia [19].
[m]Means ± 95% CI, combined quantified index [1–6] of fruiting and flowering in lowland forest (Sungei Bantang), and in 15-year-old oil palm plantations (Johor, West Malaysia) [19].
[n]Measured in $n = 5$ emergent trees in the high canopy of lowland forest Danum Valley (figure 3).
[o]Measured in $n = 6$ (temperature) and $n = 5$ (relative humidity) in 14–18-year-old oil palm trees over 24 h periods at plantation sites in Sabah (see [26] for full site details of the study site).
[p]Measured in $n = 6$ (temperature) and $n = 5$ (relative humidity) low-canopy trees over 24 h periods in lowland forest Danum Valley (figure 3).

There is some evidence that high temperatures do adversely affect arthropod abundance and activity in these habitats: when arthropod trap catches are plotted against temperature at the time of capture, they follow an inverse relationship that seems to be similar for both forest and oil palm understorey (figure 4). The increases in temperature following forest clearance are much more dramatic than any changes that are predicted to result from global warming, and are likely to be more severe for tropical than for temperate species [66].

(c) *Direct human impacts on oil palm biodiversity*

The creation of large tracts of a crop monoculture not only directly reduces biodiversity but it also creates a golden opportunity for invasion by pests and weeds, which can suppress other species and whose control can lead to yet further impacts on biodiversity. Oil palm is attacked by a wide variety of pests, including, for example, rats and herbivorous insects, and by diseases, especially those caused by fungi [67,68]. The numbers of these pest species have increased over the last 50 years as herbivores have switched from other hosts to attacking oil palm [62]. The oil palm industry has for a long time realized that the most effective way of dealing with pests is through some form of integrated pest management [69]. Nevertheless, chemicals are widely and intensively used to control oil palm pests. This is bound to have harmful direct and indirect effects on biodiversity in the oil palm landscape.

4. CONSEQUENCES OF BIODIVERSITY LOSS FOR ECOSYSTEM FUNCTIONING IN OIL PALM

There is considerable support for the notion that increased biodiversity has significant positive effects on ecosystem function, from theoretical and experimental model systems [70], but extraordinarily few real-world examples that this happens in natural ecosystems [71]. The crucial question here is whether the documented losses in animal biodiversity associated with oil palm cultivation matter in relation to ecosystem function. Taxa that show increases in abundance (figure 1) might be important in ecosystem processes and have the potential to buffer ecosystem functioning against changes caused by the losses of other species. Species diversity also provides temporal resilience for ecosystem processes and the possibility for the system to adapt to future changes [72]. We here discuss what is known about the ecosystem functioning and the provision of ecosystem services within oil palm landscapes that are potentially

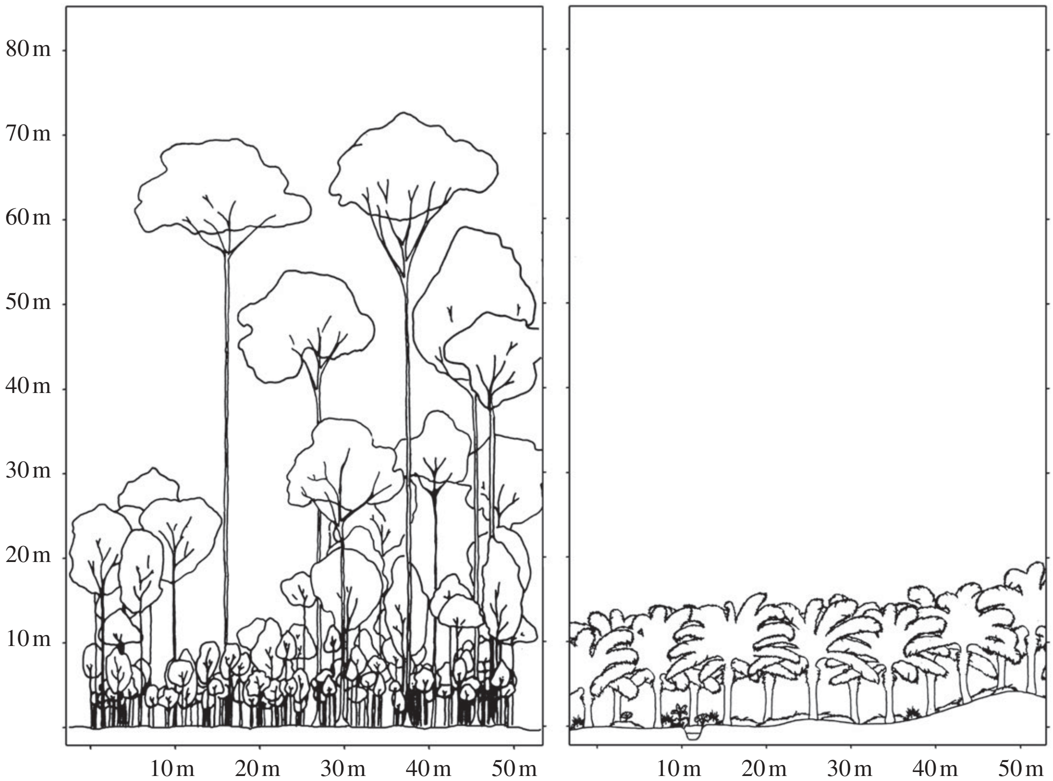

Figure 2. Lateral sections through primary forest (Danum Valley Conservation Area, Sabah) and oil palm plantation (Sabahmas, Lahad Datu, Sabah). Each section is 70 m in height by 50 m width.

mediated by arthropods: biocontrol, pollination, decomposition and soil fertility.

(a) *Biocontrol*

Oil palm pests tend to be native species that have transferred to the introduced oil palm monocultures [73]. Although there is a wide range of economically important pest taxa, the most prominent are lepidopteran insect defoliators, principally bagworms (Psychidae) and nettle caterpillars (Limacodidae) [69,74–76]. Historically, general control methods such as blanket spraying were used in an attempt to prevent outbreaks, but it became the consensus that this spraying affected the natural enemy populations of the oil palm pests [69]. Integrated pest management techniques are now standard within the industry. Particularly effective examples of this include the use of the fungus *Metarhizium anisopliae* in the control of rhinoceros beetles; adult assassin bugs (Heteroptera) in the control of a range of herbivorous insects; and barn owls (*Tyto alba*) in the management of rats [68].

Although there are many studies describing the natural enemies (especially parasitoids) of oil palm pests, the only published work that experimentally links natural predation with biological control is Koh's study of the effect of birds on herbivory in oil palm plantations [77]. It is known that oil palm insect herbivores are an important part of the diet of insectivorous birds [78], and Koh showed that by caging young oil palms in bird exclosures, herbivory was significantly increased. There is, however, no link made to bird *biodiversity*, nor is there a measured effect on oil palm yield, and, since these experiments were done on 1-year-old seedlings, they may not be relevant to mature plantations.

There is evidence that oil palm herbivory rates may be influenced by ant community composition. Herbivory rates have been shown to be negatively correlated with the occupancy of *Crematogaster* and positively correlated with the abundance of *Tetramorium* [79]. We must be wary of assuming that non-forest species have no role to play in sustaining ecosystem function in oil palm. For example, the common insectivorous oil palm birds are not forest specialists [4,77,78]. Non-native species, even those that have negative impacts in some situations, for example, the yellow crazy ant *Anoplolepis gracilipes*, which is common in oil palm [15], have been used to control herbivore populations in cocoa and coconut plantations [80].

(b) *Pollination*

Pollination of oil palm in South East Asia generally relies on a single species of weevil, *Elaiedobius kamerunicus* (Coleoptera: Curculionidae), which was introduced into the area from its native West Africa in the early 1980s, providing a huge boon to the industry, eliminating the need for hand pollination and increasing yield by around 20 per cent [81]. However, total reliance on a single species is in principle risky [72], and there are specific concerns emerging about the effectiveness of the weevil. The weevil is relatively ineffective as a pollinator in dry conditions and in heavy rain [82]; there can be high levels of attack by parasitic nematodes, which can greatly reduce the fitness of the weevil [83]; and there may be high levels of inbreeding depression [74].

One potential solution to these problems is to increase the number of pollinator species for this crop. Syed's

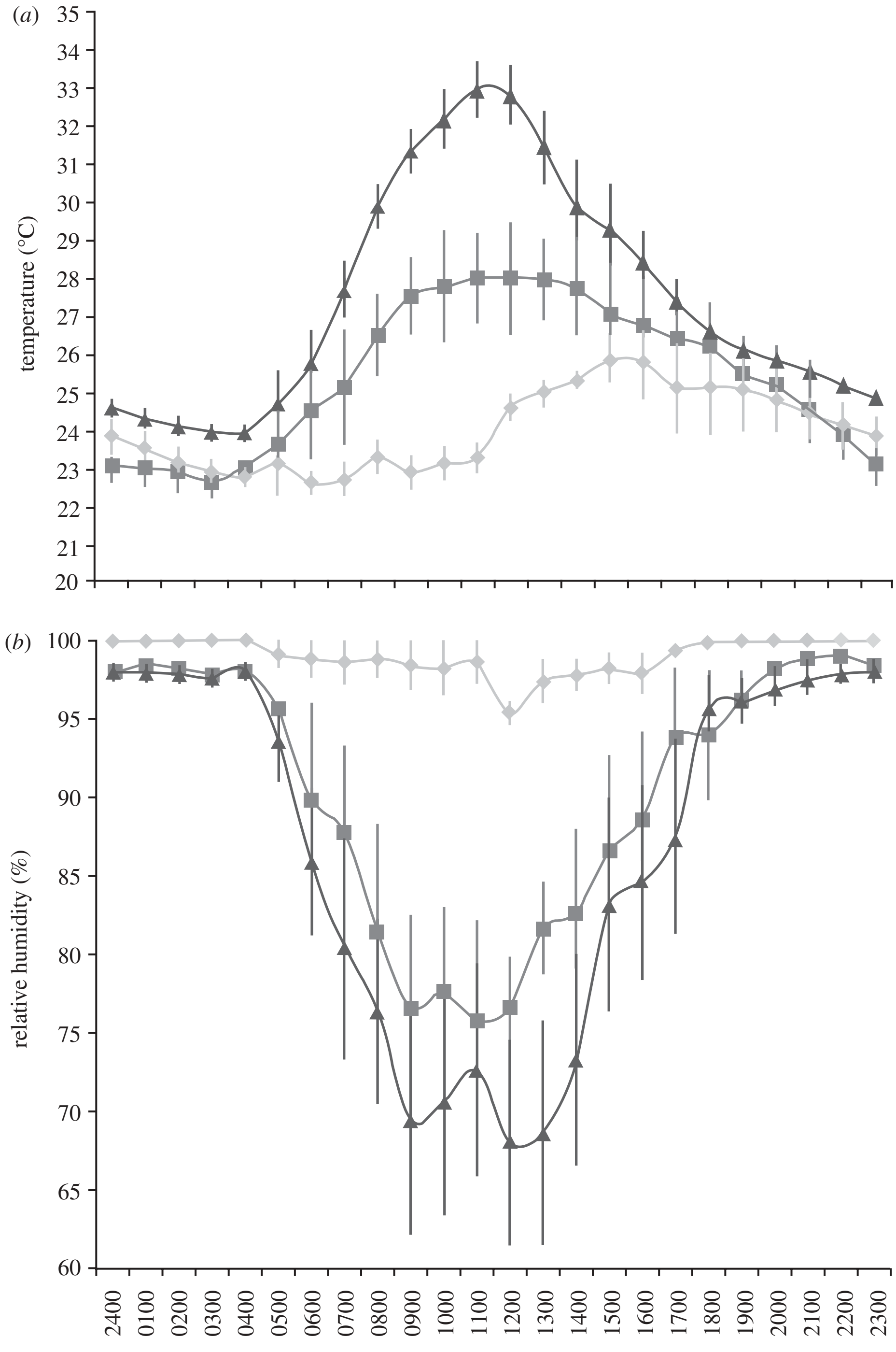

Figure 3. (*a*) Temperature and (*b*) relative humidity in the high and low canopy of primary forest (Danum Valley Conservation Area, Sabah) and in the oil palm plantation (Borneo Samudera, Lahad Datu, Sabah) over a period of 24 h. $n = 5$ for both sets of measurements. All readings taken using a LogIT DataMeter 1000 (DCP Microdevelopments, UK). Dark grey triangles, oil palm; dark grey squares, high canopy; light grey diamonds, low canopy.

original observations in Cameroon established that there was a suite of *Elaeidobius* species that were effective pollinators and that might have different microclimatic requirements [81,84]. It would therefore be possible to introduce a suite of these species, as has been done in the Manaus region of Brazil [82]. There are clear risks when introducing exotic species [85], and it would be preferable to make use of native species. A range of native pollinators of oil palm has also been recorded from Malaysia, Indonesia, South and Central America and West Africa [86]. This includes, from Malaysia *Thrips hawaiensis* (Thysanoptera) and the moth *Pyroderces* sp. [84], and in South and Central America, *Mystrops costaricensis* [86–88]. Caudwell *et al.* [82] report that, in Malaysian plantations, a high abundance of exclusively native pollinator species can support adequate pollination and fruit set. High numbers of non-*E. kamerunicus* flower visitors have been reported on palms near forest habitats, but their effectiveness in pollination is not known [86]. There is clearly a higher diversity of oil palm pollinators than is generally realized, and we need to remain flexible about their potential effectiveness, given the fragility of relying on only one pollinator.

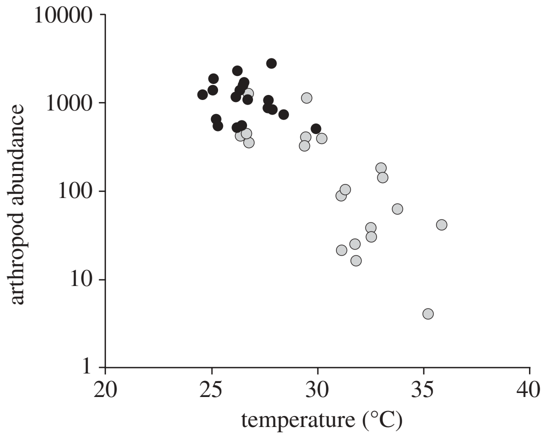

Figure 4. Arthropod abundance in 4 m^2 of leaf litter compared against temperature (using a Vaisala HM34 humidity and temperature meter) recorded at time of collection. Insect samples were taken by collecting all leaf litter in four 1 m^2 areas and extracting arthropods using the Winkler-type apparatus (for full details, see [26]). Black circles, forest; grey circles, oil palm plantation.

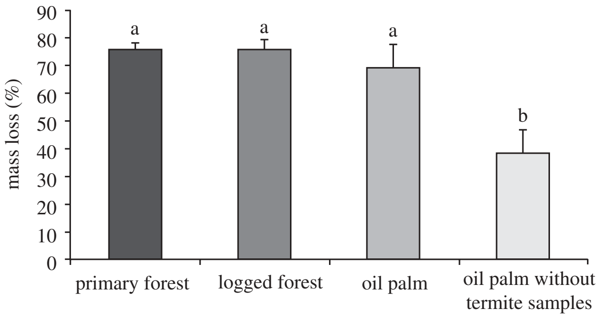

Figure 5. Mean percentage mass loss from litterbags for primary forest, logged forest and oil palm plantation habitats. There was a reduced mean percentage mass loss in the oil palm sites after the samples with obvious *Macrotermes gilvus* activity had been removed (ANOVA: d.f. = 3, $F = 5.17$, $p = 0.003$). Leaf-litter decomposition was measured using the litterbags (5 × 5 cm, of 4.5 mm mesh) of freshly fallen *Shorea johorensis* (Dipterocarpaceae) leaves (1.5 g). Litterbags were placed in the leaf litter and left for 280 days: primary forest, $n = 29$; logged forest, $n = 30$; oil palm, $n = 18$; oil palm without termite samples, $n = 9$ (for full details, see [90]).

(c) *Decomposition/soil fertility*

Forest conversion to oil palm leads to considerable changes in the soil, for example, extensive damage to the top soil, and soil compaction and erosion [89]. These changes are associated with reductions in the biodiversity and abundance of the litter itself and of the decomposer communities (tables 1 and 2; [15,18, 21,26]), but there are no reliable data on how these changes in diversity might affect decomposition and soil fertility. Litter decomposition provides another example of the potential importance of disturbance-tolerant species in providing ecosystem functions in oil palm. A litter-bag experiment showed that the mean rate of litter mass loss was not significantly different between forest and oil palm, but the mass loss that was observed in oil palm was the result of the activities of a single species of the widespread termite *Macrotermes gilvas* (figure 5).

5. METHODS FOR CONSERVATION OF BIODIVERSITY AND ECOSYSTEM FUNCTION IN OIL PALM

Given what little we know about the effects of the conversion of forest to oil palm, how can we remedy the loss of biodiversity and ecosystem functions provided within the oil palm habitat? Higher heterogeneity within an area is frequently associated with a higher diversity of species, and this complexity may be associated with factors operating at everything from the local to the landscape scale. For example, both local- and landscape-scale variables have been found to be important in structuring bird communities in forest areas in Borneo [91], and the interaction at the landscape scale between managed and natural habitats may be crucial for maintaining functional diversity within managed landscapes [92]. We will consider independently approaches that might be effective at the landscape and at the more local scale.

(a) *Landscape scale*

Non-crop areas can range from continuous adjacent forest to smaller patches maintained within the oil palm landscape on steep slopes and riverine margins. At the smallest scale, they may also be represented by single standing trees within the plantation area, such as the *Koompassia excelsa* sometimes left during clear felling as they contain nests of the honeybee *Apis dorsata*. These fragments provide both a habitat for species within the landscape and a potential source of spillover of species into the crop [93,94]. The amount of forest cover surrounding oil palm plantations has been shown to be an important predictor of the species richness of both butterflies and birds [50]. Peh *et al.* [19] suggested that adjacent forest areas may be important in providing many of the species of birds that forage within oil palm.

Regulations to influence the design of oil palm landscapes and reduce biodiversity loss are difficult to implement [95], although existing policies such as requirements to maintain forest on steep slopes and in a 30 m strip on river margins, which were designed to prevent soil erosion, do have the potential to support biodiversity. The formation of the Round Table on Sustainable Palm Oil in 2004 with a mission statement to promote the growth of sustainable palm oil (www.rspo.org) may also encourage plantation management to be more biodiversity friendly, although considerable doubts have been raised about its ability to deliver this [96,97]. Choosing areas with lower biodiversity value for cultivation is a key first step in reducing the initial impacts of oil palm expansion. Selection of heavily degraded habitats for cultivation would reduce the impacts on biodiversity of converting forested land [98]. Selecting areas that are best suited to oil palm cultivation can also help to increase yield and therefore reduce pressure on other areas [99]. One general approach for offsetting the impacts of oil palm plantations on biodiversity is to provide incentives and mechanisms to minimize further conversion of forest: these include identifying and protecting High Conversion Value forest, Reducing Emissions from Deforestation and Forest Degradation and biodiversity banking [39].

Oil palm is a long-lived crop—it may exist for 30 years—allowing time for biodiversity to develop, supporting ecosystem functions. Over half of the studies reporting the impacts of conversion of forest to oil palm on animal communities fail to report the age of the study plantation (table 1), but it is clear that the communities of animals and plants alter as a plantation ages—probably relating to changes in tree structure and closure of the canopy as the palms mature. For example, communities of birds have been found to vary with age of the oil palm and with the availability of food resources [78]. Other components of the ecosystem may also change as a plantation ages—for example, the numbers of the epiphytic bird's nest ferns (*Asplenium* spp.) increase in older plantations [58]. Management practices that aim to maintain a diverse age structure (e.g. by not clearing and replanting large areas simultaneously) may also therefore increase plantation diversity.

(b) *Local scale*

Complexity at the local scale in oil palm plantations depends on plantation management, which can control, for example, the abundance and diversity of epiphytes and of the understorey layers. Understorey vegetation has been shown to be important in maintaining the abundance and richness of beetle assemblages in oil palm in Sabah [18] and of bird communities in Guatemalan oil palm [100]. Understorey vegetation can also be important in producing increased amounts of leaf litter in plantations, which can itself support a higher diversity and abundance of taxa [18].

Indeed, this understorey complexity provides probably the best example within the oil palm landscape of the potential importance of conservation biological control—that is pest control based on the effects of habitat complexity on the biodiversity of natural enemies within the wider landscape [101]. It has for some time been assumed in the industry that beneficial planting of understorey vegetation provides vital levels of 'silent' biological control [69]. It is known that experimentally providing an artificial sugar supply significantly prolongs the life of parasitoids [75], and it is thought that the provision of nectar-rich understorey species will therefore support a greater diversity of these natural enemies. This should in turn help ensure that parasitoids do not become desynchronized from their hosts, which Basri *et al.* [75] showed was the major factor that caused outbreaks in the bagworm pest *Metisia plana*. However, we urgently need explicit demonstrations of exactly how beneficial planting might aid conservation biological control so that the practice might be adopted in a more rational manner. A further example of the importance of local complexity is the demonstration that a dense cover of ground vegetation can reduce the attacks by rhinoceros beetles on young oil palm [102].

Epiphytes are common in plantations—for example, oil palm can house significantly higher densities of the epiphytic bird's nest ferns (*A. nidus*) than primary forest (112 in 1 ha of oil palm compared with 44 in forest understorey (table 2)), probably relating to the large areas available for fern establishment on the oil palm trunks and open, light conditions that are found in plantations (and have been found to be important in determining fern abundance in primary forest areas [15]). Such epiphytes can act as an important habitat for invertebrates [15,26], probably owing in part to their more favourable microclimatic conditions [64]. It is likely that epiphytes in oil palm plantations also act as an important foraging site for birds. For example, in coffee plantations, the presence of epiphytes was found to significantly increase bird abundance owing to their importance as nesting and foraging sites [103]. It has been suggested that oil palm could be grown within an agroforestry system, thus increasing the structural diversity of the whole system [104]. However, such a strategy is likely to be impracticable as it would result in too marked a reduction in oil palm yield [105,106].

(c) *Economic costs and benefits of intervention*

Once we have a more rigorous understanding of whether we can establish a connection between biodiversity and ecosystem function, it is then essential to quantify the costs and benefits of relevant interventions within the oil palm habitat and assess the trade-off via relevant economic models. It is conceivable that the ecosystem service benefits of enhancing biodiversity are entirely negated by the increased costs of reductions in net profit and associated lack of investment in forest reserves via reduced land sparing. At the moment, although mechanisms for producing such models are being developed [99,107], we simply do not have reliable data to enable us to run these models for the costs and benefits of biodiversity in the oil palm landscape. Our view is that increasing local complexity could be economically significant, since retaining epiphytes and understorey has relatively low net costs, and has the potential for significant biodiversity benefits [100]. Developing a rigorous cost–benefit framework for interventions that might enhance oil palm biodiversity is clearly an urgent research priority.

6. CONCLUSION

The development of a biodiverse and properly functioning oil palm landscape is a vital conservation priority of the modern era. Two elements are required. First of all, ecologists need to provide robust scientific evidence that will establish whether local and landscape complexity can enhance biodiversity and how increased biodiversity might in turn support ecosystem functions, and therefore services, within this landscape. We must then use any such evidence to persuade policy makers and the industry to design oil palm landscapes that will function in a healthier and more sustainable way, providing a wide range of ecosystem services, including the conservation of diverse and charismatic species.

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