Contributed Paper

Ecological and Economic Services Provided by Birds on Jamaican Blue Mountain Coffee Farms

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Abstract: *Coffee farms can support significant biodiversity, yet intensification of farming practices is degrading agricultural habitats and compromising ecosystem services such as biological pest control. The coffee berry borer (*Hypothenemus hampei*) is the world's primary coffee pest. Researchers have demonstrated that birds reduce insect abundance on coffee farms but have not documented avian control of the berry borer or quantified avian benefits to crop yield or farm income. We conducted a bird-exclosure experiment on coffee farms in the Blue Mountains, Jamaica, to measure avian pest control of berry borers, identify potential predator species, associate predator abundance and borer reductions with vegetation complexity, and quantify resulting increases in coffee yield. Coffee plants excluded from foraging birds had significantly higher borer infestation, more borer broods, and greater berry damage than control plants. We identified 17 potential predator species (73% were wintering Neotropical migrants), and 3 primary species composed 67% of migrant detections. Average relative bird abundance and diversity and relative resident predator abundance increased with greater shade-tree cover. Although migrant predators overall did not respond to vegetation complexity variables, the 3 primary species increased with proximity to noncoffee habitat patches. Lower infestation on control plants was correlated with higher total bird abundance, but not with predator abundance or vegetation complexity. Infestation of fruit was 1–14% lower on control plants, resulting in a greater quantity of saleable fruits that had a market value of US$44–$105/ha in 2005/2006. Landscape heterogeneity in this region may allow mobile predators to provide pest control broadly, despite localized farming intensities. These results provide the first evidence that birds control coffee berry borers and thus increase coffee yield and farm income, a potentially important conservation incentive for producers.*

Keywords: coffee berry borer, coffee farms, ecosystem services, *Hypothenemus hampei*, Jamaican coffee, pest control

Servicios Ecológicos y Económicos Proporcionados por Aves en Fincas Cafetaleras en Blue Mountains, Jamaica

Resumen: *Las fincas cafetaleras pueden soportar biodiversidad significativa. Sin embargo, la intensificación de las prácticas agrícolas está degradando los hábitats naturales y comprometiendo los servicios del ecosistema tal como el control biológico de plagas. El barrenador del café (*Hypothenemus hampei*) es la principal plaga del café a nivel mundial. Los investigadores han demostrado que las aves reducen la abundancia de insectos en las fincas cafetaleras pero no han documentado el control de aves sobre el barrenador del café ni cuantificado los beneficios de las aves a la producción o al ingreso de la finca. Realizamos un experimento de exclusión de aves en fincas cafetaleras en las Blue Mountains, Jamaica, para medir el control de barrenadores del café, identificar especies potencialmente depredadoras, asociar la abundancia de depredadores y la reducción de barrenadores con la complejidad vegetal y cuantificar los incrementos en la producción de café. Las plantas de café excluidas del forrajeo de aves tuvieron significativamente mayor infestación y reproducción de barrenadores, mayor daño de frutos que las plantas control. Identificamos 17 especies potencialmente depredadoras (73% fueron especies migratorias neotropicales), y 3 especies primarias*

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comprendieron 67% de las detecciones de migratorias. La abundancia relativa promedio y la diversidad de aves en relación con la abundancia de depredadores residentes incrementaron con la cobertura de árboles de sombra. Aunque los depredadores migratorios no respondieron en general a las variables de complejidad de la vegetación, las 3 especies primarias incrementaron con la proximidad a los fragmentos de hábitat no cafetalero. La menor infestación en plantas control se correlacionó con la mayor abundancia total de aves, pero no con la abundancia de depredadores o la complejidad de la vegetación. La infestación de frutos fue 1–14% menor en las plantas control, lo que resulta en una mayor cantidad de frutos que tuvieron un valor de mercado de US$44–105/ha en 2005/2006. La heterogeneidad del paisaje en esta región puede permitir que los depredadores controlen plagas, no obstante intensidades agrícolas localizadas. Estos resultados aportan la primera evidencia del control de barrenadores por aves y el consiguiente incremento en la producción y el ingreso económico, un incentivo de conservación potencialmente importante para los productores.

Palabras Clave: barrenador del café, café Jamaiquino, control de plagas, fincas cafetaleras, *Hypothenemus hampei*, servicios del ecosistema

Introduction

A vast and expanding percentage of terrestrial habitats are altered for human settlement and commodity production. Effective biodiversity conservation must include the array of matrix components that compose fragmented landscapes (Pimentel et al. 1992; Ricketts 2001). Complex agricultural ecosystems in particular can support significant species richness (Daily 1997; Altieri 1999), but many of these systems are threatened by modern agricultural practices. Recognition of specific ecosystem processes and components present in traditional, biologically diverse agroecosystems that enable and sustain production of economically important goods could provide effective conservation incentives (Farber et al. 2006), especially in developing tropical countries (Gatzweiler 2006).

Coffee (*Coffea arabica* and *C. robusta*) is the second-most traded global commodity by developing nations after oil (Rice 1999). With global production based in the tropics, coffee farms are important components of biogeographically diverse regions (Perfecto et al. 1996; Moguel & Toledo 1999) and strategic targets for conservation. If properly managed, structurally and biologically complex coffee farms can provide habitat for a variety of taxa (e.g., Perfecto et al. 1996; Greenberg et al. 1997; Mas & Dietsch et al. 2004). In the 1970s, coffee varieties that thrive in direct sun were developed to increase production (Dietsch et al. 2004). The subsequent intensification of coffee cultivation has resulted in ecological simplification, which directly compromises biodiversity and its associated ecosystem services (Perfecto et al. 1996; Naylor & Ehrlich 1997; Perfecto & Vandermeer 2002), including the integrity and viability of natural biological pest control through the loss of predator species (Tscharntke et al. 2005).

The world's predominant coffee pest is the coffee berry borer (*Hypothenemus hampei* [*Coleoptera: Scolytidae*]), whose entire life cycle occurs inside coffee berries (Damon 2000; Chavez & Riley 2001). Gravid females bore galleries into the fruit's endosperm, where they lay their eggs and broods develop over 28–34 days (Damon 2000). At maturity females mate exclusively with their flightless male siblings, emerge gravid from the fruit in 23–28 days, and immediately seek a new coffee berry for oviposition (Brun et al. 1995). All infested fruits are separated and discarded after harvest. Therefore, the rate of berry infestation directly affects saleable crop yields and farmer income.

A variety of biological controls for berry borers have been examined (e.g., parasitoid wasps; Chavez & Riley 2001), but they have not achieved widespread implementation and economic success (Batchelor et al. 2005). Birds effectively control agricultural insect pests in temperate regions (Tremblay et al. 2001; Mols & Visser 2002); reduce arthropods of several taxonomic groups in Guatemalan (Greenberg et al. 2000), Mexican (Philpott et al. 2004), and Puerto Rican coffee farms (Borkhataria et al. 2006); and suppress simulated outbreaks of lepidopteran caterpillars in Mexican coffee farms (Perfecto et al. 2004). Nevertheless, no one has yet provided direct evidence of reduction of borers by birds or that these effects benefit crop production or farm income. Linking increases of saleable coffee berries with reductions in borers by insectivorous birds could provide a strong economic incentive to coffee farmers to promote vegetation complexity because birds and their services increase with vegetation complexity in coffee farms (Wunderle & Latta 1998; Greenberg et al. 2000; Perfecto et al. 2004).

We conducted a bird-exclosure experiment on coffee farms in the Blue Mountains of Jamaica, West Indies, to examine the ecological and economic pest-control services provided by birds. Our goals were to (1) measure reductions by birds of borer infestation, borer broods, and coffee-berry damage, (2) identify potential avian predator species of borers and determine whether their abundances increase with vegetation complexity, (3) determine whether greater pest reductions are associated with greater bird abundance and vegetation complexity, and

(4) quantify the economic value of any observed pest reductions due to birds by calculating increases in saleable coffee berries.

Methods

Study Sites

The island of Jamaica has approximately 10,000 ha in coffee cultivation (Robinson & Mansingh 1999). The coffee berry borer was inadvertently introduced to Jamaica in 1978 (Robinson & Mansingh 1999).

We selected 4 farms in the Blue Mountains within a 10-km^2 area: Clifton Mount (34 ha of coffee), Wallenford (22 ha), McGraham (6 ha), and Rowan's Royale (0.6 ha). All farms bordered the Blue and John Crow Mountains National Park, represented a range of vegetation complexity and agricultural intensification, had *C. arabica* var. *tipica* growing, and had owners willing to participate in the project for at least 1 year. In this region fruit emerges and ripens from late September through early May. Annual harvests are from January to May, with most fruit collected between late February and early April. Annual organochloride pesticides (endosulphan) were applied to Clifton Mount, Wallenford, and McGraham 4 months prior to the commencement of our study (typically 0.4 L of active ingredient/ha) and were not applied again until after project completion. Rowan's Royale is a certified organic farm and was not sprayed.

Bird Exclosures

To measure reductions of coffee berry borer infestation, brood abundance, and berry damage by birds on individual coffee plants, we randomly selected pairs of coffee plants stratified across the 4 farms ($n = 30$). The entire production area of each property was represented. The experimental plant of each pair received a bird-proof exclosure, whereas the other plant remained accessible to foraging birds and served as a control. We selected experimental coffee plants by mapping each farm's borders with a geographic positioning system (GPS, Garmin, Olathe, Kansas) and generating random points throughout the farm that were at least 10 m apart and 10 m from the farm edge with ArcView 3.3 (ESRI, Redland, California). The plant nearest the random point that was 1.5–2.5 m tall and flowering or bearing fruit was selected as the experimental plant and received the bird exclosure. The nearest plant within 1–5 m of but not touching the experimental plant that was visually determined to be similar in form and production to the experimental plant was selected as the control plant. Exclosures on Wallenford ($n = 10$) and Rowan's Royale ($n = 5$) were built in late November 2005; exclosures on Clifton Mount ($n = 10$) and McGraham ($n = 5$) were built in early January 2006. Our construction of exclosures coincided with commencement of fruit emergence and arrival of migratory birds.

Exclosures were pyramidal pole frames of cut saplings over individual coffee plants wrapped in transparent nylon gill netting (N163A 58 mm mesh, Nylon Net Company, Memphis, Tennessee) and staked down to prevent entry of ground-foraging birds. Our design is typical for other experiments in the tropics that have successfully prevented access by small birds without restricting access by aerial and sessile invertebrates (Greenberg et al. 2000; Perfecto et al. 2004; Borkhataria et al. 2006) or by *Anolis* lizards common on Jamaica and other Caribbean islands (Pacala & Roughgarden 1984; Borkhataria et al. 2006).

Coffee Berry Borer Surveys

To determine borer infestation levels on each plant, we inspected 100 berries per plant and recorded the proportion of infested berries. Berries were chosen systematically from available fruit of all levels of ripeness across the plant. We inspected berries for borer entry holes exclusively positioned at the top of the ovary. We measured initial borer infestation levels during exclosure construction and made repeated measurements in the first week of every month, January through May 2006. We report survey time as the number of months since exclosure deployment. Proportions of borer infestation were arcsine-root transformed to meet normality assumptions.

We harvested all ripe berries from exclosure and control plants each month. To determine borer brood presence and extent of berry damage, we dissected all harvested berries infested with borers. We used the depth of borer penetration into the berry (point of entry to the most distal bored area in millimeters) as a measure of berry damage. We recorded the presence or absence of a brood at any life cycle stage. Depth of penetration was natural log transformed for analysis.

Bird Surveys

We performed 20-min area searches (Bibby et al. 2000) within 400-m^2 plots ($n = 30$) centered on each exclosure to quantify relative bird abundance and diversity and identify bird species potentially responsible for observed differences in borer infestation. We alternated periods of slow walking and standing. We recorded each bird within the plot, whether it made a foraging attack within 1 min of detection (Remsen & Robinson 1990), and the vertical vegetation layer it occupied (tree, coffee, ground) during the first attack (if any). More than one individual of a species were only recorded if viewed simultaneously or discernable by sex or age. Birds flying over were not recorded. We surveyed each plot monthly from February through May between sunrise and 10:00 the morning before borer surveys.

Bird species that we observed foraging within coffee shrubs on one or more occasions and that ingest tiny invertebrates (≤3 mm, Lack 1976) were considered potential borer predators. We calculated the average total number of birds, bird species, and borer predators per plot as response variables, which were square-root transformed to meet normality assumptions.

Vegetation Complexity

Within the 400-m^2 bird plots, we measured percent shade cover, number of coffee plants (≥1 m), number of banana plants (≥1 m), and number, average height, and average diameter at breast height (dbh) of shade trees. We used a densiometer (Forestry Suppliers, Jackson, Mississippi) to measure shade cover of each plot. We took 1 reading at the north side of the exclosure and 1 at each cardinal direction 5 m from the exclosure and averaged them. We used GIS to determine elevation of each exclosure.

To further assess vegetation complexity, we visually estimated the linear distance from each plant pair ($n = 30$) to the nearest tree, habitat patch, and farm edge vegetation within a 90° arc centered on each cardinal bearing. We defined a tree as any woody, noncoffee plant >5 m tall, and a habitat patch as an area ≥10 m^2 of woody noncoffee vegetation with elements >5 m tall, both of which birds can use as "stepping stones" to move through highly disturbed areas (Wunderle 1999). We created 6 variables for each plant pair: the single nearest distance to each vegetation component (nearest tree, patch, edge) and the average distance to each component across all 4 directions (average tree, patch, edge). Nearest tree, patch, and edge were square-root transformed and average distance to tree was natural-log transformed to meet normality assumptions. Average patch and edge did not require transformations.

Ecological Analyses

To determine the effect of birds on coffee berry borer infestation over time, we used repeated measures analysis of variance. The model included farm and treatment as between-factor variables, survey period as a within-factor variable, and the 2-way and 3-way interactions. We used Tukey–Kramer tests for group comparisons.

We used chi-square analysis to compare the number of infested berries with borer broods from exclosure and control plants. To examine berry damage, we analyzed the difference in depth of borer penetration between infested berries from exclosure and control plants with 1-tailed t tests.

To avoid including collinear variables in regression models (Legendre & Legendre 1998), we entered all 4 dependent bird variables, the difference between control and exclosure plants in number of berries infested by borers (Δ_{CBB}), and all 12 independent vegetation complexity variables into a Spearman's rank correlation matrix (Greaves et al. 2006). We first chose the variable with the highest Spearman's rank correlation coefficient for all dependent variables and then eliminated all independent variables that were collinear ($r > 0.60$) with the selected variable (Beck & George 2000). We repeated this process with the remaining independent variables until we established a subset, which was then entered into a forward-stepwise regression ($\alpha = 0.15$ to enter; Anderson et al. 2000). We used linear regression to relate the final vegetation complexity variables with each dependent variable. All analyses were run in SPSS 13.0 (2005).

Economic Analysis

We interviewed farm managers to determine the number of hectares in coffee production, per-hectare yield, and price received per unit volume for each farm. To estimate the economic value of bird predation to coffee farmers, we first quantified each farm's average increase in saleable berries resulting from reductions in borer infestation (Δ_{CBB}) by subtracting the monthly borer infestation level of each control plant from its paired exclosure plant and taking the average of all surveys with a significant positive value. We translated this value into an economic benefit of birds to each farm for the 2005–2006 production season with the formula

$$\Delta_{CBB} \times \frac{\text{no.boxes}}{\text{ha}} \times \frac{\text{US\$}}{\text{box}} \times \text{ha},$$

where a box is a standard 27.2-kg unit of coffee berry harvest. We used 95% confidence intervals (CIs) for borer reduction to calculate the CIs for benefit of birds per hectare, per farm, and for the total study area.

Results

Coffee Berry Borer

Borer infestation differed significantly by farm ($F_{3,220} = 3.77, p = 0.01$). Rowan's Royale was higher than Clifton Mount and Wallenford. Exclosure plants had significantly higher borer infestation than controls ($F_{1,220} = 10.71, p = 0.001$; Fig. 1). There was no significant difference in average borer infestation across survey periods ($F_{4,220} = 0.25, p = 0.91$). There was a significant treatment-by-survey interaction ($F_{4,220} = 2.8, p = 0.026$), such that infestation rose in exclosures but declined on control plants during surveys 2 through 4 (Fig. 1). Farm-by-treatment ($F_{3,220} = 1.15, p = 0.32$), farm-by-survey ($F_{4,220} = 1.49, p = 0.12$), and the 3-way interactions ($F_{12,220} = 0.85, p = 0.6$) were not significant. Our sample size was reduced across the survey periods because coffee plants ended their fruiting cycle, no longer providing sufficient berries for surveys.

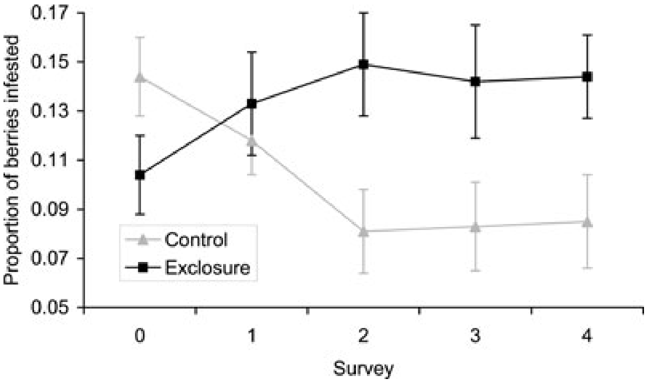

Figure 1. Mean (SE) proportion of coffee berries infested with coffee berry borers from bird-exclosure plants and control plants on 4 farms in Jamaica over 5 survey periods from November 2005 and May 2006. Our sample size was the number of control and exclosure shrub pairs, and it declined during the study because some experimental plants were completely harvested (survey 0, n = *30; 1,* n = *29; 2,* n = *28; 3,* n = *25; 4,* n = *20).*

We dissected 224 ripe coffee berries infested with borers. Berries from inside exclosures contained significantly more broods (38 of 111) than did control fruits (20 of 113; $\chi^2 = 8.63$, df = 1, $p = 0.003$), and they were bored deeper (mean [SE] = 5.48 mm [0.32]) than berries from control plants (3.87 mm [0.25]; $t = 3.76$, df = 222, $p < 0.001$). Depth of penetration remained significantly greater in exclosure berries ($n = 73$, mean = 3.68 mm [0.24]) than control berries ($n = 93$, mean = 2.94 mm [0.18]; $t = 2.22$, df = 164, $p = 0.014$) after removing the berries containing broods from analysis, which restricted the comparison to damage done by the adult and not brood activity.

Avian Predators

We made 354 total bird detections of 43 species across area search plots over 3 months. Of these, 195 detections included a foraging attack with 57% occurring in coffee shrubs, 33% in trees, 6% on the ground, and 4% in non-coffee shrubs. On average we detected 4 birds per plot (range = 0–15) and an average proportion of 47% (range = 0–100%) making a foraging attack.

Our initial cumulative list of species observed foraging in coffee during area searches included 23 species. On the basis of diet criteria (Lack 1976), we considered 17 of these species potential borer predators (Table 1). Eleven North American migrants represented over 73% of all predator detections (Table 1). We made ad hoc splits of predator groups for subsequent analyses. We separated migrant and resident species, which can exhibit different habitat associations in coffee and forest systems (Wunderle 1999). We also grouped the 3 most common migrants together as primary predators: Black-throated Blue Warbler (*Dendroica caerulescens*), American Redstart (*Setophaga ruticilla*), and Prairie Warbler (*D. discolor*). Primary predators composed 67% of all migrant detections and nearly 50% of all predator detections (Table 1). These 3 warblers are common throughout the

Table 1. Bird species identified as potential coffee berry borer predators and the average percent shade and distance to nearest habitat patch for each species on 4 coffee farms in the Blue Mountains, Jamaica.

Species	*Scientific name*	*Status*[a]	*Total predator detections*	*Shade-tree cover (%)*[b]	*Nearest habitat patch (m)*[b]
Black-throated Blue Warbler	*Dendroica caerulescens*	M	43	31	17
American Redstart	*Setophaga ruticilla*	M	24	23	21
Prairie Warbler	*D. discolor*	M	22	18	29
Arrowhead Warbler	*D. pharetra*	E	14	51	11
Jamaican Tody	*Todus todus*	E	11	32	17
Common Yellowthroat	*Geothylpis trichas*	M	10	31	15
Yellow-rumped Warbler	*D. coronata*	M	10	7	18
Banaquit	*Coereba flaveola*	R	9	36	15
Ovenbird	*Seiurus aurocapillus*	M	8	35	12
Palm Warbler	*D. palmarum*	M	8	9	29
Black-whiskered Vireo	*Vireo altiloquus*	B	7	60	9
Jamaican Vireo	*V. modestus*	E	5	68	10
Black-and-white Warbler	*Mniotilta varia*	M	4	75	3
Blue Mountain Vireo	*V. osburni*	E	2	56	35
Northern Parula	*Parula americana*	M	2	0	46
Swainson's Warbler	*Limnothlypis swainsonii*	M	1	31	60
Tennessee Warbler	*Vermivora peregrina*	M	1	31	60

[a]*Abbreviations: M, wintering migrant; B, breeding migrant; E, endemic resident, R, resident.*
[b]*The average across all detections of the species of measured vegetation values on the 400-m^2 plots in which each detection occurred.*

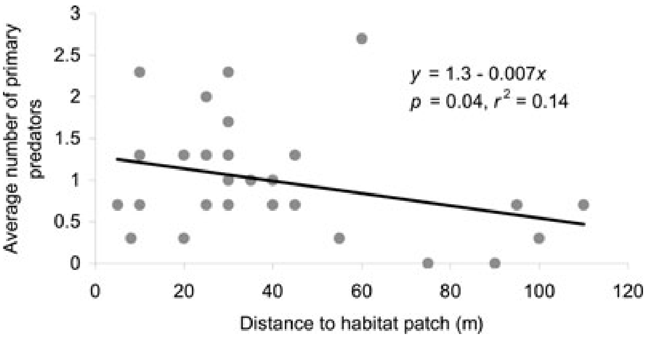

Figure 2. Distance from center of 400-m² survey plots to nearest habitat patch and the average number of detections of primary predators from February to April 2006 on coffee farms in the Blue Mountains, Jamaica.

Greater Antilles, where they co-occur in an array of habitats (Holmes et al. 1989; Wunderle & Waide 1993; Latta & Faaborg 2001).

Vegetation Complexity

Initial variable selection resulted in a subset of 5 vegetation variables for inclusion in subsequent multivariate analyses; percent shade, number of coffee shrubs, number of banana trees, distance to nearest habitat patch, and average distance to farm edge. Average number of total birds ($r^2 = 0.37$, $F_{1,28} = 16.62$, $p < 0.001$), total species ($r^2 = 0.42$, $F_{1,28} = 20.1$, $p < 0.0001$), and resident predators ($r^2 = 0.35$, $F_{1,28} = 14.9$, $p < 0.001$) increased significantly with increasing percent shade. Migrant predators were not significantly associated with any vegetation variables. In contrast, primary predators decreased with increasing distance to the nearest habitat patch ($r^2 = 0.14$, $F_{1,28} = 4.61$, $p = 0.04$; Fig. 2).

Average borer reduction (Δ_{CBB}) for experimental plant pairs across surveys 2 through 4 (Fig. 1) was not significantly associated with any measures of vegetation complexity included in the variable subset or with elevation ($r^2 = 0.04$, $F_{1,27} = 1.02$, $p = 0.3$), which ranged from 864 to 1316 m. Average borer infestation showed a significant positive correlation with average total bird species ($r^2 = 0.25$, $F_{1,28} = 9.21$, $p = 0.005$) and average total birds ($r^2 = 0.21$, $F_{1,28} = 7.31$, $p = 0.01$), but was not correlated with resident, migrant, or primary predators.

Economic Value

Control plants had 1–14% fewer fruits infested with borers than exclosure plants. All 4 farms received the same standard regional price in the 2005–2006 season of US$48/box of coffee berries. The value of pest-control services of birds to farmers ranged from US$44 to US$105/ha (Table 2). Summed across our entire 62.6-ha study area, the total economic value of increased coffee crop yield due to bird predation was US$4018 (95% CI $2805).

Discussion

Ecosystem Services Provided by Birds

Birds supplied ecologically and economically valuable services to Blue Mountain Coffee farmers in Jamaica, providing the first evidence that birds can directly benefit coffee yield and farm income via pest control. In this experiment, avian predators reduced adult borer infestation, number of borer broods, and extent of berry damage. These services likely result from avian predation of adult female borers as they search for an oviposition site or bore into the endosperm, which can take up to 8 h (Damon 2000; J.K., personal observation). During much of that time, borers may be reliable and easily detectable prey for insectivorous birds that consume small arthropods.

We assert that the pest-control services detected in this experiment were due to bird predation and were not attributable to other factors. Although we were unable to directly observe birds preying on berry borers, samples of stomach contents obtained from Black-throated Blue Warblers, American Redstarts, and Prairie Warblers at Baron Hall coffee farm in Jamaica contained 53, 56, and 44% coffee berry borers, respectively (M. Johnson & T. Sherry, unpublished data). Data for other species are not available. We did not collect samples of stomach contents because the emetic used to procure the sample may cause death in some birds (Johnson et al. 2002).

Although we did not quantify the presence of herpetofauna on experimental plants or their impact on borer infestation, monofilament nets do not exclude lizards (Pacala & Roughgarden 1984; Borkhataria et al. 2006), and we commonly observed *Anolis* lizards on exclosure

Table 2. Economic benefit of birds per hectare calculated for 4 Jamaican Blue Mountain coffee farms during the 2005–2006 production year.

Farm	*Average berry borer reduction* (Δ_{CBB})	*Boxes/ ha*	*US$/box*	*Mature coffee* (ha)	*US$ benefit of birds/ha* (95% CI)	*US$ benefit of birds/farm* (95% CI)
Rowan's Royale	0.026 (0.020)	82	48	0.6	102 (79)	62 (48)
Clifton Mount	0.012 (0.006)	77	48	34	44 (24)	1440 (775)
McGraham	0.013 (0.012)	85	48	6	53 (37)	171 (119)
Wallenford	0.024 (0.019)	91	48	22	105 (84)	2344 (1863)

and control plants throughout the study period and farms. Invertebrate samples from all 30 exclosures contained taxa ranging in size from 1 mm (e.g., Formicidae) to >5 cm (e.g., Orthoptera, M.J. & J.K., unpublished data) in length, which is consistent with other exclosure studies (Greenberg et al. 2000; Borkhataria et al. 2006). Therefore, it is unlikely that 3-mm parasitoid wasps that attack berry borer (Damon 2000) and hymenopteran pollinators that can affect the fruit set of coffee (Ricketts et al. 2004) were restricted by 58-mm mesh. Temperature and relative humidity recorded by data loggers (HOBO Pro v2, Bourne, Massachusetts) were nearly identical for exclosure and control plants, regardless of weather conditions (M.J. & J.K., unpublished data).

The decline of borer infestation on control plants over the first 2 months of the study coincides with the arrival of Neotropical migrants from North America, which nearly double Jamaica's summer population (Lack 1976). In the Blue Mountains, the coffee production season (September–May) and the harvest period (February–April) occur completely within the time migratory birds are present (September–May, Downer et al. 1990). Migrants constituted more than 60% of all birds detected on our survey plots. Despite the prevalence of wintering migrants, resident species may also provide significant pest control. Arrowhead Warblers and Jamaican Todies composed 14% of total predators and nearly 60% of resident predators detected (Table 1). Average abundance of resident predators and average bird abundance and diversity increased significantly with shade cover (Table 1).

Farms with greater vegetation heterogeneity and thus greater functional diversity of avian predator species could exhibit stronger resilience of services after disturbances such as hurricanes through "insurance" species (Loreau et al. 2003; Tscharntke et al. 2005). Avian ecosystem services may be particularly vulnerable to intensive habitat degradation and fragmentation due to the high trophic level of birds (Dobson et al. 2006) and the sensitivity of avian insectivores (Şekercioğlu et al. 2002) and Neotropical migratory species to population decline (Maurer & Haywood 1993). Research on winter territory size, habitat associations, and the movement of predator species among farms and bordering habitats is needed to better understand the relationship between landscape complexity, habitat simplification, and the provision of pest control services.

The difference in borer infestation between farms may reflect differential pesticide use. Rowan's Royale, the only certified organic coffee farm in Jamaica (D. Robinson, personal communication), had significantly higher infestation inside exclosures (mean = 0.185) than all other farms combined (mean = 0.123, $F_{1,128} = 7.29$, $p < 0.01$). Nevertheless, infestation of control plants where birds were foraging was equivalent on Rowan's Royale (mean = 0.118) and nonorganic farms (mean = 0.101, $F_{1,128} = 0.68$, $p < 0.41$), suggesting that the economic value of birds may be partly dependent on borer prevalence. Pesticides, applied 4 months before our data collection, may initially have reduced borer infestation, but bird predation appears to reduce or maintain levels at around 10% on both organic and conventional farms throughout the remainder of the season. Because of higher ambient infestation on the organic farm, more borers were removed to reach these levels. Interestingly, inbreeding by borers may foster rapid genetic resistance to Endosulphan (Brun et al. 1995), a pesticide used in the Blue Mountains since 1978 (Robinson & Mansingh 1999).

Temperature and humidity also influence borer abundance (Damon 2000). The relatively small reductions (1–14%) in berry borers on experimental plants may have reflected the cool, wet conditions typical of Blue Mountain farms (D. Robinson, personal communication). During preliminary experiments, we found reductions of 11–38% 1 month after the exclusion of birds under hotter and drier conditions of a lower-elevation farm (625 m, J.K., unpublished data). Additional experimental research on avian pest control of borers should be conducted across a range of biogeographic regions and alongside other pest-control methods to better inform integrated pest management and conservation strategies.

Mobile Predators and Landscape Heterogeneity

If birds reduce borers and increase with shade-cover, why did we not find corresponding reductions of borers with shade? Mobile agents such as birds can provide ecosystem services to areas beyond their primary habitats (Kremen 2007). In particular, migratory warblers, which composed 73% of all predator detections, use a variety of habitats with varying disturbance regimes (e.g., Confer & Holmes 1995; Johnson & Sherry 2001; Johnson et al. 2006). Detections of the 3 primary predator species declined steeply on plots further than 40–50 m from habitat patches (Fig. 2). Although our exclosures were randomly placed throughout each farm's entire cultivated area, their small sizes (0.6–34 ha), irregular borders, and abundance of internal habitat patches caused most plots to be relatively close to patches of noncoffee habitat (mean = 40 m, range = 5–110 m), distances easily traversed by foraging birds. These factors and the diversity of neighboring land parcels may dilute negative effects of intense agricultural practices by facilitating movements of certain bird species among habitat patches (Altieri 1999). The matrix of the Blue Mountains likely provides sufficient habitat in the form of forest fragments, riparian strips, and rural gardens for primary predators to exploit interspersed patches of intensive sun coffee and possibly to include them in their winter home ranges (Wunderle & Latta 1998; Latta & Faaborg 2001). Although intensively managed areas are currently benefiting from local landscape diversity, continued degradation could lead to regional deterioration of ecosystem services (Şekercioğlu et al.

2004). Further research in regions with geographically extensive agricultural intensification is urgently needed to determine at what level these ecosystem services may become significantly reduced or eliminated.

In our assessment of vegetation complexity, we did not consider species composition or diversity, which are significant factors in avian presence and use of coffee farms (Perfecto et al. 2004). The farms in our study region mostly used native tree species for shade (e.g., Blue Mahoe [*Hibiscus elatus*] and Dovewood [*Alchornea latifolia*]) mixed with some non-native species, including Caribbean pine (*Pinus caribbea*) and mango (*Mangifera* spp.). To optimize the attractiveness of farms to beneficial birds, species composition of the planned and unplanned crop and noncrop biodiversity should be considered (Perfecto & Vandermeer 2002).

Economic Value

The difference in the proportion of berries infested by borers between exclosure and control plants yielded an average benefit of US$75/ha (Table 2). The economic significance of avian services becomes more apparent when one considers Jamaica's per capita gross national income (GNI) of US$3400 in 2005 (World Bank 2006). Pest control services were equivalent to 2–69% of the per capita GNI for the lowest to highest production farms, respectively (Table 2).

These values represent the benefit to only 4 farms in the Blue Mountains of Jamaica, totaling US$4018 (118% of the per capita GNI) for the 2005–2006 season. We did not take into account other associated benefits of bird predation, such as reduced pesticide applications or the reduction of other pests. Economic benefits may be far greater on farms at lower elevations or in warmer, drier regions where borer abundances can be much higher. Furthermore, we quantified the value of increases in saleable beans to coffee producers only. The price of coffee increases as it is traded from producers to wholesalers and ultimately to retailers and consumers. The economic value of pest-control services should be considered at each market level. These substantial economic benefits depend on the natural capital of the region (Costanza et al. 1997), specifically, the heterogeneous habitats that sustain viable wintering populations of Neotropical migratory warblers and resident species of Jamaican avifauna that provide valuable ecosystem services.

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