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Can oil palm plantations be made more hospitable for forest butterflies and birds?

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Summary

1. Rising global demand for palm oil is likely to exacerbate deforestation rates in oil palm-producing countries. This will lead to a net reduction in biodiversity unless measures can be taken to improve the value of oil palm plantations.

2. Here, I investigate whether the biodiversity of oil palm plantations can be increased by determining how forest-dwelling butterflies and birds in these plantations are affected by vegetation characteristics at the local level (e.g. epiphyte prevalence) and by natural forest cover at the landscape level (e.g. old-growth forests surrounding oil palm estates).

3. Across transects, vegetation variables explained 0–1·2% of the variation in butterfly species richness and 0–7% of that in bird species richness. The most important predictors of species richness across transects were percentage ground cover of weeds for butterflies; and epiphyte prevalence and presence of leguminous crops for birds. Across estates, natural forest cover explained 1·2–12·9% of the variation in butterfly species richness and 0·6–53·3% of variation in bird species richness. The most important predictors of species richness across estates were percentage cover of old-growth forests surrounding an estate for butterflies; and percentage cover of young secondary forests surrounding an estate for birds.

4. *Synthesis and applications.* In order to maximize biodiversity in oil palm plantations, oil palm companies and local governments should work together to preserve as much of the remaining natural forests as possible by, for example, creating forested buffer zones around oil palm estates or protecting remnant forest patches in the landscape.

Key-words: agriculture, biodiversity hotspots, bird, Borneo, butterfly, conservation, reconciliation ecology, restoration ecology, Southeast Asia

Introduction

Global cropland is forecast to increase by a net $3{\cdot}5 \times 10^8$ ha by 2050 as global food demand doubles (Tilman *et al.* 2001). This is expected to have detrimental impacts on natural habitats and biodiversity worldwide (Tilman 1999). Over the past few decades, the oil palm *Elaeis guineensis* Jacq. has become one of the most rapidly expanding equatorial crops in the world (Clay 2004; Koh & Wilcove 2007). Global production of crude palm oil and palm kernel oil increased from 1·7 million tons in 1960 to 23·8 million tons in 2000, accounting for 26·4% of the global increase in production of all vegetable oils during that period (Corley & Tinker 2003). The rapid growth of the oil palm industry can be attributed to its diverse downstream uses, which include food additives, cosmetics, industrial lubricant and biodiesel (i.e. biologically-derived diesel fuel) (Corley & Tinker 2003; Clay 2004). Unless the future expansion of oil palm agriculture is regulated (e.g. through sustainable development, Corley 2006), rising global demands for palm oil is likely to exacerbate the high rates of forest conversion in major oil palm-producing countries (Koh 2007c).

Malaysia and Indonesia are two of the most cost-efficient countries in the world for oil palm agriculture due to their favourable climate, rich soils and relatively low labour costs, which allow for year-round harvesting and high fruit yields (Casson 2000). Unsurprisingly, these two countries currently lead the world in oil palm production, accounting for 80·5% (130·3 million tons [palm kernel equivalent]) of global production and 56·1% (6·7 million ha) of worldwide oil palm-cultivated area (FAO 2006). Coincidentally, Malaysia and Indonesia are located within two of the world's 34 biodiversity hotspots – Sundaland and Wallacea – which contain exceptionally high concentrations of endemic species and are undergoing widespread deforestation (Mittermeier *et al.* 2004; Sodhi *et al.* 2004; Koh 2007b). As a result, the rapid expansion of oil palm agriculture in Southeast Asia has raised serious concerns about its potential impacts on the region's biodiversity (Koh & Wilcove 2007).

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To minimize losses in natural habitats and biodiversity from oil palm agriculture, the most critical task is to identify and preserve habitats of high conservation value. However, the effective protection of large and contiguous tracts of forests in many developing countries, including Malaysia and Indonesia, is fraught with socio-political challenges (e.g. corruption), due ultimately to the overwhelming emphasis in these countries on short-term financial gains over long-term natural resource conservation (Smith *et al.* 2003; Laurance 2004; Sodhi & Brook 2006; Koh & Wilcove 2007). In addition to the traditional approach of forest reservation, there is both potential and a need to develop better management practices that reconcile oil palm agriculture and biodiversity conservation – an area of research that remains poorly addressed (Daily, Ehrlich & Sanchez-Azofeifa 2001; Rosenzweig 2003). The main objective of this study is to identify biodiversity-friendly practices in oil palm agriculture by answering the following questions: (i) To what extent would altering different vegetation characteristics at the local level (e.g. epiphyte prevalence in 100 m transects) enhance the species richness of forest-dwelling butterflies and birds (i.e. species known to occur in old-growth forests) in oil palm plantations? (ii) To what extent would retaining natural habitats at the landscape level (e.g. old-growth forests surrounding estates) make oil palm estates more hospitable for these two taxonomic groups? I use the species richness of forest-dwelling butterflies and birds as proxies of forest biodiversity for insects and vertebrates, respectively, because butterflies and birds are known to be highly sensitive to habitat disturbance and have been commonly used as bio-indicators in other studies (e.g. Furness, Greenwood & Jarvis 1993; Koh & Sodhi 2004; Thomas *et al.* 2004; Koh 2007a).

Methods

STUDY SITES AND SAMPLING PERIODS

This study was conducted in East Sabah, Malaysia, located on the island of Borneo in Southeast Asia (see Supplementary material Fig. S1). Butterflies and birds were sampled over two field seasons: the wetter months of September and October 2006 [mean rainfall = 246·5 ± 23·8 (standard error) mm mo^{-1}], and the drier months of March and April 2007 (155·3 ± 23·0 mm mo^{-1}) (Walsh & Newbery 1999). A total of 15 oil palm estates spread across three oil palm complexes were surveyed (38 489 ha in total; Supplementary material Fig. S1). Oil palm estates are individually managed plantations that ranged in size from 875 to 3575 ha; oil palm complexes are clusters of oil palm estates.

BUTTERFLY SAMPLING

Butterflies were sampled using the modified transect walk method (Caldas & Robbins 2003; Koh & Sodhi 2004). Between three and 10 standard-length (100 m) butterfly transects were randomly located within each oil palm estate and at least 1 km apart. Each transect was walked between one and three times over the entire sampling period. Transects were walked at a constant pace and with a pause for a 1-min visual census at every 10-m interval. Every unique butterfly individual spotted 20 m to each side, 20 m ahead and 20 m above was recorded once. All butterfly transects were walked between 09·00 h (~3 h after sunrise) and 15·00 h (~3 h before sunset). A total of 121 butterfly transect samples were collected. As with other studies conducted in the tropics, butterfly species from the families of Hesperiidae and Lycaenidae were excluded due to the difficulties of identifying them in the field (Hill *et al.* 1995; Koh & Sodhi 2004). To access the efficacy of the transect walk method for sampling forest-dwelling butterflies in oil palm plantations, butterflies were also trapped in 10 oil palm estates during a preliminary study (see Supplementary material). All butterflies were identified using Otsuka (1988, 1991). As the focus of this study is on forest-dwelling species, only butterfly species known to occur in Malaysia's 'primary forests' were included (referred herein as old-growth forests), based on life history information from Corbet & Pendlebury (1992) (see Supplementary material Appendix S1 for excluded species). A single unidentified individual was also excluded from the analyses (representing 0·38% of the total sample size of butterfly transects).

BIRD SAMPLING

Birds were sampled using transect surveys. Between four and 10 standard-length (100 m) bird transects were randomly located within each oil palm estate and at least 1 km apart. Each transect was walked between one and three times over the entire sampling period. Transects were walked at a constant pace and with a pause for a 1-min visual census at every 10-m interval. Every unique bird individual spotted or heard 50 m to each side, 50 m ahead and 50 m above was recorded once. All bird transects were walked between 06·00 h and 10·00 h. A total of 137 bird transect samples were collected. All birds were visually identified using the field guide of MacKinnon & Phillipps (1993). A voice recorder was used to record unfamiliar calls and songs, which were later identified using the recordings of Scharringa (2005). Only bird species known to occur in local unlogged forests in East Sabah were included in the analyses, based on a previous study (Johns 1996) (see Supplementary material Appendix S1 for excluded species). In this study, surveys included 13 individuals that could not be identified in the field, as well as four non-breeding winter visitors (blue-and-white flycatcher *Cyanoptila cyanomelana* Temminck, cattle egret *Bubulcus ibis* Linnaeus, little egret *Egretta garzetta* Linnaeus and little tern *Sternula albifrons* Pallas). These unidentified individuals and migrant species were excluded from the analyses (representing 2·71% of the total sample size of bird transects). All butterfly and bird transect surveys were conducted during fair weather (i.e. no rain or overcast sky), from 8 September to 14 October 2006 and from 20 March to 7 April 2007.

MEASUREMENTS OF VEGETATION AND LAND COVER VARIABLES

In oil palm agriculture, financial and agronomical considerations limit the changes that could be made to local level vegetation characteristics. Through interviews with senior plantation executives and preliminary field surveys, it appeared that the presence of epiphytes on palm trees, and the extent and nature of ground vegetation are variables that could both potentially affect butterfly and bird diversity, and be altered within the operational constraints of oil palm agriculture (see Supplementary material Fig. S2). Epiphytes (e.g. *Asplenium nidus* L.) grow naturally on the trunks of palm trees and may be removed if they become an obstacle to the harvesting of fresh fruit bunches. Leguminous crops (e.g. *Mucuna bracteata* DC. ex Kurz) and ferns (e.g. *Nephrolepis biserrata* Sw.) are typically established within oil palm plantations as natural cover crops to prevent soil erosion and desiccation (Corley & Tinker 2003). Beneficial plants (e.g. *Euphorbia heterophylla* L.) are planted to attract the insect predators and parasitoids of lepidopteran pests of oil palms (e.g. *Metisa plana* Walker) (Kamarudin *et al.* 1996). Weeds (e.g. *Asystasia gangetica* L.) may be removed to reduce competition with palm trees for soil nutrients. To investigate the local level effects of vegetation on butterflies and birds, the following variables were independently estimated by two different observers at the start and end points of each butterfly and bird transect: (i) epiphyte prevalence – the proportion of the nearest 10 palm trees that had epiphytes covering at least half the length of its trunk; (ii) percentage ground cover of leguminous crop within a 10-m radius; (iii) percentage ground cover of ferns; (iv) percentage ground cover of weeds; and (v) percentage ground cover of beneficial plants. The average of the start and end-point estimates of each variable from each observer was calculated. The average of this value between the two independent observers was used for subsequent analyses. To control for potential confounding effects, the following variables were recorded or calculated for each transect: (i) age of oil palms in the field where the transect was located, which ranged from 2 to 29 years old; (ii) canopy density – the average of four cardinal measurements of upper storey density using a concave spherical densiometer (Lemmon 1957); (iii) altitude, using a Global Positioning System (GPS) receiver with built-in barometric altimeter (Garmin GPSMap76CS, Garmin International Inc., Kansas City, USA); and (iv) proximity to forests – quantified as the percentage cover of natural forests within 1 km, 3 km or 5 km radius centred at each transect based on the Southeast Asia land cover data set of the Global Land Cover 2000 Project (GLC) (Stibig & Malinggreau 2003). Natural forests include both old-growth and young secondary forests as defined in the GLC (see Supplementary material Appendix S2).

To investigate the landscape level effects of natural forest cover on butterflies and birds, the percentage cover of old-growth and young secondary forests was calculated both within and surrounding each oil palm estate at 1-km, 10-km, 20-km or 30-km wide buffer zones. In addition, the area of each oil palm estate was calculated to control for potential confounding effects of the species–area-relationship (MacArthur & Wilson 1967; Rosenzweig 1995). Forest cover and estate area were calculated based on the GLC data set (Stibig & Malinggreau 2003).

STATISTICAL METHODS

To assess the overall sampling completeness of butterflies and birds, expected species accumulation curves were generated based on the analytical formula of Colwell, Mao & Chang (2004). An accumulation curve – plotted on an x-axis for sampling effort (number of transect samples collected) and a y-axis for species richness – illustrates the rate at which new species were recorded. An asymptotic accumulation curve would indicate that the sampling had been exhaustive. Additionally, the observed species richness for butterflies and birds was compared with eight estimators of their 'true' species richness: Abundance-based Coverage Estimator (ACE), Incidence-based Coverage Estimator (ICE), Chao1 estimator, Chao2 estimator, Jack1 estimator, Jack2 estimator, bootstrap estimator and Michaelis–Menten Means estimator (for formulae and detailed descriptions of each estimator, see Colwell & Coddington 1994; Chazdon *et al.* 1998; Chao 2005). The use of some of these estimators requires information on the abundance of species (e.g. ACE and Chao1). For transects that had been surveyed repeatedly, the abundance of a species in a transect was taken to be the highest number of individuals recorded during any one survey. Accumulation curves and species richness estimators were generated using the EstimateS package (Colwell 2006). Ecologists are increasingly aware of the importance of considering spatial scale effects in biodiversity studies (Hamer & Hill 2000; Hill & Hamer 2004; Koh 2007a). Diversity partitioning is a useful tool for studying the effect of spatial grain on biodiversity measurements (Arita & Rodriguez 2002; Veech *et al.* 2002; Koleff, Gaston & Lennon 2003; Clough *et al.* 2007a). For both forest butterflies and birds, the additive diversity partitioning approach was used to estimate the relative contributions of α-diversity (diversity of a transect), between-transect β-diversity (variation in species composition between transects) and between-estate β-diversity to the observed total species richness (γ-diversity) (Allan 1975; Lande 1996; Wagner, Wildi & Ewald 2000; Clough *et al.* 2007a; see Supplementary material).

To determine the local level effects of vegetation on butterflies and birds, a set of 31 candidate models were generated, representing competing hypotheses that explain variations in species richness of each taxon across the transects (see Supplementary material Appendix S3). All candidate models were fitted to the data as generalized linear mixed-effects models (GLMM) using the lmer function in R (R Development Core Team 2007), assigning each model a Poisson error distribution and a log-link function. Candidate GLMMs were fitted by coding the species richness of butterflies or birds as the response variable and individual vegetation variables or these variables in every possible combination as fixed effects in the linear predictor. The vegetation variables of epiphyte prevalence, percentage ground cover of ferns and percentage ground cover of weeds were coded as continuous fixed effects. Because leguminous crops and beneficial plants were absent in > 80% of the transects, these two variables were coded as binomial fixed effects (i.e. either present or absent). To control for their potential confounding effects, the control variables of age of oil palms, canopy density, altitude, proximity to forests (at the pre-determined spatial resolution of a 3-km radius; see Supplementary material), transect sampling effort (i.e. number of times a transect had been sampled) and the oil palm estate where the transect was located were included as random effects. Only data collected from mature oil palm fields (i.e. > 3 years post planting) were used for this part of the analysis (i.e. 117 butterfly transect samples and 130 bird transect samples). Immature fields were excluded because they are transient habitats and therefore irrelevant to the objective of determining how altering vegetation characteristics could affect butterfly and bird species richness.

To determine the landscape level effects of natural forest cover on butterflies and birds, a set of 15 candidate models were generated representing competing hypotheses to explain variations in the species richness of each taxon across the estates (see Supplementary material Appendix S4). Candidate GLMMs were fitted by coding the species richness of butterflies or birds as the response variable and individual forest cover variables or these variables in every possible combination as fixed effects in the linear predictor. The forest cover variables of percentage cover of old-growth forests within an estate, percentage cover of old-growth forests surrounding an estate (at the pre-determined spatial resolution of a 1-km wide buffer zone; see Supplementary material), percentage cover of young secondary forests within an estate and percentage cover of young secondary forests surrounding an estate (1-km wide buffer zone) were coded as continuous fixed effects. To control for their potential confounding effects, the control variables of estate area (natural log-transformed), estate sampling effort (i.e. number of transects sampled within an estate) and the oil palm complex where the estate was located were included as random effects.

The first step of the model selection procedure was to calculate the Akaike's Information Criterion corrected for small sample sizes (AIC_c) for each candidate model (Burnham & Anderson 2002). The AIC_c is an estimate of the relative Kullback–Leibler (K–L) distance between each fitted model and the unknown true mechanism that generated the data (Burnham & Anderson 2004). Next, the Akaike weight (Burnham & Anderson 2002) and McFadden's pseudo-R^2 (Veall & Zimmermann 1996) were calculated for each model. The Akaike weight reflects the weight of evidence in support of a particular model relative to the entire model set, and varies from 0 (no support) to 100% (complete support). The 'null' model used in the calculation of McFadden's pseudo-R^2 was a GLMM fitted with the respective control variables (i.e. six control variables for local level analyses and three for landscape level analyses). Therefore, the McFadden's pseudo-R^2 of each candidate model reflects the additional variance explained by the fixed effects (i.e. predictor variables of interest). The candidate model with the highest Akaike weight was selected as the K–L most parsimonious model. The model averaged variance explained by each predictor was computed by averaging McFadden's pseudo-R^2 across all models where the predictor occurs, weighted by the Akaike weight of models.

Results

GENERAL PATTERNS

A total of 30 species and 264 individuals of butterflies, and 37 species and 1695 individuals of birds were recorded during the sampling period (see Supplementary material Appendix S1). The number of species recorded in a transect ranged from 1 to 10 for butterflies (median = 1) and from 0 to 9 for birds (median = 4·5) (see Supplementary material Appendix S5). The species richness recorded in an estate ranged from 1 to 13 for butterflies (median = 5) and from 7 to 14 for birds (median = 10) (see Supplementary material Appendix S6). The expected species accumulation curves for both butterflies and birds showed signs of approaching their asymptotes (see Supplementary material Fig. S3). Compared to the eight estimators of 'true' species richness, sampling effort yielded between 55·6% and 88·6% (median = 67·4%) of the 'true' species richness for butterflies and between 70·0% and 109·2% (median = 77·9%) of that for birds. Mean α-diversity accounted for 5% and 19% of the observed total species richness for butterflies and birds, respectively (Fig. 1). Between-estate β-diversity accounted for most of the total species richness for both butterflies (76%) and birds (56%). Between-transect β-diversity was 19% and 25% of the total species richness for butterflies and birds, respectively. The percentage cover of natural forests within a 3-km radius around each transect best explained local level variations in both butterfly and bird species richness across the transects. As such, the control variable of proximity to forests was measured and analysed at this spatial resolution. The percentage cover of natural forests within a 1-km wide buffer zone surrounding each estate best explained landscape level variations in both butterfly and bird species richness across the estates. The predictor variables of percentage cover of old-growth or young secondary forests were measured and analysed at this spatial resolution.

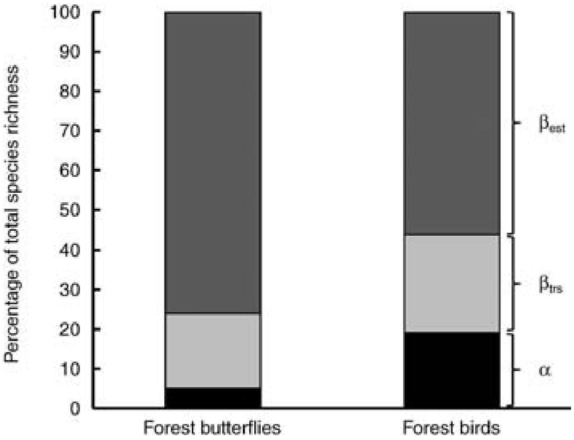

Fig. 1. Relative contributions of mean α-diversity (α), between-transect β-diversity (β_{trs}) and between-estate β-diversity (β_{est}) to species richness of forest butterflies and birds in the study sites.

LOCAL LEVEL EFFECTS OF VEGETATION CHARACTERISTICS

The most parsimonious model for explaining variations in butterfly species richness at the local level was one in which percentage ground cover of weeds was the sole predictor variable. This model accounted for 11·2% of the Akaike weights in the model set and explained 0·4% of variations in butterfly species richness across the transects. This model is described by the following equation:

$$\log(RICHNESS) = 0{\cdot}004 \times WEED + 0{\cdot}011 \times AGE - 0{\cdot}01 \times CANOPY + 0{\cdot}008 \times ALTITUDE - 0{\cdot}016 \times PROXIMITY + 0{\cdot}481 \times EFFORT_{trs} - 0{\cdot}544,$$

whereby *RICHNESS* is predicted species richness, *WEED* is percentage ground cover of weeds, *AGE* is the age of oil palms, *CANOPY* is canopy density, *ALTITUDE* is altitude, *PROXIMITY* is proximity to forests and $EFFORT_{trs}$ is transect sampling effort. This fitted model shows that butterfly species richness is expected to increase with percentage ground cover of weeds (Fig. 2a).

The most parsimonious model for birds was one that included both epiphyte prevalence and presence (or absence) of leguminous crops. This model accounted for 17·3% of the Akaike weights in the model set and explained 5·7% of the variation in bird species richness. The following equation describes this model:

$$\log(RICHNESS) = 0{\cdot}003 \times EPIPHYTE + 0{\cdot}423 \times LEGUME - 0{\cdot}003 \times AGE + 0{\cdot}002 \times CANOPY + 0{\cdot}001 \times ALTITUDE + 0{\cdot}0002 \times PROXIMITY + 0{\cdot}282 \times EFFORT_{trs} + 0{\cdot}533,$$

whereby *EPIPHYTE* is epiphyte prevalence and *LEGUME* is presence or absence of leguminous crops. The species richness of birds is expected to increase with epiphyte prevalence, and is also predicted to be higher when leguminous crops are present than when these crops are absent (Fig. 2b).

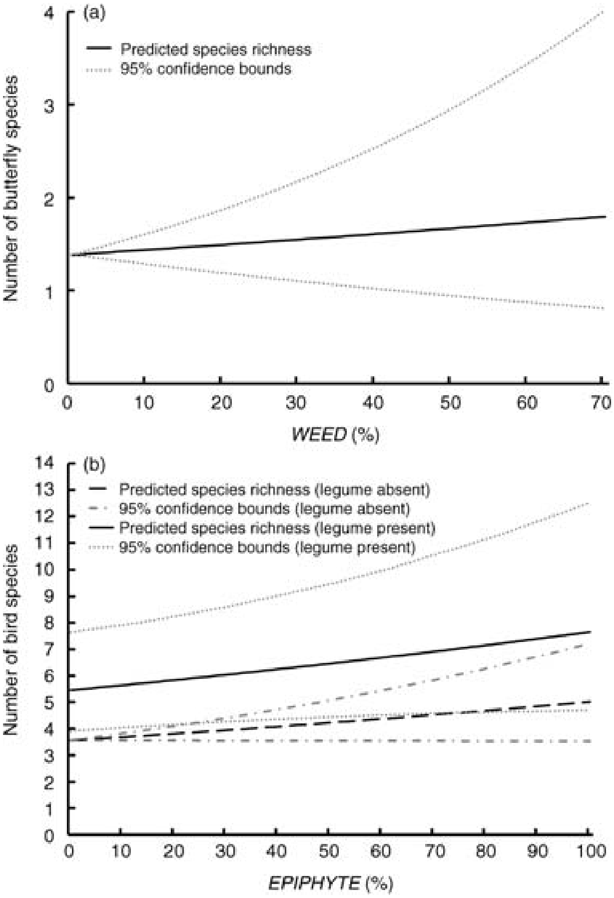

Fig. 2. Predicted number of species of (a) butterflies and (b) birds at the local level (i.e. across transects) based on the AIC$_c$-selected most parsimonious generalized linear mixed-effects model. Predictor variables were percentage ground cover of weeds (*WEED*) for butterflies, and epiphyte prevalence (*EPIPHYTE*) and presence or absence of leguminous crops (*LEGUME*) for birds. Species richness was predicted for the range of observed data values for each predictor variable. The median observed data values for the control variables of age of oil palms, canopy density, altitude, proximity to forests and transect sampling effort were used in the predictions. Confidence bounds represent the 10 000-iteration bootstrapped 95% upper and lower confidence limits.

The model averaged variance explained by each predictor variable in decreasing order of magnitude is as follows, for butterflies: percentage cover of weeds (pseudo-$R^2 = 0{\cdot}2\%$), presence of leguminous crops (pseudo-$R^2 = 0{\cdot}2\%$), percentage cover of ferns (pseudo-$R^2 = 0{\cdot}1\%$), presence of beneficial plants (pseudo-$R^2 = 0{\cdot}1\%$) and prevalence of epiphytes (pseudo-$R^2 = 0{\cdot}1\%$); for birds: presence of leguminous crops (pseudo-$R^2 = 4{\cdot}2\%$), prevalence of epiphytes (pseudo-$R^2 = 3{\cdot}1\%$), percentage cover of weeds (pseudo-$R^2 = 1{\cdot}8\%$), presence of beneficial plants (pseudo-$R^2 = 1{\cdot}1\%$) and percentage cover of ferns (pseudo-$R^2 = 1{\cdot}1\%$).

LANDSCAPE LEVEL EFFECTS OF NATURAL FOREST COVER

The most parsimonious model for explaining variations in butterfly species richness at the landscape level was one in which percentage cover of old-growth forests surrounding an estate was the sole predictor variable. This model accounted for 38·8% of the Akaike weights in the model set and explained 10·8% of the variation in butterfly species richness. This fitted model is described by the following equation:

$$\log(RICHNESS) = 0{\cdot}027 \times OLDGROWTH_{\mathrm{srd}} + 0{\cdot}576 \times \log(AREA) + 0{\cdot}149 \times EFFORT_{\mathrm{est}} - 4{\cdot}292,$$

whereby $OLDGROWTH_{\mathrm{srd}}$ is percentage cover of old-growth forests surrounding an estate, *AREA* is estate area and $EFFORT_{\mathrm{est}}$ is estate sampling effort. The fitted model shows that butterfly species richness is expected to increase with percentage cover of old-growth forests surrounding an estate (Fig. 3a).

The most parsimonious model for birds was one that included percentage cover of young secondary forests as the sole predictor variable. This model accounted for 29·5% of the Akaike weights in the model set and explained 14·4% of the variation in bird species richness. The following equation describes this model:

$$\log(RICHNESS) = 0{\cdot}023 \times YOUNGSEC_{srd} + 0{\cdot}108 \times \log(AREA) + 0{\cdot}063 \times EFFORT_{\mathrm{est}} + 0{\cdot}841,$$

whereby $YOUNGSEC_{\mathrm{srd}}$ is percentage cover of young secondary forests surrounding an estate. The species richness of birds is expected to increase with percentage cover of young secondary forests (Fig. 3b).

The model averaged variance explained by each predictor variable in decreasing order of magnitude is as follows, for butterflies, percentage cover of: old-growth forests surrounding an estate (pseudo-$R^2 = 4{\cdot}9\%$), old-growth forests within an estate (pseudo-$R^2 = 1{\cdot}4\%$), young secondary forests surrounding an estate (pseudo-$R^2 = 0{\cdot}5\%$), and young secondary forests within an estate (pseudo-$R^2 = 0{\cdot}5\%$); for birds, percentage cover of: young secondary forests surrounding an estate (pseudo-$R^2 = 5{\cdot}3\%$), old-growth forests within an estate (pseudo-$R^2 = 1{\cdot}6\%$), old-growth forests surrounding an estate (pseudo-$R^2 = 1{\cdot}1\%$), and young secondary forests within an estate (pseudo-$R^2 = 0{\cdot}5\%$).

Discussion

The sampling completeness for butterflies (~70%) and birds (~80%) in this study is comparable to that of other studies conducted in Southeast Asia (e.g. Benedick *et al.* 2006; Sodhi *et al.* 2006). Furthermore, as all analyses in this study were performed with the appropriate controls for variations in sampling effort at both the local and landscape levels, the lack of a complete sample for butterflies or birds is not expected to affect the study's main conclusions. The diversity partitioning analysis revealed that the observed total species richness across study sites was largely attributed to variations in species composition between transects and between estates (Fig. 1). Large contributions of β-diversity to overall species

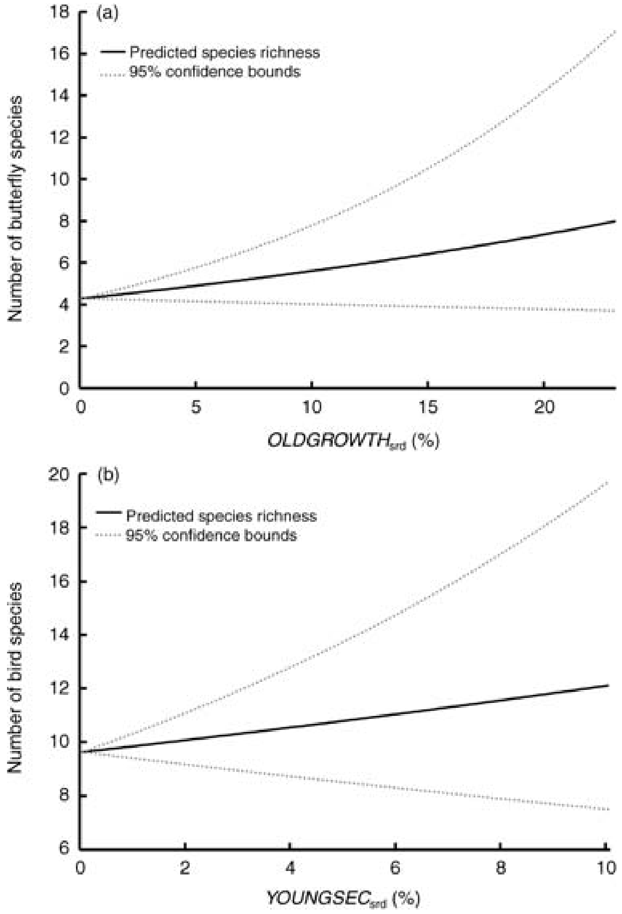

Fig. 3. Predicted number of species of (a) butterflies and (b) birds at the landscape level (i.e. across estates) based on the AIC_c-selected most parsimonious generalized linear mixed-effects model. Predictor variables were percentage cover of old-growth forests surrounding an estate ($OLDGROWTH_{srd}$) for butterflies; and percentage cover of young secondary forests surrounding an estate ($YOUNGSEC_{srd}$) for birds. Species richness was predicted for the range of observed data values for each predictor variable. The median observed data values for the control variables of estate area and estate sampling effort were used in the predictions. Confidence bounds represent the 10 000 iteration bootstrapped 95% upper and lower confidence limits.

richness patterns have also been reported in previous studies of biodiversity in agricultural landscapes (Wagner *et al.* 2000; Clough *et al.* 2007a). If species occurrences in an estate are influenced by the surrounding habitats, heterogeneity in the landscape would explain variations in species composition between estates (Clough, Kruess & Tscharntke 2007b). Similarly, differences in local vegetation characteristics within estates could explain variations in species composition between transects. Furthermore, low rates of species dispersal could also have contributed to high β-diversity relative to α-diversity (Chandy, Gibson & Robertson 2006). This hypothesis is supported by the results showing that between-estate composition of birds was less variable than that of butterflies (less mobile than birds).

LOCAL LEVEL EFFECTS OF VEGETATION CHARACTERISTICS

Vegetation characteristics explained between 0% and 1·2% of the variation in butterfly species richness across transects (see Supplementary material Appendix S3). The most parsimonious model for butterflies at the local level indicates that increasing the percentage ground cover of weeds from 0% to 70% (i.e. the maximum value recorded) would increase butterfly species richness by only 0·4 species (Fig. 2a). These results suggest that the vegetation characteristics measured in this study do not have a marked effect on forest-dwelling butterflies. A plausible explanation is that butterflies, particularly forest-dwelling species, are highly specialized with regard to their larval host plants (Koh, Sodhi & Brook 2004; Koh 2007a), such that their species richness would be largely determined by the species richness of potential larval host plants rather than the areal extent of ground vegetation. Furthermore, because many of the plant species cultivated in oil palm estates are not native to Borneo (e.g. the leguminous crop *Mucana bracteata*; Wilmot-Dear 1992), it is unlikely that native butterfly species could use them as larval resource.

Vegetation characteristics explained between 0% and 7% of the variation in bird species richness across transects (see Supplementary material Appendix S3). The most parsimonious model for birds at the local level shows that increasing epiphyte prevalence from 0% to 100% (i.e. to have epiphytes on every palm tree) would increase bird species richness by 1·5 species if leguminous crops were absent and by 2·2 species if they were present; and the presence of leguminous crops is expected to enhance bird species richness by between 1·9 species (when epiphyte prevalence is 0) and 2·6 species (when epiphyte prevalence is 100%). The positive effects of epiphyte prevalence and the presence of leguminous crops are probably due to the additional vegetation complexity that they provide to the oil palm habitat. Epiphytes might serve as an important nesting substrate for tree nesting birds that occur in oil palm plantations such as *Copsychus saularis* Linnaeus (magpie robin) (Nadkarni & Matelson 1989). Leguminous crops are likely to serve as foraging grounds for insectivorous birds such as *Rhipidura javanica* Sparrman (pied fantail) (MacKinnon & Phillipps 1993; Sekercioglu, Daily & Ehrlich 2004).

LANDSCAPE LEVEL EFFECTS OF NATURAL FOREST COVER

Natural forest cover within or surrounding an oil palm estate explained between 1·2 to 12·9% of the variation in butterfly species richness across estates (see Supplementary material Appendix S4). The most parsimonious model for butterflies suggests that increasing the percentage cover of old-growth forests surrounding an estate from 0% to 23% would increase butterfly species richness by 3·7 species (Fig. 3a). These results imply that (i) natural forests surrounding an oil palm estate are important to butterflies within the estate; and (ii) old-growth forests are more important to these butterflies than young secondary forests. As noted above, many forest-dwelling butterflies are highly host-specific and might be utilizing the natural forests surrounding oil palm estates as a source of larval host plants. Old-growth forests have a greater positive impact on butterfly species richness than young secondary forests because older forests by definition support a greater diversity of forest plant species that the larvae of forest-dwelling butterflies feed on.

Natural forest cover explained between 0·6% and 53·3% of the variation in bird species richness across oil palm estates (see Supplementary material Appendix S4). The most parsimonious model for birds reveals that increasing the percentage cover of young secondary forests from 0% to 10% would increase bird species richness by 2·5 species (Fig. 3b). These results suggest that for at least some of the bird species occurring in oil palm plantations, the surrounding natural forests remain an irreplaceable habitat for important life-history functions (e.g. reproduction).

The importance of the surrounding natural forests on butterflies and birds suggests that these forests could serve as important population sources for species occurring in oil palm plantations (Pulliam 1988). This is consistent with the conclusions of similar studies conducted in other human-disturbed habitats. For example, Koh & Sodhi (2004) showed that in Singapore, human-made parks adjacent to forest fragments had higher species richness of butterflies than isolated ones. Similarly, Raman (2006) reported that shade-coffee *Coffea canephora* L. and cardamom *Eletteria cardamomum* Maton plantations in the Western Ghats, India, adjoining natural forests had higher species richness of birds than plantations that lacked such connectivity.

Conclusions

In order to maximize biodiversity in oil palm plantations, oil palm companies and local governments should work together to preserve as much of the remaining natural forests as possible by, for example, creating forested buffer zones around oil palm estates or protecting remnant forest patches in the landscape. Although the magnitude of biodiversity enhancement (i.e. up to 3·7 species for butterflies and 2·5 species for birds) may seem low relative to the number of species in a neighbouring undisturbed lowland rain forest [for example, Danum Valley Conservation Area contains at least 85 butterfly and 103 bird species (Johns 1996; Hamer *et al.* 2006)], these additional species both are intrinsically valuable and may provide important ecosystem services for oil palm agriculture. For example, Koh (2008) recently showed that insectivorous birds in oil palm plantations contribute to the control of leaf-eating oil palm pests, which may provide the economic incentive for oil palm producers to make plantations more hospitable for biodiversity.

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Supplementary material

The following supplementary material is available for this article:

Detailed methods for butterfly trapping, diversity partitioning analysis and determination of spatial resolution for data analysis.

Appendix S1. Species lists of butterflies and birds recorded

Appendix S2. Definitions of old-growth and secondary forests

Appendix S3. Local level candidate models

Appendix S4. Landscape level candidate models

Appendix S5. Local level data

Appendix S6. Landscape level data

Fig. S1. Location of study sites.

Fig. S2. Vegetation characteristics.

Fig. S3. Expected species accumulation curves.

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