

How ants, birds and bats affect crop yield along shade gradients in tropical cacao agroforestry

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Summary

1. Tropical agroforests are diverse systems where several predator groups shape animal communities and plant–arthropod interactions. Ants, birds and bats in particular can reduce herbivore numbers and thereby increase crop yield. However, the relative importance of these groups, whether they interact, and how this interaction is affected by management and landscape context, is poorly understood.

2. We jointly manipulated access of ants, birds and bats in Indonesian smallholder cacao agroforestry across gradients of shade and distance to natural forest. We quantified arthropod abundance, pest damage and yield.

3. In control treatments, yield was highest under 30–40% canopy cover. Ant exclusion strongly reduced yield (from 600 to 300 kg ha⁻¹ year⁻¹) at 15% canopy cover. Bird exclusion impaired yield (from 400 to 250 kg ha⁻¹ year⁻¹) at 60% and enhanced yield (from 600 to 900 kg ha⁻¹ year⁻¹) at 15% canopy cover, while bats had no effect. Yield increased with forest proximity, a pattern not related to predator access.

4. No interactive effects among predator exclusions on yield, pest damage and arthropod communities were found. Ant exclusion increased numbers of herbivores below 30% canopy cover, without reducing spider abundances. Bird exclusion reduced herbivore and increased spider abundances.

5. *Synthesis and applications.* Using exclusion studies, we estimated that ants and birds cause cacao yield to vary between 100 and 800 kg ha⁻¹ year⁻¹, depending on shade-tree management. In all but the most shaded agroforests, ants were pivotal in supporting yields. Yields under low-canopy cover were strongly dependent on access by predator groups, with birds reducing rather than increasing yield. Hence, cacao farmers should refrain from disturbing ant communities and maintain 30–40% shade-tree canopy cover not only for ecophysiological reasons but also to buffer variability in predator communities.

Key-words: agricultural intensification, biocontrol, canopy cover, ecosystem services, forest distance, mesopredator release, predation, *Theobroma cacao*, trophic interactions, yield

Introduction

Predators exert top-down control and can positively or negatively influence plant development through direct and indirect interactions affecting pests and diseases (Vandermeer *et al.* 2002; Vandermeer, Perfecto & Philpott 2010). Detailed reviews covering effects of ants, birds and bats on arthropod communities and crop yield, often assessed

using exclusion experiments, underline their importance for ecosystem service provision (Philpott & Armbrecht 2006; Van Bael *et al.* 2008; Whelan, Wenny & Marquis 2008; Mooney *et al.* 2010; Kunz *et al.* 2011; Wenny *et al.* 2011; Maas *et al.* 2015b).

Ants are effective biocontrol agents, especially in tropical agroforestry. For example, in Mexican coffee arboreal ants protect trees from colonization by important pests (Gonthier *et al.* 2013). However, impacts of ants depend on the environmental context (e.g. temperature), ant species involved (Philpott & Armbrecht 2006; Gove 2007; Wielgoss *et al.* 2014), potential counterproductive effects

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on mesopredators such as spiders (Eubanks 2001), mutualism and plant-sucking trophobionts (i.e. aphids and mealbugs) that are harmful to crops. Birds have also been shown to reduce abundances of pests (Holmes, Schultz & Nothnagle 1979; Johnson *et al.* 2009), with yield losses up to 310 kg ha⁻¹ year⁻¹ prevented in coffee agroforestry, for example (Karp *et al.* 2013). Effects of birds on arthropod communities are not always that strong, can negatively affect mesopredators and do not necessarily trickle down to plants (Williams-Guillén, Perfecto & Vandermeer 2008; Maas, Clough & Tscharntke 2013). Bats have received increased attention as biocontrol agents in recent years following several seminal reports from natural forests and agroforests (Kalka, Smith & Kalko 2008; Williams-Guillén, Perfecto & Vandermeer 2008). Efforts to disentangle bird and bat effects have partly confirmed the potential of bats as biocontrol agents in agroforestry (Maas, Clough & Tscharntke 2013; Maas *et al.* 2015b) and partly suggested that negative impacts on spiders can cancel out the effects that bats may have on herbivores (Karp & Daily 2014).

Effects of these predator groups have usually been considered in isolation, using exclusion experiments conducted in only one or a handful of locations. In reality, density and diversity of predators, and thus probably also their biocontrol effect, depend on local management or landscape context (Clough *et al.* 2009; Karp *et al.* 2013). In addition, it is unclear whether impacts of the three predator groups are complementary or redundant. Few studies have tested interactive effects (but see Mestre *et al.* 2013b; Mooney 2007; Piñol *et al.* 2010; Philpott *et al.* 2004; Spiller & Schoener 2001). Finally, few studies quantify impacts on crop yield, making economic assessments difficult since plants can often compensate for damage (but see Mooney *et al.* 2010; Wielgoss *et al.* 2014; Maas, Clough & Tscharntke 2013; Karp & Daily 2014).

Here, we simultaneously investigate effects and management dependency of ant, bird and bat exclusions in 15 smallholder cacao plantations differing in the percentage of shade-tree canopy cover and distance to forest margins. In our study region, Central Sulawesi (Indonesia), results from separate experiments revealed that both ant and combined bird–bat exclusions decreased yield by ~30% (Maas, Clough & Tscharntke 2013; Wielgoss *et al.* 2014). These effects may change along canopy cover gradients as local shade-tree management impacts productivity, fruit abortion, and arthropod and vertebrate communities (Bos, Steffan-Dewenter & Tscharntke 2007a; Clough *et al.* 2009). Increasing distance from natural forest can also negatively affect the density and diversity of bird and bat communities, and therefore the degree of biocontrol (Estrada & Coates-Estrada 2002; Clough *et al.* 2009). In the present study, we addressed the following questions:

1. Does exclusion of ants, birds and bats affect cacao yield, and if so, does this change with shade-tree canopy cover or distance to forest margin?

2. Are effects of the three manipulated predator groups synergistic, additive or antagonistic?

3. What are the likely processes explaining impacts of ant, bird or bat exclusions on cacao crop yield, pest and disease infestation, and fruit set or fruit abortion?

4. What are the management implications for cacao farmers in terms of canopy cover, landscape-scale forest preservation and predator conservation?

Materials and methods

SITE SELECTION AND GRADIENTS

Fifteen smallholder *Theobroma cacao* L. plantations were selected at the eastern border of the Lore Lindu National Park in Central Sulawesi, Indonesia (Fig. 1; 1°23'31.8"S 120°18'57.55"E, ~1130 m a.s.l., 1990–3804 mm rainfall) to cover five distances to the forest margin (Fig. S1, three agroforests in each category: 0–250, 251–500, 501–1500, 1501–2500, 2501–3000 m) and three canopy cover types (Fig. S1, five agroforests in each category: <30%, 30–50%, >50%). Later, both variables were measured in metres to the forest margin or percentage of shade-tree canopy cover. The latter was measured at the experimental treatment level (within agroforest), but variability was larger between than within agroforests. Local farmers managed all agroforests and we incorporated pesticide-, herbicide- and fungicide-free areas to minimize management differences. Nonetheless, each agroforest provided a unique habitat due to agroforest size, cacao tree age/abundance, previous/nearby land-use, topography, drainage, fertilizer use (Table S18) or intercropped vegetables and fruits (Tables S2 and S3). The agroforests were separated by at least 500 m edge-to-edge distance. Two planted legume shade-tree species – *Erythrina subumbrans* Merr. and *Gliricidia sepium* Kunth – represented 30–91% of all recorded non-crop trees (Table S2, herb species in Table S3). We trimmed the herb layers every 2 months using a motor scythe. During the experiment, we recorded 49 ant and 69 bird species (Tables S4–S6).

EXCLUSION TREATMENTS

Bird and bat exclusions were implemented in 2010 (cf. Maas, Clough & Tscharntke 2013), and ant exclusions were added in April 2011; both were maintained until June 2012. Exclusions consisted of eight randomly positioned treatments (two trees each) per study site: (i) no exclusion, (ii) ant exclusion, (iii) bird exclusion, (iv) bat exclusion, (v) ant–bird exclusion, (vi) ant–bat exclusion, (vii) bird–bat exclusion and (viii) ant–bird–bat exclusion.

We used bamboo scaffolds covered with fishing nets (35 × 35 mm mesh size) to exclude birds and/or bats. The bird–bat exclusion treatments had fixed nets. Bird exclusion nets were manually opened in the morning (05:30 h) and closed in the evening (18:30 h), while bat exclusions were opened in the evening (18:30 h) and closed in the morning (05:30 h). Controls were always open. Open nets (top and all sides) were bound tightly to the scaffolds (Fig. S7). To exclude ants, we used cone-shaped insect glue rings fitted to the tree trunks (Fig. S8), thereby reducing contact between ring and trunk and preventing trunks from getting mouldy – a problem encountered while planning a previous study (Wielgoss *et al.* 2014). Thus, ant exclusion effects are

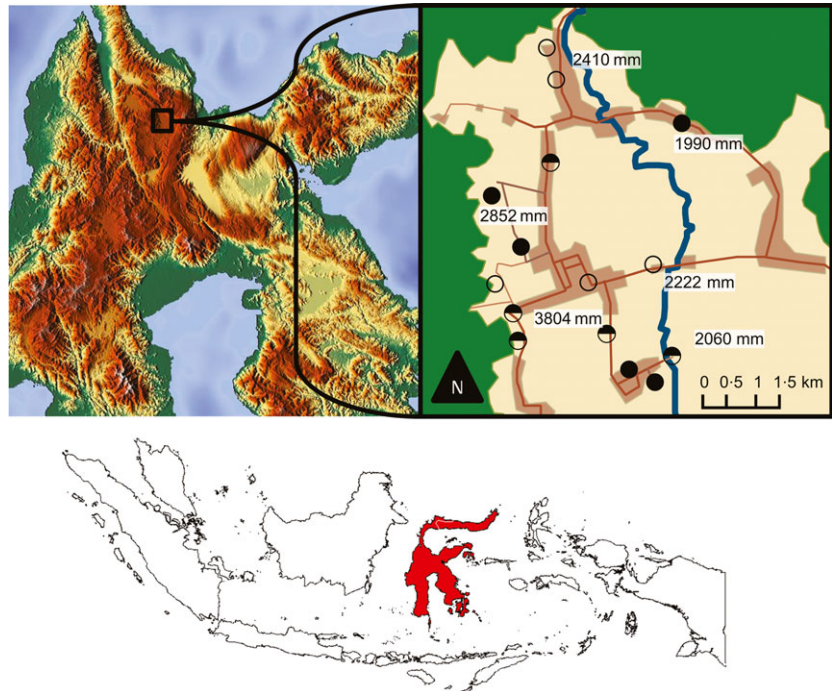


Fig. 1. Study area in the Napu valley of Central Sulawesi, Indonesia. Bottom: The red area indicates Sulawesi. Top left: Topography of Sulawesi and study area (black square). Top right: Cycles show experimental cacao agroforests, filling style indicates canopy cover (empty <30%, half = 30–50%, filled > 50%), white labels show rainfall in mm, green area indicates rain forest, reddish areas indicate houses, and bright areas indicate open land and lines indicate streets.

similar to conventional insect glue applications. We destroyed ant nests during establishment of ant exclusions, whenever discovered and during a monthly ‘search-and-destroy’ survey. Arthropod exchange through net–tree contact was avoided by regularly pruning branches to keep at least 30 cm between foliage and nets/scaffolds. Effectiveness of ant exclusion was quantified by counting ant individuals from canopy knock-down fogging samples, showing that ant abundance was strongly reduced (by 60–90%, see Results) in exclusions compared to control treatments.

SAMPLING AND SURVEYING METHODS

We obtained distances to forest margins and agroforest area using a Garmin Oregon 550 Global Positioning System device (Fig. 1). We took treatment-level digital hemispherical canopy photos and calculated percentage of canopy cover using the CIMES-FISHEYE software (Walter 2009). We measured several potentially yield-related covariates: (i) cacao tree crown volume and (ii) mean d.b.h. to represent tree size, (iii) daily mean temperature and (iv) precipitation to represent abiotic conditions, (v) non-crop tree richness known to correlate with the bird community composition (Clough *et al.* 2009), (vi) the average branch perimeter as indicator of fruit carrying capacity and (vii) the pod groove depth which indicates ‘on-fruit’ hiding opportunities for arthropods and can differ between agroforests depending on the cacao phenotype (Tables S9 and S10).

Every 2 weeks from April 2011 to May 2012, we surveyed all experimental trees counting and classifying cacao fruits by size/development and presence/absence of pest and disease symptoms and harvesting of ripe fruits (classification details, Tables S11 and S12). We separately quantified the weight of marketable and damaged beans (i.e. due to the damage of the cacao pod borer *Conopomorpha cramerella*). Damage caused by the most economically important organisms (i) *C. cramerella*, (ii) *Helopeltis sulawesi* and (iii) *Phytophthora palmivora* was assessed by counting fruit with symptoms of damage.

We recorded other pests damaging leaves, flowers and fruits (e.g. aphids, herbivorous bugs and caterpillars), as well as mesopredators (e.g. spiders, earwigs and lacewing larvae) through canopy knock-down fogging with a mixture of 5% Malathion (Fumithion 1150 ULV) and diesel fuel (Bos, Steffan-Dewenter & Tschardt 2007b; Rizali *et al.* 2013) at the end of the experiment. We fogged all treatments (covered by plastic tents) for 5 min and left the tents closed for 1 h. Fogging samples were used to test predator exclusion effects on arthropod orders.

Every 4 weeks from May 2011 to March 2012, ants were baited on trees without ant exclusions to detect effects of shade/forest distance on ant community abundance, richness and composition. We used protein (tinned tuna in brine) and carbohydrate (saturated sugar solution) baits. We identified ant/morphospecies using taxonomic literature (Bolton 1994; Fisher 2010) and regional ant collections (Rizali *et al.* 2013; Wielgoss *et al.* 2014).

Between September 2010 and June 2011, the bird community was recorded by repeated mist netting surveys and point count recordings on all 15 study sites (see Maas *et al.* 2015a for details).

STATISTICAL ANALYSES

Data from 28 harvests were summed for each agroforest and treatment. Response variables directly related to yield (total marketable yield, fruit abundance and fruit weight) were analysed in three steps. First, we fitted a full model containing the random factor ‘experimental agroforest’, and the terms of interest: (i) three binary exclusion variables and their interaction terms, (ii) agroforest-level design variables (canopy cover, forest distance) and (iii) their interaction with each exclusion treatment variable, (iv) seven covariates: crown volume, mean d.b.h., temperature, precipitation, non-crop tree richness, branch perimeter and pod groove depth. A second-order polynomial term was included for canopy cover, to allow for nonlinearity (Tschardt *et al.* 2011). Continuous explanatory variables were *z*-transformed. We fitted the model using maximum likelihood and Gaussian (marketable

yield, yield per fruit, number of harvested fruit, leaf area, leaf damage), overdispersion-corrected Poisson (arthropod abundances), or binomial (proportions of infested fruits) distribution. For Gaussian models, root- or log-transformed response variables were used to meet assumptions of homoscedasticity and (approximate) normality of the residuals. Models were assessed with variance inflation factors and diagnostic plots for residual normality, heteroscedasticity and leverage.

Secondly, retaining all variables of interest, the model was simplified by keeping those covariates that contributed to the model, as indicated by a multi-model inference procedure ('MuMIn' R-package, AIC based). The tree crown volume differed between treatments and negatively correlated with canopy cover ($F = -2.092$, $P = 0.04$). Therefore, we included crown volume as a permanent covariate during all statistical analyses. Thirdly, the same procedure was used to identify non-significant interactions that were removed for model simplification and refitted a model using restricted maximum likelihood. In the results section, variables of interest and their interactions were reported when relative variable importance values (proportion of models including the variable vs. models excluding the variable out of the best set of models, identified by delta AIC <2) exceeded 0.9 for main effect interactions and 0.7 for covariates. We used the lme4 package in R (Bates *et al.* 2014; R Core Team 2014) and reported statistical significance from the final model using ANOVA Type II, Wald chi-square test (Kuznetsova, Brockhoff & Christensen 2014).

To determine the mechanisms leading to differences in marketable yields, only predictors identified as important for marketable yield (see Appendix S13) were used on the following responses: (i) open flowers, (ii) aborted small fruits and (iii) leaf herbivory. To test patterns of herbivorous arthropod abundances, incidence of pests and disease symptoms, and beneficial arthropod abundances, we used: (i) fruit infestation of *H. sulawesi* and *C. cramerella*, (ii) Sternorrhyncha, (iii) caterpillars >10 mm, (iv) Coleoptera >10 mm, (v) Auchenorrhyncha, (vi) Dermaptera, (vii) Neuroptera larvae, (viii) hunting spiders <4 mm, (ix) hunting spiders 4–10 mm, (x) web spiders <4 mm, (xi) web spiders 4–10 mm, (xii) ants and (xiii) Diptera <4 mm.

Finally, changes in community composition were tested using species richness, diversity, evenness and composition of ants and birds along the gradients of canopy cover and forest distance. The measurements were rarefied to 737 individuals per site for ants and 122 individuals per site for birds. We conducted a

redundancy analysis and visualized community composition using Minimum Convex Polygons (MCP) at the level of the agroforest (birds) and experimental treatment (ants) and, finally, tested for the influences of canopy cover, forest distance and treatment using a permutation test ($n = 999$). Separate analyses were conducted for each variable, with both remaining variables and crown volume being set as conditions. Crown volume and treatment were not included for bird community analyses, as birds were recorded at the agroforest level.

Results

EFFECTS OF PREDATOR EXCLUSION, CANOPY COVER AND DISTANCE TO FOREST ON CACAO YIELD

Yields of control trees varied between 75% and 135% of the average productivity per hectare of 540 kg ha⁻¹ year⁻¹ for Indonesia in 2012 (Fig. 2, Appendix S13.1; yield Indonesia 2012: <http://faostat3.fao.org>). In control trees, marketable yield, proportion of fruits without pest infestation and the number of harvested fruits peaked under 30–40% shade-tree canopy cover (Figs 2 and 3g–l, Appendix S13.1–S13.3). Yield was affected by ant and bird exclusion with magnitude and direction of effects depending on shade-tree canopy cover. Yield was not affected by bat exclusion (Fig. 2, Appendix S13.1). Interactions between exclusion treatments were not significant. Independently of predator exclusions, marketable yields and numbers of harvested fruits decreased with increasing forest distance (Appendix S13.1–S13.3).

ANT EXCLUSION

Ant exclusions reduced ant abundances by 60–90% (Fig. 5a; Appendix S13.11). Marketable yield, the number of harvested fruit and fruit weight were reduced under ant exclusion (Figs 2 and 3j,m; Appendix S13.1–S13.3). Ant abundances were positively correlated with marketable yields while controlling for exclusion treatments ($\chi^2 = 7.22$, $P < 0.01$).

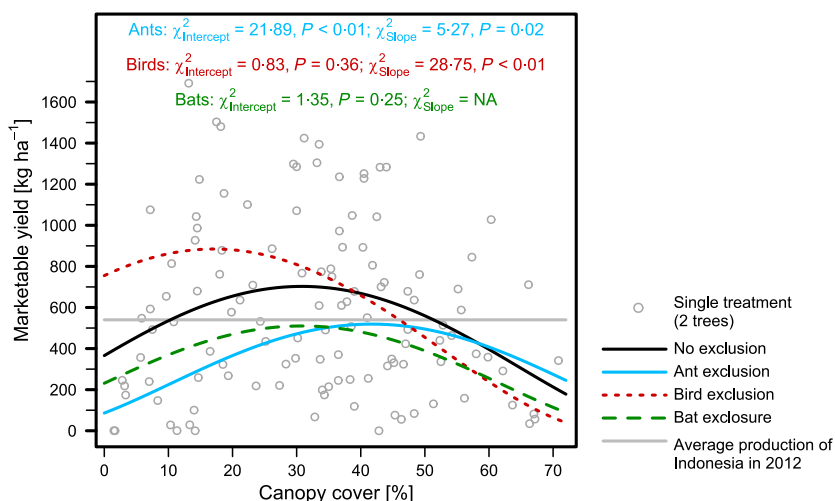


Fig. 2. Effects of predator exclusion on marketable cacao bean yield. Dry yield (y-axis) of exclusion treatments (control = continuous black, no ants = blue, no birds = dotted red, no bats = dashed green) dependent on percentage of canopy cover (x-axis), grey line marks the average cacao production of Indonesia 2012 (<http://faostat3.fao.org>), and yield was standardized to 12 months for plotting only. $\chi^2_{\text{Intercept}}$ indicates influences of predator exclusions, while χ^2_{Slope} indicates canopy cover dependency of predator exclusions.

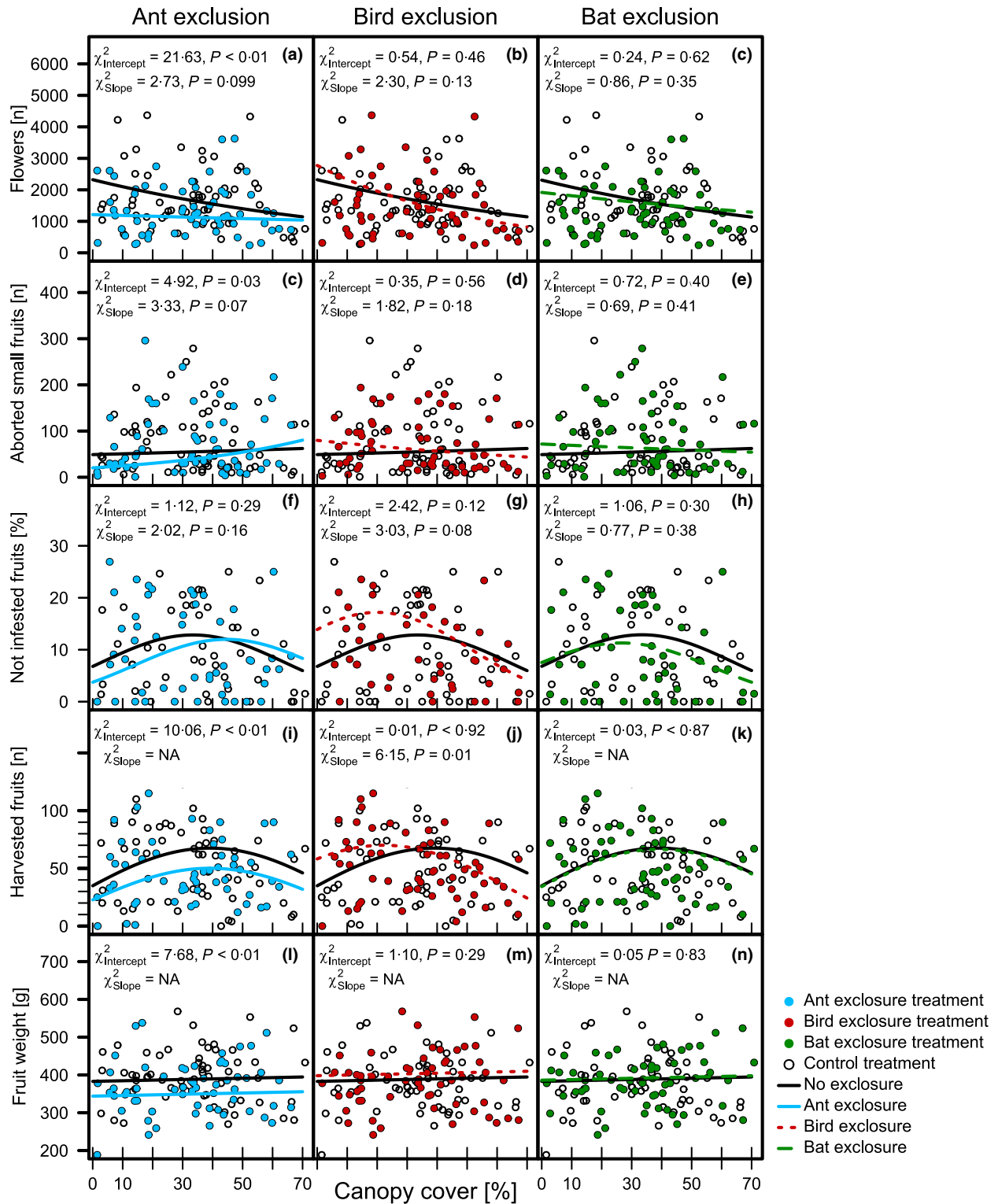


Fig. 3. Effects of predator exclusion on cacao tree phenology. Small figures show the response of cacao trees to ant (left), bird (mid) or bat (right) exclusion related to canopy cover (x-axis), each circle/dot corresponds to two trees, line types: control = continuous black, no ants = blue, no birds = dotted red, no bats = dashed green. $\chi^2_{\text{Intercept}}$ indicates influences of predator exclusions, while χ^2_{Slope} indicates canopy cover dependency of predator exclusions.

Below 30% canopy cover, ant exclusions were associated with fewer flowers, and a trend towards fewer aborted small fruits compared to control treatments

(Figs 3a,d; Appendix S13.4 and S13.5). Ant exclusion did not affect pest and disease incidence at fruits (Fig. 3g; Appendix S13.6). Canopy cover above 50% reversed the

differences in aborted small fruits, with higher numbers in ant exclusions than in controls (Fig. 3d). Losses of flowers and small fruits were reflected in reduced numbers of harvested fruits under ant exclusion (Fig. 3j; Appendix S13.3). Additionally, fruit weight was reduced in the absence of ants (Fig. 3m; Appendix S13.2).

Abundances of lepidopteran caterpillars (>10 mm) and beetles significantly increased in response to ant exclusions while abundances of caterpillars (0–4 mm) and leafhoppers remained unaffected (Figs 4a–j; Appendix S13.7–S13.10). Leaf damage was increased in ant exclusions below 30% canopy cover ($\chi^2 = 6.54$, $P = 0.01$; Appendix S13.16).

Spiders were largely unaffected by ant exclusion, with only a trend towards small web-building spiders being more frequent in ant exclusions below 30% canopy cover. (Fig. 5d,g; Appendix S13.12 and S13.13). Below 30% canopy cover, earwigs were absent, but when present, their abundance was reduced in ant exclusions (Fig. 5j; Appendix S13.14). Small beetles were more abundant under ant exclusion and with above 50% canopy cover (Fig. 5m; Appendix S13.15).

BIRD EXCLUSION

Compared to controls, marketable cacao yields were slightly reduced in bird exclusions when canopy cover was above 50%. Canopy cover below 30% led to higher yields in bird exclusions (500 kg ha⁻¹ year⁻¹ to 830 kg ha⁻¹ year⁻¹, Fig. 2; Appendix S13.1). Comparable patterns were found for flowers, aborted small fruits, fruits without damage by pests such as *H. sulawesi* and *C. cramerella*, and harvested fruits (Figs 3b–h; Appendix S13.4–S13.7). Amounts of non-infected and harvested fruits were significantly correlated ($\chi^2 = 32.87$, $P < 0.01$). The fruit weight remained unaffected by bird exclusion (Fig. 3n; Appendix S13.3).

Caterpillar and beetle abundances remained unaffected by bird exclusion, but abundances of Auchenorrhyncha were reduced (Figs. 4b–k, Appendix S13.7–S13.10). Simultaneously, web-building spider abundance increased, although this effect was only significant for large individuals (4–10 mm), where it was stronger over 50% canopy cover (Fig. 5h, Appendix S13.13). Increases in small web spiders (<4 mm) were marginally significant and tended to be higher with canopy cover <30% (Fig. 5e, Appendix S13.12). Small beetles (<4 mm) tended to be less abundant with more than 30% canopy cover (Fig. 5n, Appendix S13.15). Earwigs had lower densities due to bird exclusion, an effect restricted to canopy cover higher than 40% (Fig. 5k, Appendix S13.14). Ants were not significantly affected by bird exclusion (Fig. 5b, Appendix S13.11). Yield effects of bird exclusion persisted when adding ant abundance as a model covariate. Small dipterans were less frequent under bird exclusions ($\chi^2_{\text{Bird exclusion}} = 6.59$, $P = 0.01$; Appendix S15.17 in Supporting Information).

BAT EXCLUSION

Excluding bats had no significant effect on marketable yield. No effect could be detected on flowers, aborted small fruits, fruit infestation by pests and diseases, harvested fruits or fruit weight (Figs 2 and 3c–o; Appendix S15.1–S15.6). Bat exclusion was associated with higher numbers of leaf hoppers and, for canopy cover over 50%, higher numbers of large caterpillars (4–10 mm) (Fig. 4f,l, Appendix S15.7/10). Small caterpillars or beetles remained unaffected (Fig. 4a,i, Appendix S15.7/9). Bat exclusion did not affect mesopredators smaller than 4 mm in body length, but was associated with higher spider and earwig abundance (Fig. 5c–o, Appendix S15.11–15).

ANT AND BIRD DIVERSITY ALONG THE CANOPY COVER AND FOREST DISTANCE GRADIENT

Ant species composition (redundancy analysis, Fig. S14) was similar across those treatments where ants were present ($F = 0.76$, $P = 0.84$), but ant species composition strongly changed with percentage of canopy cover ($F = 2.81$, $P = 0.001$) and forest distance ($F = 2.93$, $P = 0.001$). Species composition of the local bird assemblage (redundancy analysis, Fig. S15) changed due to forest distance ($F = 1.31$, $P = 0.03$), but did not respond to canopy cover ($F = 1.12$, $P = 0.33$). Shannon index, species evenness and rarefied species richness of ants and birds were independent of canopy cover and forest distance (Fig. S16).

Discussion

Access by predators, percentage of shade-tree canopy cover and distance to forest margin had economically relevant impacts on cacao yield. While the negative effect of forest distance was independent of predator exclusion, percentage of canopy cover affected the impact of predators. Yield peaked at 30–40% canopy cover. Canopy cover below 15% or above 55% resulted in less than half of the optimum yield. Ant exclusion reduced yields at 15% canopy cover from 600 to 300 kg ha⁻¹ year⁻¹. Bird exclusion decreased yields at 60% canopy cover from 400 to 250 kg ha⁻¹ year⁻¹. Unexpectedly, bird exclusion increased yields at 15% canopy cover from 600 to 900 kg ha⁻¹ year⁻¹. Bats had no effect on yield.

Canopy cover-dependent effects of ant and bird exclusions in agroforests have never been shown previously, despite several recent studies targeting these groups in tropical agroforestry (Wielgoss *et al.* 2014; Maas *et al.* 2015b). Our results can partly be explained by patterns in yield formation, as well as impacts on herbivorous and predatory arthropods that were quantified by fogging the experimental trees at the end of the study period.

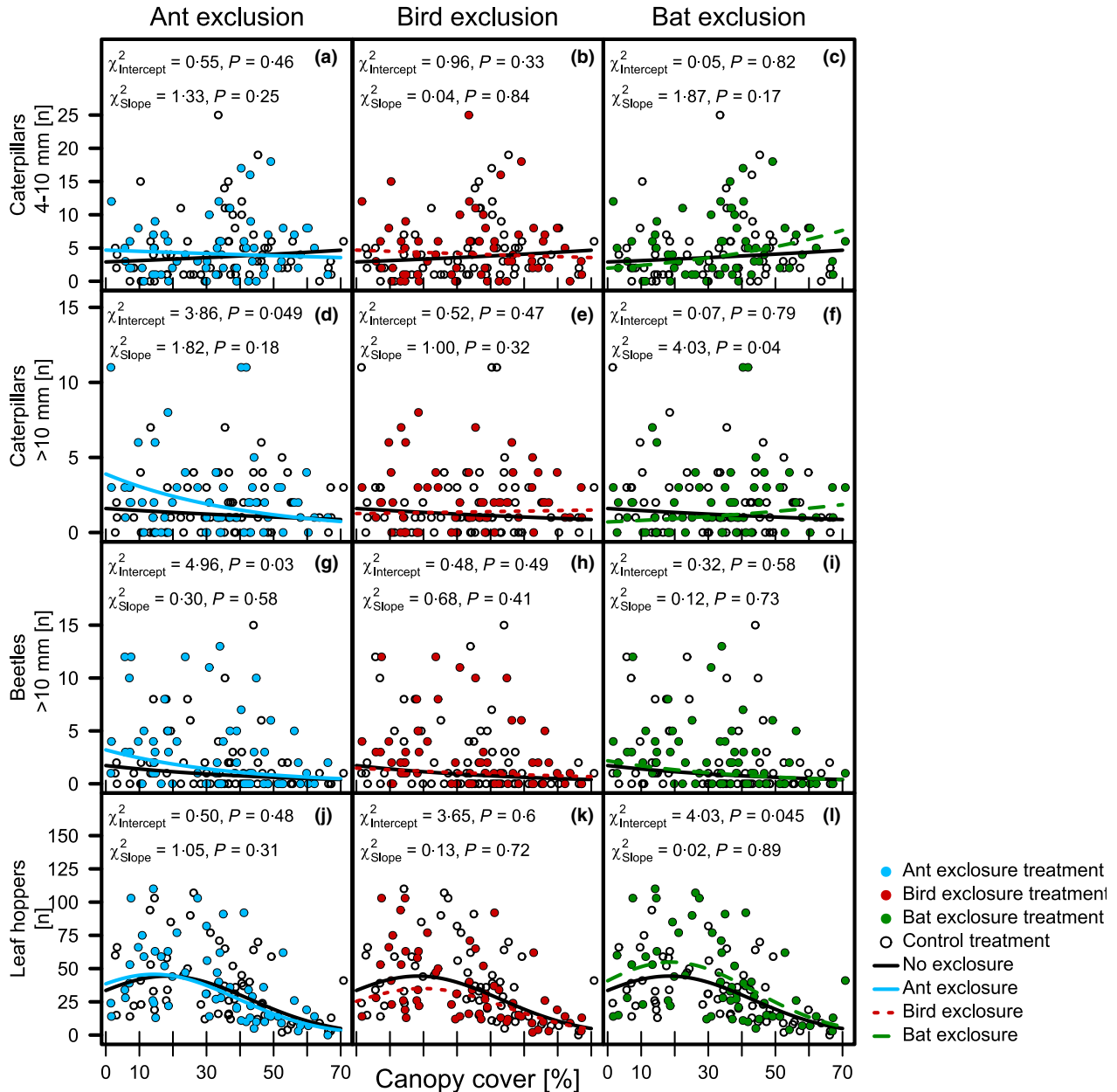


Fig. 4. Effects of predator exclusion on cacao tree herbivores. Small figures show the response of herbivores to ant (left), bird (mid) or bat (right) exclusion related to canopy cover (x-axis), each circle/dot corresponds to two trees, line types: control = continuous black, no ants = blue, no birds = dotted red, no bats = dashed green, $\chi^2_{\text{Intercept}}$ indicates influences of predator exclusions, while χ^2_{Slope} indicates canopy cover dependency of predator exclusions.

CANOPY COVER-DEPENDENT EFFECTS OF ANTS

Ants affect plants by tending/defending or predating/displacing herbivores, but also predating/displacing predators (such as spiders) and pollinators, spreading propagules of plant pathogens (Wielgoss *et al.* 2014), pollinating flowers, predating/dispersing seeds and changing soil conditions (Bartlett 1961; Way 1963; Mestre *et al.* 2013b; 2014). Their ecological dominance in tropical agroforestry systems likely affects trees in multiple ways (e.g. plant growth, leaf and fruit development). In our study, impacts of ant exclusion have their likely cause in the interaction of arboreal ants and other arboreal organisms such as

herbivores: ants were excluded from trees and not the ground below, tent-building species able to spread pathogens were absent, and ants are not able to pollinate cacao (Leston 1970). Interference between ants and spiders has been reported from tree crops (Piñol, Espadaler & Cañellas 2012; Mestre *et al.* 2012; Mestre, Bucher & Entling 2014 but see Marín & Perfecto 2013). Here, and in contrast to what was observed in response to bird exclusion, no significant change in spider abundance occurred under ant exclusion, suggesting that ants do not limit the abundance of spiders. Instead, ants reduced abundances of herbivores such as caterpillars and beetles that damage not only leaves but also cacao flowers (YC personal observa-

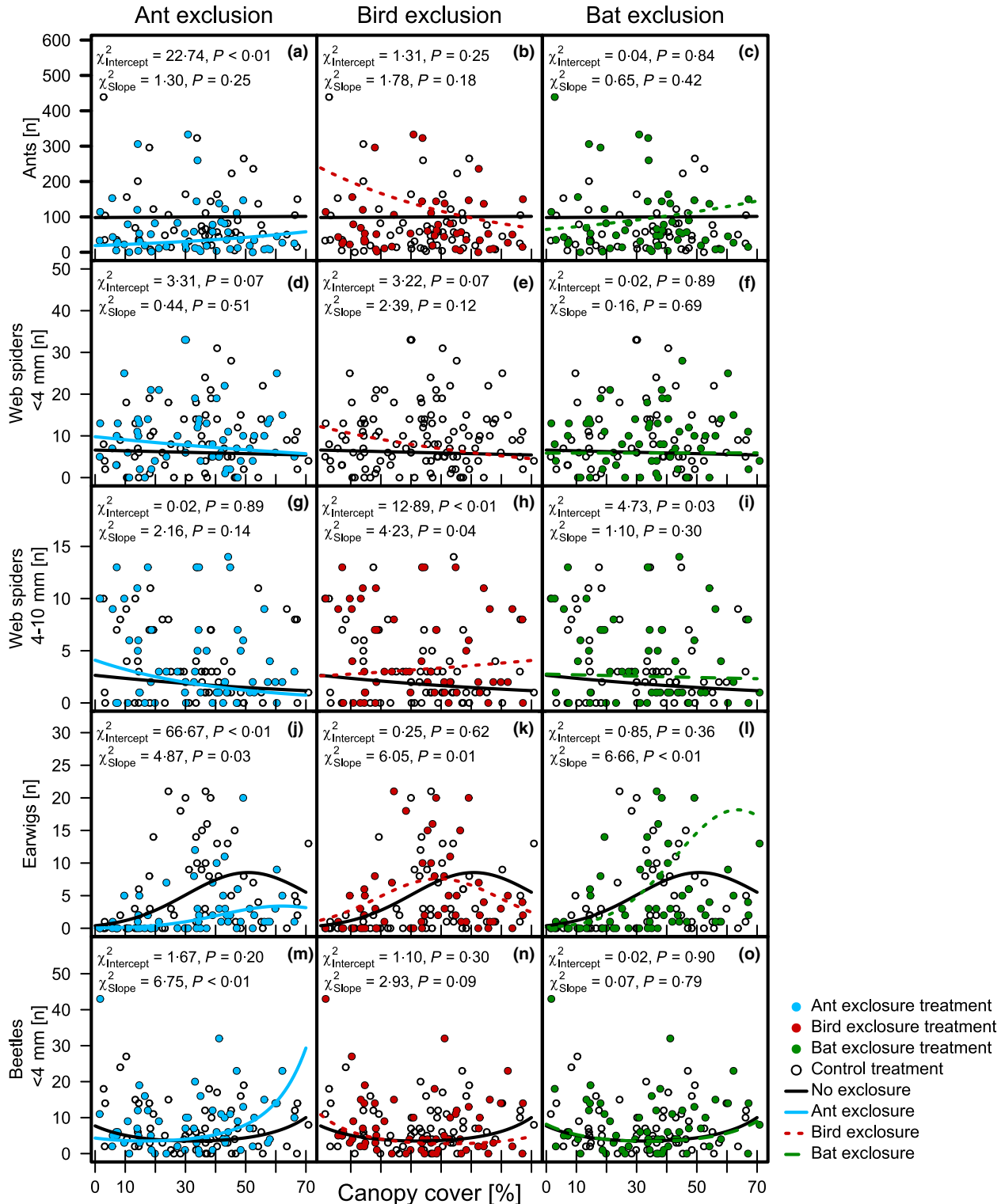


Fig. 5. Effects of predator exclusion on cacao tree mesopredators. Small figures show the response of mesopredators to ant (left), bird (mid) or bat (right) exclusion related to canopy cover (x-axis), each circle/dot corresponds to two trees, line types: control = continuous black, no ants = blue, no birds = dotted red, no bats = dashed green. $\chi^2_{\text{Intercept}}$ indicates influences of predator exclusions, while χ^2_{Slope} indicates canopy cover dependency of predator exclusions.

tion; Bos, Steffan-Dewenter & Tscharrntke 2007a; Maas, Clough & Tscharrntke). Increased herbivore abundance, parallel increased leaf damage and fewer flowers under ant exclusion probability resulted in fewer fruits.

Simultaneously, reinforcing negative effects on yield, fruit weight was reduced when ants were absent, which is associated with infestation by fruit-damaging pests such as *H. sulawesi* and *C. cramerella* (Wielgoss et al. 2014). Impacts

of ants on crop yield, including their economic importance, are similar to those reported from sites situated in the same region at lower altitudes (Wielgoss *et al.* 2014), but our results demonstrate that ant predation effects were only economically relevant for agroforests providing <40% canopy cover. Generally, low-shade conditions can be more stressful for cacao trees, both in terms of eco-physiology, and in terms of herbivory (De Almeida & Valle 2007; Tschardtke *et al.* 2011). These findings are in accordance with our results, showing that small beetles and caterpillar densities increased under low-shade conditions. Besides this, we could show that there was significant ant species turnover across the gradient in canopy cover. It thus cannot be excluded that ant species more dominant under low-canopy cover conditions provide a more effective pest control than species dominant under high-canopy cover.

BIRD EXCLUSIONS CAN DECREASE OR INCREASE YIELDS DEPENDING ON CANOPY COVER

Against expectation, excluding birds led to more fruits and higher proportions of healthy fruit below 30% canopy cover. Lowered or similar yields under bird exclusion would have been expected throughout the canopy cover gradient, but were observed only in relation to canopy cover above 40%. We assume that the effects of excluding birds are caused by the absence of insectivorous birds, of which 31 species were recorded at cacao canopy level (Maas *et al.* 2015a). Indeed, none of the bird species recorded feed on cacao fruits. Woodpecker damage can occasionally be seen on fruit (YC personal observation), but is likely to only affect fruit with prior pest infestation. Pollination reduction due to bird exclusion is unlikely, since cacao flowers are very small and pollinated by midges, not birds (Leston 1970). The bird community composition did not change with canopy cover, suggesting that shade dependency of yields under bird exclusions may be due to observed differences in arthropod pest and mesopredator densities along the gradient. Generally, there was little response in herbivore abundance to bird exclusion. Leafhopper numbers were depressed and earwig numbers promoted under bird exclusion when canopy cover was below 30%. This, together with lower numbers of damaged fruits under bird exclusion, points to indirect positive effects on herbivores by birds (e.g. mesopredator predation) under little-shaded conditions where herbivory affects cacao trees more severely (Tschardtke *et al.* 2011). The exact mechanism is unclear, as the fogging data show only a trend towards increases in predator densities at canopy cover below 30% for ants and small web spiders with increases and decreases at canopy cover above 50% for larger web spiders and earwigs, respectively. Generally, increased abundances of predators, such as ants, spiders and earwigs, under bird exclusions, are common (Gunnarsson 2007; Williams-Guillén, Perfecto & Vandermeer 2008; Piñol *et al.* 2010; Maas, Clough & Tschardtke 2013; Mestre *et al.* 2013a). Overall, increases in

most predatory arthropods and decreases in individual herbivores due to bird exclusion suggest mesopredator release and may at least partly explain the ambivalent effects of birds on cacao yield in our study, although food web data will be necessary to confirm this. The impact of lower abundances in small Dipterans (<4 mm), which includes cacao-pollinating Ceratopogonidae (Leston 1970), is unknown, yet could conceivably reduce pollination and thereby cause yield losses (Groeneveld *et al.* 2010).

BATS

In 2010, at least 16 insectivorous bat species were recorded in agricultural areas around the Lore Lindu National Park in two separate studies by Graf and Boonman (unpublished data, Table S17). Several of the species glean insects from leaves or perch on plants to prey on arthropods associated with plants and might therefore be relevant to our experimental exclusions. However, bat exclusion did not affect yield, or yield-related plant variables, but enhanced abundances of leafhoppers, large caterpillars, and earwigs and large spiders, that is both herbivorous and predatory arthropods. Bats have strong effects on arthropod communities in tropical forests and agricultural systems (Kalka, Smith & Kalko 2008; Williams-Guillén, Perfecto & Vandermeer 2008; Wanger *et al.* 2014). In coffee, bats can promote herbivorous arthropods by reducing spider densities and, as a result, do not necessarily provide biocontrol (Karp & Daily 2014). A previous study from cacao in our study region, however, showed bats were instrumental in decreasing pests (Maas, Clough & Tschardtke 2013). This suggests that impacts of bats could be strongly dependent on the net balance of arthropod herbivores and predators, with bat impacts on both groups cancelling out any top-down effect on the plants in the present study. Leaf-gleaning bats are less abundant in agricultural systems than in natural forest (Phommexay *et al.* 2011) suggesting natural forests are sources of bats for nearby agroforests, but we did not find any evidence for forest distance-dependent effects of bats.

STUDY LIMITATIONS AND CAVEATS

The extent to which we can causally underpin the detected significant effects is limited by the study design in some respects. First, the impact of forest distance on yield, while significant, cannot be fully elucidated, as it seems not to involve the manipulated predators. Secondly, while we tried to control for variables that could not be standardized, unwanted exclusion effects may have occurred. For instance, reduced earwig abundances under ant exclusion may have been due to the ant exclusion rings partly excluding crawling earwigs. While this may have led to overestimated impacts of ants under high-canopy cover, impacts of ants were strongest below 30% canopy cover, where earwigs were scarce, so our conclusions on ant effects are robust. Moreover, earwig abundances that increased over

40% canopy cover in bat exclusions did not affect cacao yield. Thirdly, we cannot exclude that the presence of nets deterred certain birds or bats from foraging inside the agroforests, due to the risk of collision. Finally, the drawback of a long study duration was the impossibility of adequately surveying arthropods during the whole course of the experiment. Parallels between herbivores and predators recorded through fogging, and cacao tree variables recorded over the whole study duration, allow us to draw hypotheses on mechanisms, but not to formally test them.

MANAGEMENT RECOMMENDATIONS

Impacts of ants and birds on cacao yield are economically relevant, but depend on shade-tree management. In all but most shaded agroforests, ants were pivotal in supporting yields, reducing populations of herbivorous insects rather than other beneficial organisms such as spiders. This confirms the importance of ants for the economic performance of cacao agroforestry in Central Sulawesi. Farmers should be aware of changes in ant communities due to shifts in management or species invasion, and avoid destroying ant nests, as commonly done for weaver ants, for example (YC & PG personal observation). Moreover, current cacao farming methods entail self-shaded or low-shaded (~10% shade-tree canopy cover) plantations impairing arthropod and plant diversity (Rice & Greenberg 2000). The observation that, on average, shade-tree canopy cover of 30–40% yielded most, suggests that farmers should maintain such intermediate canopy cover levels not only for ecophysiological reasons (Tscharntke *et al.* 2011), but also to buffer variability in predator communities. Our data suggests that beneficial effects of forest proximity on yield were unlikely to be related to pest limitation services by ants and birds. However, positive effects of forest proximity on predation of dummy caterpillars, mediated by higher abundances of a locally common white-eye species *Zosterops chloris*, have been demonstrated in our study area (Maas *et al.* 2015a), and together these results suggest that farmers should have an interest in the stability of forest margins, which are threatened by encroachment.

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Data accessibility

Data are available through EFForTS-Information System (<https://efforts-is.uni-goettingen.de>) and Dryad Digital Repository doi: 10.5061/dryad.90329 (Gras *et al.* 2016).

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Supporting Information

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

Fig. S1. Schematic experimental design.

Table S2. Non-crop tree species within chemical application free area.

Table S3. Herbal plant species.

Table S4. Discovered ant species.

Table S5. Discovered bird species.

Table S6. Ant and bird community.

Fig S7. Open bat exclusion.

Fig. S8. Conical-shaped ant exclusion rings (without insect glue).

Table S9. Potentially yield influencing variables (additional to the predator exclusion).

Table S10. Characteristics of experimental trees and plantations at treatment level.

Table S11. Fruit development categories.

Table S12. Pest and disease categories.

Appendix S13. ANOVA Tables.

Fig. S14. RDA – Management, landscape, and predator access manipulation influences on the ant community composition (morpho species level).

Fig. S15. RDA – Management and landscape effects on the bird community (species level).

Fig. S16. Visualization of bird and ant community composition related to shade cover and forest distance.

Table S17. Bat species.