

Trait-dependent declines of species following conversion of rain forest to oil palm plantations

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Abstract Conversion of natural habitats to agriculture reduces species richness, particularly in highly diverse tropical regions, but its effects on species composition are less well-studied. The conversion of rain forest to oil palm is of particular conservation concern globally, and we examined how it affects the abundance of birds, beetles, and ants

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according to their local population size, body size, geographical range size, and feeding guild or trophic position. We re-analysed data from six published studies representing 487 species/genera to assess the relative importance of these traits in explaining changes in abundance following forest conversion. We found consistent patterns across all three taxa, with large-bodied, abundant forest species from higher trophic levels declining most in abundance following conversion of forest to oil palm. Best-fitting models explained 39–66 % of the variation in abundance changes for the three taxa, and included all ecological traits that we considered. Across the three taxa, those few species found in oil palm tended to be small-bodied species, from lower trophic levels, that had low local abundances in forest. These species were often hyper-abundant in oil palm plantations. These results provide empirical evidence of consistent responses to land-use change among taxonomic groups in relation to ecological traits.

Keywords Biodiversity · *Elaeis guineensis* · Malaysia · SE Asia · Stable isotope

Introduction

Agriculture is the main driver of tropical deforestation (Kissinger et al. 2012), and the expansion of oil palm plantations threatens tropical forests in Asia, Latin America, and Africa (Butler and Laurance 2009; Laurance et al. 2010; Wilcove and Koh 2010). Conversion of forest to oil palm plantation reduces species richness and abundance, and alters species composition in a range of taxa (Fitzherbert et al. 2008; Danielsen et al. 2009; Sodhi et al. 2010). Previous studies have suggested that habitat- and diet-specialist, and restricted-range species may be most at risk from conversion of tropical forest to oil palm (Danielsen and Heegaard 1995; Aratrakorn et al. 2006; Chey 2006; Peh et al. 2006; Fitzherbert et al. 2008), but it is unclear whether there is any consensus in such patterns among major taxonomic groups. Integrated analyses of existing data provide the potential to obtain new insights, and to examine ecological and phylogenetic variables known to be important for explaining species' responses to land-use change (McKinney 1997; Henle et al. 2004).

Ecological response traits (henceforth termed 'ecological traits'), such as body size and feeding guild, group species together according to shared responses to environmental disturbances and are often strongly associated with functional effect traits (henceforth termed 'functional traits'), which classify species based on their shared effects on particular ecosystem functions (Lavorel and Garnier 2002). Consequently, assessing how different ecological traits are affected by land-use changes can reveal concurrent impacts on ecosystem functioning (Hooper et al. 2005; de Bello et al. 2010). More directly, response traits can help to understand mechanisms driving species declines and aid conservation efforts by predicting species groups at greatest risk from land-use changes (McGill et al. 2006; Williams et al. 2010). For example, studies have demonstrated that certain feeding guilds are more sensitive to habitat disturbance than others (Gray et al. 2007; Attwood et al. 2008), and predatory species, particularly large-bodied or specialist predators, are especially sensitive to

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disturbance and land-use changes (e.g., Kareiva 1987; McKinney 1997). Other species traits associated with vulnerability to extinction following habitat fragmentation, land-use change and disturbance include local rarity, large body size, and small geographic range size (e.g., Terborgh 1974; McKinney 1997; Henle et al. 2004). Conversely, omnivores tend to be more resilient to land-use changes (e.g., McKinney 1997; Henle et al. 2004). Mechanisms underlying these trait sensitivities include a reliance on highly specialised resources, and greater energy requirements resulting in low population densities and the need for larger home ranges (e.g., Henle et al. 2004; Damuth 1981).

In cases where ecological traits are associated with functional traits, it is possible to infer direct relationships between declining traits and ecosystem processes. For example, Larsen et al. (2005) showed that larger-bodied dung beetles were more susceptible to extinction following habitat loss and were more functionally efficient than smaller-bodied beetles. Declines in larger-bodied beetles following habitat loss reduced rates of dung burial, an important ecosystem function. The same study also showed that declines in bee abundance and species richness following habitat disturbance reduced pollination rates (Larsen et al. 2005). For vertebrates, long-distance seed dispersal depends disproportionately on a few larger-bodied frugivorous birds and mammals, with decreased abundances of frugivorous birds directly reducing rates of seed dispersal (Moran et al. 2009; Velho et al. 2012). Furthermore, the loss of top predators can cause trophic cascades through food-webs, leading to a hyper-abundance of seed predators and herbivores, and subsequent reductions of seedling and sapling density (Terborgh et al. 2001). Comparison of species responses across different taxonomic and functional groups may thus help to predict ecological consequences of land-use change for ecosystem functioning (Lewis 2009; Morris 2010; Sodhi et al. 2010).

Ecological traits have been widely used to study land-use changes, but very few studies have used them to assess the impacts of converting rain forest to oil palm, and none of these have considered multiple ecological traits across several taxonomic groups. In this study, we assess (i) the relative importance of different ecological traits for explaining changes in abundance following conversion to oil palm, and (ii) the congruence of trait-specific responses across different taxonomic groups. We use a multi-taxon approach, focusing on birds, ants and beetles, which provides greater insight into community level effects than would a single taxon study (Fazey et al. 2005). We use abundance data extracted from published studies to test the hypothesis that, across the three taxonomic groups, species vary in their sensitivity to the conversion of forest to oil palm, and that locally rare, range-restricted, predatory, and large-bodied species show the greatest declines in abundance following the conversion of forest to oil palm. For birds, we account for potential confounding effects of phylogeny (Sibley and Ahlquist 1990) by using phylogenetically independent analyses, but suitable phylogenetic information is not currently available for ants or beetles.

Methods

We focused on birds, ants and beetles as three ecologically diverse taxa, thereby including vertebrates and invertebrates, social and non-social insects, and taxa representing a range of different feeding groups. We excluded taxa which contain only a single feeding group (e.g., herbivorous Lepidoptera), as it is not possible to quantitatively compare changes in abundance between guilds in such taxa. We searched ISI Web of Knowledge (WoK) for studies examining changes in abundance in forest and large-scale, mature (>10 years) oil palm habitats. We used the following key words: ('oil palm') AND (('biodiversity') OR

(‘bird(s)’ OR (‘avian’) OR (‘ant(s)’) OR (‘beetle(s)’) OR (‘coleoptera’) OR (‘species richness’) OR (‘composition’) OR (‘abundance’) OR (‘forest’)). We also searched reference lists and citations of studies found from these searches. To ensure our quantitative analyses were robust, we limited our search to peer-reviewed literature. Four otherwise suitable studies had to be excluded from analyses because abundance data for individual species or genera were unavailable (Danielsen and Heegaard 1995; Aratrakorn et al. 2006; Turner and Foster 2009; Brühl and Eltz 2010).

The final dataset used for analysis was from six published studies which compared extensive tracts of selectively logged, or in one case unlogged, forest with oil palm sites in SE Asia (Malaysia). Studies were limited to those from SE Asia to avoid biogeographical differences in species responses (e.g., Gray et al. 2007). Studies comparing forest and oil palm at more than one location contributed more than one dataset to the analyses (Peh et al. 2006) and so these studies provided a total of seven datasets for analysis; four for birds (total of 188 species), two for ants (207 species) and one for beetles (91 genera). For those studies with unequal sampling effort in different habitats, we randomly selected an equal number of samples from each habitat for analysis (Peh et al. 2006; Sheldon et al. 2010). We excluded species or genera recorded only as singletons from the analyses to avoid errors due to insufficient sampling. This cut-off value was chosen to maximise the number of species/genera analysed, and followed sensitivity analyses that showed that findings were qualitatively similar for thresholds of two, five or ten individuals per species or genus.

We analysed ant data averaged across the two studies comparing oil palm to unlogged forest (Fayle et al. 2010) and to logged forest (Lucey and Hill 2012). To examine whether combining data from logged and unlogged forest sites affected our findings, we compared final parameter estimates from analyses of the combined ant dataset ($n = 207$ species) with those from just the selectively logged forest dataset ($n = 92$ species). The parameter estimates were not qualitatively different between these analyses, and so the combined dataset was used to maximise the number of ant species analysed. This approach of combining the two studies is supported by recent studies showing little difference between species assemblages in unlogged and selectively logged forest (Berry et al. 2010; Edwards et al. 2011; Woodcock et al. 2011).

Bird names were assigned according to Sibley and Monroe (1990), ants according to Bolton et al. (2006), and beetles according to Bouchard et al. (2011 and the Universal Biological Indexer and Organizer project (www.ubio.org)). Ant analyses included morphospecies that represent unique species, but that have not yet been ascribed to known species. However, because morphospecies were not named consistently across studies, we analysed morphospecies data from only the most species-rich dataset (Fayle et al. 2010) to avoid pseudoreplication.

Traits examined and guild classification

We examined the traits of body size, local population size, geographic range size, and trophic position or feeding group classifications of species (hence forth termed ‘feeding guild’). Data on bird body mass and ant body size were from Dunning (2009) and ant-web.org, respectively and average values by genus were used if species-level values were unavailable (birds: 6/188 species, and ants 175/207 species); data on bird geographic range sizes were from Birdlife International (2011); local population size was calculated as the mean total abundance of species/genera in forest sites. Our measure of ant abundance (see “Analyses” below) gives a robust measure of population size that is independent of colony size. There were no data available for ant or beetle geographical range sizes, or for beetle body sizes.

Table 1 Species were assigned to feeding guilds based on information in published studies

Feeding guild	Description	Food source
Birds		
Carnivore	Carnivore, raptor	Vertebrates (inc. fish), carrion
Frugivore ^a	Frugivore	Fruit, berries
Granivore ^a	Granivore, seed eater	Seeds, grain (not fruit)
Insectivore	Insectivore	Insects, invertebrates
Nectarivore	Nectarivore	Nectar, pollen
Omnivore	Omnivore, opportunist	Combination of other guilds, with no single primary food source
Beetles		
Algivore ^b	Algivores, bryophages	Algae, lichen, and mosses
Fungivore	Fungivore	Fungi
Herbivore	Herbivore, xylophage	Any living plant matter
Saprophage	Saprophage, coprophage	Dung, carrion, dead organisms but not fungi
Predator	Predator	Living invertebrates (and vertebrates)

^a Lambert (1992) was not used to classify granivores or frugivores as it did not differentiate between seed and fruit eaters, classifying both as frugivores

^b Hunt et al. (2007) included moss-feeding Byrrhidae, genera of which are included in the beetle dataset from this study, in the algivore guild

Birds were assigned to one of six feeding guilds based on Wong (1986), Lambert (1992), Cleary et al. (2007), Jeyarajasingam and Pearson (1999), MacKinnon and Phillipps (1999) and Phillipps and Phillipps (2009) (Table 1). Beetles were assigned to guilds based on classifications in Hunt et al. (2007). Three bird species and 14 beetle genera were excluded from analyses, due to a lack of consensus in feeding guild assignment (birds), or where feeding guild was unknown (beetles).

Assigning species or genera to feeding guilds is possible for well-studied groups, such as birds. However, for hyper-diverse and poorly studied rainforest taxa, assigning guilds is challenging and often impractical (Blüthgen et al. 2003), particularly given that feeding habits of many species do not fall into discrete categories (Petchey and Gaston 2002). However, it is possible to examine the feeding habits of species using analysis of stable isotope ratios (Layman et al. 2007). Nitrogen isotope ratios ($^{15}\text{N}:^{14}\text{N}$, expressed as $\delta^{15}\text{N}$ values) are particularly useful in determining trophic positions because $\delta^{15}\text{N}$ values increase by approximately 2.5–3.5 ‰ during each trophic transfer (Vanderklift and Ponsard 2003). $\delta^{15}\text{N}$ values can therefore be converted into direct measures of trophic position (Post 2002), with trophic positions of approximately 2 indicating a plant-based diet and a trophic position ≥ 4 likely to indicate an entirely carnivorous diet. Ants were assigned trophic positions according to stable isotope data from Woodcock (2011), based on ants sampled from continuous primary forest in Sabah, Malaysia (see Woodcock et al. 2012 for details on methodology). Differences in morphospecies classifications meant that for most ants (178/207 species) species-level data on trophic position were not available, and so species were assigned average values by genus, following Gibb and Cunningham (2011). Six ant species were excluded from analyses because data were not available for any members of the genus. This genus-averaging approach is supported by the observation that, for adequately sampled taxa, the standard deviation of trophic level for different species

within each genus (mean $\sigma = 0.31$) was only fractionally higher than the standard deviation for different colonies of each species (mean $\sigma = 0.27$) (Woodcock 2011).

Analyses

Analyses were conducted separately for bird species (four datasets), ant species (two datasets), and beetle genera (one dataset). Ants may form large nests of thousands of individuals, and so individuals sampled at the same sampling point are unlikely to provide independent data. We thus analysed the incidence of species at sites (henceforth termed ‘abundance’), based on their presence or absence at individual sampling points within sites (e.g., Woodcock et al. 2011). Beetle analyses were conducted at the genus level, in line with the predominantly genus level identification in the original study (Chung et al. 2000). We computed changes in the abundance of species (birds and ants) or genera (beetles) between sampling locations in forest and oil palm. Following Gray et al. (2007), the mean change in abundance per guild was calculated as:

$$\frac{\sum_{i=1}^{Sg} \frac{n_{op} - n_f}{n_{op} + n_f}}{Sg} \quad (1)$$

where S = number of species/genera in the guild, g , and n = abundance of a species/genus (i) in oil palm (op) and forest (f). For 29 bird species and 20 ant species recorded in multiple studies, we computed the average change in abundance across studies. Data were then standardised according to total abundance of species/genera in forest and oil palm. Thus Eq. 1 weights all species/genera equally according to abundance with possible values ranging from +1, when all individuals are found only in oil palm, to -1 when all individuals are found only in forest.

We conducted separate analyses for the three taxa, containing the following variables; for birds: feeding guild (categorical), local population size (continuous), body mass (continuous) and geographical range size (continuous); for ants: trophic position, local population size and body size (all variables continuous); for beetles: feeding guild (categorical), and local population size (continuous).

We employed an information-theoretic approach to identify and select the best models for explaining changes in abundance in each of our three taxa. For each taxon, we constructed models with all possible combinations of the variables described above. We then fitted general linear models to the data for ants and beetles and phylogenetic generalised linear models (PGLS, see Freckleton et al. 2002) to the data for birds. The PGLS analysis was carried out using the most extensive estimate of avian phylogeny (Sibley and Ahlquist 1990). It is based on Pagel’s (1999) measure of phylogenetic independence (λ), which unlike many other statistical phylogenetic approaches, allows continuous and categorical variables to be analysed together (Pagel 1999). The PGLS method determines a maximum likelihood value for λ , which is then used to correct for phylogenetic non-independence in the data. λ ranges from 0 to 1, where 0 indicates the relationship between traits to be independent of phylogeny and 1 signifying that more closely related species are more likely to have the same trait values.

Prior to final analyses, model diagnostic plots were checked for homogeneity of variance and normality of residuals, following Faraway (2006). Non-homogeneous variances and non-normal residuals were corrected by the following transformations: \log_{10} (bird geographical range size and body mass, ant body size and population size, and beetle population size), \log_{10} square-root (ant change in abundance) and cube root transformation

(bird population sizes). After transformation, all continuous predictor variables were standardised to equivalent scales by subtracting the mean value and dividing by twice the standard deviation (Grueber et al. 2011). This means that effect sizes can be used to directly compare the relative importance of each predictor variable for explaining changes in abundance, and that main effect estimates are still interpretable for models that included interaction terms (Schielzeth 2010; Grueber et al. 2011).

Models were ranked according to their AIC_c values (Burnham and Anderson 2002; Mazerolle 2006), which are commonly used for model selection and account for potential biases due to small sample sizes. The smaller the AIC_c value, the better the model's fit (Burnham and Anderson 2002). We calculated the difference in AIC_c value between each model and the best model (delta AIC_c : Δ_i). Best models were selected as those with Δ_i values <2 . If there were multiple models with Δ_i values <2 , we carried out model-averaging across these models or, if no other model had a Δ_i value <2 , we used the parameters estimates from the single best model (Burnham and Anderson 2002). This allowed estimation of effect sizes and confidence intervals (CIs) for each predictor variable: effect sizes for continuous variables were slope estimates, whereas estimates for categorical feeding guilds were mean changes in abundance for each guild. To assess the overall goodness-of-fit of best models, adjusted R^2 values are presented.

Results

From six published studies we extracted seven datasets, allowing us to analyse responses of 188 bird species, 207 ant species, and 91 beetle genera, which ranged from endemic to ubiquitous taxa. Birds and beetles spanned 10 feeding guilds, and ant species ranged from herbivorous species (trophic position = 2.0) to entirely carnivorous species (trophic position = 4.7). Ant body lengths varied from 0.5 to 8.0 mm and bird body masses from 5.6 g to 2.9 kg.

For birds, overall species richness in forest declined by 43 % following conversion to oil palm (175 species in forest vs. 99 in oil palm), and abundance declined by 18 % following conversion (3,812 individuals in forest vs. 3,122 in oil palm). For ants, both species richness and abundance declined by 61 % following conversion (190 species and 1,003 incidences in forest vs. 74 species and 388 incidences in oil palm) and for beetles there was a 52 % decline in generic richness (85 genera in forest vs. 41 in oil palm) and a 54 % decline in abundance (984 individuals in forest vs. 450 in oil palm) following conversion.

Selection of best models and model confidence

All the ecological variables we examined were present in the best models for all three taxa (Table 2). For birds, the model with the lowest AIC_c value contained the ecological predictor variables of feeding guild, body size, local population size, and geographical range, without any interactions. Both of the best ant models contained all three predictor variables of trophic position, body mass, and local population size, as well as an interaction between trophic position and body size. The best beetle model also contained both predictor variables of feeding guild and local population size. Overall model confidence was high for all three taxa, with 43 % of the variation in the data set explained in the best bird model, 39 % in the best ant model and 66 % in the best beetle model (Table 2).

Table 2 Best models were selected based on AIC_c values

Model	Log-lik	K	AIC _c	Δ_i	Rank	$\exp(-\Delta_i/2)$	w_i	w_j	Adj R ²
Birds									
Mass + pop + range + guild	-144.53	9	308.07	0.0	1	1.00	0.31	1.00	0.43
Guild + pop + range	-145.72	8	308.25	0.2	2	0.91	0.28	1.10	0.42
Mass + guild + pop*range	-144.01	10	309.27	1.2	3	0.55	0.17	1.82	0.43
Guild + pop*range	-145.44	9	309.88	1.8	4	0.40	0.12	2.47	0.42
Guild + range + mass*pop	-144.33	10	309.91	1.8	5	0.40	0.12	2.50	0.43
Ants									
Pop + trophic*size	-115.81	4	241.91	0.0	1	1.00	0.65	1.00	0.39
Trophic*size + trophic*pop	-115.36	5	243.13	1.2	2	0.54	0.35	1.84	0.39
Beetles									
Guild + pop	-11.29	6	37.94	0.0	1	1.00	1.00	1.00	0.66

We computed parameter estimates by using model-averaging across the best models listed above. For each taxon, best models were those with $\Delta_i < 2$

Log-likelihood the overall model fit with no adjustment for the number of parameters, *K* the number of parameter estimates in the model, w_i the Akaike weight, representing the model's relative strength compared to other best models, and w_j the evidence ratio of the best models compared to the top-ranked model. AIC_c and Δ_i are explained in "Methods". *mass* body mass, *pop* local population size, *range* geographic range, *trophic* trophic position, *size* body size

Best predictors of sensitivity to conversion

Presented below are effect sizes and 95 % confidence intervals for each variable included in best models. Effect sizes for continuous variables are slope estimates of the variable against change in abundance, whereas estimates for categorical feeding guilds are mean changes in abundance for each guild. Parameter estimates from bird analyses indicated that different feeding guilds varied in their sensitivity to the conversion of forest to oil palm, although some guilds had low sample sizes (Fig. 1). Insectivores (effect size: -0.48; 95 % CIs: -0.63, -0.34) and frugivores (effect size: -0.55; CIs: -0.76, -0.34) declined most in abundance following forest conversion, whilst nectarivores showed smaller declines (effect size: -0.40; CIs: -0.77, -0.026). In contrast, omnivores (effect size: -0.21; CIs: -0.46, 0.045) showed no significant decline in abundance following conversion of forest to oil palm.

Local population size, body mass, and geographical range size all had significant effects on the change in abundance of bird species following conversion to oil palm. Local population size had by far the greatest relative impact, with an estimated effect size of -0.75 (CIs: -0.92, -0.59), followed by geographic range size with an estimated effect size of 0.36 (CIs: 0.20, 0.53), and body mass had the smallest relative impact on change in abundance with an estimated effect size of -0.19 (CIs: -0.37, -0.010). Therefore, in decreasing order of importance, bird species with large local population sizes in forest, small geographic ranges, and large bodies declined most in abundance following conversion to oil palm (Fig. 1).

In ant analyses, trophic position and local population size both had significant impacts on change in abundance. In addition, the highly significant positive interaction between trophic position and body size (effect size: 1.23, CIs: 1.01, 1.46) was by far the most important factor explaining changes in ant abundance, suggesting that large-bodied,

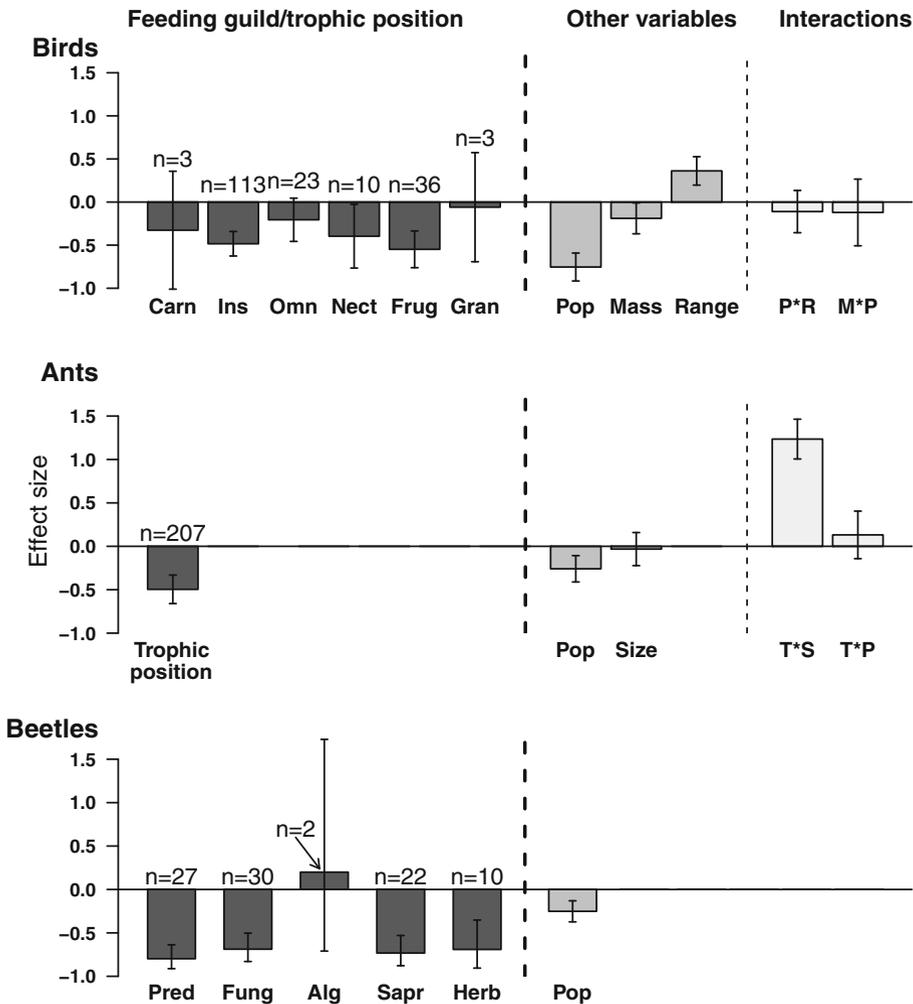


Fig. 1 Model-averaged effect sizes of different predictor variables for abundance change of birds, ants, and beetles between forest and oil palm. We present model-averaged effect sizes for all variables included in the best models. Effect sizes for continuous variables and interactions are estimated slope values of standardised variables/interactions against abundance change. Effect sizes for categorical feeding guilds are estimated mean abundance changes of each bird and beetle feeding guild. N.B. ants were not classified into trophic categories and so the effect size plotted is for the continuous variable trophic position. Sample sizes for the number of species/genera in each feeding guild are shown. For all estimates, *error bars* give model-averaged 95 % CIs. *Trophic* trophic position, *Pop* population size, *Mass* body mass, *Range* geographic range, *M*R* body mass*geographic range, *M*P* body mass*population size, *T*S* trophic position*body size, *T*P* trophic position*population size, *Carn* carnivores, *Ins* insectivores, *Omn* omnivores, *Frug* frugivores, *Gran* granivores, *Nect* nectarivores, *Pred* predators, *Fung* fungivores, *Alg* algivores, *Sapr* saprophages, *Herb* herbivores

carnivorous ants declined most in oil palm (Fig. 1). Trophic position was the second best predictor of change in abundance (effect size: -0.50 , CIs: -0.66 , -0.33), followed by local population size (effect size: -0.26 , CIs: -0.41 , -0.11). The effect of body size on its own was not significantly different from zero (effect size: -0.03 , CIs: -0.22 , 0.16).

Therefore, in decreasing order of importance, large-bodied ants with more carnivorous diets, carnivorous ants in general, and ants with large local population sizes in forest were particularly vulnerable to conversion to oil palm.

The beetle analyses suggest that feeding guild was not as important for predicting abundance change as for birds and ants, with all guilds except for algivores declining similarly in oil palm. Algivores appear to be more abundant in oil palm than in forest but there were only two genera in this guild, resulting in large confidence intervals (effect size: 0.20, CIs: $-0.71, 1.73$). All other guilds declined in abundance following conversion. The largest decline was for predators with an effect size of -0.80 (CIs: $-0.91, -0.64$), followed by saprophages (effect size: -0.73 ; CIs: $-0.88, -0.53$), fungivores (effect size: -0.69 ; CIs: $-0.83, -0.50$) and herbivores (effect size: -0.69 ; CIs: $-0.91, -0.35$). Whilst this suggests that predators may have declined slightly more than other guilds following conversion, population size appeared to be a better predictor of vulnerability for beetles (estimate: -0.25 , CIs: $-0.37, -0.13$). Therefore, genera with large local population sizes in forest declined most in abundance in oil palm.

Similarity of responses among taxa

Across taxonomic groups, there were consistent declines in the abundance of large-bodied and locally abundant forest species, and of species from higher trophic levels following conversion of forest to oil palm. Therefore, species occurring at highest abundances in oil palm plantations tended to be small-bodied species, from lower trophic levels, that are locally rare in forest. Following land-use conversion, relative abundance patterns of species/genera were also less evenly distributed within the three taxa. In each taxon, a small number of species/genera were dominant and became hyper-abundant in oil palm (see supplementary online material 1).

Influence of phylogeny

Comparison of phylogenetic and non-phylogenetic bird analyses revealed little difference in estimated variable parameters (Fig. 2). Model selection in the non-phylogenetic analyses identified a set of three best models, which were the first, third and fifth best models in the phylogenetic analyses. In the phylogenetic bird analyses, the maximum likelihood value of λ for each of the five best models deviated significantly from 1 ($p < 0.0001$ in all cases) but not from 0 ($p > 0.16$ in all cases). Thus, there was little evidence that any of the traits considered were related to phylogeny. Although caution is required when extrapolating trends across taxa, the phylogenetic independence of bird analyses may lend support to the validity of the non-phylogenetically adjusted ant and beetle analyses.

Discussion

Conserved trait declines

Our results showed consistent responses across taxa in terms of which ecological traits were most affected by conversion of forest to oil palm. The most abundant species in oil palm tended to occur at very low abundances or be absent in forest, and large-bodied species and those from higher trophic levels also occurred at much lower abundances in oil

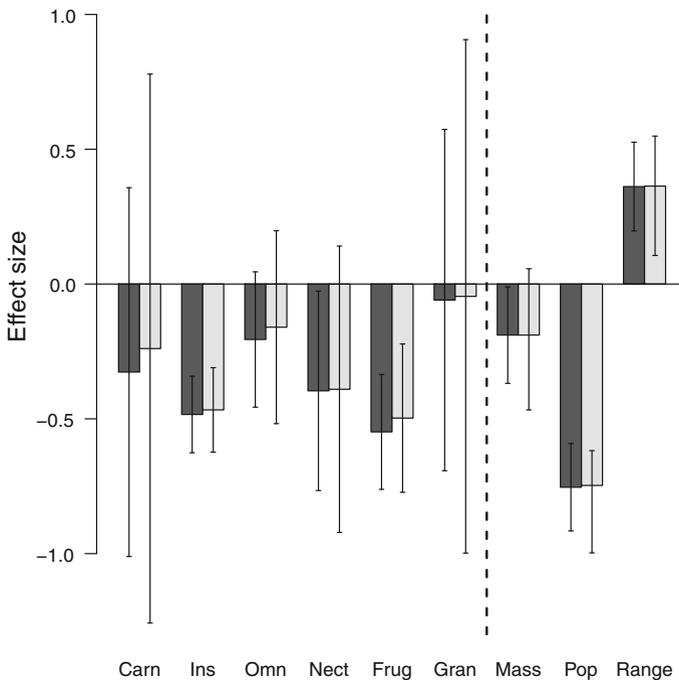


Fig. 2 Effect sizes of predictor variables from bird analyses with (*dark grey bars*), and without (*light grey bars*) adjustment for phylogeny. Effect sizes and CIs for continuous and categorical variables, number of species in each guild, and guild abbreviations as in Fig. 1

palm than in forest. This study provides quantitative evidence for consistent patterns in the sensitivity of ecological traits across different taxonomic groups following the conversion of forest to oil palm. Our results show that across three ecologically diverse taxonomic groups, species found in oil palm plantations consistently tend to be small-bodied species, from lower trophic levels, that are locally rare in forest.

Drivers of trait declines

Our results on consistent patterns of declines in traits in different taxa following conversion of forest to oil palm suggest that there may be consistent extinction drivers acting across taxonomic groups. In tropical forest habitats, very high plant diversity supports high structural diversity, which underpins high animal diversity (Novotny et al. 2006). The structurally simple oil palm environment with very low non-palm plant diversity (largely restricted to herbaceous ground cover and epiphytic ferns e.g., Foster et al. 2011) may drive many specialised species extinct and favour more generalist and disturbance-tolerant species that occur at only low abundances in forest. This shift from habitat complexity to simplicity could explain the declines in frugivorous and insectivorous birds. These were the most species rich guilds in our analyses (insectivores: 107 species, frugivores: 35 species) and, thus might be expected to exhibit the greatest niche specialisation in forest (e.g., to avoid competition). The declines of these guilds following habitat conversion may be explained by this specialisation, and by the lack of suitable fruit-bearing trees and invertebrate-rich vegetation layers in the homogenous oil palm environment. Declines of

large-bodied and higher trophic level species in oil palm may be explained by cascading bottom-up effects of reduced resource availability disproportionately affecting the species with greater energy requirements and lower population densities (e.g., Damuth 1981).

Our finding that abundant forest species decline most in oil palm does not agree with previous studies showing high vulnerability of rare species (e.g., McKinney 1997; Henle et al. 2004), but this is likely to be explained by two factors. Firstly, the scale at which rarity is defined is critical in explaining whether “rare” species are shown to be more or less vulnerable to extinction following habitat disturbances (McKinney 1997). For example, whilst you would expect high vulnerability of rare species defined by restricted geographic distributions or IUCN Red Listings, our definition of rare species as those with small local population sizes in forest may include geographically widespread, disturbance-associated taxa that occur at low abundances in forest. Indeed, this is supported by our results showing that bird species with smaller geographic ranges declined more in abundance following conversion of forest to oil palm.

Secondly, much of the earlier evidence on the vulnerability of rare species is from studies of forest disturbance and fragmentation (McKinney 1997; Henle et al. 2004), which compare the same habitats under varying levels of disturbance. By contrast, forest and oil palm are distinct habitats, and our results demonstrate that many relatively common forest species cannot persist in oil palm habitats.

We maximised the number of species in our analyses by including all species occurring more than once. However, when only forest species were included in analyses we still found declines of abundant forest species following conversion. Given that the majority of species declined in abundance following conversion, the slope of the relationship between population size and change in abundance is likely to be driven by those few species that increase in abundance in oil palm and so our findings do not preclude the loss of rare forest species, as well as the loss of more abundant forest species, in plantations. In oil palm, the small-bodied species from lower trophic levels, that tended to be locally rare in forest, but that dominated these agricultural sites were probably able to exploit the few crop-associated resources found in the plantations. Similarly, widespread and omnivorous bird species that are not reliant on a single food source were also more abundant in plantations (Gregory and Gaston 2000; Walker 2006).

Hyper-abundance of species on plantations

We observed a few species reaching very high abundances in oil palm sites in all three taxa (see supplementary material 1). For example, most insectivorous and frugivorous bird species declined in plantations, although some species, such as *Macronous gularis* (Striped Tit-babbler), *Orthotomus sericeus* (Rufous-tailed tailorbird), and *Psittacula longicauda* (Long-tailed parakeet) were highly abundant in oil palm plantations. Similar patterns have also been shown in butterflies (Lucey and Hill 2012), moths (Chey 2006), termites (Hassall et al. 2006), rats (Wood and Chung 2003, Bernard et al. 2009), and frugivorous bats (Danielsen and Heegaard 1995), whereby oil palm plantations typically support a small number of species that occur at much higher abundances than observed in forest habitats. For example, Lucey and Hill (2012) showed that plantations support just 54 % of forest species, yet overall butterfly abundance was >3.5 times higher in plantations than in forest. The same trends have also been observed following other land-use changes (e.g., Terborgh et al. 2001; Laurance et al. 2002; Feeley and Terborgh 2006; Gardner et al. 2007; Nichols et al. 2007). Oil palm monocultures can provide a hyper-abundance of just a few resources (e.g., palm fruit and palm fronds) that can be exploited by a few species, which can

subsequently achieve very high abundances. However, the restricted range of resources present in plantations means that most resources required to support forest species are absent.

Our results illustrate substantial turnover of species with different ecological traits between forest and oil palm. Many of the traits considered are also functional traits (e.g., body size, feeding guild), implying inherent differences in the way that the forest and plantation systems function ecologically. Essential ecosystem functions in forest may not be important in oil palm plantations, either because they are replaced by plantation management practices, for example the addition of fertilisers in place of natural nutrient cycling, or because there is little requirement for them in monoculture plantations (e.g., seed dispersal). However, in plantations, there may still be risks associated with a reliance on a few numerically dominant species for ecosystem functioning, and more data are required on whether or not a few dominant species in oil palm plantations can compensate for the loss of many specialised forest species (e.g., Loreau et al. 2001; Foster et al. 2011; Peh and Lewis 2012).

Conclusions

Our results show that across three ecologically diverse taxonomic groups there were consistent patterns in the sensitivity of species to land-use change, and that species occurring in oil palm plantations were more likely to be small-bodied species, from lower trophic levels that are present at very low abundances in forest. All three taxonomic groups contained a few species that were hyper-abundant in oil palm, presumably because they could exploit the few highly abundant crop-associated resources present in plantations. Observed declines of large-bodied, higher trophic level, forest species may be a response to the low diversity of available resources in homogenous plantations. Consistent responses to land-use change among the three taxonomic groups in relation to species' ecological traits imply that similar mechanistic drivers affect species' responses to land-use conversion, and infer differences in ecosystem functioning between forest and oil palm habitats.

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