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LETTER

Bats and birds increase crop yield in tropical agroforestry landscapes

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Abstract

Human welfare is significantly linked to ecosystem services such as the suppression of pest insects by birds and bats. However, effects of biocontrol services on tropical cash crop yield are still largely unknown. For the first time, we manipulated the access of birds and bats in an enclosure experiment (day, night and full enclosures compared to open controls in Indonesian cacao agroforestry) and quantified the arthropod communities, the fruit development and the final yield over a long time period (15 months). We found that bat and bird exclusion increased insect herbivore abundance, despite the concurrent release of mesopredators such as ants and spiders, and negatively affected fruit development, with final crop yield decreasing by 31% across local (shade cover) and landscape (distance to primary forest) gradients. Our results highlight the tremendous economic impact of common insectivorous birds and bats, which need to become an essential part of sustainable landscape management.

Keywords

Biodiversity conservation, biological control, ecosystem services, enclosure field experiment, land-use management, mesopredators, multitrophic interactions, shade cover, Southeast Asia, *Theobroma cacao*.

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INTRODUCTION

Ecosystem services such as biological control of pests contribute to human welfare, especially for the world's poor (Millennium Ecosystem Assessment 2005; Boyd & Banzhaf 2007). Recent studies paid particular attention to the impacts of both diurnal and nocturnal flying predators in different tropical habitats (Kalka *et al.* 2008; Williams-Guillén *et al.* 2008; Morrison & Lindell 2012), but there is no publication showing the influence of birds and bats on arthropod suppression and crop productivity. It has not yet been analysed in a long-term experimental approach considering effects on arthropods and final yield across spatial scales. This is partly due to the complexity of predator–prey interactions, which are often nonlinear, change in space and time, and include direct as well as indirect effects (e.g. Brown *et al.* 2001; Vandermeer *et al.* 2010; Singer *et al.* 2012), making predictions difficult. For example, insectivorous birds, which decrease the numbers of leaf-chewing insects can indirectly enhance forest tree growth by reduction of leaf damage (Marquis & Whelan 1994), whereas intermediate densities of minor pests in other ecosystems can be favourable, if they inhibit infestation of major pests (Wielgoss *et al.* 2012).

Flying vertebrates like birds and bats are considered effective arthropod predators in the tropics (e.g. Whelan *et al.* 2008; Kunz *et al.* 2011; Morrison & Lindell 2012), but can also impact predatory insects and spiders, releasing lower trophic levels from potential pest control (e.g. Lundberg & Moberg 2003). Such mesopredator release (e.g. of predatory spiders and ants) could lead to reorganisation of local food web structure and consequentially, unexpected changes in crop productivity, underlining the need for empirical studies that consider the complexity of interactions both in space and time with their relation to crop yield.

We conducted an extensive enclosure field experiment, including 15 months of continuous data collection to investigate the effects of biological control by birds and bats on diurnal and nocturnal insect communities, cacao fruit development, crop yield and leaf herbivory in Indonesian tropical cacao agroforests differing in local

shade tree management and distance to primary forest. Such long-term empirical studies (conducted over a period of 12 months or more) better account for variation of environmental and seasonal fluctuations (e.g. Williams-Guillén *et al.* 2008; Singer *et al.* 2012), changing peaks of population densities and crop yield, which have never been considered in previous enclosure experiments. They also provide for larger sample sizes and higher completeness of species inventories (e.g. Novotný & Basset 2000).

Landscape structure influences local communities and ecosystem services (e.g. Tscharntke *et al.* 2012), especially the biological control of insect pests (Bianchi *et al.* 2006) as well as species richness and diversity of birds and bats (Faria *et al.* 2006). Both distance to forest margin and available amount of shade trees are known to be critical variables in explaining the composition of bird (Clough *et al.* 2009) and bat (Faria *et al.* 2006) communities, in particular of forest species.

Last but not least, the majority of research on the functional role of birds and bats is available from the Neotropics (e.g. Van Bael & Brawn 2005; Kalka *et al.* 2008; Williams-Guillén *et al.* 2008; Morrison & Lindell 2012), while knowledge from other tropical regions is urgently needed to understand global patterns of biodiversity-related ecosystem services.

We tested the hypotheses that: (1) the absence of top predators (birds and bats) does not only influence the abundance of phytophagous insects and mesopredators (predatory ants and spiders) but also (2) affects cacao crop yield. Furthermore, we hypothesised that (3) these effects depend on shade tree availability in the cacao plantations (Clough *et al.* 2011; Tscharntke *et al.* 2012), and on the distance to the next closed forest block (Clough *et al.* 2009), a likely source of foraging insectivorous birds.

To our knowledge, we present the first results from a comprehensive enclosure experiment relating predation of birds and bats to changes in mesopredators (predatory insects and spiders), phytophagous insects, and the development and damage of fruits over more than one year. In particular, we quantified crop yield, the final ecosystem service integrating all intermediate services (Mace *et al.*

2012), and found that bats and birds induced crop yield increases consistently across local (shade cover) and landscape (distance to primary forest) gradients.

MATERIAL AND METHODS

Establishment of long-term enclosures

All sites were situated at the northern tip of Napu Valley in Central Sulawesi, Indonesia (1°25' 32" S, 120°18'54" E). After an initial mapping of the study area, we selected 15 smallholder cacao plantations as sites for our enclosure experiments in March 2010 (Fig. 1).

Each site represented a unique combination of two gradients:

(1) Local shade tree cover: With reference to Steffan-Dewenter *et al.* (2007) and based on measurements in the field, we quantified local shade tree canopy cover in per cent and classified it as low (0–25%), medium (25–50%) or high (more than 50%). In all of our study sites, shade was predominately provided by planted legume shade trees (*Erythrina* sp. and *Gliricidia* sp.; $n = 2148$; see Table S5), which are favoured in many agroforestry systems (e.g. Tscharntke *et al.* 2011). Single shade tree species from the families Euphorbiaceae (e.g. candle nut tree) and Lauraceae (e.g. avocado) occurred in two thirds of the plots, but were much less common ($n = 87$ and 86 respectively). We used mean shade tree cover per site, which was calculated from two shade cover surveys in June 2010 and Feb-

ruary 2011, using digital photographs of the treatment canopy at each site (Panasonic DMC-TZ7EG-K) and processing software Image J (Rasband 1997–2010).

(2) Distance to primary forest: Distance to primary forest was determined using satellite pictures and GPS data (Garmin 12 Map, GARMIN International, Inc., Olathe, KS, USA) from the study area and measured as the distance (range: 0–3500 m) from the edge of the study site to the edge of the closed forest block. There were no secondary forest patches between the cacao plantations and the primary forest of the adjacent national park (Lore-Lindu National Park).

All cacao plantations were larger than 0.5 ha (range: 0.5–1.5 ha) and at least 500 m apart from each other. They were managed by local farmers without applications of insecticides, herbicides or other chemical compounds. We rented 8 cacao trees per site during the period of the study (January 2010 until August 2011). Trained field assistants maintained the experimental plots (see Table S2). Study tree and site characteristics are listed in more detail in the Supporting Information (see Table S1).

In each cacao plantation, four enclosure treatments (Fig. 2) were established: (1) Day-time enclosure of birds (Day ex.); (2) Night-time enclosure of bats (Night ex.); (3) Total enclosure of both birds and bats (Full ex.); (4) Control treatment with no enclosure (Con).

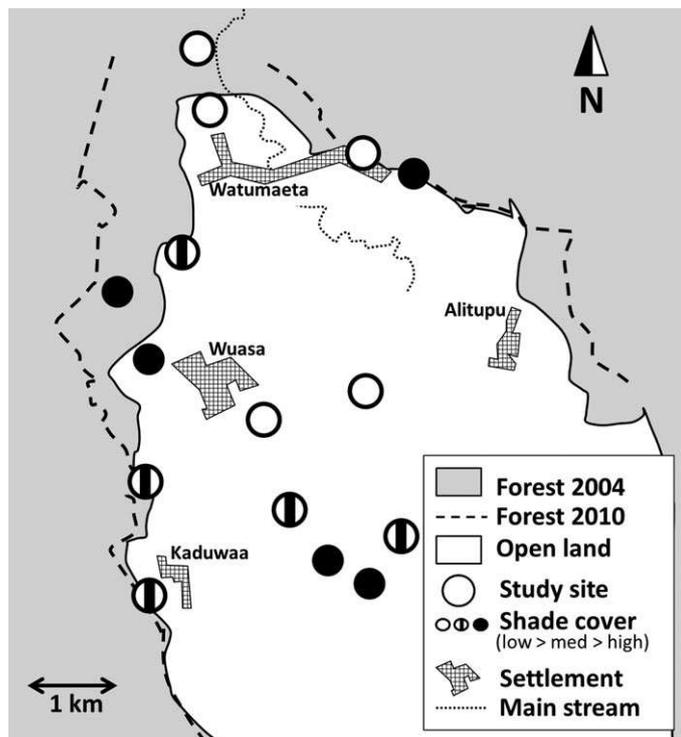


Figure 1 Schematic map of study sites. Grey parts indicate the closed primary forest block of the Lore Lindu National Park in 2004. The dashed line represents the forest margin measured in our study (2010). White area represents the human dominated open land of the Napu valley (with all other habitat types, including agricultural systems). Our 15 cacao agroforestry study sites are plotted as circles, which indicate the amount of shade cover: 0–25% (empty); 25–50% (half filled) and more than 50% (filled black).



Figure 2 One of the four enclosure treatments per site (Day, Night and Full Enclosure in addition to a non-caged Control) with two cacao trees (*Theobroma cacao*) within the enclosure construction of bamboo and nylon monofilament (mesh size: 2 × 2 cm).

Each of the four enclosure treatments contained two 2.5–4 m high cacao trees. The foliage of the study trees and the enclosure net were always spaced 1–2 m. Except for the control, each treatment was surrounded by an enclosure cage built by a bamboo construction and commercial nylon monofilament with a mesh size of 2 × 2 cm (following Van Bael & Brawn 2005; Kalka *et al.* 2008; Williams-Guillén *et al.* 2008). The enclosures prevented access by all bird and bat species but allowed access by arthropods, including large spiders and Lepidoptera (*personal observation*; see also Morrison & Lindell 2012). The enclosure nets were opened and closed like curtains daily in the morning hours (5:30 am) and in the evening (6:30 pm) to avoid/allow access from all directions. The total enclosure was always closed and cleaned from fallen shade tree leaves if necessary. In total, 120 cacao trees from 60 enclosure treatments on 15 cacao plantation sites were included in our study.

After 8 weeks of training of Indonesian assistants and optimisation of methods and survey schedules, we started our standardised, repeated surveys in May 2010 and finished in August 2011 (15 months of continuous data collection; see Table S2). Additional mist netting of birds (see Table S3) and data from bat mist netting 23 km apart from our study area (see Table S4) were used to identify excluded species and families. The most abundant insectivorous bird species excluded within our sites were: *Dicaeum aureolimbatum*, *D. celebicum*, *Nectarinia jugularis*, *Zosterops chloris* and *Z. atrifrons* (see Table S3). Excluded insectivorous bat species from the western border of the Lore Lindu national park mostly belong to the genera *Hipposideros*, *Myotis*, *Megaderma* and *Rhinolophus* (Graf 2010, see Table S4).

Arthropod communities

Every month, B. M. observed the arthropod community of each study tree on each site twice: During day-time (7 am until 1 pm) and during night-time (8 pm until 2 am). We used a time standard of 25 min per survey round and tree to observe all insects and spiders on the different parts of the tree. Starting on the ground, we observed stem, branches and tree foliage visually and documented the observed arthropods with digital photographs (Panasonic DMC-TZ7EG-K). For each insect or spider, we noted as many attributes as possible and necessary for the best available identification (e.g. colour, morphological characteristics and body size). In the field, we identified insects and spiders at least to order level and estimated the size (in mm). We recorded the respective position on the tree (branch, stem, fruit, flower or leaf) and activity (eating or hunting) of each observed individual. The number of insects that occurred in groups larger than 20 individuals was estimated and re-checked after the survey using the photographs. Final identification was done using various references (e.g. Zborowski & Storey 2010) and photographic material from the surveys, which was archived after each survey.

For statistical analysis, we used seven groups of the most common arthropod groups that are expected to play an essential role within the multitrophic interactions on cacao trees (of seven target orders), either being at least partly phytophagous (Coleoptera imagines and Lepidoptera larvae), mesopredators (ants and spiders), phytophagous ant trophobionts (aphids) and/or mainly night active consumers (Orthoptera and Blattodea). Lepidopteran larvae were the only larvae group which was abundant enough (Table 1) to perform a separate analysis (in contrast to Coleoptera larvae). As flow-

Table 1 Arthropod abundances

No. of individuals	Arthropod groups						
	Leplarv	Coleo	Ants	Spiders	Aphids	Ortho	Blatto
(a) Woody parts	486	1101	9711	3580	1343	97	374
(b) Tree foliage	1973	2469	1047	1330	5704	250	18
(I) Day	1665	2062	9367	3228	5352	108	162
(II) Night	794	1508	1391	1682	1695	239	230
TOTAL	2459	3570	10758	4910	7047	347	392

Total numbers (*n*) of the most common arthropod groups observed on (a) woody cacao tree parts (stem, branches, fruits and flowers) or (b) the cacao foliage. Differences between arthropod numbers in daytime and night-time surveys (I and II) are shown above the total count of arthropods (TOTAL). Short names of the groups relate to the following: Lepidoptera larvae (leplarv), Coleoptera imagines (coleo), wingless Formicidae (ants), Araneae (spiders), Aphididae (aphids), Orthoptera (ortho) and Blattodea (blatto).

ers and fruits of cacao grow on the tree stem (cauliflore) and we were interested in quantifying fruit development, we analysed arthropods on the stem of the cacao trees (including tree stem, branches, fruits and flowers) separately from those on the tree foliage (two different response variables). Each of the seven arthropod groups showed up with a minimum of 250 individuals at least at the woody tree parts or the tree foliage.

Cacao pests, fruit production, flowers and yield

The cacao fruits were surveyed in two steps. First, every 2 weeks, the number of small, medium and large cacao fruits was counted (according to the methods of Wielgoss *et al.* 2012) and fruit pests were quantified, including feeding marks of *Helopeltis sulawesii* Stone-dahl (Heteroptera, Miridae) and cacao pod borer *Conopomorpha cramerella* Snellen (Lepidoptera: Gracillariidae) feeding symptoms as well as cherrille wilt (early abortion of small cacao fruits smaller than 5 cm).

In addition to the cacao fruits, we counted all cacao flowers (2011–2012) on each tree. Cacao flower and fruit survival strongly depend on multiple factors such as fruit abortion, diseases and pollination and are determined during the first few weeks of fruit development (Bos *et al.* 2007).

The total number of cacao flowers was used in our analyses. In a second step, all harvested cacao fruits were opened and diseases of the fruit content were recorded (e.g. cacao pod borer damage). Finally, the cacao seeds were dried in separate drying boxes for each treatment per site. The dry cacao seeds (kg/treatment) represent cacao yield in our analyses. Cacao yield was further sorted into first class and second class cacao beans to determine effects on the top quality yield. In total, we recorded 75576 cacao fruits of all size classes (including multiple counts of single fruits which developed during the survey and were therefore counted more than once). Altogether, 4071 cacao fruits were produced and harvested on all sites during our experiment.

Herbivory

On each study tree, leaf damage (in %) caused by phytophagous insects (and not by fungi, virus infection or sunburn) was quantified by a trained assistant. Every month, we marked a new group of 10 freshly developed (red coloured and soft) cacao leaves on one or

two branches of each study tree, and surveyed them three times (every 10 days). The selection of leaves was determined by the leaf production on the tree itself: very young cacao leaves have an intensive red colour, in contrast to leaves older than a few days, which change their colour increasingly to green, and are not of primary interest for herbivores (personal observation; see also Van Bael & Brawn 2005). We measured the leaves' lengths and widths (in cm) to calculate the leaf area according to an algorithm developed by Marc Adams (personal communication: $n = 97$, $R^2 = 0.997$): $\text{Area} = (\text{Length} \times 0.4807)^2$. For analyses, we used the absolute leaf loss per tree calculated as the product of leaf area and leaf damage. In total, we investigated 34 400 leaves in 30 rounds.

Statistical analysis

We used linear mixed-effects models (lme) with site as a random factor to test for the effects of vertebrate exclusion (treatments were grouped within site) on the observed parameters.

Adequacy of models checked graphically by plotting residuals against fitted values. The variables shade tree cover and distance to forest margin were centred by subtracting the mean to improve the interpretation of multiplicative and interaction terms in the models. The distribution of the response variable was assumed to be normal (yield, number of fruit, leaf loss), over-dispersed binomial (incidence of damage by pests and diseases) or right-skewed (arthropod counts and number of cacao flowers). The number of all arthropod counts and cacao flowers per treatment was log-transformed (natural logarithms) before analyses. Cacao fruit damage incidences were calculated as the relative proportion of pest infection relative to the total number of harvested cacao fruits ($n = 4071$) or proportion of cherelle wilt pods relative to the total fruit set including black cacao pods ($n = 10362$). For the analyses of cacao yield, harvested cacao fruits and small cacao fruits, untransformed raw data were used. All data were aggregated at study site and study treatment level.

Exclusion treatment, mean shade cover (%) and distance to forest (in metres) were used as fixed effects in all initial full models. To produce the final model, we took the models using Maximum Likelihood and dropped all three- and two-way interactions from the full model that did not reach statistical significance in the Likelihood Ratio Test (LRT). Significance of remaining interaction terms and explanatory variables not entering any interaction term was also assessed using LRT and a manual approach in which single terms were dropped one by one from the full model to investigate effects of the single terms.

To plot the effect of the exclusions relative to the control treatment, we calculated the difference between each study treatment (Day ex., Night ex. and Full ex.) and the control treatment. Coefficients and respective SE's between exclusion treatment and the tested parameters were determined from the models' summary statistics. Differences between groups were considered significant when $P < 0.05$. All analyses were conducted using R version 2.15.1 (R Development Core Team 2007).

RESULTS

Responses of the arthropod community

In total, we observed 47406 nocturnal and diurnal insects and spiders belonging to 16 orders and 65 families, from which 32537 indi-

viduals from seven target arthropod orders (from at least 46 families) were included in our analyses (Table 1). All arthropod groups responded with significant increases to the absence of birds, bats or both predators in the full exclusion and in at least one of the two cacao tree parts (foliage vs. woody parts). The following results from post hoc tests are displayed in Fig. 3 and listed in detail in the (see Table S5). On the woody parts of the cacao trees, where flowers and fruit develop, the abundance of the main chewing insect groups, the Coleoptera and larvae of Lepidoptera, increased in the full exclusion and the day exclusion relative to the control treatment ($P < 0.05$, Tukey test; Fig. 3/I a and b). These groups were also often observed actively feeding on cacao flowers. Spiders increased also strongly on woody tree parts in all exclusion treatments ($P < 0.05$, Tukey test; Fig. 3/I d). Phloem-feeding aphids increased in the full exclusions on both tree positions ($P < 0.05$, Tukey test; Fig. 3/I and II e). Interestingly, mainly night-active insects like Orthoptera and Blattodea increased only within the night exclusions and on both tree parts ($P < 0.05$, Tukey test; Fig. 3/I and II f and g). In contrast, predominantly day-active insects like Coleoptera and Lepidoptera larvae increased only in the day exclusions, and only in their main microhabitat, the tree foliage ($P < 0.05$, Tukey test; Fig. 3/II a and b). Spiders were much less abundant on the tree foliage (only 27% of the whole spider sample) and increased there only within day exclusions, whereas ants in the tree foliage strongly increased in the night and under full exclusion of birds and bats ($P < 0.05$, Tukey test; Fig. 3/II c and d). Abundance of aphids, which were observed to attack young flowers and fruits and were attended by ants, were the only herbivore group that was negatively related to cacao yield ($F_{1,44} = 7.459$, $P = 0.009$; see Table S7).

Cacao yield

In total, we recorded 50114 small cacao fruits, 5648 medium-size fruits and 15743 large fruits (including multiple counts of fruits over different survey rounds) during 28 survey rounds on our study sites, resulting in a final count of 4071 ripe and harvested fruits. The number of harvested fruits represents the total amount of cacao fruit production in the exclusion cages. These fruits were used to determine the representative cacao yield per treatment and study site.

In the control treatments, a mean cacao yield (dry cacao beans) of 0.1 kg per treatment and month was obtained over the whole duration of the experiment. The total amount of cacao yield was closely related to the amount of selected first class cacao beans ($R^2 = 0.81$, d.f. = 58, $n = 1680$). The absence of birds and bats in the full exclusion ($P = 0.004$) and night exclusion ($P = 0.032$), but not in the day exclusion, caused a significant decrease of crop yield compared to the control treatment ($P < 0.05$, Tukey test; Fig. 3a). The number of harvested cacao fruits was significantly reduced in all experimental treatments, compared to the mean productivity in the control treatment (all $P < 0.05$, Tukey test; Fig. 4a). The negative effect of bird and bat exclusion was also significant for earlier stages of the cacao fruit development: the number of cacao flowers (log-transformed) and small fruits decreased in day exclusions, or night and full exclusion treatments respectively (see Fig. S1 and Table S6). We calculated the mean reduction of crop yield per site and year (July 2010 until June 2011) following bird and bat exclusion, and translated this loss to an economical value. Relative to the

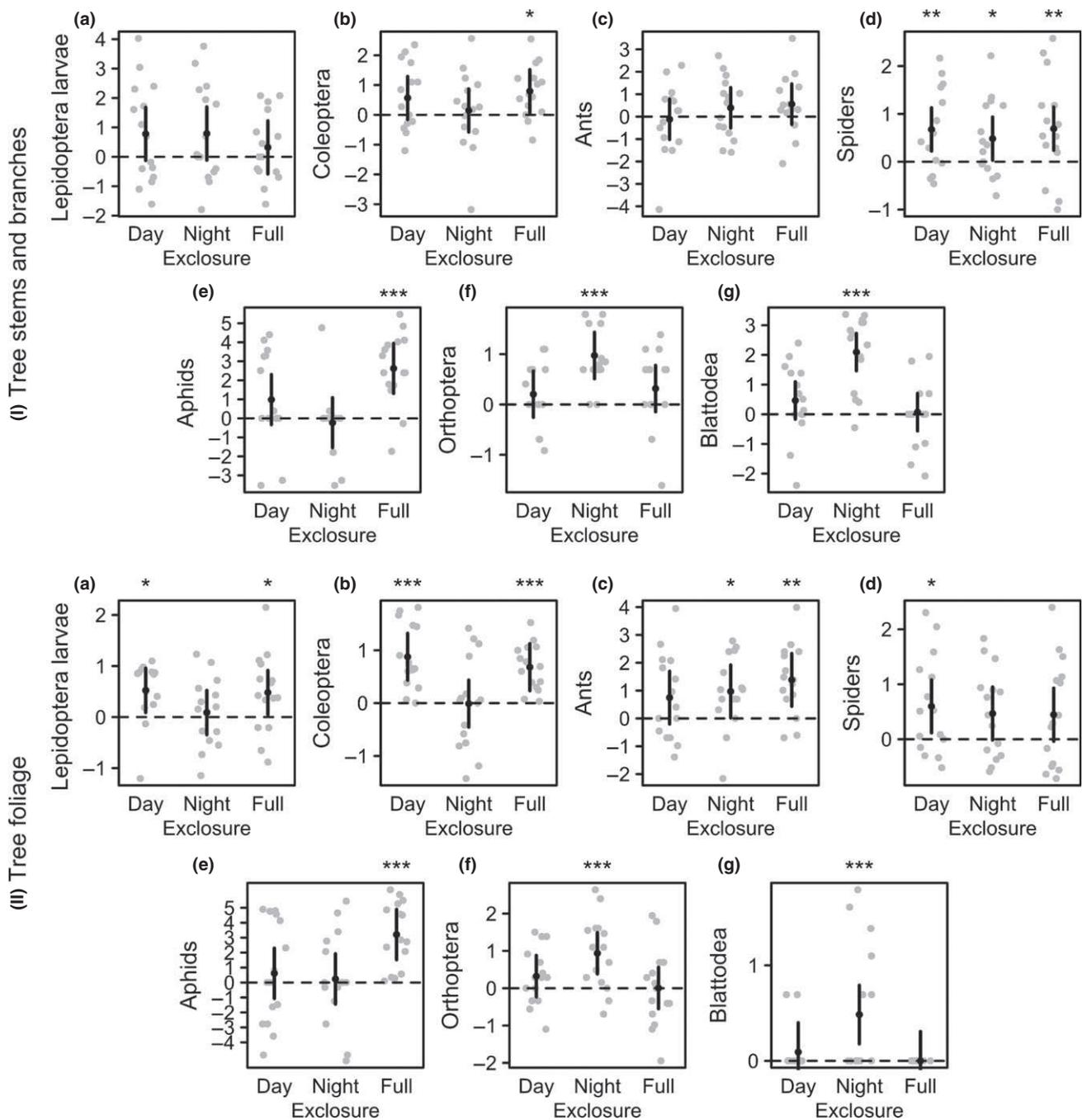


Figure 3 Effects of daytime, night-time and full closures of birds and bats on abundances of seven arthropod groups (a–g) observed on (I) woody parts of the cacao trees (stem, branches, cauliflore fruits and flowers) or (II) on the cacao tree foliage. Observed abundance of all groups increased in the enclosure treatments relative to the unmanipulated control treatment (dashed line at zero level). For each enclosure treatment, the mean number of individuals is displayed in black (\pm 95% confidence intervals) and original data on study site-level (15 circles per treatment) are shown in grey. This allows a direct visual interpretation of treatment effects on single arthropod groups. All individual numbers were log-transformed before analyses. Asterisk symbols represent statistical significance for P -values below 0.05, 0.01 and 0.001 (*, ** and ***).

controls, the mean crop yield in the full enclosures was reduced by 31%. Related to the mean size of one enclosure treatment within the cacao plantations (16.43 m²) and the mean yield outcome in the control (1051.73 kg yield per ha and year), this reduction equals approximately 326 kg yield per ha and year which are lost due to the absence of birds and bats. According to the current ICCO daily prizes of cacao beans (mean of 2.25 USD/kg in 2013) this reduction leads to an estimated economical loss of 730 USD per ha and

year. The negative effects of bird and bat enclosure on crop yield remain across differences in local shade cover or distance to the nearest forest ($P > 0.05$).

Fruit pests, leaf herbivory and spatial scales

Neither the damage by the notorious pest species *Helopeltis sulawesii* and *Conopomorpha cramerella* nor leaf herbivory were affected by the

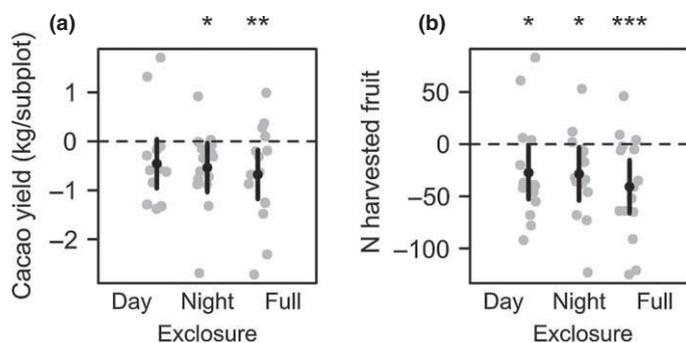


Figure 4 Results from linear mixed effect models (lme) and performed Tukey Test's for multiple comparisons of means. The amount of cacao yield (a) decreased as consequence of the exclusions of birds and bats in daytime, night-time and full exclusions from cacao trees. In case of the decreased number of harvested cacao pods (b) this difference was significant in all experimental treatments relative to the control. Asterisk symbols represent statistical significance for p -values below 0.05, 0.01 and 0.001 (*, ** and ***).

exclusion treatments in their abundance ($P > 0.05$, see Fig. S1 and Table S6). The negative effects of bird and bat exclusion on crop yield remain across differences in local shade cover or distance to the nearest forest ($P > 0.05$). Lepidoptera larvae were the only arthropod group showing positive significant responses to the local and landscape gradients (leplarv: $F_{1,13} = 4.686$, $P = 0.05$). This group increased in abundance on sites that were both highly shaded and located at higher distances from the primary forest. All other observed arthropod groups (observed total numbers on both tree positions) occurred in similar abundances across both gradients ($P > 0.05$).

DISCUSSION

Day and night exclusions of birds and bats in tropical cacao agroforestry did not only increase the abundance of phytophagous insects, ants and spiders, but also caused an economically important reduction in crop yield (31% or 730 USD per ha and year), consistently across gradients of shade cover and distance to primary forest.

Effects on the arthropod communities

Bat and bird exclusions caused higher densities of phytophagous insects, despite increases in densities of mesopredators such as spiders and ants. Phytophagous insects (which occurred in high abundances) were expected to have a high impact on young leaves, cacao flowers and fruits. These effects were only partially detected. As expected, the number of leaf-eating chewing insects (Coleoptera and Lepidoptera larvae) increased in the day exclusions, whereas mainly night-active groups such as Blattodea and Orthoptera increased in the night exclusions (Fig. 3).

Leaf damage did not significantly increase (contrary to our expectations), and was not directly related to insect abundances. Similarly, Williams-Guillén *et al.* (2008) did not find an effect of exclusions on leaf area losses in coffee agroforestry. We observed several arthropod groups (predominately larvae of Lepidoptera and few Coleoptera larvae) on cacao flowers during our insect surveys and assume that the herbivory on flowers may be of significant importance for the development of the crops, a mechanism which needs to be studied further in detail.

Coleoptera and Lepidoptera (especially their larvae) are known to be effectively reduced in their abundance by birds with effects on host plants across different habitat types (Van Bael & Brawn 2005; Barber & Wouk 2012; Morrison & Lindell 2012). On the other hand, arthropod groups which might have been under-represented in former studies due to several reasons such as polyphagy, sampling artifacts and genuine rarity (Novotný & Basset 2000), showed strong responses within our exclusion treatments. In particular, Orthoptera form a substantial part of the diet of gleaning insectivorous bats (e.g. Belwood & Morris 1987; Kalka & Kalko 2006). In contrast to Coleoptera and Lepidoptera, Orthoptera feed on plant foliage throughout their life cycles; individuals are usually rare, but relatively large and high in biomass.

These increases in the abundance of phytophagous insects occurred despite a concurrent increase in mesopredator abundance in response to the exclusions. Prugh *et al.* (2009) and Brashares *et al.* (2010) define 'mesopredator release' broadly, as the expansion in density or distribution of a middle-rank predator, resulting from a decline in the density or distribution of an apex predator.

Spiders, which greatly increased in both nocturnal and diurnal exclusions, are abundant predators that can reduce insect pest populations in terrestrial habitats and can curtail plant damage by lowering the numbers of herbivores (Van Bael & Brawn 2005; Sanders & van Veen 2011). Spiders were the second most observed arthropods in our samplings, which accords with other cacao studies from Sulawesi (Klein *et al.* 2002).

Night-active arthropods strongly declined in abundance in the night-time exclusions which raises the question if and how activity patterns of diurnal and nocturnal predators (Meyer *et al.* 2004) and their prey are the result of a potential avoidance strategy.

Ants were the most abundant arthropod group observed and ants on the tree foliage responded to the absence of flying vertebrates with strong increases in the night-time and full exclusions. Ant species like *Anoplolepis gracilipes*, *Crematogaster* sp., and *Monomorium floridicola* were very abundant in our study sites, and are potential predators of pests in cacao plantation (Rizali *et al.* 2012). Although ants are considered important mesopredators, especially in the tropics (e.g. Conner *et al.* 2010), they can also provide disservices such as enhancement of their plant-sucking trophobionts (Wielgoss *et al.*, unpublished data).

In our study, both ants and aphids (which were ant attended) increased in the exclusions. As aphids attacked flowers and young fruits, their damage might have been significant and may at least partly explain flower and young fruit losses. Furthermore, the fact that aphid density was significantly related to the reductions in final yield pointed to a potentially major role of aphids in cacao yield reduction.

Interestingly, the well-known insect pests of cacao, the *Helopeltis* bugs and the cacao pod borer, were not affected by bat and bird exclusion. The main reason appeared to be that the cacao pod borer, which is a major cacao pest (Wielgoss *et al.* 2012), spends most of its immature stages hidden inside the cacao pod and therefore is not at all a conspicuous prey.

Effects on cacao yield and fruit productivity

Cacao crop yield was significantly reduced in the night-time exclusion and the full exclusion of flying vertebrates, where it decreased by 31% (Fig. 4). This impressive ecological impact of bats and birds

(730 USD per ha and year), is an important argument for public policy makers, farmers and conservationists alike for sustainable management of this service, which is provided by common bird and bat species.

Furthermore, this service might even be enhanced by effective management focused on those bird and bat species that exhibit the greatest beneficial impact on cacao fruit development.

Neotropics vs. Paleotropics

This study presents the first results of bird and bat exclusions from a paleotropical system. Previous studies focused on the Neotropics (e.g. Van Bael *et al.* 2003; Kalka *et al.* 2008; Williams-Guillén *et al.* 2008; Morrison & Lindell 2012), the natural origin of *Theobroma cacao*. Although cacao has been introduced to Indonesia, and now covers 1.5 million hectares of cacao production area (the largest in South-East Asia), it is likewise affected by ecological processes, diseases and pests.

Comparing Neotropics with Paleotropics, differences in species richness and species specialisation are conspicuous. Williams-Guillén *et al.* (2008) reported more than 120 bird species and 45 bat species present in Mexican organic coffee plantations. Bird and bat mist netting in agroforestry systems in Sulawesi recorded 13 bat species (see Table S4) and 71 bird species (see Table S7). In general, the species richness of birds and bats in neotropical agroforestry is higher than in the Old World tropics, but the mean proportion of endemic species is highest in Southeast Asia (Sodhi *et al.* 2010). Ongoing conversion of agroforests into simplified agricultural systems can result in shifts towards less specialised bird communities with altered proportions of functional groups (e.g. loss of insectivorous bird species) and cause reduced avian ecosystem functions in these systems (Tschardtke *et al.* 2008; Sekercioglu 2012).

Migratory birds were found to be of high importance in Neotropical systems, where they showed the strongest correlation with reduced arthropod densities (Van Bael *et al.* 2008). The presence of migratory bird species might influence the effectiveness of arthropod suppression due to an increased diversity of the bird assemblage, which results in a higher probability of present insectivorous species (e.g. Van Bael *et al.* 2008). In our study, no migratory birds were recorded.

Contrary to Neotropical studies conducted on forest sites, which detected increased leaf herbivory in bird and bat exclusions in natural habitats (e.g. Van Bael & Brawn 2005; Kalka *et al.* 2008), no significant effect on leaf damage could be found in Mexican agroforestry (Williams-Guillén *et al.* 2008). This is consistent with our findings, except for the dependency on seasonal effects found by Williams-Guillén *et al.* (2008). Such differences in herbivory could be caused by changing food resource use of insects. Cacao insects feed on cacao flowers, whereas flower herbivory does not appear to be important in coffee. Generally, the ecology of cacao flowers as well as their pollination remain largely unstudied and should be included in future research.

Although ecosystem services in agroforestry might be often provided by common species, this does not decrease its potential to support also endangered natural forest species. Recommended management practices like increasing numbers of shade tree species (Clough *et al.* 2011), exposing roosting boxes (Morrison & Lindell 2012) and planting fruit trees (Tschardtke *et al.* 2011) to augment resources for insectivorous birds and bats may become part of bio-

diversity-friendly management by smallholder farmers (Bhagwat *et al.* 2008) and need to be realised in the near future to prevent losses of ecological services and high biodiversity.

CONCLUSIONS

The functional importance of birds and bats for tropical agroforestry is demonstrated in our study by the effective suppression of arthropod densities and the impressive increase of cacao crop yield by almost a third. We provide new arguments for wildlife-friendly management of agroecosystems, which is not only important for sustaining rural livelihoods, but also for the potential conservation of endangered species. For a better understanding of the role of birds and bats in tropical agroforestry, further research on biotic interactions shaping their services (e.g. effects on predatory arthropods like ants and spiders) as well as on interactions with other ecosystem services (e.g. pollination) needs to be conducted. These studies should be performed on appropriate scales accounting for temporal (e.g. seasonal effects, migrations, annual breeding cycles) and spatial variation (e.g. local and landscape effects; elevational gradients). Taking into account larger spatial and temporal scales into management practices might even facilitate the beneficial impact of birds and bats on agroforestry crops.

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STATEMENT OF AUTHORSHIP

All authors designed the research. Installation of the experiments, field work, data collection and data processing was done by BM. YC and BM analysed the data. BM wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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