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LETTER

Forest bolsters bird abundance, pest control and coffee yield

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Abstract

Efforts to maximise crop yields are fuelling agricultural intensification, exacerbating the biodiversity crisis. Low-intensity agricultural practices, however, may not sacrifice yields if they support biodiversity-driven ecosystem services. We quantified the value native predators provide to farmers by consuming coffee's most damaging insect pest, the coffee berry borer beetle (*Hypothenemus hampei*). Our experiments in Costa Rica showed birds reduced infestation by ~ 50%, bats played a marginal role, and farmland forest cover increased pest removal. We identified borer-consuming bird species by assaying faeces for borer DNA and found higher borer-predator abundances on more forested plantations. Our coarse estimate is that forest patches doubled pest control over 230 km^2 by providing habitat for ~ 55 000 borer-consuming birds. These pest-control services prevented US$75–US$310 ha-year^{-1} in damage, a benefit per plantation on par with the average annual income of a Costa Rican citizen. Retaining forest and accounting for pest control demonstrates a win–win for biodiversity and coffee farmers.

Keywords

Agriculture, agro-forestry, bat, bird, conservation biological control, countryside biogeography, ecosystem services, landscape complexity, natural enemies, tropical forest.

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INTRODUCTION

Agriculture is intensifying and expanding rapidly, threatening the substantial biodiversity that persists in tropical farming countryside (Tilman *et al.* 2011; Fischer *et al.* 2008; Philpott *et al.* 2008; Perfecto *et al.* 2009; Karp *et al.* 2011; Melo *et al.* 2013). In particular, removal of natural habitat within and around farms fundamentally alters biological communities (Philpott *et al.* 2008; Perfecto *et al.* 2009; Mendenhall *et al.* 2011; Melo *et al.* 2013). Native predators of crop pests are particularly sensitive to habitat loss because natural habitat provides predators with alternative prey, refuges during disturbances, and sites for breeding, hibernation and roosting (Landis *et al.* 2000; Bianchi *et al.* 2006; Chaplin-Kramer *et al.* 2011; Jirinec *et al.* 2011). Therefore, maintaining natural habitat is hypothesised to improve farm yields by supporting predators of crop pests.

Whether landowners maintain natural habitat ultimately depends on a suite of trade-offs largely centred on yield and income. Very few studies, however, have quantified the relationships that determine the outcomes of these trade-offs (Ricketts *et al.* 2004). Oilseed rape is the only crop in which avoided pest damage has been quantified in relation to natural habitat presence on farms (Thies & Tscharntke 1999; Thies *et al.* 2003; Chaplin-Kramer *et al.* 2011). Complex predator–prey dynamics and research biases towards temperate systems make quantifying changes in pest control difficult (Bianchi *et al.* 2006; Chaplin-Kramer *et al.* 2011). Resolving these complexities requires analysing the effects of natural habitat adjacent to crops on the predators of crop pests, the pests themselves and predation rates. Relying on just one measure may obscure underlying trends. For example, natural habitat may boost both predators and pests, making predator abundance alone a poor proxy for pest control (Bianchi *et al.* 2006; Chaplin-Kramer *et al.* 2011).

Our investigation focuses on pest-control services provided by native birds and bats to tropical coffee plantations. Coffee has a retail value of ~ US$90 billion, making it one of the most economically important tropical crops (Vega *et al.* 2003; Jaramillo *et al.* 2011). Twenty million households make their livelihoods by its cultivation, and ~ 10 million ha in more than 50 countries are dedicated to its production (Vega *et al.* 2003). Recently, traditional 'shade-grown' coffee practices have been largely abandoned for 'full-sun' practices (Perfecto *et al.* 2009). Shade tree removal and clearing natural habitat adjacent to coffee plantations fundamentally alters biological communities (Philpott *et al.* 2008; Williams-Guillén & Perfecto 2010; Karp *et al.* 2011; Mendenhall *et al.* 2011). For example, tree removal affects predators of insects and herbivorous insects, some of which may be damaging pests (Perfecto *et al.* 2004; Williams-Guillén *et al.* 2008; Karp *et al.* 2011). How such changes in biological communities will ultimately affect pests and agricultural yields remains unclear.

Coffee's most damaging insect pest is the coffee berry borer (*Hypothenemus hampeii*), a ~ 2 mm beetle native to Africa, where coffee originated. Recently, the pest has spread to nearly every major coffee-producing country (Burbano *et al.* 2011; Jaramillo *et al.* 2011). Borer infestations can be devastating, with harvest losses greater than 75%, and no failsafe method of control (Vega 2004). Pesticides are largely ineffective because the borer resides within the coffee berry's seed coat and because borers rapidly evolve resistance (Brun *et al.* 1995). Furthermore, endosulfan (the primary pesticide, a neurotoxin) poses significant human health and environmental risks (Roberts *et al.* 2007). While biological control with introduced parasitoids has had only limited success (Damon 2000), native insectivores may help reduce infestations (Kellermann *et al.* 2008; Jaramillo *et al.* 2010; Johnson *et al.* 2010; Larsen & Philpott 2010).

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Native birds have been shown to consume the borer on Jamaican coffee plantations, likely when borers are dispersing or during the up to 8 h it takes to drill into coffee berries (Damon 2000; Kellermann *et al.* 2008; Johnson *et al.* 2010).

In this study, we evaluate bird- and bat-mediated control of the borer and ask whether conserving countryside forest elements for borer-consuming birds and bats affects coffee yield. We define countryside forest elements as ribbons and clusters of tropical native habitat weaving through farmland, often too small or with configurations too complex for most remote sensing techniques to detect (Mendenhall *et al.* 2011). Native predators of the borer may rely on forest elements for moving through non-forested agricultural lands, roosting and sources of alternative prey (Kellermann *et al.* 2008; Johnson *et al.* 2010; Jirinec *et al.* 2011). These activities may take place at multiple scales, as predators may utilise forest both embedded within plantations and in surrounding landscapes (Jirinec *et al.* 2011). Whether forest elements increase pest control and boost yields at any scale, however, is unknown. We capitalise on a landscape comprised of coffee plantations, pastures and forest elements in southern Costa Rica to identify borer predators, quantify bird and bat predation of borers, and measure how borer-predator abundances, borer infestations and crop damage change with deforestation.

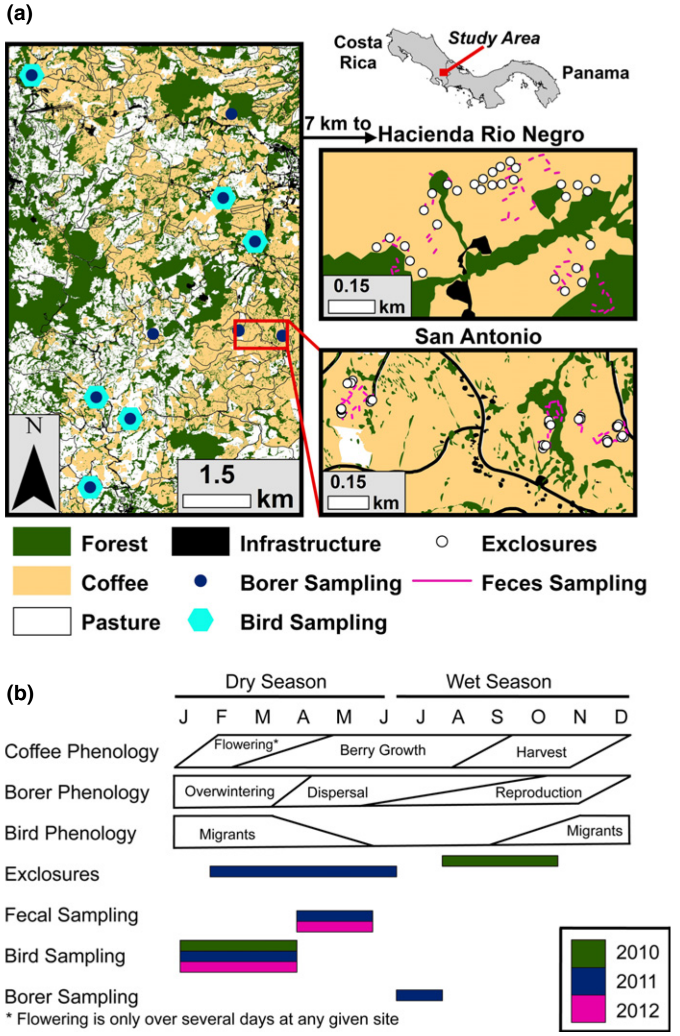
METHODS

Study sites

We quantified bird- and bat-mediated control of the coffee berry borer beetle in southern Costa Rica near the Organization for Tropical Studies' (OTS) Las Cruces Biological Station. Our study sites were situated at ~ 1100 m elevation in the Coto Brus Valley, between the Talamanca and Coastal ranges, where annual precipitation and temperature average 3600 mm and 17–24 °C respectively (Fig. 1a). The valley was previously covered in premontane tropical wet forest, but was largely deforested in the 1950s and 1960s (Sansonetti 1995). We studied coffee (*Coffea arabica*) plantations, all of which were 'sun coffee' with 25 ± 6% seasonal canopy cover directly over the coffee shrubs – mostly from nitrogen-fixing 'Poró' trees (*Erythrina* spp.) and banana/plantain plants (*Musa* spp.). 'Shade-grown coffee,' cultivated under a full canopy of trees, is largely absent from our study area.

Our core experiment focused on two plantations, 'San Antonio' and 'Hacienda Rio Negro'. Both plantations apply a combination of fertiliser, herbicide and fungicide throughout the year. The plantations primarily manage the borer by removing unharvested and fallen berries after harvest (December to February) to suppress borer populations between growing seasons (Fig. 1b). In addition, Rio Negro applies low doses of endosulfan at the end of June (2010: 0.35 L ha^{-1}; 2011: 0.5 L ha^{-1}) and erects borer traps when borers are undergoing maximal dispersal (20 ha^{-1} in April to May).

The two plantations, however, were purposely chosen to differ in some respects to help verify that trends in bird and bat predation were general, at least within the region. San Antonio is a small, 30 ha plantation in a largely deforested region. In contrast, Rio Negro is a Rainforest Alliance-certified, commercial operation, with 250 ha of coffee in production. Rio Negro maintains two 80 ha forest elements, and abuts La Amistad National Park, a 570 000 ha reserve that spans southern Costa Rica and northern Panama.



* Flowering is only over several days at any given site

Figure 1 Locations and timing of pest-control experiments in Coto Brus, Costa Rica from 2010 to 2012. (Panel a) Landscape map (left) shows bird mist-net sampling sites ($n = 6$ plantations) and borer sampling sites ($n = 9$ plantations with two survey locations at San Antonio). Insets show the locations of exclosures and faecal sampling sites (mist-net locations) at the two core plantations: Hacienda Rio Negro and San Antonio. (Panel b) Coffee, borer and bird phenology overlaid with our data collection timeline. Exclosure experiments ran through all stages of coffee production. Faecal sampling coincided with the height of borer dispersal. Bird sampling occurred when migrant birds were present. Finally, borer sampling took place as dispersal waned and beetles could be easily censused.

Exclosure experiment

We excluded birds and bats from coffee shrubs with exclosures made from bamboo frames enveloped in mesh nets. Mesh size was small enough to exclude birds and bats, but large enough to allow passage for large insects (1.5in^2 net; Nylon Net Co.; N163A) (Kellermann *et al.* 2008; Johnson *et al.* 2010). At San Antonio, we constructed 36 exclosures (~ 2 m × ~3 m × ~2 m), each surrounding four coffee shrubs. Exclosures were assigned to one of four treatments: permanent (excluding birds and bats), diurnal (excluding birds), nocturnal (excluding bats) or open controls. Bird exclosures were closed at sunrise and opened at sunset; bat exclosures were closed at sunset and opened at sunrise. Blocks of these four exclosure treatments were separated by at least 50 m, and placed along a gradient of nearby forest cover, with some blocks located adjacent to forest patches and others located in completely deforested areas (Fig. 1a). At Rio Negro, we constructed 60 exclosures (~1 m × ~1 m × ~2 m) around single shrubs, thirty of which were permanently closed and thirty of which were an open frame. Like San Antonio, pairs of exclosures and controls were placed together, and in areas of high and low forest cover.

The experiment took place over a wet (July to October 2010) and a dry season (February to June 2011). At morning and evening for every day during these periods, we raised and lowered exclosures at San Antonio to differentiate bird and bat-mediated control of the borer. Before and after the wet season, we surveyed shrubs for borers by counting the proportion of berries with borer entry holes. We only surveyed shrubs for borers at the end of the dry season experiment, as berries had not yet formed at the beginning of the experiment. For each shrub, we chose the seventh branch from the top, and systematically examined 100 berries for borer entry holes at the top of the ovary, beginning our surveys at the distal end of the branch. We dissected 560 berries without the entry hole, and never found the borer. We also collected up to 20 attacked berries from each shrub at the end of the first phase of the experiment. We then randomly chose five berries for dissection, noted borer presence, and measured the depth of the entry hole as a measure of the stage of infestation (Kellermann *et al.* 2008).

Economic analyses

We acquired coffee production data and farmgate prices through interviews with producers and the Instituto de Café de Costa Rica (Table 1). No price data were publicly available for Rio Negro, so value was estimated from San Antonio prices. We calculated the increase in the proportion of berries infested after excluding birds (Δborer) at San Antonio (Kellermann *et al.* 2008). At Rio Negro, we analysed the effect of excluding birds and bats together. To calculate the benefit of borer predators per hectare, we used the formula:

$$[\text{Production (kg)} * \Delta \text{ borer} * \text{Price(US\$)}]/\text{Area(ha)} \tag{1}$$

For 2011, we calculated Δborer indirectly at San Antonio, as the experiment ended in June, approximately 3 months before harvest began (Fig. 1b). We surveyed the per cent of berries infested (BI) in control shrubs at harvest, and estimated infestation on shrubs in exclosures, had the experiment continued:

$$\%\text{BI}_{\text{Controls,Fall'11}} * [\%\text{BI}_{\text{Exclosure,Spring'11}}/\%\text{BI}_{\text{Controls,Spring'11}}] \tag{2}$$

We then used Equation 1 to calculate bird and bat predation value at harvest in 2012. The experiment continued through harvest at Rio Negro; therefore, predation value was estimated directly.

Identifying borer predators

Identifying the predator species that consume crop pests is crucial to understanding pest-control dynamics (Karp *et al.* 2013). The borer, however, is ~ 2 mm long, and spends the majority of its lifecycle feeding within coffee berries. Therefore, obtaining characteristic borer fragments from faecal pellets or witnessing predation events is infeasible. DNA analysis of bird and bat faecal samples provided us with a novel opportunity to identify the borer's predators (King *et al.* 2008; Zeale *et al.* 2010).

Table 1 Economic analysis of bird-mediated control of the borer. At Rio Negro, bird and bat effects are combined

	San Antonio		Rio Negro	
	2010 Harvest	2011 Harvest	2010 Harvest	2011 Harvest
Area (ha)	30	30	225	247
Coffee production (kg)	29 900	38 410	156 722	570676
% Infested (control)	4.60 (1.7)	6.4 (1.2)	5.8 (1.4)	3.9 (.9)
% Infested (no birds)	8.50 (2.5)	11.6 (2.2)*	9.3 (1.9)	6.0 (1.1)
% Diff (excluded-control)	3.9 (2.4)	5.1 (1.0)	3.5 (1.4)	2.1 (.8)
Total ratio (excluded per control)	1.8	1.8	1.6	1.5
Production saved (kg)	1200 (700)	2000 (400)	5500 (2200)	11 600 (4300)
Coffee price (US$ kg^{-1})	3.03	4.75	3.03†	4.75†
Value saved (US$)	3500 (2200)	9400 (1800)	17 000 (6800)	55 100 (20 300)
Production saved per ha (kg)	40 (20)	70 (10)	25 (10)	50 (20)
Value saved per ha	120 (70)	310 (60)	75 (30)	220 (80)

*Exclosure experiment did not continue past spring, 2011. We estimated the per cent of berries infested within exclosures using total ratios from fall, 2010 and spring, 2011 (see methods).

†Price data were not available for Rio Negro. We used San Antonio prices.

Mean values are reported; values in parentheses are standard errors.

We acquired faecal samples from birds and bats at San Antonio and Rio Negro during April and May 2010, corresponding to the height of borer dispersal and thus vulnerability to predation. On each plantation, we arrayed sixty 12 × 2.5 m mist-nets composed of 32 mm mesh. Nets were placed in the same area as the exclosure experiment, in areas of high and low forest cover (Fig. 1a). At each plantation, we also placed at least 10 nets inside forest elements. Bird surveys began at sunrise and continued for 5–6 h, using standard mist-netting protocol (Ralph *et al.* 1993). Bat surveys began at sunset and continued for 4 h. Birds and bats were placed in cotton bags that were previously bleached to prevent contamination. They were then walked to a nearby processing station, identified and individually marked. Shortly after processing, animals were released and their cotton transport bags were checked for faecal samples. We used sterilised tweezers to obtain faeces from transport bags, storing samples immediately in vials of 95% ethanol. To determine the efficacy of this approach, we also conducted feeding trials with three insectivorous bird species – Rufous-capped Warbler (Basileuterus rufifrons), Rufous-breasted Wren (Pheugopedius rutilus) and Plain Wren (Cantorchilus modestus). We fed birds 2, 4 or 8 borers, kept them in mesh-net cages for up to 1.5 h and collected faecal samples.

We extracted DNA from faeces using DNA Stool Mini Kits (Qiagen) and a modified extraction protocol to increase yields (Zeale *et al.* 2010). We amplified a 185bp segment of mitochondrial

DNA (Cytochrome oxidase I or COI) using published borer-specific primers (Jaramillo *et al.* 2010). Polymerase chain reactions were carried out in 12.2 μL reactions consisting of 8.3 μL deionised water, .3 μL 10 μg μL^{-1} Bovine Serum Albumin (BSA), .45 μL 10 mM dNTPs, 1.41 μL 10× PCR buffer, .61 μL 50 mM $MgCl_2$, .28 μL 20 mM forward primer, .28 μL 20 mM reverse primer, 0.06 μL 5 U μL^{-1} Taq Platinum (Invitrogen, Life Technologies, CA, USA) and .6 μL template DNA. We used a 2-min denaturation at 95 °C, followed by 50 cycles of 22 s at 94 °C, 22 s at 55 °C and 30s at 72 °C, and finally an incubation of 8 min at 72 °C. We then visualised products with gel electrophoresis, and sent all products of approximately correct size for sequencing (Elim BioPharm, Hayward, CA, USA). We identified samples as containing borer DNA if they matched reference sequences with > 99% similarity.

Bird and borer surveys

We assessed the effect of forest element cover on borer-consuming bird abundances with three years of bird mist-net surveys (2010–2012) at six coffee plantations in the Coto Brus Valley (Mendenhall *et al.* 2011) (Fig. 1a). These plantations were all owned by smallholder producers, and were chosen to vary in the amount of shade trees and forest patches embedded within and surrounding the plantations. Specifically, the plantations ranged in forest element cover from ~ 10 to ~ 30%. Mist-netting protocols consisted of twenty, 12 × 2.5 m, mist-nets in 3–5 ha plots, and took place between January 25 and May 12. Sites were visited three times each, with each visit averaging 5–6 h, beginning at sunrise. Birds were captured, banded with a unique leg band, aged and sexed, and released on-site shortly after processing.

We also surveyed these six plantations and three additional plantations, for borer infestations (Fig. 1a). On each plantation, we haphazardly chose three sites that were separated by at least 50 m, and surveyed four coffee shrubs per site for borers, using the same methods as in the exclosure experiment. Berries were not dissected. Each plantation was visited once, in July 2011.

Statistical analyses

We tested the effect of bird and bat exclusion on borer infestation with generalised linear mixed models (GLMMs) (Zuur *et al.* 2009). We modelled proportion data using binomial distributions and spatial non-independence of treatment blocks and cages as nested random effects. These models included a variable indicating whether birds were excluded, a variable indicating whether bats were excluded, their interaction (both or neither excluded), and interactions with season. Significance was tested with backwards model selection, utilising Aikaike Information Criteria and log-likelihood tests (Zuur *et al.* 2009).

We also tested whether forest element cover increased pest control using a 2 m-resolution land-use map of the Coto Brus Valley. The map was manually digitised from orthorectified aerial photographs taken in 2003 and 2005, spanning 236 km^2 and encompassing San Antonio but not Rio Negro (Mendenhall *et al.* 2011). We computed the fraction of forest element cover in concentric circles surrounding each exclosure at multiple scales to determine the contributions of forest cover to pest control both on the farm and in the surrounding landscape. Specifically, we calculated forest element cover at 16 scales, using concentric circles with radii between 60 and 500 m (60, 70, 80, 90, 100, 125, 150, 175, 200, 225, 250, 300, 350, 400, 450 and 500 m). There was not sufficient variation in forest cover to examine radii less than 60 m, and sites were not sufficiently separated to evaluate radii greater than 500 m. We examined the interaction of bird and bat presence with forest element cover at each scale in GLMMs to assess changes in bird predation with forest element cover. Treatment blocks and cages were modelled as nested random effects. Each scale was analysed in a separate GLMM to avoid collinearity. We report the range of scales in which the relationship between pest control and forest element cover was significant.

We also assessed whether forest element cover negatively correlated with borer infestation severity at nine plantations across the Coto Brus Valley (Fig. 1). We included elevation as a covariate, as elevation has been found to determine borer abundance in previous studies (Avelino *et al.* 2012). Again, we used GLMMs and a model selection framework, including blocks and sites as nested random effects and repeating GLMMs at the same spatial scales as pest-control analyses (concentric circles of 60–500 m radii).

Finally, we examined the influence of forest element cover on borer predators. We computed the proportion of forest element cover for each of the six plantations that we had surveyed for birds, using 60–500 m radii. We then calculated the total captures of unique individuals over our three census years at each plantation as a proxy for borer-consuming bird abundance. Finally, we related the abundance and number of borer predator species at each plantation to forest cover across scales with linear regression. All statistics were conducted in R; GLMMs were implemented in the 'lme4' package (R Development Core Team 2010).

Mapping borer-predator abundance and pest control

Using the relationships derived from GLMMs, we projected borer-predator abundance and pest control across our 230 km^2 study area on all coffee plantations. Our projections were at a 2 m resolution, the same resolution as the orthorectified land-use map available for our study area (Mendenhall *et al.* 2011). We estimated the value forest elements provide plantation owners by linking the value realised on coffee plantations back to contributing forest elements. Specifically, for pest control, we calculated the avoided pest damage (kilograms of coffee ha^{-1}) that coffee plantations received from forest elements within 60 m. This was accomplished by multiplying the per cent change in borer infestation after bird exclusion by average coffee yield (San Antonio farm: 1138.5 kg ha^{-1}). Similarly, we calculated the increase in borer-predator density (birds ha^{-1}) that each forest element provided to coffee plantations within a 400 m radius. We then equally allocated these values back to all contributing 2 × 2 m pixels of forest. Next, we isolated and individually identified all forest elements across our study area by implementing 6, 12 and 18 m width pinch points. Finally, we summed the pest-control value (kilograms of avoided pest damage) and predator-abundance value (number of borer-consuming birds) of all 2 × 2 m pixels in each forest element. In this way, we calculated the pest-control and predator-abundance values for each forest element across our study landscape.

RESULTS

We found that birds significantly reduced borer infestations at both plantations and in both seasons (Fig. 2; Table 2). Borer infestation almost doubled when birds were excluded from foraging on coffee

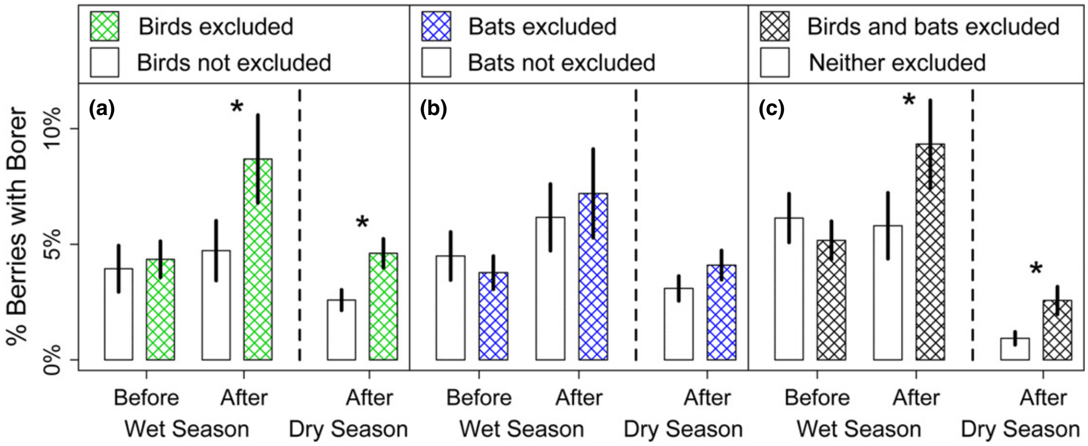


Figure 2 Birds reduced borer infestations at two Costa Rican coffee plantations. (Panel a) Before bird exclusion at the small plantation, shrubs in exclosures and controls did not differ in infestation; however, infestation almost doubled after birds were excluded in both seasons. (Panel b) Excluding bats caused no significant increase in infestation in either season. (Panel c) Trends at the commercial plantation mirrored the small plantation. Asterisks denote significance ($P < 0.05$) under log-likelihood tests, comparing nested models.

Table 2 Effects of bird and bat exclusion on borer infestation

Farm	Time	Model	AIC	χ^2	P
San Antonio	Pre-experiment (before wet season)	~ Birds × Bats + RE	404.5		
		~ Birds + Bats + RE	402.9	0.37	0.542
		~ Birds + RE	403.0	2.16	0.141
		~ RE	**404.1**	**3.11**	**0.078**
Rio Negro	Pre-experiment (before wet season)	~ Both + RE	172.2		
		~ RE	**173.1**	**2.87**	**0.09**
San Antonio	Post-experiment (wet and dry seasons)	~ Birds × Bats + Birds : Season + Bats : Season + Season + RE	903.9		
		~ Birds + Bats + Birds : Season + Bats : Season + Season + RE	902.0	0.03	0.85
		~ Birds + Bats + Bats : Season + Season + RE	902.2	2.19	0.14
		~ Birds + Bats + Season + RE	902.2	2.01	0.16
		~ Birds + Season + RE	**902.1**	**1.96**	**0.16**
		~ Season + RE	914.6	14.5	<0.01
		~ RE	1027.7	115.1	<0.01
Rio Negro	Post-experiment (wet and dry seasons)	**~ Both × Season + RE**	**338.9**		
		~ Both + Season + RE	341.2	4.35	0.04
		~ Both + RE	388.1	48.8	<0.01
		~ RE	637.0	250.9	<0.01

Birds = Variable indicating if birds were excluded; Bats = Variable indicating if bats were excluded;
Both = Variable indicating if both birds and bats were excluded; Season = Variable indicating the wet or dry season; ':' indicates an interaction; RE, Random effects. San Antonio: cages nested in blocks. Rio Negro: blocks.
Significance was assessed via backwards model selection with log-likelihood tests. Bolded text indicates the best model after model selection.

shrubs, rising from 4.6 to 8.5% in the wet season and from 2.7 to 4.8% in the dry season. In contrast, bats did not significantly reduce borer infestations. These effects were consistent for the two seasons at San Antonio; however, we measured a greater effect of predator exclusion in the dry than wet season at Rio Negro (Table 2). We also found that borers drilled deeper when birds (but not bats) were excluded, an average of 7.1 mm vs. 6.6 mm (San Antonio: $\Delta AIC = 5.5$, $\chi^2 = 7.70$, $P < 0.005$; Rio Negro: $\Delta AIC = 1.89$, $\chi^2 = 3.47$, $P = 0.049$). Because bat exclusion did not significantly increase borer infestation, we ascribe observed changes in borer abundances to birds.

Bird predation conferred significant economic benefits to coffee farmers (Table 1). At San Antonio, birds saved 40–70 kg ha-year^{-1} of coffee from borer infestation, a value of US\$120–\$310 ha-year^{-1}. At Rio Negro, predation saved 25–50 kg ha-year^{-1} (US\$75-\$220 ha-year^{-1}). By multiplying the benefit per hectare by plantation size, we estimated bird predation saved the San Antonio plantation US\$3500–US\$9400 year^{-1}.

We identified some of the species responsible for providing these benefits by assaying 522 faecal samples from 75 bird ($n = 469$ samples) and 13 bat species ($n = 53$ samples) for fragments of borer DNA. Assays were not limited to samples from insectivores but rather included all trapped birds and bats. Borer detection rates were low; reflecting both the low probability of trapping an insectivore after it had recently fed on a borer and degradation of borer DNA upon passing through the gut. Indeed, in feeding trials in which birds were fed two, four and eight borers, we detected the borer in ~ 10, ~ 20 and ~ 70% of samples respectively. Despite these low detection rats, we found that five bird species were borer predators: Buff-throated Foliage-Gleaner (Automolus ochrolaemus; detected in one of five samples), Rufous-breasted Wren (Pheugopedius rutilus; one of five), Rufous-capped Warbler (Basileuterus rufi-

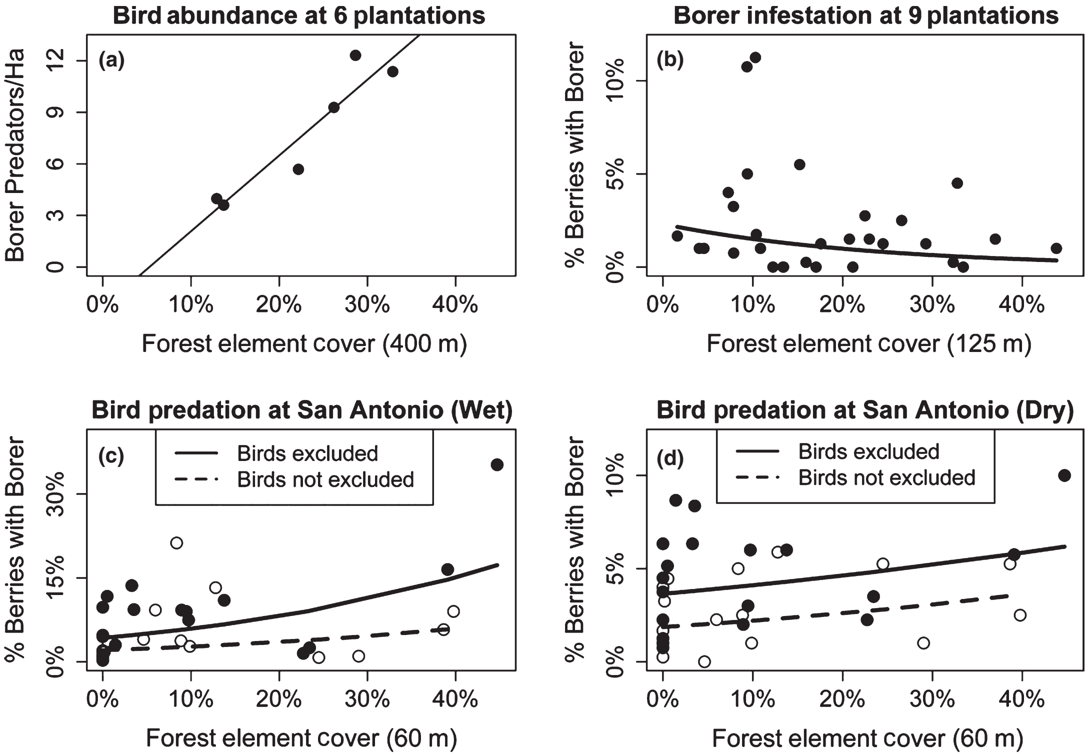


Figure 3 Effect of forest element cover on borer-predator abundance, borer infestations and bird-mediated pest control. (Panel a) Borer predators reached higher abundances on plantations with higher forest element cover, measured as the fraction of forested area within 400 m of mist-net survey locations. Bird surveys were conducted over 3 years at six coffee plantations. (Panel b) At nine coffee plantations, the per cent of berries with borer damage declined as forested area increased. This relationship was most significant when forest element cover was measured within a 125 m radius of survey locations. (Panel c) At low levels of forest element cover, borer infestation levels were similar when birds were excluded and when birds were present. As forest element cover increased, the difference in infestation between exclosures and controls increased. This trend occurred in the wet but not the dry season (Panel d). Forest element cover was measured within 60 m of each exclosure.

frons; 4 of 30), White-tailed Emerald (Elvira chionura; one of two) and Yellow Warbler (Setophaga petechia; one of six).

These species were more common on coffee plantations with higher forest element cover. This result was robust to spatial scale. Borer-predator abundance increased with forest element cover when calculated with 225–500 m concentric circle radii around the study sites (Table S1). The strongest relationship was at 400 m (Fig. 3a; $r^2 = 0.86$, $P < 0.01$). The same trend occurred at other scales, but was not significant. More of the five borer-consuming bird species were also present on plantations with higher forest element cover (significant for radii of 225–500 m; Table S1)

We also found evidence that borer infestations decreased with increasing forest element cover. We observed more severe borer infestations in areas of low forest element cover (Fig. 3b). This relationship was significant for concentric circle radii of 70–175 m (Table S2). Forest cover at a 125 m radii explained the most variation in borer infestation, which was very similar to another Costa Rican landscape (150 m) (Avelino *et al.* 2012).

Finally, we found evidence that forest element cover increased bird control of the borer. In the wet season, excluding birds in areas of higher forest cover caused a larger increase in borer infestation than in areas of lower forest cover (Fig. 3c; Table S1). Again, this relationship was robust to the choice of concentric circle radii: the trend did not change across scales and remained significant at 60–250 m radii (Table S2). The relationship was largely a result of a block of 16 shrubs adjacent to a forest element (< 10 m). When removed, the trend was no longer significant ($\chi^2 = 0.56$, $P = 0.45$).

Using these relationships, we projected the abundance of borer-consuming birds and the amount of coffee (kg) saved by birds on coffee plantations across our 230 km^2 study area. We then calculated the value of every forest element, both in terms of the additional borer-consuming birds and additional coffee yield provided to nearby coffee plantations (Fig. 4; Fig. S1/S2). Our very coarse estimate based on capture frequencies is that forest increased borer-predator abundance on coffee plantations by ~ 55 000 birds across ~ 5300 ha of coffee. On average, forest elements doubled bird-mediated pest control from 2 to 4% berries saved.

Forest elements owned and voluntarily maintained by private landowners provided the vast majority of this benefit. The Las Cruces Biological Reserve, the only formally protected area in our study area, provided < 1% of the total pest control. On the other hand, very small forest elements, ~ 1 ha in size, provided ~ 50% of the total pest-control value and provided habitat for ~ 50% of the total pest-eating birds (Fig. 4c/f). These results were maintained regardless of whether forest elements were isolated by 6, 12 or 18 m pinch points (Fig. S1/S2).

DISCUSSION

Despite the coffee berry borer beetle having arrived in Costa Rica in 2000 (Staver *et al.* 2001) and at our study sites in 2005 (M. Rojas *pers. comm.*), native birds have already begun consuming this damaging pest. Borers also drilled deeper into coffee berries in the absence of birds, indicating a progression of infestation (Kellermann *et al.* 2008).

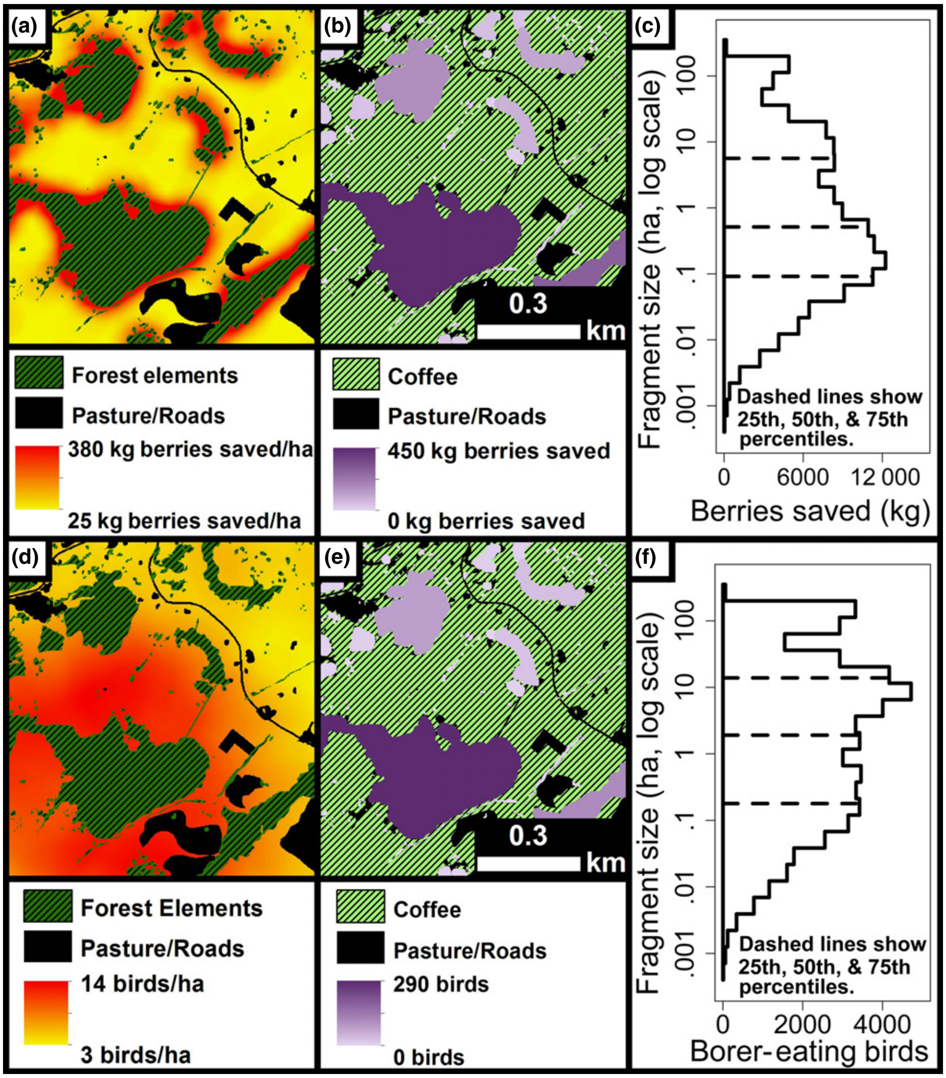


Figure 4 Linear models that included forest cover were used to map pest control (Panel a) and borer-consuming bird abundance (Panel d) on coffee plantations. Models predicted that forest elements embedded in coffee plantations increased bird-mediated pest control (Panel b) and borer-consuming bird abundance (Panel e) on nearby coffee plantations. Small forest elements were more numerous than large elements, providing most of the total pest-control value (Panel c) and habitat for borer-consuming birds (Panel f). Histograms show the benefit that forest elements of differing sizes provided to coffee plantations. Dotted lines represent 25th, 50th and 75th percentiles of the total pest-control value (total kg berries saved from infestation by birds) and total borer-consuming bird value (total birds foraging in coffee but relying on forest elements) across the study region.

We found little evidence, however, that bats serve as significant borer control agents, despite previous observations that bats limit arthropods in a tropical coffee plantation (Williams-Guillén *et al.* 2008). Low bat predation may reflect borer diurnality. Light stimulates borer dispersal, with peak flight in the afternoon (Damon 2000). Accordingly, at one plantation, we observed a greater effect of excluding bats and birds in the dry than wet season, when borers were at peak dispersal (Damon 2000).

Despite bats' limited role, birds prevented significant borer damage to coffee shrubs, representing a gain per plantation approximately equal to Costa Rica's per-capita income (The Little Green Data Book 2012). This value will likely increase as the borer invasion continues. The borer arrived recently, and only ~ 2% of coffee berries were infested across our study area. Once longer established, the borer can cause much more severe infestations – > 75% crop losses have been recorded in many countries (Vega 2004). Climate change may also increase infestation severity (Jaramillo *et al.* 2009, 2011). Because the borer reaches a maximum reproductive rate at an average daily temperature of 26.7 °C (Jaramillo *et al.* 2009) and the average daily temperature on coffee plantations in our study sites is 20 ± 0.5 °C, an increase in temperature could increase infestation severity. If infestation increases, pest-control value would also likely increase, as borers become a more significant food source (Railsback & Johnson 2011). Jamaican coffee plantations already support this claim with more yield saved in a country where borers are longer established (Kellermann *et al.* 2008; Johnson *et al.* 2010).

Conserving bird populations by maintaining countryside forest elements on farmland may therefore represent a critical component of borer control strategy. We found that borer-consuming birds increased in abundance and exerted stronger control on borer populations on plantations with higher forest element cover. Correspondingly, we observed less severe borer infestations on plantations with more forest elements. Further, birds are not the borer's only predators. Twig-nesting ants, e.g., consume the borer and decline in intensively managed coffee plantations (Larsen & Philpott 2010). Similarly, neotropical herpetofauna are known to regulate arthropod abundances in coffee plantations, but further study is needed to determine whether they regulate the borer and the extent to which they rely on countryside forest elements (Borkhatariam *et al.* 2006). Regardless, our results support the idea that countryside forest elements can increase pest control by bolstering the predators of pests on farmland.

Very few other studies have traced the benefits of maintaining natural habitat on farmland back to pest infestations and avoided crop damage, focusing instead on direct effects on predators (Thies & Tscharntke 1999; Thies *et al.* 2003; Chaplin-Kramer *et al.* 2011). In our study, predator abundance increased, pest infestation decreased and predation rates increased with increasing forest element cover, suggesting that forest mitigates borer infestations by bolstering insectivorous bird populations. Countryside conservation activities that account for pest-control services may thus provide a win–win for biodiversity and farmers' livelihoods.

Managing land for agricultural production and biodiversity simultaneously, however, is controversial. So-called 'land sparing' advocates suggest that we maximise yields through agricultural intensification and set aside large reserves for biodiversity (Fischer *et al.* 2008; Phalan *et al.* 2011). Ensuing debate has focused almost exclusively on food production and biodiversity, neglecting other critical ecosystem processes and services (Phalan *et al.* 2011; Mendenhall *et al.* 2012). Our spatial projections suggest that unprotected, countryside forest elements weaving through farmland provided 99% of the total pest-control benefits to coffee farmers. Similarly, complex forest element configurations provision crop pollination services better than isolated protected areas (Ricketts *et al.* 2004; Brosi *et al.* 2008). Protected areas are and will continue to be important for safeguarding biodiversity, ecosystem services and human wellbeing (Bruner *et al.* 2001; Chan *et al.* 2006; Andam *et al.* 2010; Laurance *et al.* 2012). Our findings suggest that conservation activities in farmland can provide similar benefits, potentially without reducing yields (Fischer *et al.* 2008; Clough *et al.* 2011).

CONCLUSION

Globally, agricultural intensification is rapidly replacing ribbons and clusters of natural habitat elements on farmland with monocultures that may appear as buffets for pests and wastelands for their predators (Bianchi *et al.* 2006; Chaplin-Kramer *et al.* 2011). Nearby natural habitat has been shown to improve coffee quality and yield by promoting bee pollination (Ricketts *et al.* 2004). Here, we report consistent relationships between forest elements, predators, pests, and pest-control services. These lines of evidence show that forest elements may also improve yields by bolstering pest-control services. Future work should focus on extending these analyses to other locations, to other predator-pest networks, and to inform more general, spatially explicit models for pest-management programmes. Whether our results will be consistent in different systems is an open question. There is evidence, however, that increasing natural habitat in landscapes dominated by temperate annual crops (e.g. oilseed rape and corn) also increases biological control (Thies & Tscharntke 1999; Meehan *et al.* 2012). Regardless, our results show that adjusting agricultural practices to conserve countryside forest elements, and associated biodiversity, may limit losses from the most damaging pest of one of the world's most economically important crops.

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AUTHOR CONTRIBUTIONS

DSK, CDM, PRE, EAH, GCD designed the research; DSK, CDM, RSF collected data; DSK, NC analysed data; DSK, CDM, PRE, EAH, GCD wrote the manuscript.

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