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Pest reduction services by birds in shade and sun coffee in Jamaica

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Abstract

The reduction of insect pests by birds in agriculture may provide an incentive for farming practices that enhance the conservation value of farms for birds and other wildlife. We investigated pest reduction services by insectivorous birds on a coffee farm in Jamaica, West Indies. Our results suggest that birds reduced insect pests on our study site. Infestation by the coffee berry borer *Hypothenemus hampei*, the world's most damaging insect pest in coffee, was significantly elevated on coffee shrubs from which birds were experimentally excluded from foraging. Overall, we estimated the economic value of the reduction of coffee berry borer by birds on the 18 ha farm to be US\$310 ha^{-1} for the 2006 harvest season. These results provide additional evidence that birds can reduce numbers of economically damaging pests and enhance crop yields in coffee farms. Differences in the magnitude of pest reduction within the farm may have resulted from variation in shade management and surrounding habitats, and these factors merit further investigation.

Introduction

Ecosystem services are processes that help sustain and fulfill human life (Daily, 1997), and they can provide powerful incentives for conservation (Gatzweiler, 2006). Valuable ecosystem services in agricultural settings include nutrient cycling, crop pollination and the biological control of pests, especially insects (Swift, Izac & van-Noordwijk, 2004; Tscharntke *et al*., 2005). Coffee farms are useful study systems for examining ecosystem services because they occur in tropical regions of high biodiversity and are economically critical to many developing countries – coffee is second only to oil as the leading legal export in Latin America (O'Brien & Kinnaird, 2003; Vandermeer, 2003).

Shaded coffee farms can supply habitat for native biodiversity, especially forest birds attracted to overstory shade trees (Greenberg *et al*., 1997; Moguel & Toledo, 1999; Donald, 2004; Johnson *et al*., 2006). However, modern 'sun coffee' cultivation techniques can increase short-term yields but offer little conservation value (Perfecto *et al*., 1996). Market values offer a modest economic incentive for the retention of traditional cultivation techniques via environmentally labeled premium-priced coffees, but additional incentives are needed for farmers to retain shade trees (Gobbi, 2000; Perfecto *et al*., 2005).

Several studies indicate that birds can reduce overall arthropod numbers in traditionally managed coffee farms (Greenberg *et al*., 2000; Perfecto *et al*., 2004; Borkhataria, Callazo & Groom, 2006; Johnson *et al*., 2009). A recent study conducted in the Blue Mountain highlands of Jamaica provided the first evidence that these effects directly benefit crop production and farm income (Kellermann *et al*., 2008). This study extends previous work by comparing bird reduction of pests between areas under shade and sun cultivation, and by addressing the effect of bird predation on coffee insect pests in a different region at a lower elevation (<500 m), where much of the world's coffee is grown (Rice, 1999).

Ecological theory predicts that characteristics such as habitat complexity and species diversity or abundance of bird assemblages should influence the strength of bird effects (Van Bael *et al*., 2008), prompting the expectation that birds should reduce insects more in shade than in sun coffee. We examined the effect of birds on insect pests in a coffee farm with areas under sun and shade cultivation by testing three predictions: (1) bird abundance and diversity should be higher in shade than in sun coffee; (2) pest infestation should be elevated on shrubs from which birds are experimentally excluded from foraging; (3) any observed effects of birds on insects should be stronger in shade than in sun coffee. Lastly, we aimed to quantify the economic value of any observed reductions in pests due to birds by calculating increases in saleable coffee berries.

Materials and methods

We worked on the Kew Park Coffee Farm near Betheltown, Jamaica (300 m; 18°16′N, 77°04′W). The farm (17.7 ha) contained *Coffea arabica* var. *typical*, with dense second growth forest extending along one side of the farm, and pasture, mixed agriculture and rural housing surrounding the other sides. Banana trees (*Musa* sp.) occurred sporadically between coffee rows throughout the farm. About 70% of the farm was shaded by *Inga vera*, *Swietenia mahagoni*, *Cedrela odorata*, *Ceiba pentandra*, *Terminalia latifolia* and various fruit trees (e.g. *Mangifera indica*, *Ficus* spp.). The farm is a 'commercial polyculture' farm as described in the coffee farm nomenclature provided by Moguel & Toledo (1999). Some shade trees were planted recently (2002–2005) in the remainder of the farm ($\sim$30%), but they were short (≤ 2 m), providing almost no shade or habitat for forest birds, so we considered this area 'sun coffee' (this area was free of trees large enough to provide shade from 1990 until the time of this study; Fig. 1). Shade cover was estimated with a densiometer (Forestry Suppliers Inc., Jackson, MS, USA) at 109 points distributed systematically across the entire farm. We delineated shade coffee and sun coffee areas of the farm by walking homogeneous areas with shade greater or less than 20%, respectively, with a hand-held global positioning unit. Coffee tree age and structure and fruit phenology were similar between the sun and shade areas. An organochlorine insecticide, endosulfan, was applied annually in mid to late summer (July–August 2005; *c.* 0.4 L of active ingredient ha^{-1}), and was not applied again until after project completion. Other measures to reduce insect pests included removal of overripe unharvested berries in January 2006, after the harvest season.

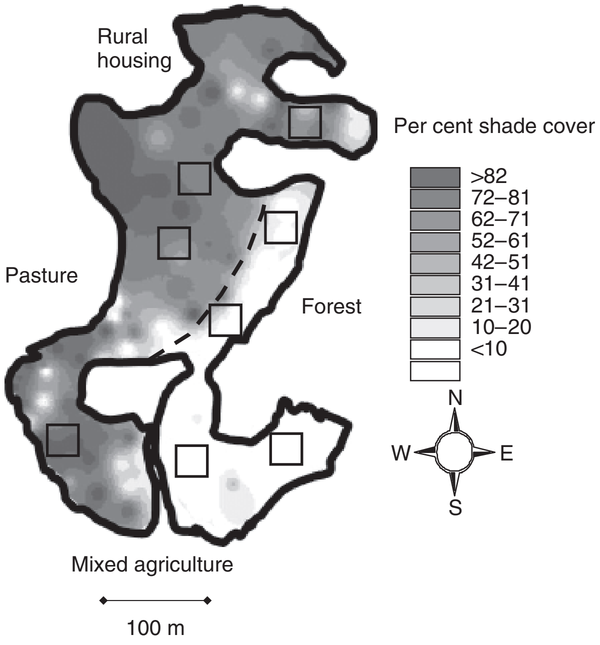

Figure 1 Kew Park Coffee Farm, Westmoreland, Jamaica. The dashed line separates the shade coffee from the sun coffee within the farm and the squares indicate the locations of eight bird survey plots that also included experimental bird exclosures. Shade cover was estimated at 109 points systematically distributed throughout the farm. We used a spline interpolator in the Spatial Analyst extension for ArcView 3.3 (ESRI, Redlands, CA, USA) to create the shade surface depicted. Adjacent habitats are shown with text.

Bird surveys

Bird abundance peaks in Jamaica in the winter months (October–April), when migratory warblers are present (Johnson *et al.*, 2005). We conducted our bird surveys in November–December 2005. Bird abundance was estimated with three 10-min area searches (Bibby *et al.*, 2000) conducted 0700–1000 CST on each of eight randomly positioned 30×30 m plots, four in shade coffee and four in sun coffee areas (Fig. 1). All plots were separated by at least 80 m. During the plot surveys, we recorded each species detected within the plot and the vegetation layer it occupied (understory or canopy). Species were classified as migratory or resident (non-migratory) and insectivorous or not following classification in Lack (1976) and Kellermann *et al.* (2008), and depicted in Table 1.

Bird exclosures and pest infestation

The world's most important insect pest in coffee is the coffee berry borer *Hypothenemus hampei*, a tiny (<3 mm) beetle (Damon, 2000). Gravid adult females bore into coffee berries and lay a brood of 30–120 eggs; the larvae feed, mature and mate with their siblings inside the berry; and gravid adult females emerge 23–28 days later to disperse to another berry before dying (Damon, 2000). At middle to low elevations in Jamaica (<500 m), berries are present on coffee nearly 12 months of year, with harvesting in August–November and fruit initiation and development occurring in December–July. Berry borer can produce four to eight generations during the fruiting period (Damon, 2000), and they typically bore into berries at early to mid-stages of fruit development (in our system, December–May, greatly overlapping the period of migratory peak bird presence, October–April).

We used bird-proof exclosures to compare coffee berry borer infestation in the 2006 fruiting season in the presence and absence of bird predation. In October and November 2005, we built four exclosures in the shade coffee and four in the sun coffee, in the center of each bird survey plot (Fig. 1). We constructed exclosures with transparent nylon gill netting (N163A 58 mm diagonal mesh, Nylon Net Co., Memphis, TN, USA) wrapped around a wooden pole frame over three coffee plants in a row, tied shut with twine and staked into the ground to prevent entry of ground foraging birds. The exclosures did not restrict access by *Anolis* lizards, butterflies, bees or other invertebrates (Pacala & Roughgarden, 1984; Borkhataria *et al.*, 2006). Three control plants were selected for each exclosure from a parallel row of coffee 2–3 m away. On each shrub, we inspected 100 berries chosen systematically across all plant heights, sides, inner and outer portions of the branches and over various fruit sizes and levels of ripeness. We recorded the proportion of inspected berries that had diagnostic berry borer entrance holes. We performed berry inspections on each experimental and

Table 1 Maximum number of birds detected on three 10-min area searches conducted on eight 30 × 30 m plots centered on bird exclosures ($n=4$ in shade, 4 in sun), Kew Park Farm, Jamaica November–December, 2005

Resident species[a]	Shade	Sun
Red-billed streamertail *Trochilus polytmus*	5	0
Jamaican mango *Anthracothorax mango*	3	0
Vervain hummingbird *Mellisuga minima*	1	0
Jamaican tody *Todus todus* UI	4	1
Jamaican woodpecker *Melanerpes radiolatus* I	2	0
Jamaican elaenia *Myiopagis cotta* I	1	0
Sad flycatcher *Myiarchus barbirostris* I	2	2
Jamaican becard *Pachyramphus niger* I	2	0
Loggerhead kingbird *Tyrannus caudifasciatus* I	2	0
White-chinned thrush *Turdus aurantius* UI	2	0
Bananaquit *Coereba flaveola* I	7	1
Jamaican euphonia *Euphonia jamaica*	2	0
Black-faced grassquit *Tiaris bicolor* U	3	5
Yellow-faced grassquit *Tiaris olivacea* U	1	9
Gr. Antillean bullfinch *Loxigilla violacea* UI	2	0
Orangequit *Euneornis campestris* I	3	1
Jamaican oriole *Icterus leucopteryx* I	1	0
Prairie warbler *Dendroica discolor* UIM	3	0
Northern parula *Parula americana* IM	2	0
American redstart *Setophaga ruticilla* UIM	3	3
Black-throated blue warbler *Dendroica caerulescens* UIM	5	4
Black and white warbler *Mniotilta varia* IM	4	0
Ovenbird *Seiurus aurocapillus* UIM	1	0
Common yellowthroat *Geothlypis trichas* UIM	0	4

[a] Letters indicate whether or not a species commonly foraged in the understory (U), ingests insects (I) or is a migratory winter visitor in Jamaica (M).

control shrub at the time of exclosure construction in 2005 (initial survey) and again in April, May and June 2006. Fruits inspected in these months set, grew and were susceptible to berry borer infestation over the previous 5–8 months (December–April), coincident with migrant bird abundance (October–April) and our bird surveys (November–December). Data from two shade exclosures in April were removed from analysis due to damage between sampling periods; they were repaired and used in subsequent analyses.

Data analysis

To determine if bird abundance was higher in shade coffee than in sun coffee, we used Aspin-Welch t-tests for unequal variance to compare the abundance of all birds, insectivores, insectivores detected in the understory, migrants and residents ($n = 4$ plots in each stratum). The three replicates were averaged for each bird plot for analyses of abundance, and the maximum number of individuals detected at a plot in a given survey was used to calculate Shannon-Weiner indices of diversity for shade and sun. Rarefaction was used to subsample species richness and community similarity was assessed between shade and sun plots with the Jaccard and Bray–Curtis indices of similarity (Stiling, 1999). Bird abundance data were normally distributed. We used one-tailed tests based on the expectation that bird abundance should be positively related to shade cover.

We ran a repeated measure ANOVA on the difference in coffee berry borer infestation between each exclosure and its control shrubs (i.e. a subject was an exclosure-control pair, averaged over the three shrubs in each); the within-subject factor was date (initial, April, May and June surveys), and the between-subject factor was shade category (shade vs. sun). To normalize the response variable, we took the natural log of the difference in proportion of infestation $+1/6$; variances were not significantly different between sun and shade areas. The within-subjects effect of date tested the prediction that pest infestation should increase (relative to controls) on shrubs from which birds were experimentally excluded from foraging, and the between-subjects effect of shade category tested the prediction that this response differed between shade and sun coffee. We used Tukey-Kramer *post hoc* comparison tests to compare mean values for dates and shade category. To examine effects of bird exclosures on coffee berry borer infestation within a shade stratum, we ran one-sample t-tests on the difference between exclosure and control infestation (H_0 mean difference = 0). We used one-tailed tests based on the *a priori* prediction that this difference should be >0. We used two-sample t-tests to compare controls between sun and shade areas.

Economic calculations

Farm managers and owners provided data on the number of boxes of coffee produced per acre for the 2006 harvest season. The price farmers received per 'box' (27.2 kg of fruit) of coffee in 2006 was obtained from the Jamaican Coffee Industry Board. We quantified the farm's average proportional yield increase in saleable berries resulting from reductions of berry borer due to bird predation (Δ_{pred}) as the difference in berry borer infestation level of each exclosure and its paired control sample, averaged over all sample units and across all but the initial sampling periods (April, May, June 2006). This value was translated into an economic benefit of birds for the 2006 production season using the formula

$$\Delta_{\text{pred}} \times \frac{\text{boxes}}{\text{ha}} \times \frac{\text{US}}{\text{box}} \times \text{ha}$$

A 95% confidence interval was generated around the economic benefit value by applying the upper and lower 95% confidence limits for Δ_{pred}. We lacked sufficiently precise yield data to examine economic effects separately for shade and sun strata.

Results

Bird abundance and diversity

Twenty-four species of birds were detected within the coffee farm (Table 1). Species richness was 23 in the shade and nine in the sun; after rarefaction species richness was 17.62 ± 1.5 in the shade. Fifteen species were unique to shade, one species was unique to sun, and nine species were detected in both. The Jaccard index of community similarity was 0.33, and the Bray–Curtis index was 0.62. Shannon-Weiner indices of diversity were 2.99 and 1.95 in shade and sun, respectively. The abundance of all birds, insectivores, insectivores detected in the understory and resident species was higher in shade than in sun coffee (Table 2). Among these groups, the difference was most pronounced for insectivores (178% higher in shade) and least pronounced for understory insectivores (28% higher in shade). Abundance of migrants was statistically similar in shade and sun coffee.

Bird exclosure and pest infestation

The difference in infestation between exclosures and controls was negligible at the initial surveys, but increased significantly after birds were excluded (within subjects ANOVA: $F_{3,15} = 14.20$, $P = 0.0001$, Fig. 2). The initial difference in infestation between exclosures and controls (October/November 2005) was significantly lower than the differences recorded in April, May and June 2006, which were not significantly different from each other. On control shrubs subject to bird predation, berry borer infestation rates ranged from 11 to 21% and were similar between shade and sun in each month and April–June averaged (April $t_4 = 0.34$, $P = 0.748$, May $t_6 = 0.98$, $P = 0.365$, June $t_6 = 0.99$, $P = 0.359$, April–June $t_6 = 0.82$, $P = 0.444$; Fig. 2). Inside exclosures, infestation rates peaked at over 40% in the sun, but only rose to about 19% in the shade. The difference in infestation between exclosures and controls was greater in the sun than in the shade (between subjects ANOVA: $F_{1,6} = 11.11$, $P = 0.016$). In the shade, the difference in infestation between exclosure and control shrubs was significantly greater than zero in May ($t_3 = 2.63$, $P = 0.039$)

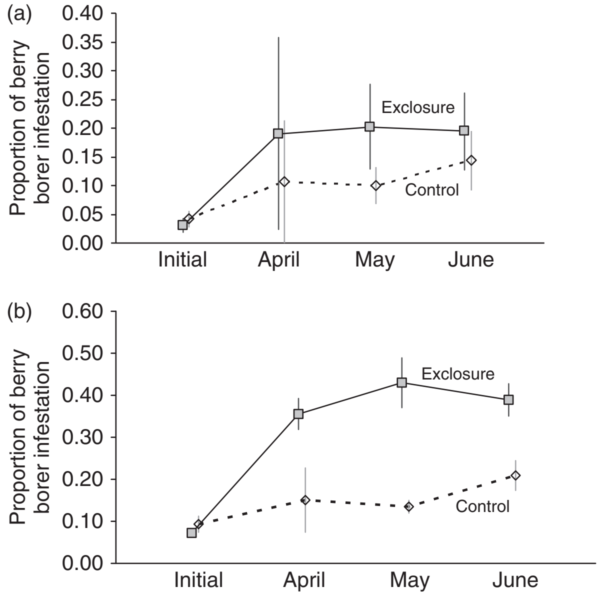

Figure 2 Proportion of berries showing evidence of coffee berry borer *Hypothenemus hampei* infestation on coffee shrubs in (a) shade and (b) sun coffee at the Kew Park Farm, Jamaica. Berries were surveyed inside eight bird exclosures (four in shade, four in sun) and on adjacent control shrubs when exclosures were built (initial survey, October/November 2005) and in April, May and June 2006. Sample size for shade exclosures was reduced to two in April and three in May due to temporary damage to the exclosures. Data are means ± 1 SE. Points are slightly offset on the *x*-axis to show error bars.

Table 2 Abundance (mean ± 1 SE) of birds in shade and sun coffee at the Kew Park Farm, Westmoreland, Jamaica, November–December 2005

Bird group	Shade coffee	Sun coffee	*t*	d.f.	*P*
All birds	11.83 ± 1.65	5.58 ± 0.25	3.75	3.14	0.015
Insectivores	8.33 ± 1.08	3.00 ± 0.19	4.86	3.19	0.010
Insectivores in understory	3.83 ± 0.32	3.00 ± 0.19	2.25	4.91	0.038
Migrants	3.08 ± 0.16	2.33 ± 0.36	1.91	4.12	0.063
Residents	8.56 ± 1.39	3.25 ± 0.57	3.55	3.97	0.012

Estimates were based on three 10-min areas searches conducted on an eight 30 × 30 m plot centered on each bird exclosure (n=4 in shade, 4 in sun). Degrees of freedom are reduced (from 6) due to unequal variances via Aspin-Welch corrections to standard *t*-tests.

and April–June averaged ($t_3 = 3.40$, $P = 0.021$), but not in April or June individually ($t_1 = 1.33$, $P = 0.205$ and $t_3 = 1.96$, $P = 0.072$, respectively, Fig. 2). In the sun, the difference in infestation between exclosure and control shrubs was significantly greater than zero in all months individually (April $t_3 = 3.23$, $P = 0.024$; May $t_3 = 4.81$, $P = 0.009$; June $t_3 = 6.06$, $P = 0.009$) and April–June averaged ($t_3 = 7.77$, $P = 0.002$). The interaction between effects of date and shade/sun was not significant ($F_{3,15} = 1.45$, $P = 0.25$).

Economic value of pest reduction

The farm produced 113.7 boxes of coffee per hectare in 2006. All farms in the region received the same regional standard price for the 2006 season of US$22.69 per box of coffee berries, yielding a gross crop value of US$2579 ha^{-1} (US$45 632 in total). The estimated value of pest reduction services of birds to the Kew Park in terms of increased volume of saleable berries was US$310 ha^{-1} (95% CI: US$183–US$437) or US$5485 (95% CI: US$3246–US$7723) in total.

Discussion

Ecosystem and economic services provided by birds

Our results suggest that bird predation impacted insect pests on our study farm. Coffee berry borer infestation was elevated on coffee shrubs from which birds were experimentally excluded from foraging (Fig. 2). These results provide additional evidence that birds can reduce numbers of economically damaging pests such as the coffee berry borer (Kellermann *et al*., 2008) and add to the body of evidence from Guatemela (Greenberg *et al*., 2000), Mexico (Philpott *et al*., 2004), Panama (Van Bael *et al*., 2008) and Puerto Rico (Borkhataria *et al*., 2006) suggesting birds reduce insects in general on coffee farms.

Ecosystem services provided by birds in coffee farms can increase farm production and farmer revenue (Kellermann *et al*., 2008), creating an incentive for farmers to adopt farming practices attractive to insectivorous birds. Bird abundance and diversity are clearly associated with shade vegetative complexity (Tables 1 and 2, Philpott *et al*., 2008), and a recent meta-analysis suggests that bird suppression of insect abundance is positively associated with both bird abundance and diversity (Van Bael *et al*., 2008). Farmers and farm policy-makers seeking to enhance bird abundance and diversity should retain or establish shade trees (Greenberg *et al*., 1997), non-coffee habitat within and adjacent to farms (Kellermann *et al*., 2008), arboreal epiphytes (Cruz-Angon & Greenberg, 2005) and nearby forest patches (Perfecto *et al*., 2003).

Coffee berry borer is the world's most damaging insect pest in coffee farms, with estimated annual losses valued at over US$500 million (Damon, 2000; Baker, Jackson & Murphy, 2002), so it is important to pursue effective, environmentally sensitive measures for control. Though neither was currently in practice on our study farm, farmers in Jamaica and elsewhere in the Neotropics have experimented with releases of parasitic wasps (especially *Cephalonomia stephanoderis* and *Prorops nasuta*; Baker *et al*., 2002; Jaramillo *et al*., 2005) and the use of traps (e.g. BROCAP®, Centre de cooperation international en recherché agronomique pour le développement (CIRAD), Montpellier, France; Dufour *et al*., 2004) to help control coffee berry borer. Although *C. stephanoderis* can successfully establish populations in the field, *P. nasuta* has rarely persisted for longer than 15 months in the field when pest abundance is low, and neither parasitoid has achieved economically meaningful pest control (Barrera *et al*., 1990; Damon, 2000; Batchelor *et al*., 2005). The traps reportedly are most effective during periods of dispersal, as gravid females leave their berries in search of new ones to colonize (Cloclet da Silva, Ventura & Morales, 2006). In contrast, our observations suggest that birds most often glean coffee berry borer from berries as they are boring through the epidermis, that is, after they have successfully dispersed to a coffee berry (M. D. Johnson & J. L. Kellermann, pers. obs.). Thus, bird predation may remove pests 'missed' by the traps, providing an additive (rather than compensatory) agent of biological control.

We estimated the economic value of the reduction of coffee berry borer by birds on the farm we studied to be US$5485 (US$310 ha^{-1}), or approximately 12% of the total crop value. Unfortunately, no data are available to compare the efficacy and costs of insecticides, wasps or traps relative to bird predation. Indeed, there is no available data of the efficacy of the most commonly used insecticide – endosulfan – on coffee berry borer in the Caribbean. Endosulfan is toxic to birds (Hudson, Tucker & Haegele, 1972), but it degrades quickly and no study has quantified direct or indirect effects of endosulfan on birds in coffee farms.

Our results suggest that birds provided economic and ecosystem services in this study, and they were more abundant in shade coffee than in sun coffee, but we did not find support for the prediction that the effect of birds on insect pests was greater in shade than in sun. The effect of bird exclusion on coffee berry borer infestation was significantly weaker, not stronger, in shade coffee than in sun coffee (Fig. 2). There may be several explanations for this apparent paradox.

First, it is important to note that our study site was small (18 ha) and is only one farm under two different forms of cultivation, and effects could have arisen from extrinsic factors. The sun coffee area was narrow and surrounded by shade coffee or forest patch, and thus it may have contained a higher abundance or diversity of birds than larger sun coffee farms. The reduction in pest infestation attributed to birds could be the result of birds visiting the coffee from surrounding natural habitats (Kellermann *et al*., 2008), a benefit that might not be seen in a large-scale sun coffee farm without adjacent forest. In addition, unaccounted factors, such as pruning schedule, soil conditions, drainage, etc. could partially explain observed differences between sun and shade areas of the farm.

Second, optimally foraging generalist predators such as plant-gleaning insectivorous birds should switch toward alternative prey or broaden their diets as a given prey species diminishes in relative abundance (Stephens & Krebs, 1986). There also may be a higher abundance or diversity of prey for insectivorous birds in shade (Greenberg *et al.*, 2000), causing low-quality prey such as the small hard-bodied coffee berry borer to be less preferred in shade than in sun. In our exclosure experiment, coffee berry borer infestation in the absence of bird predation was considerably higher in sun than in shade (compare exclosure data in Fig. 2a and b). However, berry borer infestation was not significantly different on control shrubs in shade and sun coffee (~11–21%, compare control data in Fig. 2a and b). Thus, birds may have reduced coffee berry borer abundance in both sun and shade to a point where their profitability diminished, but because of higher ambient levels in the sun stratum, this reduction was of a greater magnitude in sun than in shade.

Third, a stronger apparent effect of the exclosures on coffee berry borer in sun than in shade may have been caused by other predators. In the absence of bird predation (inside exclosures), pest infestation was higher in sun than in shade, suggesting something other than birds may have been limiting the pests in shade. Other researchers have found variation in ambient pest infestation across a range of farm variables, including shade (Beer *et al.*, 1998), though these patterns are inconsistent. Complex trophic interactions among arthropods have been documented in coffee systems (Philpott *et al.*, 2004), and cessation of bird predation could release insect predators (such as spiders and ants) that could in turn suppress insect pests (Borkhataria *et al.*, 2006). We did not examine intra-guild trophic structure, but it is reasonable to expect the diversity of insects to increase with increasing shade and habitat complexity (Philpott *et al.*, 2008). Foliage-gleaning bats, which were excluded by our experimental design, can also influence arthropod abundance (Williams-Guillén, Perfecto & Vandermeer, 2008). However, in Jamaica no bat species is considered primarily a foliage gleaner, although *Macrotus waterhousii* will occasionally glean insects from foliage (Genoways *et al.*, 2005). This species is larger than most foliage-gleaning birds in our system (16–20 g) and may not take prey as small as coffee berry borer.

Finally, a greater apparent reduction of coffee berry borer by birds in sun than in shade coffee could also be caused by differential abundance of certain types of birds between sun and shade. For example, our finding that birds were more abundant in shade coffee was largely due to canopy-dwelling species, and these birds may have had little impact on small understory insects such as coffee berry borer. Alternatively, the reduction of pests may have been caused mainly by one or just a few species that were disproportionately common in sun coffee. Our area searches did not provide adequate information to test for significant differences in the relative abundance of individual species between sun and shade; moreover, complete diet information is not available to identify the bird species responsible for berry borer depredation. However, limited diet information indicates that Black-throated blue warblers *Dendroica caerulescens*, American redstarts *Setophaga ruticilla* and Prairie warblers *Dendroica discolor* all ingest the pest (M. D. Johnson & T. W. Sherry, unpubl. data), and these three species were not more common in sun than in shade (Table 1).

Comparison with other work

We found a 40% reduction of coffee berry borer in shade coffee, and a 58% reduction in sun. Other experiments have shown significant effects of birds on large (>5 mm) arthropods (Greenberg *et al.*, 2000; Perfecto *et al.*, 2004; Philpott *et al.*, 2004; Borkhataria *et al.*, 2006), but effects on small insects have been less consistent. Effect sizes on small insects in other studies have ranged from 10 to 20% (Van Bael *et al.*, 2008), and no study except Kellermann *et al.* (2008) reported an effect of bird predation on coffee berry borer, which found a 60–70% reduction in the Blue Mountain highlands of Jamaica, though the overall infestation rate was much lower there than in this study.

These results coupled with those of Kellermann *et al.* (2008) document significant ecosystem and economic services provided by birds to coffee farms at both high (>1000 m) and middle (~300 m) elevations in Jamaica. This may provide a powerful incentive for bird conservation locally, and future research should seek to establish if these effects are widespread elsewhere in the Caribbean and other coffee-growing regions. However, despite strong associations of birds with shade trees, neither this project nor Kellermann *et al.* (2008) could confirm that reduction of berry borer by birds increased with increasing shade cover. Thus, while our results provide an incentive for bird conservation in coffee farms in general, they did not reveal clear evidence that pest reduction services are more pronounced with shade on small farms in heterogeneous landscapes. Future work should explore the influence of surrounding habitats on bird consumption of insects, possible prey-switching behaviors as pests become increasingly scarce and the influence of trophic interactions involving non-avian natural enemies of insect pests in coffee.

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References

Baker, P.S., Jackson, J.A.F. & Murphy, S.T. (2002). *Natural enemies, natural allies*. California: The Commodities Press.

Barrera, J.F., Moore, D., Abraham, Y.J., Murphy, S.T. & Prior, C. (1990). Biological control of the coffee berry borer, *Hypothenemus hampei*, in Mexico and possibilities for further action. *Proceedings of the Brighton crop protection conference, pests and diseases – 1990*. Vol. 1: 391–396. British Crop Protection Council (Ed.). Farnham, Surrey: British Crop Protection Council.

Batchelor, T.P., Hardy, I.C.W., Berrera, J.F. & Pérez-Lachaud, G. (2005). Insect gladiators II: competitive interactions within and between bethylid parasitoid species of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Biol. Control* **33**, 194–202.

Beer, J., Muschler, R., Kaas, D. & Somarriba, E. (1998). Shade management in coffee and cacao plantations. *Agrofor. Syst*. **38**, 139–164.

Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S. (2000). *Bird census techniques*. 2nd edn. Massachusetts: Academic Press.

Borkhataria, R.R., Collazo, J.A. & Groom, M.J. (2006). Additive effects of vertebrate predators on insects in a Puerto Rican coffee plantation. *Ecol. Appl*. **16**, 696–703.

Cloclet da Silva, F., Ventura, M.I. & Morales, L. (2006). Capture of *Hypothenemus hampei* Ferrari (Coleoptera, Scolytidae) in response to trap characteristics. *Sci. Agric*. **63**, 567–571.

Cruz-Angon, A. & Greenberg, R. (2005). Are epiphytes important for birds in coffee plantations? An experimental assessment. *J. Appl. Ecol*. **42**, 150–159.

Daily, G.C. (Ed.). (1997). *Nature's services*. Washington: Island Press.

Damon, A. (2000). A review of the biology and control of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Bull. Entomol. Res*. **90**, 453–465.

Donald, P.F. (2004). Biodiversity impacts of some agricultural commodity production systems. *Conserv. Biol*. **18**, 17–37.

Dufour, B.P., Gonzáles, M.O., Maurico, J.J., Chávez, B.A. & Ramírez, R. (2004). International Science Colloquium on Coffee: the Association Scientifique Internationale pour le Café. *Proceedings of the 20th colloquium of the Association for Science and Information on Coffee (ASIC)*, Bangalore, India.

Gatzweiler, F.W. (2006). Organizing a public ecosystem service economy for sustaining biodiversity. *Ecol. Econ*. **59**, 296–304.

Genoways, H.H., Baker, R.J., Bickham, J.W. & Phillips, C.J. (2005). *Bats of Jamaica*. Special Publications of the Museum of Texas Tech University, 48.

Gobbi, J.A. (2000). Is biodiversity-friendly coffee financially viable? An analysis of five different coffee production systems in western El Salvador. *Ecol. Econ*. **33**, 267–281.

Greenberg, R., Bichier, P., Angon, A.C., MacVean, C., Perez, R. & Cano, E. (2000). The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. *Ecology* **81**, 1750–1755.

Greenberg, R., Bichier, P., Angon, A.C. & Reitsma, R. (1997). Bird populations in shade and sun coffee plantations in central Guatemala. *Conserv. Biol*. **11**, 448–459.

Hudson, R.H., Tucker, R.K. & Haegele, M.A. (1972). Effect of age on sensitivity: acute oral toxicity of 14 pesticides to mallard ducks of several ages. *Toxicol. Appl. Pharmacol*. **22**, 556–561.

Jaramillo, J., Bustillo, A.E., Montoya, E.C. & Borgemeister, C. (2005). Biological control of coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae) by *Phymastichus coffea* (Hymenoptera: Eulophidae) in Colombia. *Bull. Entomol. Res*. **95**, 467–472.

Johnson, M.D., Levy, N.J., Kellermann, J.L. & Robinson, D.E. (2009). Effects of shade and bird predation on arthropods and leaf damage on coffee farms in Jamaica's Blue Mountains. *Agrofor. Syst*., **76**, 139–148.

Johnson, M.D., Sherry, T.W., Holmes, R.T. & Marra, P.P. (2006). Measuring habitat quality for a migratory songbird wintering in natural and agricultural areas. *Conserv. Biol*. **20**, 1433–1444.

Johnson, M.D., Sherry, T.W., Strong, A.M. & Medori, A. (2005). Migrants in Neotropical bird communities: an assessment of the breeding currency hypothesis. *J. Anim. Ecol*. **74**, 333–341.

Kellermann, J.L., Johnson, M.D., Stercho, A.M. & Hackett, S.L. (2008). Ecological and economic services provided by birds on Jamaican Blue Mountain coffee farms. *Conserv. Biol*. **22**, 1177–1185.

Lack, D. (1976). *Island biology, illustrated by the landbirds of Jamaica*. Berkeley: University of California Press.

Moguel, P. & Toledo, V.M. (1999). Biodiversity conservation in traditional coffee systems of Mexico. *Conserv. Biol*. **13**, 11–21.

O'Brien, T.G. & Kinnaird, M.F. (2003). Caffeine and conservation. *Science* **300**, 587.

Pacala, S. & Roughgarden, J. (1984). Control of arthropod abundance by *Anolis* lizards on St. Eustatius (Neth. Antilles). *Oecologia* **64**, 160–162.

Perfecto, I., Mas, A., Dietsch, T. & Vandermeer, J. (2003). Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. *Biodivers. Conserv*. **12**, 1239–1252.

Perfecto, I., Vandermeer, J.H., López, G., Ibarra-Nuñez, G., Greenberg, R., Bichier, P. & Langridge, S. (2004). Greater predation of insect pests in a diverse agroecosystem: the role of resident neotropical birds in shade coffee farms. *Ecology* **85**, 2677–2681.

Perfecto, I., Vandermeer, J.H., Mas, A. & Soto Pinto, L. (2005). Biodiversity, yield, and shade coffee certification. *Ecol. Econ*. **54**, 435–446.

Perfecto, I.P., Rice, R.A., Greenberg, R. & Van Der Voort, M.E. 1996. Shade coffee: a disappearing refuge for biodiversity. *BioScience* **46**, 598–608.

Philpott, S.M., Arendt, W.J., Armbrecht, I., Bichier, P., Diestch, T.V., Gordon, C., Greenberg, R., Perfecto, I., Reynoso-Santos, R., Soto-Pinto, L., Tejeda-Cruz, C., Williams-Linera, G., Valenzuela, J. & Zolotoff, J.M. (2008).

Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees. *Conserv. Biol.* **22**, 1093–1105.

Philpott, S.M., Greenberg, R., Bichier, P. & Perfecto, I. (2004). Impacts of major predators on tropical agroforest arthropods: comparisons within and across taxa. *Oecologia* **140**, 140–149.

Rice, R.A. (1999). A place unbecoming: the coffee farm of Northern Latin America. *Geogr. Rev.* **89**, 554–579.

Stephens, D. & Krebs, J.R. (1986). *Foraging theory*. Princeton: Princeton University Press.

Stiling, P. (1999). *Ecology, theories and applications*. 3rd edn. Upper Saddle River: Prentice-Hall Inc.

Swift, M.J., Izac, A.-M.N. & van-Noordwijk, M. (2004). Biodiversity and ecosystem services in agricultural landscapes – are we asking the right questions? *Agric. Ecosyst. Environ.* **104**, 113–134.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.* **8**, 857–874.

Van Bael, S.A., Philpott, S.M., Greenberg, R., Bichier, P., Barber, N.A., Mooney, K.A. & Gruner, D.S. (2008). Birds as predators in tropical agroforestry systems. *Ecology* **89**, 928–934.

Vandermeer, J.H. (Ed.). (2003). *Tropical agroecosystems*. Boca Raton: CRC Press.

Williams-Guillén, K., Perfecto, I. & Vandermeer, J. (2008). Bats limit insects in a tropical agroforestry system. *Science* **320**, 70.