LETTER

Wildlife-friendly oil palm plantations fail to protect biodiversity effectively

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Abstract

Expansion of agriculture is a principal driver of biodiversity losses in the tropics, prompting suggestions that plantations should be made more hospitable to wildlife. Such "wildlife-friendly" practices contrast with the alternative "land sparing" strategy, which promotes separation of agricultural and conservation areas. Focusing on the wildlife-friendly strategy of retaining fragments of forest within the agricultural matrix, here we report the abundance and diversity of birds within oil palm plantations, fragments, and contiguous forest. Abundances of imperiled bird species were 60 times lower in fragments and 200 times lower in oil palm than in contiguous forest. Forest fragments also did not increase bird abundances in adjacent oil palm, had lower species richness than contiguous forest, and had an avifaunal composition that was more similar to oil palm than to contiguous forest. Therefore, from a conservation perspective, any investment in the retention of fragments would be better directed toward the protection of contiguous forest.

Introduction

The most pervasive threat to tropical biodiversity is the conversion of natural ecosystems to agricultural crops (Sala *et al.* 2000; Tilman *et al.* 2001; Sodhi *et al.* 2004). With world food demand expected to more than double by 2050 (Tilman *et al.* 2002) and a rapidly growing biofuel market (Koh 2007; Koh & Ghazoul 2008; Corley 2009), agriculture is likely to continue to drive declines in natural ecosystems and the species they contain for the foreseeable future. Decisions about how to manage existing agricultural land and where to create new croplands will therefore have profound effects on the conservation of tropical biodiversity, as well as economic development and poverty alleviation in tropical nations (Sachs *et al.* 2009).

One of the most rapidly expanding crops in the tropics is oil palm *Elaeis guineensis* (Fitzherbert *et al.* 2008). The majority of global palm oil production occurs in Malaysia and Indonesia (80%; Fitzherbert *et al.* 2008), where over half of the expansion of oil palm between 1990 and 2005 occurred at the expense of forest and where the rate of forest clearance for oil palm is increasing (Koh & Wilcove 2007; Koh & Wilcove 2008). Such loss of lowland rainforest (≈ 50% of original forest cover; Sodhi *et al.* 2004) has resulted in the sharpest declines of biodiversity in any biogeographic region (Butchart *et al.* 2004).

How to make oil palm a more environmentally friendly crop is therefore a critical conservation question (Fitzherbert *et al.* 2008; Koh *et al.* 2009). Several authors have promoted strategies that enhance biodiversity within oil palm landscapes, such as production of oil palm beneath shade trees, diverse agro-forestry on plantation boundaries, and maintenance of forest patches within plantations (Bhagwat & Willis 2008; Fitzherbert *et al.* 2008; Koh 2008b; Koh *et al.* 2009). Meanwhile, many of the largest palm oil producers have expressed a desire to implement environmentally friendly management, resulting in the Roundtable on Sustainable Palm Oil (RSPO) certification program (RSPO 2007). The RSPO promotes the protection of forest fragments that have High Conservation Value (HCV) within existing plantations, plus avoiding conversion of HCV forests into new oil plantations, as a means of mitigating losses of biodiversity. Moreover, some producers have voluntarily retained, protected, or created fragments within their plantations (Koh *et al.* 2009). Such strategies are also promoted in other regions (Chan & Daily 2008; Harvey *et al.* 2008; Scherr & McNeely 2008). In Brazil, for example, landowners clearing forest for agriculture are legally bound to leave a proportion of their land as forest fragments, which are protected under law (Jenkins *et al.* 2010).

Retaining forest fragments could have several benefits. Fragments might harbor populations of forest-dependent species that would otherwise not be able to persist in the agricultural landscape (Benedick *et al.* 2006; Koh 2008b) and they could maintain landscape-scale connectivity by acting as "stepping stones" between contiguous areas of forest (Laurance 2008; Lees & Peres 2009). They might also provide socioeconomic benefits, such as biocontrol of pests if predators living in the forest fragments also forage in the plantations (Koh 2008a), and fragments could reduce soil erosion from adjacent croplands.

The protection of forest fragments follows the philosophy of "wildlife-friendly" farming (Green *et al.* 2005), in that fragments are advocated for protecting and improving biodiversity at the plantation level. Fragments vary in size and follow a continuum from "fine-grained" inclusion of biodiversity with the smallest to "coarse-grained" inclusion with larger fragments (Fischer *et al.* 2008). The wildlife-friendly continuum finishes at "land sparing," which involves spatially separating agriculture from biodiversity conservation by maximizing the productivity of agricultural lands to increase the area of contiguous natural ecosystems that can be protected for biodiversity (Green *et al.* 2005; Ewers *et al.* 2009). Largest fragments might thus be sufficiently course-grained to be considered land spared.

Assuming that companies and civil society are willing to pay for conservation measures to mitigate the effects of oil palm on biodiversity, the question becomes how to achieve the maximum biodiversity benefits with the area and budget available. Fragments and other strategies aimed at promoting biodiversity within individual plantations represent a direct cost to companies, especially if those companies engage in active management of these features (e.g., monitoring of wildlife, rehabilitation of degraded areas). Land sparing also has inherent costs (e.g., paying for effective protection), and whether a more wildlife-friendly or a more land sparing approach is most appropriate will also depend on the prevailing governance and socioeconomic environments.

Here, we evaluate the conservation benefit side of this cost–benefit question. We report bird abundances, species richness, and species composition in plantations, fragments, and contiguous forest for the entire avifauna and also for the subset of birds that are considered to be at greatest risk of extinction (Birdlife International 2009). We also examine whether or not forest fragments increase bird abundance within oil palm plantations themselves. We use these data to infer the effect of different land use strategies on birds and we find that by every measure, contiguous forest better protects birds than do forest fragments within the plantation matrix and larger fragments are more effective than smaller ones.

Materials and methods

Site description

Fieldwork was conducted from May–September 2008 within the Ulu Segama-Malua Forest Reserve and oil palm estates in Sabah, Borneo (4º 58′ N, 117° 48′ E). Sampled forest had been selectively logged during the 1970s–1980s and again during 2001–2007, resulting in ca. 100–160 m^3 of timber extracted per hectare (Whitmore 1984). Sampled fragments were logged and isolated as the clearance frontier moved across eastern Sabah in the 1960s and early 1970s. The sampled oil palm estates had mature trees (planted 20–30 years ago) with a density of 100 palms/ha.

Avifaunal sampling

Birds were sampled at five sites within logged forest and a further five within oil palm, each separated by > 7 km. We also sampled within 12 fragments of logged forest surrounded by oil palm and separated by > 1 km from contiguous forest. Fragments were between 0.7 and 87 ha in area (mean = 21.1 ha ± 8.4 standard error [SE]) with a mean minimum distance of 1.2 km ± 0.5 SE (range = 150 m to 5 km) to the nearest other fragment in the landscape. An earlier study revealed that fragments separated by > 80 m of open land are isolated to forest bird species (Bierregaard *et al.* 1992).

Birds were sampled using timed point-counts with an unlimited radius at stations along semipermanent transects at each site (Lees & Peres 2006). Stations were placed at 250 m intervals (192 stations in total, comprising 12 at each site in contiguous forest and oil palm, plus six within each forest fragment). Necessarily, however, the distance between stations in the smallest fragments was reduced to ~50 m due to area constraints (Lees & Peres 2006).

Birds were sampled by walking transects between 05:45 and 10:30 during fine weather on three consecutive days at sites in contiguous forest and oil palm, and on two consecutive days in forest fragments. On each occasion, a single experienced observer (DPE or SLM) noted birds seen or heard during a 15-minute sampling period at each station. A recorder (TCM5000, Sony, Japan) and microphone (ME66, Sennheiser, Wennebostel, Germany) were used to record unknown vocalizations, which were subsequently checked against known calls or by ornithological experts of the region. All birds were recorded apart from Apodidae and Hirundinidae, which are difficult to detect and identify within a closed canopy.

Analysis

We investigated the impacts of habitat type (oil palm, forest fragment, or contiguous forest) and fragment area on the abundance of birds of different levels of conservation priority. Bird abundance was the observed abundance recorded during each sampling period, and since this is a count, it was modeled as a Poisson-distributed variable with a log link. The effects of random differences between sites, between days (2 or 3 days nested within each site) and between sampling points (6 or 12 points nested within each site) were accounted for using generalized linear mixed-effect models implemented within the lme4 package in *R* 2.8.0 (R Development Core Team 2008). In the notation of lme4, the random effects were (1 | site) + (1 | site:point) + (1 | site:day) (see also Table S1). We first analyzed the summed counts of all bird species, and then analyzed the subset of bird species classed as near-threatened or threatened (Birdlife International 2009), which henceforth we term "priority" birds.

Species richness of all birds and of priority birds was compared between habitat types using only the first 2 days of census at the first six points on the transect for each forest and oil palm site, thus equalizing effort across habitats. We compared both the total number of species per site and the number of species controlling for differences in bird abundance (splitting the transects into between 1 and 6 consecutive sets of points in order to obtain segments with an average of 50 individuals). Numbers of all species and numbers of priority species were log-transformed ($\log_e(1+S)$) and then analyzed using linear models. In the analysis controlling for abundance, we used a linear mixed-effects model with a random effect of site (whereas in the analysis of total number of species there was only one observation per site).

To determine how species composition differed among oil palm, fragments, and contiguous forest, we examined species-abundance matrices using CAP v. 3.1 software (PISCES Conservation Ltd, Oxford, UK). Abundance matrices of all birds were standardized as proportions to account for differences among sites in total abundance. Ordination of sites according to species similarity (Bray-Curtis index; Magurran 2004) was achieved using nonmetric multi-dimensional scaling (MDS; see Clarke & Warwick 2001), allowing transects with more similar species assemblages to be placed closer together in reduced dimensional space. To test for differences among forest types in species composition, we then used an Analysis of Similarity (ANOSIM), which is a nonparametric permutations test. Qualitatively similar results were found using square-root transformed data.

We then examined whether or not forest within the oil palm matrix had a positive effect on birds within the nearby oil palm. We analyzed whether the abundance of birds within oil palm increased with proximity to forest, measured as the minimum distance to the nearest patch of forest, and with size of the nearest forest fragment. We again used generalized linear mixed-effect models within the lme4 package in R, using the previous random effects. This analysis was run for all birds and for priority birds.

Results

We recorded a total of 174 species, of which 51 were priority species. By every measure, fragments were less valuable for birds than a similar area of contiguous forest (Table 1; see also Table S1). Compared to contiguous forest, fragments had a 60-fold lower abundance of priority birds and 1.8 times fewer birds overall (see also Figures 1a and 1b). Fragments even had a lower abundance of birds overall than oil palm, but they did have a higher abundance of priority birds (average three-fold higher than oil palm). Additionally, oil palm had a 200-fold lower abundance of priority birds than contiguous forests.

There was a strong effect of fragment area on the abundance of priority birds (Figure 1b), but not on the abundance of all birds (Figure 1a, Table 1). The biggest fragments started to approach, but were still eight times lower than, the abundance of priority birds within contiguous forest (Figure 1b). By extrapolation, fragments would have to be hundreds or thousands of hectares (mean = 700 ha; 95% CI = $116–2.5\times10^5$ ha) to have the same abundance of priority birds as contiguous forest. Our confidence intervals are large, since we are extrapolating in log-log space, but fragments would clearly have to be much bigger than almost all of those currently existing in palm-oil estates.

Table 1 Parameters of fixed effects in generalized linear mixed models of bird abundances in fragments compared with oil palm, contiguous forest, and area. *Z* tests are used to test whether parameters coefficients differ from zero. Poisson models have a log link, so parameters are in units of log (birds recorded per 15 minute count). The exponential of the parameter is also given for ease of interpretation, e.g., the value 1.5 means that oil palm has 1.5 times the overall abundance of birds as fragments.

		All birds				Priority birds			
Data set	Model parameter	Estimate	S.E.	*P*	exp(estimate)	Estimate	S.E.	*P*	exp(estimate)
Overall	Oil palm (compared to fragment)	0.42	0.20	0.032	1.524	−1.23	0.91	0.18	0.292
	Forest (compared to fragment)	0.60	0.20	0.0021	1.830	4.08	0.78	<0.00001	59.0
Fragments alone	Area	0.13	0.08	0.12	1.137	0.91	0.22	0.00005	2.483

Fragments also had lower species richness of all birds and of priority birds than contiguous forest, even after controlling for the lower numbers of individuals in samples (Figures 1c and 1d; all birds, $P < 0.0001$; priority birds, $P < 0.0001$; see Table S2 for full model outputs).

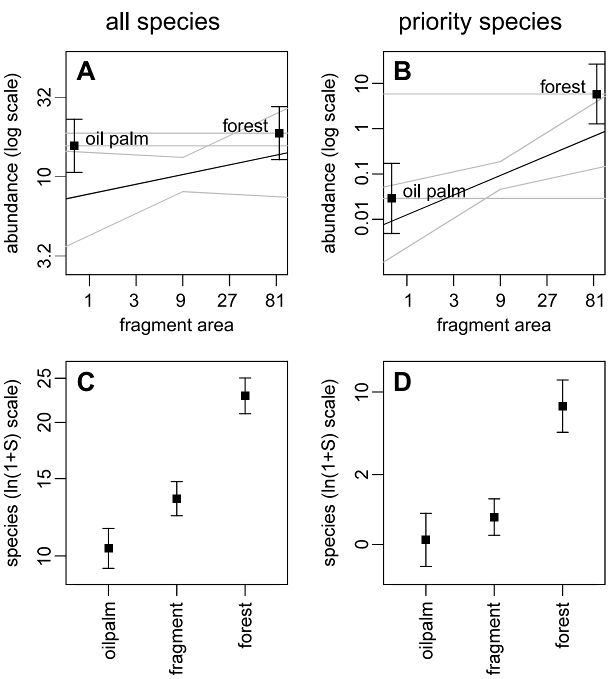

Figure 1 Forest fragments compared to oil palm and contiguous forest in terms of abundance (**a, b**) and species richness (**c, d**), of all birds (**a, c**), and of priority birds (**b, d**). Means and 95% CIs are shown, based on fitted models (see Table 1 and S1–S2 for model details and Figure S1 for raw data on abundance). Confidence intervals apply to the fixed parameters and illustrate the significance of the fixed effects. Note that uncertainty in *predicting* the abundance of any randomly chosen site would be bigger than this because of the random effects. In (**a, b**), the abundance per 15 minute sample for fragments is plotted against log fragment area. For comparison purposes the oil palm abundance is plotted at the area of the smallest fragment, and the contiguous forest abundance is plotted at the area of the largest fragment.

In turn, oil palm had lower species richness of all birds than fragments, but not of priority birds, again after controlling for numbers of individuals (Figures 1c and 1d; all birds, $P = 0.0002$; priority birds, $P = 0.11$; see Table S2). Additionally, for priority species, there was a species–area relationship indicating that larger fragments hold more species per count than do smaller fragments ($P = 0.008$), but this relationship did not hold for all species ($P > 0.1$; see Table S2).

Patterns of species-abundance differed among the habitat types (Figure 2; ANOSIM: $R = 0.72$, $P = 0.001$). However, while species assemblages in fragments were different from those in oil palm ($R = 0.31$ $P = 0.018$), assemblages in fragments were far more similar to those in oil palm than to those in contiguous forest ($R = 1.0$,

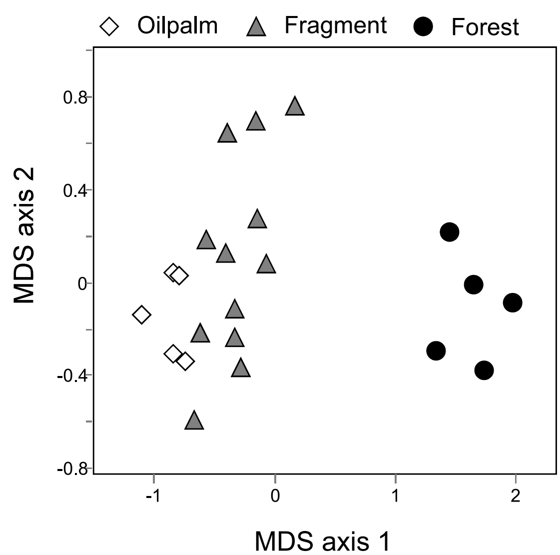

Figure 2 Nonmetric multidimensional scaling (MDS) ordination of the avifauna in each forest type. Average dissimilarity between forest types: oil palm versus fragment = 54%; forest versus fragment = 83%; forest versus oil palm = 90%.

$P = 0.001$; Figure 2). The avifaunal assemblage of contiguous forest and oil palm also differed ($R = 1.0$, $P = 0.001$), and were the least similar between habitat types (Figure 2).

Despite having a lower abundance, lower richness, and different composition of birds than contiguous forest, fragments might offer a net benefit to conservation if their presence enhances the abundance of birds in the nearby oil palm (Koh 2008b). However, there was no evidence that bird abundances in oil palm were significantly higher closer to fragments (Figure S2; all species, $P = 0.3$; priority species, $P = 0.09$; accounting for the size of the nearest fragment offered no improvement to the models).

Moreover, under a hypothetical landscape-planning scenario, any cost of "removing" fragments, in terms of losses of abundance of priority birds from the agricultural matrix, would be very likely outweighed by the benefit of "offsetting" a similar area of contiguous forest. We first calculate the total abundance of priority birds in an oil palm-forest fragment mosaic (Δ_{OP+FF}) of area A as:

$$(1/60 \times P_{FF} \times A) + (1/200 \times (1 - P_{FF}) \times A) = \Delta_{OP+FF} \times A$$

Where 1/60 is the proportional abundance of birds in forest fragments compared to contiguous forest, 1/200 is the proportional abundance in oil palm compared to contiguous forest, and P_{FF} is the proportion of estate area as forest fragments.

If we then conservatively assume that *all* priority birds found in the oil palm are lost when fragments are removed, we can calculate the total abundance of priority birds of "offset" land in contiguous forest (Δ_{CF}) as:

$$1 \times P_{FF} \times A = \Delta_{CF} \times A.$$

In this case, when P_{FF} is just 0.5% of plantation area or greater, $\Delta_{CF} \geq \Delta_{OP+FF}$ and a "land sparing" approach would be the better strategy. Additionally, contiguous forest offsets would also likely represent a net benefit in terms of priority bird species richness, since the removal of fragments could only result in the loss of the single priority species recorded in oil palm and since contiguous forest is far more priority species rich than are fragments (Figure 1d; Table S2).

Discussion

Given the rate at which forests in Southeast Asia are being converted to oil palm and given the growing interest in oil palm agriculture in other tropical regions, scientists, policy makers, and palm-oil producers are developing conservation strategies that reduce biodiversity losses associated with this crop. Focusing on the "wildlife-friendly" strategy of retaining forest fragments in the oil palm matrix, our data strongly suggest that forest fragments have lower abundances and diversities of birds compared to contiguous logged forests, that fragments have a species composition more similar to that of oil palm than of contiguous forest, and that the spatial juxtaposition of fragments and oil palm in the landscape has little effect on these patterns of bird diversity. Consequently, there is little evidence that making existing or proposed oil palm plantations more hospitable to biodiversity will benefit the vast number of species now threatened by the expansion of oil palm agriculture, and this study instead highlights the importance of retaining large areas of contiguous logged forest for biodiversity protection (Berry *et al.* 2010).

We did not investigate whether other taxa might react differently to birds. While we cannot rule out this possibility, it is likely that the strong trends revealed by birds, which are reasonable indicators of general patterns across taxa (Howard *et al.* 1998; Barlow *et al.* 2007; Berry *et al.* 2010), will follow for other groups. Forest fragments may facilitate the dispersal of forest-dependent species across the oil palm landscape (Laurance 2008; Lees & Peres 2009), although the large distances between contiguous forests blocks are likely to limit this potential benefit. Fragments might also provide benefits independently of biodiversity considerations, such as reducing soil erosion, but we argue that retention of fragments should not be regarded as an effective strategy to increase biodiversity value per se within oil palm plantations.

Our data thus strongly suggest that retaining contiguous forest wherever possible in Southeast Asia would be the most effective strategy for conserving biodiversity. Furthermore, if forest fragments are to be preserved within plantations, then larger fragments are more beneficial than smaller ones. We therefore propose a shift away from promoting strategies that aim to bring biodiversity into plantations (RSPO 2007; Bhagwat & Willis 2008; Fitzherbert *et al.* 2008; Koh 2008b; Koh *et al.* 2009; Ghazoul *et al.* 2010), in favor of a landscape approach that protects larger areas of forest externally (Phalan *et al.* 2009; Struebig *et al.* 2010).

Since palm-oil companies are currently expending funds to make existing oil palm plantations more wildlife-friendly (Koh *et al.* 2009), we suggest that these funds should be directed toward a biobanking scheme (e.g., Carroll *et al.* 2009) that protects contiguous forest outside the agricultural matrix. Similarly, in landscapes where proposed oil palm license areas are dominated by non-forest habitats but also include small patches of forest, our data suggest that biodiversity conservation will be better served by converting the entire area through a land sparing approach and the palm-oil company paying a biobank to offset a contiguous area of forest equal to or greater than the area of forest lost. Biobanks have the additional benefit of securing protected land, whereas wildlife-friendly features are owned by palm-oil companies, which could remove these features if production philosophies shift away from "green" agriculture. We believe, therefore, that where suitable governance and socioeconomic conditions prevail, a biobanking strategy would be a far more effective method for conserving tropical biodiversity in regions where large areas of natural ecosystems are threatened with agricultural conversion.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Standard deviation of random effects in generalized linear mixed models of bird abundances.

Table S2 Differences between habitats in species richness

Figure S1 Forest fragments compared to oil palm and contiguous forest in terms of bird abundance per point count.

Figure S2 The effect of distance from the nearest forest on the abundance of birds within oil palm.

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References

Barlow, J., Gardner T.A., Araujo I.S. *et al*. (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proc Natl Acad Sci USA* **104**, 18555–18560.

Benedick, S., Hill J.K., Mustaffa N. *et al*. (2006) Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments. *J Appl Ecol* **43**, 967–977.

Berry, N.J., Phillips O.L., Lewis S.J. *et al*. (2010) The high value of logged tropical forests: lessons from northern Borneo. *Biodiv Conserv* **19**, 985–997.

Bhagwat, S.A., Willis K.J. (2008) Agroforestry as a solution to the oil-palm debate. *Conserv Biol* **22**, 1368–1370.

Bierregaard, R.O., Lovejoy T.E., Kapos V., Dossantos A.A., Hutchings R.W. (1992) The biological dynamics of tropical rainforest fragments. *Bioscience* **42**, 859–866.

Birdlife International. (2009) Species factsheets. Available from: http://www.birdlife.org. Accessed August 2009.

Butchart, S.H.M., Stattersfield A.J., Bennun L.A. *et al*. (2004) Measuring global trends in the status of biodiversity: red list indices for birds. *PLoS Biol* **2**, 2294–2304.

Carroll, N., Fox J., Bayon R. (2009) *Conservation and biodiversity banking: a guide to setting up and running biodiversity credit trading systems*. Earthscan Publications, London, UK.

Chan, K.M.A., Daily G.C. (2008) The payoff of conservation investments in tropical countryside. *Proc Natl Acad Sci USA* **105**, 19342–19347.

Clarke, K.R., Warwick R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation*. *2nd edition*. Primer-E, Plymouth, UK.

Corley, R.H.V. (2009) How much palm oil do we need? *Environ Sci Policy* **12**, 134–139.

Ewers, R.M., Scharlemann J.P.W., Balmford A., Green R.E. (2009) Do increases in agricultural yield spare land for nature? *Glob Change Biol* **15**, 1716–1726.

Fischer, J., Brosi B., Daily G.C. *et al*. (2008) Should agricultural policies encourage land sparing of wildlife-friendly farming? *Front Ecol Environ* **6**, 380–385.

Fitzherbert, E.B., Struebig M.J., Morel A. *et al*. (2008) How will oil palm expansion affect biodiversity? *Trends Ecol Evol* **23**, 538–545.

Ghazoul, J., Koh L.P., Levang P. (2010) Checking the reality check. *Trends Ecol Evol* **25,** 8–9.

Green, R.E., Cornell S.J., Scharlemann J.P.W., Balmford A. (2005) Farming and the fate of wild nature. *Science* **307**, 550–555.

Harvey C.A., Komar O., Chazdon R. *et al*. (2008) Integrating agricultural landscapes with biodiversity conservation in the Mesoamerican hotspot. *Conserv Biol* **22**, 8–15.

Howard, P.C., Viskanic P., Davenport T.R.B. *et al*. (1998) Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature* **394**, 472–475.

Jenkins, C.N., Alves M.A.S., Pimm S.L. (2010) Avian conservation priorities in a top-ranked biodiversity hotspot. *Biol Conserv* **143**, 992–998.

Koh, L.P. (2007) Potential habitat and biodiversity losses from intensified biodiesel feedstock production. *Conserv Biol* **21**, 1373–1375.

Koh, L.P. (2008a) Birds defend oil palms from herbivorous insects. *Ecol Appl* **18**, 821–825.

Koh, L.P. (2008b) Can oil palm plantations be made more hospitable for forest butterflies and birds? *J Appl Ecol* **45**, 1002–1009.

Koh, L.P., Ghazoul J. (2008) Biofuels, biodiversity, and people: understanding the conflicts and finding opportunities. *Biol Conserv* **141**, 2450–2460.

Koh, L.P., Levang P., Ghazoul J. (2009) Designer landscapes for sustainable biofuels. *Trends Ecol Evol* **24**, 431–438.

Koh, L.P., Wilcove D.S. (2007) Cashing in palm oil for conservation. *Nature* **448**, 993–994.

Koh, L.P., Wilcove D.S. (2008) Is oil palm agriculture really destroying tropical biodiversity? *Conserv Lett* **1**, 60–64.

Laurance, W.F. (2008) Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. *Biol Conserv* **141**, 1731–1744.

Lees, A.C., Peres C.A. (2006) Rapid avifaunal collapse along the Amazonian deforestation frontier. *Biol Conserv* **133**, 198–211.

Lees, A.C., Peres C.A. (2009) Gap-crossing movements predict species occupancy in Amazonian forest fragments. *Oikos* **118**, 280–290.

Magurran, A.E. (2004) *Measuring biological diversity*. Blackwell Science Ltd., Oxford, UK.

Phalan, B., Fitzherbert E.B., Rafflegeau S., Struebig M.J., Verwilghen A. (2009) Conservation in oil-palm landscapes. *Conserv Biol* **23**, 244–247.

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

RSPO (2007) Roundtable on sustainable palm oil (RSPO): principles and criteria for sustainable palm oil production. Including indicators and guidance. Available from: http://www.rspo.org. Accessed August 2009.

Sachs, J.D., Baillie J.E.M., Sutherland W.J. *et al*. (2009) Biodiversity conservation and the millennium development goals. *Science* **325**, 1502–1503.

Sala, O.E., Chapin F.S., Armesto J.J. *et al*. (2000) Biodiversity – Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774.

Scherr, S.J., McNeely J.A. (2008) Biodiversity conservation and agricultural sustainability: towards a new paradigm of 'ecoagriculture' landscapes. *Phil Trans R Soc Lond B*, **363**, 477–494.

Sodhi, N.S., Koh L.P., Brook B.W., Ng P.K.L. (2004) Southeast Asian biodiversity: an impending disaster. *Trends Ecol Evol* **19**, 654–660.

Struebig, M.J., Paoli G., Meijaard E. (2010) A reality check for designer biofuel landscapes. *Trends Ecol Evol* **25**, 7–8.

Tilman, D., Cassman K.G., Matson P.A., Naylor R., Polasky S. (2002) Agricultural sustainability and intensive production practices. *Nature* **418**, 671–677.

Tilman, D., Fargione J., Wolff B. *et al*. (2001) Forecasting agriculturally driven global environmental change. *Science* **292**, 281–284.

Whitmore, T.C. (1984) *Tropical rain forests of the Far East. 2nd edition*. Clarendon Press, Oxford, UK.

