QUANTIFYING PEST CONTROL SERVICES BY BIRDS AND ANTS

IN KENYAN COFFEE FARMS

By

Megan Milligan

A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science

In Natural Resources: Wildlife

Committee Membership

Dr. Matthew Johnson, Committee Chair

Dr. Mark Colwell, Committee Member

Dr. Tim Bean, Committee Member

Dr. Yvonne Everett, Graduate Coordinator

December 2014

ABSTRACT

QUANTIFYING PEST CONTROL SERVICES BY BIRDS AND ANTS IN KENYAN
COFFEE FARMS

Megan Milligan

Ecosystem services, such as pest control and pollination, are critical benefits of

biodiversity necessary for agricultural production. Predators, including insectivorous

birds and ants, can provide important biological controls in agroecosystems, boosting

crop yield and helping to offset the need for expensive inputs such as pesticides. With

agricultural demand projected to increase in the future, two broad management strategies,

termed land sparing and land sharing, have been proposed to conserve biodiversity while

still meeting increased agricultural demand. Understanding the related impacts of habitat

and landscape characteristics on the delivery of ecosystem services can better inform

managers seeking to promote these benefits of biodiversity. In order to better understand

these relationships, I conducted a sentinel pest experiment to investigate predation levels

in response to a novel pest on coffee farms in central Kenya. The frequency of predation

decreased significantly with increasing distance from adjacent forest fragments and was

correlated with bird species richness. Predation was also significantly higher on shade

compared to sun coffee farms. The mechanism through which the bird and ant

communities are effecting pest removal is less clear, but encouraging particular

preferential predators could positively influence pest control. In conclusion, a land

sharing approach, via both the integration of shade trees and the conservation of small

forest fragments within a farm, can support increased levels of pest control services provided by both birds and ants in Kenyan coffee farms.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

Society's dependence on ecosystem services and their importance, particularly with regards to agriculture, has gained increasing awareness (Daily 1997, Bianchi et al. 2006, Sekercioglu 2006, Van Bael et al. 2008, Jedlicka et al. 2011, Wenny et al. 2011, Tscharntke et al. 2012, Johnson and Hackett, under review). Ecosystem services are defined broadly as the benefits people obtain from ecosystems and are divided into four categories: cultural, provisioning, supporting, and regulating (MEA 2005). Regulating ecosystem services, such as water purification and pest control, are critical benefits of biodiversity that are essential to agricultural productivity.

One limiting factor in agriculture, particularly in the developing world, is the availability of expensive inputs, such as fertilizers and pesticides (Ndang'ang'a et al. 2013). By encouraging the provisioning of ecosystem services, including pest control, farmers could decrease their reliance on costly chemical inputs. Birds are highly mobile and, with over 50% of all species primarily insectivorous, are ideal providers of pest control services (Wenny et al. 2011). Birds have been shown to decrease insects in a variety of systems (Bock et al. 1992, Mols and Visser 2002, Kellermann et al. 2008, Jedlicka et al. 2011, Karp et al. 2013). Furthermore, studies have shown that birds not only reduce pest populations, but that plants respond with higher levels of productivity (Whelan et al. 2008, Mooney et al. 2010). In addition to birds, ants have been shown to reduce pest populations in agroecosystems (Way and Khoo 1992, Perfecto and Castiñeiras 1998, Vandermeer et al. 2002, Armbrecht and Perfecto 2003, Philpott and Armbrecht 2006) and, as they operate on a different spatial scale from birds (Armbrecht

and Perfecto 2003), could provide complementary pest control services.

The role of such ecosystem services will only become more important in the future: according to the United Nations' Food and Agriculture Organization, food demand is projected to increase by 70 percent worldwide between 2005 and 2050 (FAO 2009). This increase in demand is fueled both by a rising human population and a shift in preferences, with greater consumption of meat and dairy products, as well as luxury items, including coffee (Balmford et al. 2012). Meeting the rising food demand will require some combination of increased land conversion and intensified production. Both courses of action represent serious threats to biodiversity. Two divergent strategies to optimize agricultural production and conservation of biodiversity have emerged and generated a significant amount of debate: the so-called land sparing and land sharing strategies (Green et al. 2005). In land sparing systems, agricultural areas are managed intensively, creating the maximum agricultural yield from a minimal area, so that other areas can be "spared for nature" (Green et al. 2005). Land sharing, on the other hand, encourages biodiversity within each farm (Fischer et al. 2008). This might be achieved by including areas that are structurally similar to native vegetation or having high levels of heterogeneity within the farmed area or along the margins. These two strategies are often represented as opposite ends of a continuum of management practices (Fischer et al. 2008), but others argue that the effects of different land management schemes depend on their spatial extent (Tscharntke et al. 2005, Smith et al. 2010) and that a combined strategy integrating both land sparing and land sharing approaches may be the best option to achieve conservation objectives (Troupin and Carmel 2014). Encouraging wildlife that

provide ecosystem services, such as pest control, could actually elevate yield, so that reductions in intensity, either from incorporating heterogeneity within the farm or preserving other land for nature, would not result in a net loss to the farmer.

In order to promote beneficial ecosystem services such as pest control, it is necessary to understand the effects of different agricultural management strategies on biodiversity. Coffee is the most valuable tropical export crop in the world, with a value of approximately US $90 billion (Jaramillo et al. 2011). Management of coffee farms can therefore significantly influence biodiversity, because of the crop's high value and its cultivation in the tropics. Coffee has received attention in the debate of land sparing versus land sharing due to the range of available management practices both on the farm and at the landscape scale, which enables comparison of current management practices (Chandler et al. 2013). Shade coffee, or coffee grown under a tree canopy, is a widely promoted example of the land sharing strategy because it can support significant on-farm biodiversity (Tejeda-Cruz and Sutherland 2004). In contrast, monocultures of sun coffee, which have lower vegetation complexity, are typically characterized by lower on-farm biodiversity but higher crop yields. If this higher production can offset yield lost on land protected for biodiversity, then sun coffee paired with preserved forest fragments may constitute land sparing. Despite a strong pattern suggesting that shade coffee supports greater biodiversity than sun monocultures (Armbrecht and Perfecto 2003, Perfecto et al. 2003, Philpott et al. 2006, Philpott and Armbrecht 2006, Raman 2006, Kellermann et al. 2008, Philpott et al. 2008, Philpott et al. 2012), there is no clear consensus regarding the effects of land sharing versus land sparing management strategies on biodiversity, in part

because few studies have examined the differences explicitly (but see Phalan et al. 2011 and Chandler et al. 2013). In addition, surrounding habitats can play a role, with adjacent forest being found to exert a stronger influence on bird populations than farm attributes such as the presence of shade trees (Bátary et al. 2011).

Encouraging optimal land allocation for biodiversity can, in turn, benefit agriculture. The "insurance hypothesis" (McNaughton 1977, Tscharntke et al. 2005) holds that biodiversity stabilizes an ecosystem and buffers environmental disruptions, such as the expansion and irruption of agricultural pests in response to climate change. Coffee berry borer (*Hypothenemus hampei*), the most important biological coffee pest worldwide (Jaramillo et al. 2006), is projected to expand in both range and abundance due to warming temperatures in East Africa (Jaramillo et al. 2011). Therefore, it is vital to gain a better understanding of the provisioning of natural pest control services and important underlying influences.

Both bird and ant populations play a role in the provisioning of natural pest control services. There is strong evidence that bird population characteristics, such as diversity and composition, affect the provisioning of these services. Studies have shown that bird species richness (Perfecto et al. 2004, Van Bael et al. 2008), bird density (Perfecto et al. 2004), functional richness (Philpott et al. 2009), both species richness and predator abundance (Jedlicka et al. 2011), and the presence of migratory species (Van Bael et al. 2008) are all positively correlated with the top-down control of pests. Bird species richness and bird density are often intertwined, with diversity increasing with observed abundance (Perfecto et al. 2004). Consequently, the direct mechanism by which

diversity influences predation is often difficult to determine (Perfecto et al. 2004, Van Bael et al. 2008, Philpott et al. 2009). The influence of diversity could reflect i) the sampling effect, i.e., higher diversity increases the probability of a very efficient predator being present (Perfecto et al. 2004, Van Bael et al. 2008, Philpott et al. 2009); or ii) species complementarity, including either facilitation or niche differentiation (Philpott et al. 2009), representing the idea that a more diverse suite of predators will consume a greater variety of prey (Van Bael et al. 2008). Despite the suite of work in the Neotropics, very few studies have examined pest control services provided by birds in Africa (De Beenhouwer et al. 2013).

In addition to birds, ants have also been shown to be pest control agents in a variety of agroecosystems (Way and Khoo 1992, Perfecto and Castiñeiras 1998, Philpott and Armbrecht 2006), including coffee (Vandermeer et al. 2002, Armbrecht and Perfecto 2003), but their role in ecosystem functioning is less straightforward. In addition to their role as predators, many ant species cultivate scale insects (superfamily *Coccoidea*) that are common coffee pests (Vandermeer et al. 2002). However, the mutualistic relationship between ants and the scale insects also provides indirect benefits to the coffee plant by reducing populations of other arthropods (Perfecto and Vandermeer 2006). For example, many ant species have been shown to forage directly on coffee pests, including coffee berry borer (Armbrecht and Perfecto 2003, Armbrecht and Gallego 2007) and some species are small enough to penetrate the holes made by the borer (Armbrecht and Perfecto 2003), thus providing a form of control not possible from birds alone.

While the relationships between biodiversity and level of intensification, as well

as between bird and ant communities and pest control services are well documented (Vandermeer et al. 2002, Armbrecht and Perfecto 2003, Perfecto et al. 2004, Van Bael et al. 2008, Philpott et al. 2009, Jedlicka et al. 2011), only a few studies have examined the direct effects of farm and landscape variables on pest predation. In the few studies examining direct effects, pest control was positively associated with measures of vegetation complexity (Philpott and Armbrecht 2006, Armbrecht and Gallego 2007), had no relationship with measures of vegetation (Kellermann et al. 2008, Philpott et al. 2009) or was actually negatively correlated with vegetation complexity, potentially due to higher ambient levels of pests in sun coffee (Johnson et al. 2010). Coffee berry borer abundance did decrease with greater levels of forest cover on farms in Costa Rica (Karp et al. 2013) and a simulation model based on data from Jamaican coffee farms found that the presence of forest patches decreased coffee berry borer infestations, but only until up to a certain amount of forested area (Railsback and Johnson 2014). Thus, these patterns appear to vary regionally, and additional studies are needed to elucidate the relationships further. Many studies have examined the relationships between both bird and ant populations and management intensification in different agricultural systems in the Neotropics. However, almost no work has been conducted on these subjects in Africa, a major coffee-producing region (De Beenhouwer et al. 2013).

I investigated how pest removal was affected by habitat and landscape characteristics and predator populations by conducting a sentinel pest experiment in central Kenya. I compared the frequency of pest removal to landscape characteristics, farm vegetation complexity, and both bird and ant community parameters. Based on

previous work conducted in the Neotropics, I predicted that 1) total pest removal would be higher with closer proximity to forest fragments; 2) total pest removal would be higher in shade than sun coffee systems; 3) farms with higher bird abundance, overall species richness, and/or insectivore abundance would have higher levels of pest removal; and 4) ants would provide pest control services in addition to those provided by birds.

METHODS

Study System

I conducted this study in Nyeri County of Central Kenya (Figure 1), which covers

an area of 3,337 km^2 and has a population density of 208 people per km^2 (USAID

Kenya). Roughly 24.5% of the population lives in urban areas, with the majority of those

living in the county's largest city, also named Nyeri (USAID Kenya). Average annual

rainfall ranges from 500 mm to 1500 mm and average temperatures vary from 12°C to

27°C. The region has two internationally recognized Important Bird Areas, one of which,

Aberdares Mountains, is adjacent to the study area (Bennun and Njoroge 1999).

Nyeri County is centered in the fertile highlands of Kenya. The region is very

agriculturally productive and coffee and tea are both major cash crops. Coffee farms

range from large estates to small-scale plots, and cultivation practices include both sun

coffee and shade coffee. In this study area, farms were either sun coffee (0% canopy

cover) or shade monoculture as classified by Moguel and Toledo (1999). Shade coffee is

not very common in this region, and shade farms that existed had less canopy cover and

vegetative diversity than has been described for shade farms in the Neotropics (Moguel

and Toledo 1999). Overall, I monitored 21 sites for pest predation, including 11 sites in

sun coffee and 10 sites in shade coffee (Figure 2). A single site consisted of two transects

of pest presentation stations (see Sentinel Pest Experiment) and all sites were a minimum

of 250 m apart to preserve independence. The sole exception was two sites which were a

minimum of 75 m apart, but were judged to be independent based on low bird recapture

rates between the sites (C. Smith, Humboldt State University, unpublished data). Sites were located on a total of five farms and, as all farms covered large areas or included many non-contiguous segments, multiple sites were located within each farm's boundaries. I initially identified farms using GoogleEarth (Version 7.1.2.2041) images, selecting the final sites on the ground. Sites were chosen based on availability, as determined by the cooperation of the farmers. The eleven sites located in sun coffee were spread across the following farms: Jungle Estate (51 ha), Dedan Kimathi University of Technology (DKUT) Farm (120 ha), Sasini Farms (210 ha) and Hill Estate (334 ha). The ten sites located in shade coffee were on the following farms: Jungle Estate, Kihuri Estate (18.55 ha), and Sasini Farms.

Figure 1. Location of the study area denoted by the red circle, in central Kenya.
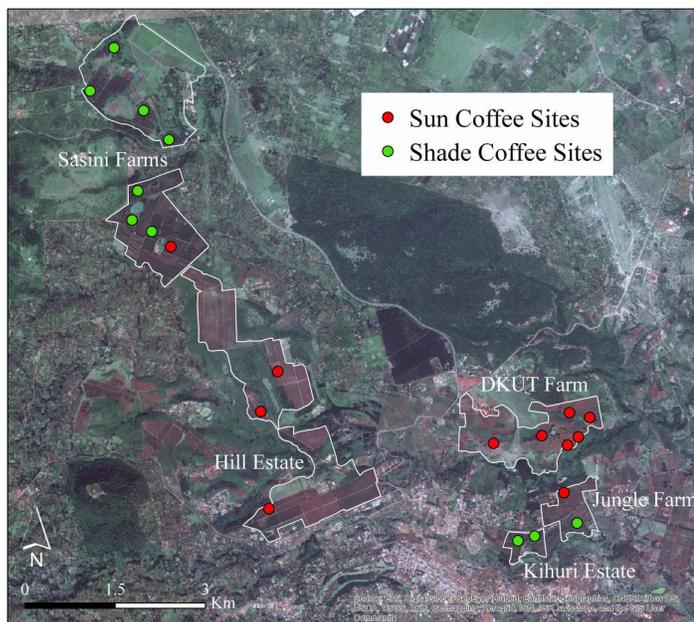
Figure 2. Map of the study sites, with green dots denoting sites in shade coffee and red dots denoting sites in sun coffee. Farm boundaries are outlined and labeled. Aerial imagery is from an ESRI basemap.

Sentinel Pest Experiment

Previous studies examining avian control of coffee pests in other regions of the world have focused on coffee berry borer, as it is one of the most prevalent and destructive pests of coffee (Kellermann et al. 2008, Karp et al. 2013). However, low infestation rates of coffee berry borer in the study region rendered this line of inquiry impractical. Therefore, I performed a sentinel pest experiment to simulate elevated levels of a novel insect pest and examined the predictions outlined above. In the literature, sentinel pest experiments are commonly used to compare relative predation pressure under varying conditions and have been used to relate predation rates to bird populations and distributions (Jedlicka et al. 2011) and to structural diversity (Perfecto et al. 2004). This experiment controlled the location and quantity of pests, thus allowing the response rate to be measured in relation to each of the relevant variables, such as distance to forest fragment and the presence of shade trees. All sentinel pest experiments were performed during a four week period from December 2012 to January 2013 and a six week period from December 2013 to January 2014.

Conducting a simulated pest outbreak with a known agricultural pest, such as coffee berry borer, was impractical for two reasons. Most importantly, it would likely meet significant resistance from the region's farmers. Additionally, the morphology and life cycle of coffee berry borer is difficult to manipulate. Thus, for the experiment I chose larger insects that were easier to manipulate and posed no threat to cooperating farmers. The maize stemborer caterpillar (*Sesamia calamistis*) is a common crop pest in Africa

and is commercially available from the International Centre of Insect Physiology and Ecology (ICIPE), an insect research organization based in Kenya, from whom I obtained third instar larvae. This experiment mimicked a dramatic increase in abundance of a novel insect pest (Perfecto et al. 2004). While lepidopteran larvae are relatively rare on coffee plants (arthropod sampling revealed an average of 0.03 larvae per branch; Perfecto et al. (2004) found an average of 2.1 larvae per coffee plant on farms in Mexico), they are an important food item for birds and thus a good indicator of overall insect removal rates. While this approach cannot reveal true pest removal rates, it can provide a measure of predation in relation to forest fragments and farm vegetation complexity (*sensu* Perfecto et al. 2004).

Due to the low prevalence of shade coffee in the study region, no shade farms directly adjacent to forest fragments were available. Therefore, I only examined the effect of forest edge on sun coffee farms. Every sun coffee site contained two transects a minimum of 100 m apart. Each transect consisted of pest presentation stations placed at 0 m, 10 m, 25 m, 50 m, 75 m, 100 m, 125 m, and 150 m from the forest fragment edge (Figure 3). This design allowed the effect of distance to forest edge on pest removal to be analyzed on sun farms using stations from 0-100 m. I excluded stations at 125 m and 150 m on the transect from the distance analyses because they were often less than 100 m from the opposite edge and did not accurately represent the corresponding distances from an adjacent forest fragment. Shade coffee sites had 100 m long transects, also a minimum of 100 m apart, located a minimum of 25 m from the coffee edge (Figure 4), with pest presentation stations positioned at six stations along the transect. Preliminary analyses

suggested that the edge effect from forest fragments decreased significantly by 25 m (see Results for full analyses). Therefore, for comparisons of pest removal on sun and shade coffee sites, I excluded presentation stations at 0 m and 10 m from sun coffee sites and distance was not included as a variable, yielding six stations per transect in both sun and shade sites, all a minimum of 25 m from the nearest forest edge (Figure 4). By excluding presentation stations closer to the edge, the potential edge effect should also be removed, thus allowing the comparison of vegetation structure between sun and shade coffee farms.

A pest presentation station consisted of caterpillars on three adjacent coffee plants. Each coffee plant had two caterpillars placed on a single leaf at a height of 1.5 m and in the same cardinal direction. I pinned caterpillars to the leaf with a black enamel insect pin (Bioquip #3) inserted through the caterpillar's thorax, allowing a limited amount of natural movement, and secured below the leaf with green painter's tape to ensure that the pins could not fall off or be removed by the wiggling caterpillar. I placed caterpillars by dawn (between 6:00 and 6:20) each morning to eliminate predation by bats and other nocturnal predators, and checked and collected them by 12:15 local time. The discovery during the 2013-2014 field season that ants were a potentially significant source of predation prompted a modification to the setup of the pest presentation stations. During the second half of the 2013-2014 field season, I protected half of the branches with an ant barrier that was a mixture of Mortein® Insect Spray (active ingredients: Allethrin [2.09 g/kg] and Resmethrin [0.39 g/kg]) and petroleum jelly (Vaseline®) to prevent access by ants. Field trials proved that the ant barrier effectively excluded ants for a minimum of 12 hours. I placed the substance sufficiently far (e.g., 0.25 m) from the caterpillars to prevent

either interference with the experiment or any impact on the birds.
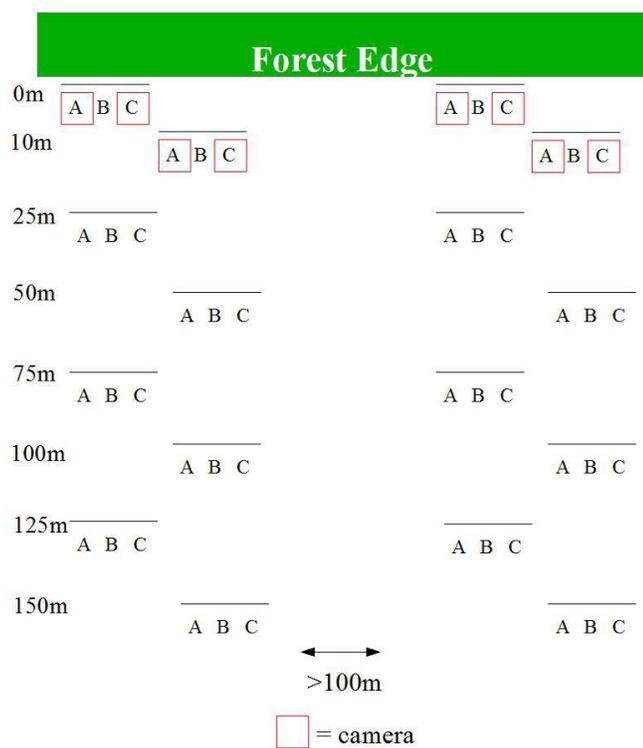
Figure 3. Experimental design of the sentinel pest experiment in sun coffee farms. Each letter (A, B, C) represents a single coffee plant with two caterpillars on the same leaf. Motion-sensor cameras are marked with a red box and were placed by plants at 0 m and 10 m from the forest fragment.

Coffee Edge

25m   —————   —————
       A B C   A B C

50m   —————   —————
             A B C   A B C

75m   —————   —————
       A B C   A B C

100m   —————   —————
         A B C   A B C

125m—————   —————
       A B C   A B C

150m   —————   —————
        A B C   A B C

                        ←——→
                       >100m
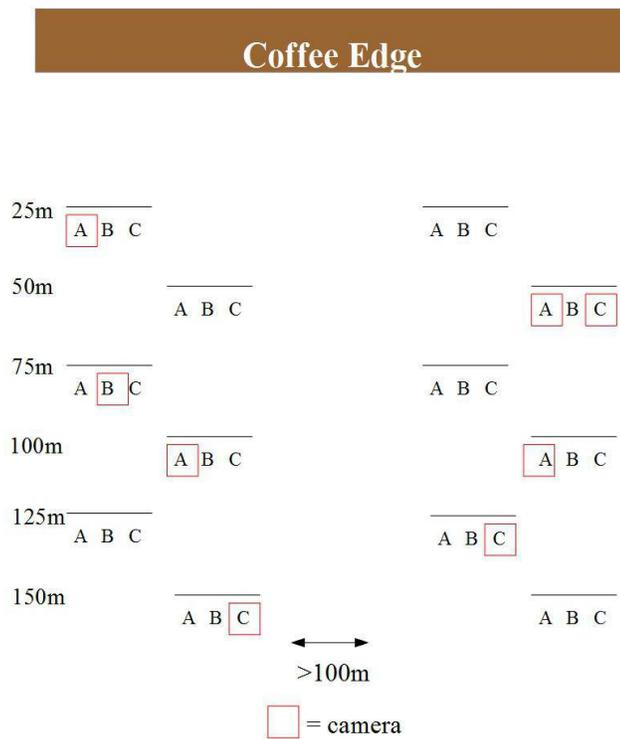
☐ = camera

Figure 4. Experimental design of the sentinel pest experiment in shade coffee farms. Each letter (A, B, C) represents a single coffee plant with two caterpillars on the same leaf. Example locations of motion-sensor cameras are marked with a red box. Cameras were placed at random plants throughout the site.

I set up motion sensor cameras (Reconyx HC500 HyperFire Semi-Covert IR) at a sample of the presentation stations (see Figures 3 and 4) in an attempt to determine which species were preferentially feeding on the caterpillars. On average, eight cameras were placed at each site for a total of 122 camera-stations in the study. As predation was expected to be significantly higher close to the forest edge, I placed cameras at stations 0 and 10 m from the forest edge in sun coffee to increase the probability of capturing a predation event on the camera. In shade coffee, I randomly placed cameras throughout the site. Cameras provided information about predation events but proved too slow to capture many events and did not yield sufficient observations to perform statistical analyses. Camera data did, however, provide information about some of the species responsible for predation, which allowed a subset of the bird population to be classified as 'preferential predators' for the analysis.

The raw data for each plant was the number of caterpillars remaining in the afternoon. For purposes of analysis, the response was the proportion of caterpillars removed from each triad of plants, which yielded an observation of predation at each distance.

Landcover Variables

In order to test the impact of distance on predation, distance from the forest edge was controlled by the experimental placement of pest presentation stations. However, adjacent forest fragments differed in size and quality. To examine whether the size of conterminous forest affects pest removal, I digitized the adjacent forest fragment in

GoogleEarth by identifying contiguous areas dominated by trees. I estimated the area of

each resulting fragment in ArcMAP 10.1. While the amount of forested area has been

shown to influence pest removal (Karp et al. 2013), the forest fragments in this study

were often embedded within much larger fragments of non-coffee land that, while not

necessarily dominated solely by trees, differed in composition and quality. To capture

such differences in the larger fragments, I calculated the proportion of each landcover

type within a buffer around each net. I utilized a radius of 125 m because that

corresponded with the geographic scale of small- to medium-sized bird movements and

was found to explain the most variation in avian control of pest infestations in other

systems (Karp et al. 2013). I digitized landcover layers in GoogleEarth based on the color

and texture of the satellite image and on-the-ground knowledge of the habitat types. The

resulting layers were divided into the following landcover types: trees, brush, sun coffee,

shade coffee, human (man-made structures), water, and other. I calculated the percentage

of each landcover type within a 125 m buffer in Program R (Version 3.0.1) using the

rgeos (Version 0.3-4) package.

<center>Vegetation Variables</center>

To test the prediction that shade coffee supports higher levels of pest control, I

analyzed the influence of the farm's vegetation complexity on predation. At each pest

presentation station, I sampled coffee and shade tree vegetation in a 5 m radius plot. For

coffee, measurements included: coffee density (the proportion of the 5 m radius sample

plot covered by coffee bushes), number of coffee bushes, percent understory (height <1.5

m) cover, percent midstory (height 1.5 to 5 m) cover, and the average height of both the

mid- and understory. I calculated the volume of the understory vegetation as the volume

of a cylinder representing the sample plot that extended to the average understory

vegetation height. I calculated the volume of the midstory vegetation in the same manner

but included only vegetation between 1.5 and 5 m tall, thus excluding any understory

vegetation in the plot. Measurements of shade trees included: percent shade cover

(measured with a densiometer [Forestry Suppliers, Jackson, Mississippi]), an estimate of

shade tree density using the point-quarter method (Krebs 1989), and the distance to

nearest tree in each quadrant (measured using a rangefinder), its species and both canopy

depth (the distance from the bottom to the top of the tree canopy) and trunk height (the

distance from the ground to the bottom of the canopy). I measured tree height with a

clinometer if too tall to estimate (e.g., greater than 15 m). I also calculated the number of

trees within 50 m of each plot to coincide with data collected during the 2012-2013 field

season. A tree was defined as a woody, non-coffee plant greater than 5 m tall. I

calculated tree density, or the number of trees per 100 m^2, using the number of trees

within 50 m to allow for consistency between sample years. I also calculated shade tree

diversity for each transect using the Shannon-Wiener diversity index based on the

proportion of trees of each species occurring within 25 m (Gotelli and Ellison 2013).

Using the point-quarter tree distances from the 2013-2014 season and the distance to

nearest tree from the 2012-2013 season, I calculated the number of trees of each species

within 25 m. As the data from the 2012-2013 season included only the distance to the

single nearest tree, I calculated the number of trees within 25 m of a pest presentation

station as a quarter of the total trees within 50 m and estimated the proportions of each species (only two were observed at the relevant sites) based on their relative frequencies.

Bird Variables

I obtained information on bird species richness, abundance and composition from concurrent research being conducted to quantify bird populations at each study site (C. Smith, proposed MS thesis, Humboldt State University). Two transects of mist nets followed the spatial sampling design of the sentinel pest experiment. Mist nets were run after the sentinel pest experiment to avoid altering bird behavior during the experiment (but within 28 days). At each individual site, twelve or sixteen nets were run for a total of 12-15 hours over three consecutive days. Birds were captured, measured, banded, and released. Bird capture rates (per 100 net hours) provided an index of bird abundance, and I calculated species richness as an average of the number of species captured at each distance for the distance analysis and for each transect for the other analyses (See Model Development and Selection below), because the capture rate was too low to allow for sufficient precision to estimate species richness at a net level. I classified species into five foraging guilds based on established groupings (Kissling et al. 2007): insectivores, omnivores, granivores, frugivores, and nectarivores. Predictor variables used in the analysis included total abundance, species richness, insectivore abundance and abundance of preferential predators identified using the camera data.

Ant Variables

An index of ant abundance at each distance was calculated using tuna fish baits

(Philpott et al. 2006). A strip of tuna 4-5 cm wide was placed on each coffee trunk approximately 1 m above the ground. Baits were examined 30 minutes after they were placed, the number of ants present was counted and, when necessary, samples were collected for identification by the National Museums of Kenya.

<center>Arthropod Variables</center>

I conducted a survey of overall arthropod abundance on the coffee plants to determine the extent to which the sentinel pest experiment elevated ambient larval abundance. This information is essential to put any observed effects of birds into context, as previous work suggests top-down effects of birds on insects may be maximized at intermediate insect densities that trigger diet switches, but can become less if pest abundance and reproduction overwhelm local bird densities (Rotenberry et al. 1995; Hogstad 2005). Birds are opportunistic, often taking advantage of abundant or profitable prey (Rotenberry et al. 1995). At low densities, insects may not be profitable enough to alter foraging strategies, while, conversely, birds may not be able to exert a sufficient top-down effect to control insect populations at very high densities. Following the protocol established by Johnson (2000), I surveyed the arthropod community at each pest presentation station by taking 2-3 branch samples. I chose branches randomly from the same part of the plant where the caterpillars were placed in the sentinel pest experiment. I quickly enclosed branches in a cloth pillowcase fitted with a drawstring and then shook them to dislodge all arthropods into the pillowcase. I checked branches for arthropods after sampling to ensure that all insects were captured in the sample. I then identified

arthropods to order in the field and recorded the number and length of individuals in each

order. Derived measurements for each pest presentation station used in analysis included

the average total number of arthropods, the average number of arthropod orders, and the

average length of all arthropods at that station.

Bird vs. Ant Predation

Both birds and ants (*Pheidole megacephala*) were observed removing caterpillars

in the sentinel pest experiment. To determine underlying mechanisms driving predation

by each taxon, I assigned pest removals to either birds or ants based on the following

criteria: any leaves that were observed to have ants on them upon collection were

determined to be removed by ants. As ants were always observed to consume both

caterpillars, any single caterpillar that was removed with no evidence of ants on the

second one, was determined to be removed by birds. Any caterpillars removed from

branches protected by the ant barrier were determined to be removed by birds, because

ants were not observed to penetrate that barrier. I defined all removals that did not satisfy

the above criteria as unknown and did not include them in the analyses specifically

examining bird or ant predation. Of the 173 caterpillars removed, a total of 88 were

classified as unknown.

Model Development and Selection

This experiment included five similar analyses that addressed separate but related

questions (Figure 5). The first three analyses examined the underlying mechanisms

driving total pest removal, while the last two analyses appraised pest removal by birds

and ants separately. The first analysis focused primarily on the effect of distance on pest removal. The second analysis concentrated on the effect of farm type (sun vs. shade coffee) on pest removal. The third analysis examined the effects of both farm type and the presence of arthropods on pest removal. The fourth and fifth analyses separated pest removal by birds and ants, respectively, and examined mechanisms driving observed patterns. Because only sun coffee farms were directly adjacent to forest fragments in this study system, the first analysis (distance) could only be performed on this subset of the data. In addition, arthropod data were not collected during the 2012-2013 field season, so the third analysis only included data from the 2013-2014 field season. As a result, the five analyses examined slightly different datasets, but all were approached in the manner described below.

In this experiment, the measure of predation was a binomial variable, the proportion of caterpillars removed at a pest presentation station, which is not normally distributed. In addition, the predictors were a mixture of fixed and random effects. To allow extrapolation to other settings, the site and transect were nested random effects. All other predictors were fixed effects to test their impact on predation. The non-normal distribution of the data required a generalized model, while the mixture of fixed and random effects necessitated a linear mixed model, so a generalized linear mixed model (GLMM) was used to determine the relative importance of the different variables as predictors of pest removal (Bolker et al. 2008).

Due to the large number of predictor variables under consideration, I used hierarchical model selection to build a set of candidate models for each analysis that were

compared using the corrected Akaike's Information Criterion (AICc) (Burnham et al.

2011). The null model included both random effects, but no fixed effects. Vegetation

variables were the first fixed effects considered as they presumably have a foundational

influence on the other factors analyzed. Initially, I examined the variance inflation factors

(VIFs) of the vegetation variables to determine that there was no multicollinearity, thus

allowing all the variables to be considered in combination. I then employed a variety of

evaluation steps to determine the best vegetation model. First, I examined the AICc of

each model with a single variable and if the variable increased the AICc over the null

model containing only random effects, I discarded it. Second, I calculated the marginal R^2

values for each single variable model following the method outlined by Nakagawa and

Schielzeth (2013). I retained the vegetation variables with relatively high marginal R^2

values in the top model. I used the R package glmmLasso (Version 1.2.2) as a supporting

tool and variables that proved significant using this method were generally those that

lowered the AICc and those with high marginal R^2 values. The result of this process

yielded a top vegetation model that was included in the subsequent analysis.

     Once I chose a top model including only vegetation variables, I then considered

other variables dependent on the particular analysis (see Figure 5). I considered the top

model(s) from the previous step in combination with the next set of variables to build a

final candidate model set. All the vegetation variables were significantly correlated with

farm type (sun or shade), so, where indicated (Figure 5), the top vegetation model was

compared to a model containing the simple binary variable of farm type to see which

model better captured the differences between farms. I did not evaluate bird predictor

variables in combination to better determine through which mechanism the bird

community was driving pest removal. Similarly, arthropod variables were not considered

together, with the exception of abundance and length. I averaged the final models to yield

coefficient estimates and variables were considered significant if their 95% confidence

intervals did not overlap zero. I then assessed model fit by computing both marginal and

conditional R^2 values following the method described by Nakagawa and Schielzeth

(2013). For a detailed explanation of each analysis, see Appendix A.
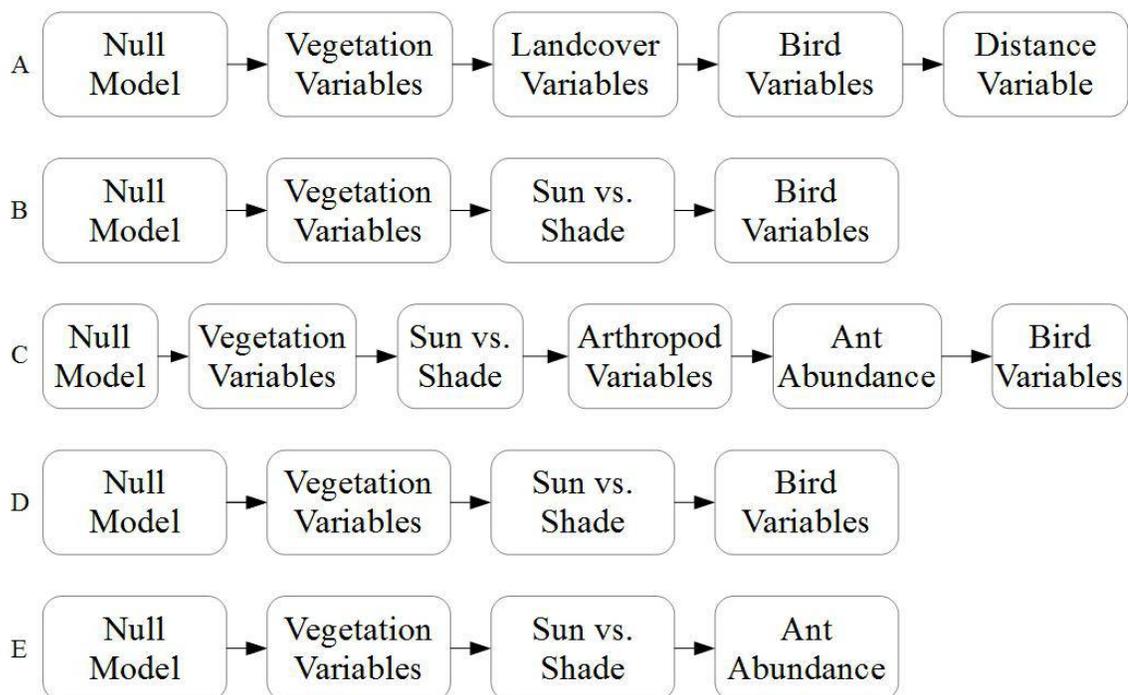
Figure 5. Steps in the hierarchical model selection process in the distance analysis (A), farm type analysis (B), arthropod analysis (C), bird predation analysis (D), and ant predation analysis (E). Analyses A-C examined total removal, and analyses D and E examined known bird and ant removal, respectively. I considered vegetation variables first in relation to the null model, which just included random effects, and then added other variables to the top vegetation model in the order indicated. Landcover variables included fragment size, proportion of area covered by trees, proportion of area covered by coffee, and proportion of area covered by brush. Bird population variables included total abundance, species richness, abundance of insectivores, and the abundance of preferential predators as determined by the camera data. Arthropod variables included total abundance, diversity and average size. The vegetation variables were significantly correlated with farm type (sun or shade), so I compared the top vegetation model to a model containing the simple binary variable of farm type where indicated.

RESULTS

I conducted the sentinel pest experiment on a total of 21 sites spread over five

farms. Predation ranged between zero and 100% at individual pest presentation stations,

with a mean of 11-12% of the caterpillars being removed. Birds removed an average of at

least 4.5% of the caterpillars and ants removed an average of at least 1.9% of the

caterpillars. A total of 85 bird species were captured and, of those species, I classified 36

as insectivores (for a complete list, see Appendix B). Cape Robin-chats (*Cossypha caffra

iolaema*), Common Bulbuls (*Pycnonotus barbatus*), and White-eyed Slaty Flycatchers

(*Melaenornis fischeri*) were identified eating the caterpillars in the sentinel pest

experiment using motion-activated camera footage. Therefore, I included a variable

representing the abundances of these three species as preferential predators. Bird data

collected from mistnets are summarized in Appendix B.

Distance Analysis

A mean of 12.0% of the pest presentation stations used in the distance analysis

were depredated. Among the vegetation variables, the best predictors of pest removal

included canopy cover, volume of midstory vegetation, tree density, and trunk height.

When examined in combination with the top vegetation model, none of the landcover

variables improved the AICc, but each landcover model had a small portion of the model

weight. Therefore, I examined each landcover variable individually compared to the null

model. As none improved the AICc fit over the null model, I did not include landcover

variables in any further analysis. When bird population parameters were analyzed with

the vegetation variables, the best model included total bird abundance, with 75% of the

model weight spread between a model including both the vegetation variables and bird

abundance and a model including only the vegetation variables. In the final set of

candidate models, the variable of distance was in all five top models, representing 100%

of the model weight (Table 1). The single strongest model (ΔAICc = 0, model weight =

0.59) included distance, bird species richness and the vegetation variables. The second

strongest model included distance, total bird abundance and vegetation variables, but it

represented only 15% of the model weight. The only variables whose confidence

intervals did not overlap zero when the coefficients were model averaged were distance

(95% CI β = -0.0405 – -0.0103, Figure 6), species richness (95% CI β = -1.0006 –

-0.0802), and canopy cover (95% CI β = 0.0003 – 0.0333; see Appendix C for all βs).

The marginal R^2 and conditional R^2 for the top model were 0.02 and 0.33, respectively.

Farm Type Analysis

Over all sites (sun and shade), a mean of 11.9% of the pest presentation stations

were depredated. Among the vegetation variables, the best predictors of pest removal

included canopy cover, coffee density and shade tree diversity. These three vegetation

variables in combination were better predictors of pest removal than the simple binary

variable of farm type and so were included in all further models. When combined with

the bird population parameters, the model with the strongest support (Table 2; ΔAICc=0,

model weight=0.35) included the vegetation variables and the abundance of insectivores.

However, model weight was spread fairly evenly over the top model and the following

two models, which included just the vegetation variables (ΔAICc = 0.76, model weight = 0.24), and vegetation and species richness (ΔAICc=0.83, model weight=0.23), respectively. Canopy cover (95% CI β = 0.0051 – 0.0262, Figure 7) and coffee density (95% CI β = -0.0418 – -0.0035; see Appendix C for all βs) were the only variables whose confidence intervals did not overlap zero when the coefficients were model averaged. The marginal R^2 and conditional R^2 for the top model were 0.03 and 0.39, respectively.

Arthropod Analysis

A mean of 11.5% of pest presentation stations analyzed in the arthropod analysis were depredated. Among the vegetation variables, the best predictors of pest removal were canopy cover and shade tree diversity. These two vegetation variables were better predictors of pest removal than the simple variable of farm type and so were included in later models. When arthropod abundance variables were included, the model with the strongest support (ΔAICc = 0, model weight = 0.65) included vegetation variables, total arthropod abundance, and arthropod size. The strongest two models represented 94% of model weight and so were included in further analyses. Considered in combination with the top two arthropod models, ant abundance was also an important predictor of pest removal (ΔAICc = 0, model weight = 0.56). With the addition of bird population parameters, no single model had overwhelming support (Table 3). Vegetation variables, arthropod abundance, arthropod size and ant abundance were all in the top five models. Bird variables found in the top five models, in decreasing order of significance, were bird abundance (ΔAICc = 0.23, model weight = 0.16), bird species richness (ΔAICc = 0.35,

model weight = 0.15), and abundance of insectivores (ΔAICc = 0.86, model weight = 0.11). Canopy cover (95% CI β = 0.0096 – 0.0326) and arthropod size (95% CI β = 0.0876 – 0.4544; see Appendix C for all βs) were the only variables whose confidence intervals did not overlap zero when the coefficients were model averaged. The marginal R^2 and conditional R^2 for the top model were 0.05 and 0.39, respectively.

Bird Predation Analysis

Using criteria to distinguish avian predation, birds removed 56 of the 85 depredated caterpillars assigned to birds or ants, and between zero and 83% at the individual pest presentation stations, with a mean of at least 3.9%. Among the vegetation variables, the strongest predictors of avian pest removal were coffee density, volume of midstory vegetation, tree density, trunk height and shade tree diversity. These variables were better predictors of avian pest removal than the simple variable of farm type. In combination with the bird community variables, the model with the most support included both vegetation variables and the abundance of insectivores (Table 4; ΔAICc = 0, model weight = 0.36). Variables whose confidence intervals did not overlap zero when the coefficients were model averaged included shade tree diversity (95% CI β = -3.464 – -0.2176), total abundance (95% CI β = 0.0006 – 0.0095) and species richness (95% CI β = 0.0081 – 0.1147; see Appendix C for all βs). The marginal R^2 and conditional R^2 for the top model were zero and 0.34, respectively.

Ant Predation Analysis

Using criteria to distinguish ant predation, ants removed 29 of the 85 depredated

caterpillars assigned to birds or ants, and between zero and 100% at the individual pest

presentation stations, with a mean of at least 3.6%. Vegetation variables that were the

strongest predictors of ant removal included volume of midstory vegetation and tree

density. However, the addition of vegetation variables and ant abundance did not improve

the AICc over the null model (Table 5).

Table 1. Support for the final set of models predicting the probability of caterpillar depredation in the distance analysis.

Model	K	AICc	ΔAICc	w_i	Cumulative w_i	LL
Vegetation + Species Richness + Distance	9	262.87	0.00	0.59	0.59	-121.62
Vegetation + Total Abundance + Distance	9	265.59	2.72	0.15	0.74	-122.98
Vegetation + Distance	8	265.94	3.07	0.13	0.87	-124.32
Distance	4	268.01	5.14	0.05	0.91	-129.83
Vegetation + Insectivore Abundance + Distance	9	268.04	5.17	0.04	0.96	-124.20
Vegetation + Preferential Predator Abundance + Distance	9	268.23	5.36	0.04	1.00	-124.30
Vegetation + Abundance	8	275.38	12.50	0.00	1.00	-129.04
Vegetation	7	275.55	12.67	0.00	1.00	-130.27
Vegetation + Preferential Predator Abundance	8	275.91	13.04	0.00	1.00	-129.31
Vegetation + Species Richness	8	277.50	14.63	0.00	1.00	-130.10
Vegetation + Insectivore Abundance	8	277.81	14.94	0.00	1.00	-130.26
Null	3	293.98	31.11	0.00	1.00	-143.89

Vegetation model includes the following variables: canopy cover, volume of midstory vegetation, tree density, and trunk height. Preferential predator abundance includes the individual abundances of Cape Robin-chats, Common Bulbuls, and White-eyed Slaty Flycatchers. Models were ranked based on the corrected Akaike's Information Criterion (AICc), ΔAICc, and Akaike weights (w_i). AICc is based on 2 x log likelihood (LL) and the number of parameters (K) in the model. Cumulative model weights (Cumulative w_i) are also reported.

Figure 6. Model prediction of the probability of predation at increasing distance from an adjacent forest fragment. Dashed lines represent 95% confidence intervals. Points represent the actual proportion of caterpillars removed in the sentinel pest experiment and were jittered to make overlapping points distinctly visible.

Table 2. Support for the final set of models predicting the probability of caterpillar depredation in the farm type analysis.

Model	K	AICc	ΔAICc	w_i	Cumulative w_i	LL
Vegetation + Insectivore Abundance	7	508.81	0.00	0.35	0.35	-247.16
Vegetation	6	509.57	0.76	0.24	0.58	-248.60
Vegetation + Species Richness	7	509.64	0.83	0.23	0.81	-247.58
Vegetation + Preferential Predator Abundance	7	511.32	2.50	0.10	0.91	-248.41
Vegetation + Total Abundance	7	511.58	2.76	0.09	0.99	-248.54
Null	3	517.27	8.46	0.01	1.00	-255.58

Vegetation model includes the following variables: canopy cover, coffee density, and shade tree diversity. Preferential predator abundance includes the individual abundances of Cape Robin-chats, Common Bulbuls, and White-eyed Slaty Flycatchers. Models were ranked based on the corrected Akaike's Information Criterion (AICc), ΔAICc, and Akaike weights (w_i). AICc is based on 2 x log likelihood (LL) and the number of parameters (K) in the model. Cumulative model weights (Cumulative w_i) are also reported.

Figure 7. Model prediction of the probability of predation with increasing canopy cover. Dashed lines represent 95% confidence intervals. Points represent the actual proportion of caterpillars removed in the sentinel pest experiment.

Table 3. Support for the final set of models predicting the probability of caterpillar depredation in the arthropod analysis.

Model	K	AICc	ΔAICc	w_i	Cumulative w_i	LL
Vegetation + Arth. Abun. + Arth Size + Ants	8	402.39	0.00	0.17	0.17	-192.83
Vegetation + Arth. Abun. + Arth Size + Ants + Bird Abun.	9	402.62	0.23	0.16	0.33	-191.84
Vegetation + Arth. Abun. + Arth. Size + Ants + Bird Richness	9	402.74	0.35	0.15	0.48	-191.90
Vegetation + Arth. Abun. + Arth. Size + Ants + Insectivore Abun.	9	403.26	0.86	0.11	0.59	-192.16
Vegetation + Arth. Size + Ants + Bird Abun.	8	403.67	1.28	0.09	0.68	-193.46
Vegetation + Arth. Size + Ants	7	403.76	1.37	0.09	0.77	-194.59
Vegetation + Arth. Size + Ants + Bird Richness	8	403.84	1.45	0.08	0.85	-193.55
Vegetation + Arth. Abun + Arth. Size + Ants + Preferential Predator Abun.	9	404.53	2.13	0.06	0.91	-192.80
Vegetation + Arth. Size + Ants + Insectivore Abun.	8	404.58	2.19	0.06	0.97	-193.92
Vegetation + Arth. Size + Ants + Preferential Predator Abun.	8	405.89	3.49	0.03	1.00	-194.57
Null	3	421.76	19.37	0.00	1.00	-207.82

Vegetation model includes the following variables: canopy cover and shade tree diversity. Preferential predator abundance includes the individual abundances of Cape Robin-chats, Common Bulbuls, and White-eyed Slaty Flycatchers. Models were ranked based on the corrected Akaike's Information Criterion (AICc), ΔAICc, and Akaike weights (w_i). AICc is based on 2 x log likelihood (LL) and the number of parameters (K) in the model. Cumulative model weights (Cumulative w_i) are also reported.
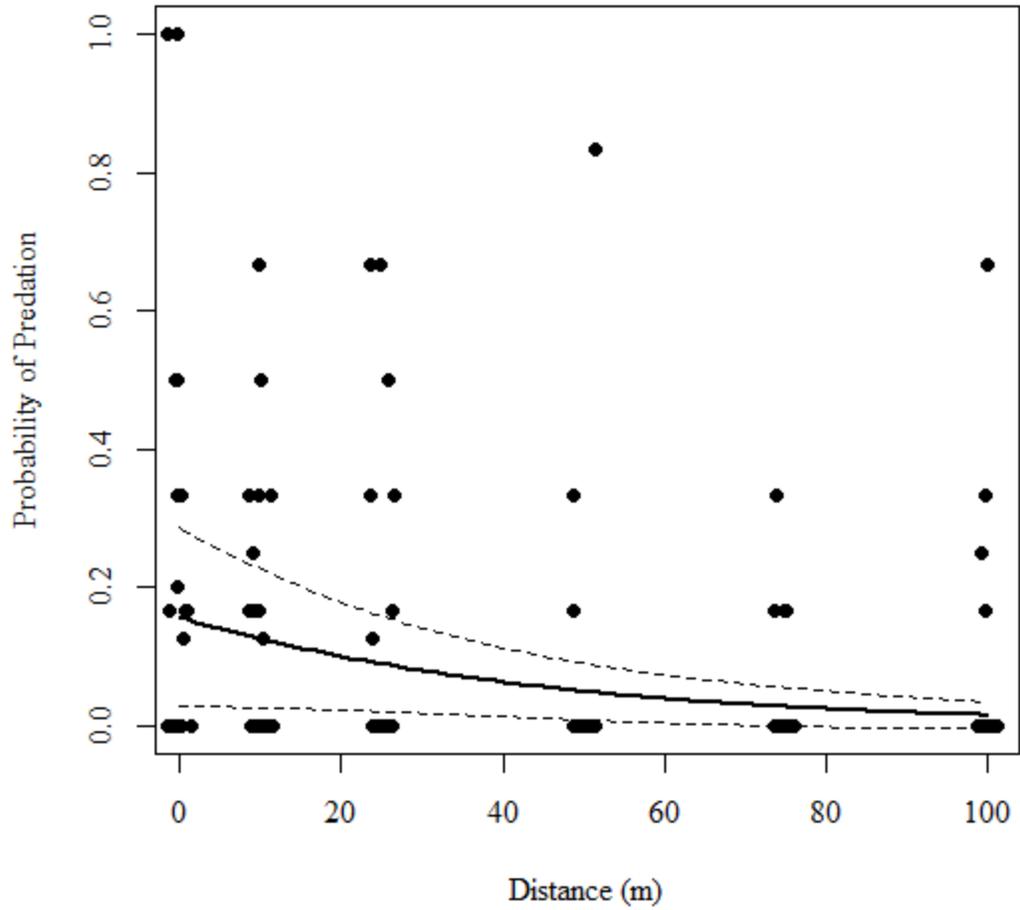
Table 4. Support for the final set of models predicting caterpillar depredation in the bird predation analysis.

Model	K	AICc	ΔAICc	w_i	Cumulative w_i	LL
Vegetation + Insectivore Abundance	9	277.37	0.00	0.36	0.36	-129.29
Vegetation + Species Richness	9	278.00	0.63	0.26	0.62	-129.60
Vegetation + Total Abundance	9	278.45	1.08	0.21	0.83	-129.83
Vegetation + Preferential Predator Abundance	9	280.10	2.73	0.09	0.92	-130.65
Vegetation	8	280.35	2.98	0.08	1.00	-131.86
Null	3	287.22	9.85	0.00	1.00	-140.56

Vegetation model includes the following variables: canopy cover, volume of midstory vegetation, tree density, trunk height, and shade tree diversity. Preferential predator abundance includes the individual abundances of Cape Robin-chats, Common Bulbuls, and White-eyed Slaty Flycatchers. Models were ranked based on the corrected Akaike's Information Criterion (AICc), ΔAICc, and Akaike weights (w_i). AICc is based on 2 x log likelihood (LL) and the number of parameters (K) in the model. Cumulative model weights (Cumulative w_i) are also reported.
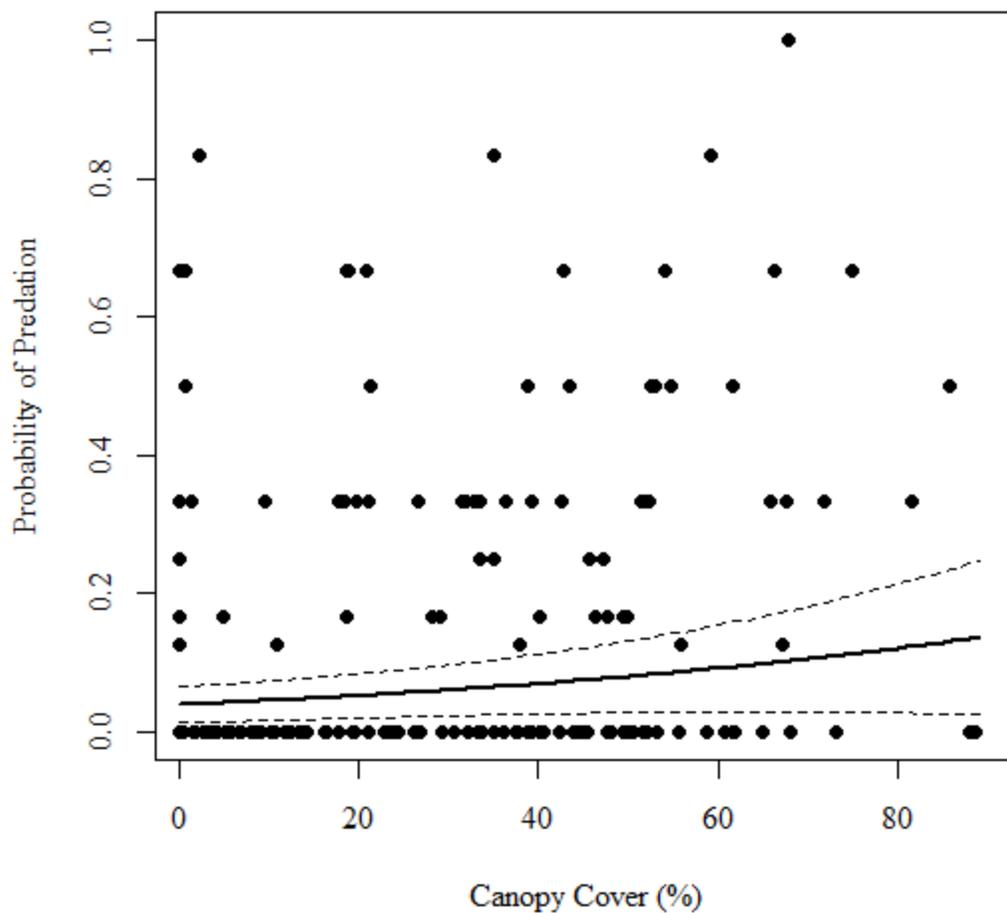
Table 5. Support for the final set of models predicting caterpillar depredation in the ant predation analysis.

Model	K	AICc	ΔAICc	w_i	Cumulative w_i	LL
Null	3	115.62	0.00	0.43	0.43	-54.75
Vegetation	5	117.01	1.39	0.21	0.64	-53.35
Farm Type	4	117.62	2.00	0.16	0.80	-54.71
Vegetation + Ant Abundance	6	117.90	2.28	0.14	0.94	-52.74
Farm Type + Ant Abundance	5	119.52	3.90	0.06	1.00	-54.61

Vegetation model includes the following variables: volume of midstory vegetation and tree density. Models were ranked based on the corrected Akaike's Information Criterion (AICc), ΔAICc, and Akaike weights (w_i). AICc is based on 2 x log likelihood (LL) and the number of parameters (K) in the model. Cumulative model weights (Cumulative w_i) are also reported.

DISCUSSION

Results of the sentinel pest experiment indicate that pest removal on coffee farms is influenced by both how a farm is managed and by its surroundings. Pest removal was positively associated with shade tree canopy and negatively associated with distance to an adjacent forest fragment.

Canopy cover, the defining characteristic of shade coffee, was significantly positively correlated with pest removal in all the models examining total predation, a finding consistent with some studies (e.g., Perfecto et al. 2004, Philpott and Armbrecht 2006, Armbrecht and Gallego 2007). The inclusion of shade trees could prompt a numerical response in both birds and ants foraging in coffee (Kellermann et al. 2008, Van Bael et al. 2008, Philpott et al. 2009), reflecting the tendency of predators to aggregate in areas of high prey density (Godfray and Pacala 1992). Alternatively, higher pest removal with increasing shade cover may be due to a functional response, whereby birds are more likely to detect and consume large and profitable prey like caterpillars when they can search for them from above. However, this finding differs from other studies that found no relationship between avian pest control and any measures of vegetation complexity, including canopy cover (Kellermann et al. 2008, Philpott et al. 2009) or actually found a negative correlation with vegetation complexity (Johnson et al. 2010). Even so, the most comparable study examining the removal of lepidopteran larvae also found a positive relationship between canopy cover and pest removal (Perfecto et al. 2004), whereas studies that found no relationship examined predation of coffee berry borer (Kellermann et al. 2008, Philpott et al. 2009). Therefore, it is possible that increased canopy cover may

enhance the profitability of searching for large and relatively conspicuous prey such as lepidopteran larvae, but have a smaller effect on less conspicuous or rewarding prey items such as coffee berry borer.

Pest removal was also positively correlated with proximity to an adjacent forest fragment. Birds may nest or roost in forest patches and venture into the farm edge to forage (Jirinec et al. 2011). This finding underscores that adjacent habitat can contribute to the delivery of an ecosystem service by mobile organisms (Kellermann et al. 2008, Wenny et al. 2011, Karp et al. 2013), and can provide an incentive for habitat protection near farm edges. However, other landscape variables, including fragment size and the amount of forested area within a given radius, were not associated with pest control. In this system, small patches of forest on farm edges may be sufficient to deliver insectivorous birds and ants into the farm, contrasting with other studies suggesting that forest cover increased avian control of coffee berry borer on farms in Costa Rica (Karp et al. 2013) and in Jamaica (Railsback and Johnson 2014). It is possible that the levels of infestation mimicked by the sentinel pest experiment were either too low or too high to detect a possible influence of forest cover. The forest fragments included in this study were also necessarily limited by availability. As a result, it was not possible to capture the ideal range of sizes and so any effect might have been too subtle to observe. In addition, the landscape variables analyzed may have been too coarse or not captured relevant characteristics. For example, while the amount of forest in the area was analyzed, the variable did not capture any differences in the quality of the forested area, such as species composition or structural diversity.

Taken together, these results suggest that a land sharing approach, incorporating both shade trees within the farm and small forest patches on farm edges, could promote increased pest control services. Land sharing encourages biodiversity within the farm, and shade coffee, a widely promoted example of this strategy, has been positively linked to both biodiversity (Raman 2006, Philpott et al. 2006, Kellermann et al. 2008, Philpott et al. 2012) and pest control (Philpott and Armbrecht 2006, Armbrecht and Gallego 2007). The strategy of land sparing, on the other hand, maximizes yield with intensification on the farm, with the resulting low biodiversity offset by protected (spared) habitat elsewhere. This strategy was not examined explicitly here, but the finding that pest removal was not related to size of adjacent forest fragment suggests that it may not facilitate ecosystem services provided by birds and ants in this study system.

Other significant vegetation variables negatively influencing pest removal included coffee density and shade tree diversity. Lower coffee densities could increase avian foraging success by making prey more conspicuous, resulting in the negative relationship seen here. In contrast to coffee densities, greater shade tree diversity would be expected to positively affect bird and ant diversity and thus pest control services, as has been shown on coffee farms in Mexico (Perfecto et al. 2004). However, the majority of shade coffee farms in this study system had very low levels of tree diversity, so these results should be interpreted with caution. Sites with a greater range of shade tree diversity should be included in future studies to determine if this result extends to other regions.

In addition to the influences of farm type and the surrounding habitat on pest

removal services provided by both birds and ants, the distribution or foraging behavior of these predators could also be driven by the availability of arthropod prey. While the effect of arthropod abundance was not significant, arthropod size was significantly positively correlated with pest removal. This suggests that bird and ant predators may respond to the quality of available prey and perhaps have a more appropriate search image for large arthropods, which could translate in a higher rate of sentinel pest detection in shade coffee.

The frequency of pest removal in this study was a result of a combination of avian and ant predation, but results suggest that an average of at least 4.5% (of a total average of 11.9%) was caused by birds. Biodiversity has been linked to ecosystem stability and resilience (the "insurance hypothesis", McNaughton 1977, Tscharntke et al. 2005), and, as this will become increasingly important with the expansion of pests as a result of climate change, it is important to understand the effect of the avian community on the provisioning of pest control services. In the full farm type analysis, bird abundance, species richness and the abundance of preferential predators were all positively correlated with pest removal, coinciding with results of previous studies that found positive relationships between bird abundance (Perfecto et al. 2004), bird diversity (Perfecto et al. 2004, Van Bael et al. 2008) and predator abundance (Jedlicka et al. 2011) with the top-down control of pests. However, as none of these bird community variables received overwhelming support in the analysis, the mechanisms mediating the positive influence of the bird community on pest removal deserve further study. Bird species richness is often related to vegetation complexity (Greenberg et al. 1997, Philpott et al. 2009),

which, in turn, affects predator foraging efficiency (Grabowski 2004). Thus, the relationships observed between the bird community and pest removal could reflect habitat influences. However, while local habitat clearly has an effect on pest removal, the inclusion of bird variables in the majority of the top models suggests that the bird community has an influence in addition to that explained by the vegetation variables. Bird species richness is often directly related to abundance, with diversity increasing with observed abundance (Perfecto et al. 2004). While it is therefore difficult to separate the independent impacts of either diversity or abundance, there are several potential explanations for the positive relationship between pest removal and either bird richness or abundance. This relationship could reflect the sampling effect, or the idea that higher diversity increases the probability of a very efficient predator being present (Perfecto et al. 2004, Tscharntke et al. 2005, Van Bael et al. 2008, Philpott et al. 2009). Alternatively it could signify species complementarity, whereby a more diverse group of predators consumes a greater diversity of prey (Tscharntke et al. 2005, Van Bael et al. 2008, Philpott et al. 2009). While these mechanisms are intertwined, the abundance of individual species was a better predictor of removal than the abundance of insectivores, suggesting that a few species could be driving pest removal.

While species richness had a positive effect on pest removal in the broader farm type analysis, it actually had a significant negative effect on removal in the distance analysis, which included only sun coffee sites. Species richness at the sun coffee sites was most likely driven by granivorous species, which were very abundant in the interior of the sun coffee plantations, where they were frequently observed foraging on the

understory vegetation (M. Milligan, personal observation), whereas the majority of insectivores were either forest generalist or forest visitor species (Bennun et al. 1996). Therefore changes in species richness might not reflect differences in the species assemblages responsible for pest predation. In addition, the abundance of insectivores was a poor predictor and was actually negatively related to pest removal. Functional richness has often been described as a more accurate predictor of ecosystem services (Philpott et al. 2009), and previous studies found insectivore abundance (Van Bael et al. 2008), functional richness (Philpott et al. 2009) and predator abundance (Jedlicka et al. 2011) to be positively correlated with the control of pests. While higher insectivore abundance would be expected to increase pest removal, 36 out of the 85 bird species detected in this study were classified as primarily insectivorous and it is possible that this is too broad a classification to be meaningful. While the grouping of preferential predators was intended to capture finer-scale influences of particular species, only three species (Cape Robin-chats, Common Bulbuls, and White-eyed Slaty Flycatchers) were definitively identified using remote cameras. Therefore, it is likely that this classification failed to capture other important species that would have made the variable more meaningful.

While ants (*Pheidole megacephala*) clearly provided some form of pest removal, none of the measured variables, including both vegetation characteristics and ant abundance, were good predictors of ant pest removal. Previous studies have found that multiple species in the genus *Pheidole* forage on coffee pests, including coffee berry borer (Armbrecht and Perfecto 2003, Armbrecht and Gallego 2007), making them good

candidates for pest control. Multiple studies also found ant diversity (Armbrecht and Perfecto 2003, Perfecto et al. 2003, Philpott et al. 2006, Philpott and Armbrecht 2006, Philpott et al. 2008) but not abundance (Philpott et al. 2006) to be negatively correlated with management intensification, but none have linked ant population characteristics directly to pest control services. Simple abundance may not be the driving factor behind ant predation. Other factors, such as food availability (Philpott and Armbrecht 2006), a colony's stage of development (Vandermeer et al. 2002), the availability of preferred nesting sites including shade trees (Philpott and Armbrecht 2006), environmental conditions (Armbrecht and Perfecto 2003), or ecological interactions (Philpott and Armbrecht 2006), could play a more important role in driving ant behavior.

Other influences, including weather, mammalian predation, or human or mechanical error could be responsible for the removal seen in the sentinel pest experiment, but these explanations are unlikely. If removals were due to weather, or human or mechanical error, the result would likely be a random pattern, not the predictable influence of shade and distance to forest fragment apparent here. Caterpillars were placed just before dawn every morning to exclude nocturnal predators, such as bats, and mammals were rarely observed in the coffee during the day. In addition, all experiments were conducted in areas where the coffee was not being actively picked to avoid any outside influence of coffee workers. Consequently the patterns observed in this experiment are most likely a result of some combination of avian and ant predation.

In summary, both birds and ants are providing important ecosystem services. The sentinel pest experiment mimicked a dramatic increase in a novel insect pest (from 0.03

to 2 lepidopteran larvae per branch) and a combination of birds and ants were able to provide meaningful reductions in pest abundance. The mechanism through which the bird and ant communities are effecting pest removal is less clear, but encouraging particular preferential predators could positively influence pest control. Despite uncertainty about the method through which predators are influencing pest control, the different farm types and surrounding habitat had a clear impact on pest control services. With coffee pests such as coffee berry borer projected to expand in both range and abundance with climate change (Jaramillo et al. 2011) and the impacts of different management strategies on pest populations being highly context-dependent (Jonsson 2014), the provisioning of natural pest control services will only increase in importance. In conclusion, these results suggest that a land sharing approach, via both the integration of shade trees and the conservation of small forest fragments within a farm, can support increased levels of pest control services provided by both birds and ants in Kenyan coffee farms.

REFERENCES

Armbrecht, I., and I. Perfecto. 2003. Litter-twig dwelling ant species richness and predation potential within a forest fragment and neighboring coffee plantations of contrasting habitat quality in Mexico. Agriculture, Ecosystems and Environment 97:107-115.

Armbrecht, I., and M. C. Gallego. 2007. Testing ant predation on the coffee berry borer in shaded and sun coffee plantations in Colombia. Entomologia experimentalis et Applicata 124:261-267.

Balmford, A., R. Green, and B. Phalan. 2012. What conservationists need to know about farming. Proceedings of the Royal Society B: Biological Sciences 279:2714-2724.

Bátary, P., A. Báldi, D. Kleijn, and T. Tscharntke. 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proceedings of the Royal Society B: Biological Sciences 278:1894-1902.

Bennun, L., C. Dranzoa, and D. Pomeroy. 1996. The forest birds of Kenya and Uganda. Journal of East African Natural History 85:23-48.

Bennun, L., and P. Njoroge. 1999. Important bird areas in Kenya. NatureKenya, Nairobi, Kenya.

Bianchi, F. J., C. J. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proceedings of the Royal Society B: Biological Sciences 273:1715–1727.

Bock. C. E., J. H. Bock, and M. C. Grant. 1992. Effects of bird predation on grasshopper densities in Arizona grasslands. Ecology 73:1706-1717.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. White. 2008. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127-135.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23-35.

Chandler, R. B., D. I. King, R. Raudales, R. Trubey, C. Chandler, and V. J. A. Chavez. 2013. A small-scale land-sparing approach to conserving biological diversity in tropical agricultural landscapes. Conservation Biology 27:785-795.

Daily, G. C. 1997. Nature's services: societal dependence on natural ecosystems. Island Press, Washington, DC, USA.

De Beenhouwer, M., R. Aerts, and O. Honnay. 2013. A global meta-analysis of the biodiversity and ecosystem service benefits of coffee and cacao agroforestry. Agriculture, Ecosystems and Environment 175:1-7.

Fischer, J., B. Brosi, G. C. Daily, P. R. Ehrlich, R. Goldman, J. Goldstein, D. B. Lindenmayer, A. D. Manning, H. A. Mooney, L. Pejchar, J. Ranganathan, and H. Tallis. 2008. Should agricultural policies encourage land sparing or wildlife-friendly farming? Frontiers in Ecology and the Environment 6:380-385.

Food and Agriculture Organization of the United Nations (FAO). 2009. State of Food

Insecurity in the World 2009. FAO, Rome, Italy.

Godfray, H. C. J., and S. W. Pacala. 1992. Aggregation and the population dynamics of parasitoids and predators. The American Naturalist 140:30-40.

Gotelli, N. J., and A. M. Ellison. 2013. A primer of ecological statistics. Sinauer Associates Inc., Sunderland, Massachusetts, U.S.A.

Grabowski, J. H. 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. Ecology 85:995-1004.

Green, R. E., S. J. Cornell, J. P. W. Scharlemann, and A. Balmford. 2005. Farming and the fate of wild nature. Science 307:550-555.

Greenberg, R., P. Bichier, and J. Sterling. 1997. Bird populations in rustic and planted shade coffee plantations of Eastern Chiapas, Mexico. Biotropica 29:501-514.

Hogstad, O. 2005. Numerical and functional responses of breeding passerine species to mass occurrence of geometrid caterpillars in a subalpine birch forest: a 30-year study. Ibis 147:77–91.

Jaramillo, J., C. Borgemeister, and P. S. Baker. 2006. Coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae): searching for sustainable control strategies. Bulletin of Entomological Research 96:223-233.

Jaramillo, J., E. Muchuga, F. E. Vega, A. Davis, C. Borgemeister, and A. Chabi-Olaye. 2011. Some like it hot: the influence and implications of climate change on coffee berry borer (*Hypothenemus hampei*) and coffee production in East Africa. PLoS ONE 6(9).

Jedlicka, J. A., R. Greenberg, and D. K. Letourneau. 2011. Avian conservation practices strengthen ecosystem services in California vineyards. PLoS ONE 6(11).

Johnson, M. D. 2000. Evaluation of an arthropod sampling technique for measuring food availability for forest insectivorous birds. Journal of Field Ornithology 71:88-109.

Johnson, M. D., J. L. Kellermann, and A. M. Stercho. 2010. Pest reduction services by birds in shade and sun coffee in Jamaica. Animal Conservation 13:140-147.

Johnson, M. D. and S. Hackett. Why birds matter economically. Chapter *in* Why birds matter. Under review, University of Chicago Press, Illinois, USA.

Jonsson, M., I. A. Raphael, B. Ekbom, S. Kyamanywa, and J. Karungi. 2014. Contrasting effects of shade level and altitude on two important coffee pests. Journal of Pest Sciences 1-7.

Karp, D. S., C. D. Mendenhall, R. F. Sandi, N. Chaumont, P. R. Ehrlich, E. A. Hadly, and G. C. Daily. 2013. Forest bolsters bird abundance, pest control and coffee yield. Ecology Letters 16:1339-1347.

Kellermann, J. L., M. D. Johnson, A. M. Stercho, and S. C. Hackett. 2008. Ecological and economic services provided by birds on Jamaican Blue Mountain coffee farms. Conservation Biology 22:1177-1185.

Kissling, W. D., C. Rahbek, K. Böhning-Gaese. 2007. Food plant diversity as broad-scale determinant of avian frugivore richness. Proceedings of the Royal Society B 274:799-808.

Krebs, C. J. 1989. Ecological Methodology. HarperCollins Publishers, New York, New York, USA.

McNaughton, S. J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. American Naturalist 111:515-525.

Millennium Ecosystem Assessment [MEA]. 2005. Ecosystems and human well-being: Synthesis. Millenium Ecosystem Assessment, Island Press, Washington, DC.

Moguel, P., and V. M. Toledo. 1999. Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology 13:11-21.

Mols, C. M. M., and M. E. Visser. 2002. Great tits can reduce caterpillar damage in apple orchards. Journal of Applied Ecology 39:888-899.

Mooney, K. A., D. S. Gruner, N. A. Barber, S. A. Van Bael, S. M. Philpott. 2010. Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. Proceedings of the National Academy of Sciences USA 107:7335-7340.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133-142.

Ndang'ang'a, P. K., J. B. M. Njoroge, K. Ngamau, W. Kariuki, P. W. Atkinson, and J. Vickery. 2013. Avian foraging behaviour in relation to provision of ecosystem services in a highland East African agroecosystem. Bird Study 60:156-168.

Perfecto, I. and A. Castiñeiras.1998. Deployment of the predaceous ants and their conservation in agroecosystems. Pages 269-289 *in* P. Barbosa, editor. Conservation Biological Control. Academic Press, Baltimore, MD, USA.

Perfecto, I., A. Mas, T. Dietsch, and J. Vandermeer. 2003. Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. Biodiversity and Conservation 12:1239-1252.

Perfecto, I., J. H. Vandermeer, G. L. Bautista, G. I. Nuñez, R. Greenberg, P. Bichier, and S. Langridge. 2004. Greater predation in shaded coffee farms: the role of resident neotropical birds. Ecology 85:2677-2681.

Perfecto, I., and J. Vandermeer. 2006. The effect of an ant-hemipteran mutualism on the coffee berry borer (*Hypothenemus hampei*) in southern Mexico. Agriculture, Ecosystems and Environment 117:218-221.

Phalan, B., M. Onial, A. Balmford, and R. E. Green. 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. Science 333:1289-1291.

Philpott, S. M., and I. Armbrecht. 2006. Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predator function. Ecological Entomology 31:369-377.

Philpott, S. M., I. Perfecto, and J. Vandermeer. 2006. Effects of management intensity and season on arboreal ant diversity and abundance in coffee agroecosystems. Biodiversity and Conservation 15:139-155.

Philpott, S. M., W. J. Arendt, I. Armbrecht, P. Bichier, T. V. Diestch, C. Gordon, R. Greenberg, I. Perfecto, R. Reynoso-Santos, L. Soto-Pinto, C. Tejeda-Cruz, G. Williams-Linera, J. Valenzuela, and J. M. Zolotoff. 2008. Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and

trees. Conservation Biology 22:1093-1105.

Philpott, S. M., O. Soong, J. H. Lowenstein, A. L. Pulido, D. T. Lopez, D. F. B. Flynn, and F. DeClerck. 2009. Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. Ecological Applications 19:1858-1867.

Philpott, S., and P. Bichier. 2012. Effects of shade tree removal on birds in coffee agroecosystems in Chiapas, Mexico. Agriculture, Ecosystems and Environment 149:171-180.

Railsback, S. F., and M. D. Johnson. 2014. Effects of land use on bird populations and pest control services on coffee farms. Proceedings of the National Academy of Sciences 111:6109-6114.

Raman, T. R. S. 2006. Effects of habitat structure and adjacent habitats on birds in tropical rainforest fragments and shaded plantations in the Western Ghats, India. Biodiversity and Conservation 15:1577-1607.

Rotenberry, J. T., R. J. Cooper, J. M. Wunderle, and K. G. Smith. 1995. When and how are populations limited? The roles of insect outbreaks, fire, and other natural perturbations. Pages 55–64 *in* T. E. Martin and D. M. Finch, editors. Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review. Oxford University Press, New York, New York, USA.

Sekercioglu, C. H. 2006. Increasing awareness of avian ecological function. Trends in Ecology and Evolution 21:464-471.

Smith, H. G., E. Öckinger, and M. Rundöf. 2010. Biodiversity and the landscape ecology of agri-environment schemes. Aspects of Applied Biology 100:225-232.

Tejeda-Cruz, C., and W. J. Sutherland. 2004. Bird responses to shade coffee production. Animal Conservation 7:169-179.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecology Letters 8:857-874.

Tscharntke, T., Y. Clough, T. C. Wanger, L. Jackson, I. Motzke, I. Perfecto, J. Vandermeer, and A. Whitbread. 2012. Global food security, biodiversity conservation and the future of agricultural intensification. Biological Conservation 151:53-59.

Troupin, D., and Y. Carmel. 2014. Can agro-ecosystems efficiently complement protected area networks? Biological Conservation 169:158-166.

Van Bael, S. A., S. M. Philpott, R. Greenberg, P. Bichier, N. A. Barber, K. A. Mooney, and D. S. Gruner. 2008. Birds as predators in tropical agroforestry systems. Ecology 89:928-934.

Vandermeer, J., I. Perfecto, G. I. Nuñez, S. Philpott, and A. G. Ballinas. 2002. Ants (*Azteca* sp.) as potential biological control agents in shade coffee production in Chiapas, Mexico. Agroforestry Systems 56:271-276.

Way, M. J. and K. C. Khoo. 1992. Role of ants in pest-management. Annual Review of Entomology 37:479-503.

Wenny, D. G., T. L. DeVault, M. D. Johnson, D. Kelly, C. H. Sekercioglu, D. F. Tomback,

and C. J. Whelan. 2011. The need to quantify ecosystem services provided by birds. The Auk 128:1-14.

Whelan, C. J., D. G. Wenny, and R. J. Marquis. 2008. Ecosystem services provided by birds. Annals of the New York Academy of Sciences 1134:25-60.

APPENDIX A

<u>Distance analysis</u>

The first analysis focused on the effect of distance to an adjacent forest fragment on pest removal and the impact of bird community characteristics on that relationship. Within this subset, the following variables were considered and introduced into the hierarchical analysis in this order: 1) measured vegetation variables, 2) landcover characteristics, 3) bird community variables, including total abundance, species richness, abundance of insectivores, and the abundance of preferential predators as determined by the camera data, and 4) distance to adjacent forest fragment. Only sun coffee sites with adjacent forest fragments were included in this analysis.

Hierarchical model selection was used to first examine vegetation variables in isolation and determine a top vegetation model. Following the selection of a top vegetation model, landcover variables were then added individually to the top vegetation model. Landcover variables were also examined individually in relation to the null model to determine whether model weights were due to the inclusion of vegetation variables or improved by the landcover variables under consideration. Variables analyzed included fragment size, proportion of area covered by trees, proportion of area covered by coffee, and proportion of area covered by brush. The three landcover types examined were chosen based on their direct relevance for the bird populations potentially responsible for pest removal and their high prevalence in the study area. Variables that had a significant amount of the weight or that significantly decreased the AICc were retained for consideration in the top candidate model set. This process yielded a top model that

included the most important vegetation and landcover variables.

Individual bird community variables were then added to the top model which potentially included vegetation and landcover variables. Bird community variables were not considered in combination to better ascertain through which of the alternative mechanisms the bird community was affecting pest removal. The best models, potentially including vegetation, landcover and bird variables, were retained based on the criteria described above. Once a candidate model set had been assembled following these steps, the distance variable was added to determine if it was still a significant predictor after controlling for the other factors. The result of this process was a final candidate model set that potentially included vegetation, landcover, bird community and distance variables.

<u>Farm type analysis</u>

The second analysis concentrated on the effect of farm type, specifically the difference between sun and shade coffee, on pest removal. Variables considered included 1) measured vegetation variables and 2) the same bird community parameters included in the previous analysis. All sites were included in this analysis. Vegetation variables were considered first and selected following the same procedure described above to yield a top model. All the vegetation variables were significantly correlated with farm type (sun or shade), so the top vegetation model was compared to a model containing the simple binary variable of farm type to see which model better captured the differences between farms. Once a model was chosen to reflect differences in farm type, individual bird community variables were considered to create the final candidate model set.

Arthropod analysis

The third analysis examined the effect of background arthropod levels on pest removal. Variables considered included 1) measured vegetation variables, 2) arthropod community parameters, including abundance, diversity and average size, 3) ant abundance, and 4) the same bird community variables included in the previous two analyses. Only sites from the 2013-2014 field season were examined in this analysis due to a lack of arthropod data from the 2012-2013 field season. A top vegetation model was selected and compared to a model containing only the variable of farm type. The top model was then considered with individual arthropod variables and ant abundance. As with the analysis of bird variables described above, arthropod variables were not evaluated in combination, with the exception of abundance and length, to determine which aspect of the arthropod community was driving pest control. After controlling for arthropod variables, bird variables were analyzed to determine if they still played a role in pest removal.

Bird predation analysis

The fourth analysis paralleled the second analysis, but examined the effect of farm type on pest removal by birds, specifically. Pest removal by birds was determined following the criteria outlined above. Once a top vegetation model was selected, bird community variables were considered individually to create a final candidate model set.

Ant predation analysis

The fifth analysis mimicked the fourth analysis, but instead examined the effect of farm type on pest removal by ants specifically, defined using the criteria outlined above.

A top vegetation model was analyzed with the variable of ant abundance to determine a

set of candidate models.

APPENDIX B

Bird species captured during mist-netting and their guild classifications
G = Granivore, N = Nectarivore, I = Insectivore, O = Omnivore
Preferential predators identified with remote cameras are denoted with an asterisk (*)

Species	Latin Name	Guild
African Citril	*Serinus citrinelloides*	G
African Dusky Flycatcher	*Muscicapa adusta interposita*	I
African Firefinch	*Lagonosticta rubricata hildebrandti*	G
African Golden Weaver	*Ploceus subaureus aureflavus*	G
African Green Pigeon	*Treron calva gibberifrons*	F
African Paradise Flycatcher	*Terpsiphone viridis*	I
African Yellow Warbler	*Chloropeta natalensis massaica*	I
Amethyst Sunbird	*Nectarinia amethystina kalckreuthi*	N
Baglafecht Weaver	*Ploceus baglafecht*	O
Black Saw-Wing	*Psalidoprocne holomelas massaicus*	I
Black-And-White Mannikin	*Lonchura bicolor*	G
Blackcap	*Sylvia atricapilla dammholzi*	O
Black-Crowned Tchagra	*Tchagra s. senegala*	I
Black-Headed Weaver	*Ploceus cucullatus*	O
Brimstone Canary	*Serinus sulphuratus sharpii*	G
Bronze Mannikin	*Lonchura cucullata scutata*	G
Bronze Sunbird	*Nectarinia k. kilimensis*	N
Brown Parisoma	*Parisoma lugens jacksoni*	I
Brown-Crowned Tchagra	*Tchagra australis emini*	I
Cape Robin-Chat*	*Cossypha caffra iolaema*	I
Chestnut Sparrow	*Passer eminibey*	G
Chin-Spot Batis	*Batis molitor*	I
Cinnamon-Chested Bee-Eater	*Merops oreobates*	I
Collared Sunbird	*Anthreptes collaris garguensis*	O
Common Bulbul*	*Pycnonotus barbatus*	O
Common Fiscal	*Lanius collaris humeralis*	I
Common Waxbill	*Estrilda astrild*	G
Common Whitethroat	*Sylvia communis icterops*	O
Crimson-Rumped Waxbill	*Estrilda rhodopyga centralis*	G
Emerald-Spotted Wood Dove	*Turtur chalcospilos*	G
Golden-Breasted Bunting	*Emberiza flaviventris kalaharica*	O
Green-Headed Sunbird	*Nectarinia verticalis viridisplendens*	O
Grey-Backed Camaroptera	*Camaroptera brachyura*	I

Species	Latin Name	Guild
Grey-Capped Warbler	*Eminia lepida*	I
Grey-Headed Sparrow	*Passer griseus*	O
Hinde's Babbler	*Turdoides hindei*	I
Holub's Golden Weaver	*Ploceus xanthops*	O
Lesser Honeyguide	*Indicator minor teitensis*	O
Lesser Masked Weaver	*Ploceus i. Intermedius*	O
Little Rock Thrush	*Monticola r. rufocinereus*	I
Marico Sunbird	*Nectarinia mariquensis suahelica*	O
Marsh Warbler	*Acrocephalus palustris*	I
Montane White-Eye	*Zosterops poliogaster*	O
Northern Brownbul	*Phyllastrephus strepitans*	I
Olivaceous Warbler	*Hippolais pallida elaeica*	I
Olive Thrush	*Turdus olivaceus abyssinicus*	O
Pale Flycatcher	*Bradornis pallidus murinus*	I
Purple Grenadier	*Uraeginthus ianthinogaster*	G
Rattling Cisticola	*Cisticola chiniana*	I
Red-Billed Firefinch	*Ulagonosticta senegala ruberrima*	G
Red-Billed Quelea	*Quelea quelea aethiopica*	G
Red-Cheeked Cordon-Bleu	*Uraaeginthus b. begalus*	G
Red-Collared Widowbird	*Euplectes ardens*	O
Red-Faced Cisticola	*Cisticola erythrops sylvia*	I
Red-Fronted Barbet	*Tricholaema diademata*	O
Red-Throated Wryneck	*Jynx r. ruficollis*	I
Rufous Chatterer	*Turdoides r. rubiginosus*	I
Rufous Sparrow	*Passer r. rufocinctus*	G
Rufous-Naped Lark	*Mirafra africana*	I
Rüppell's Robin-Chat	*Cossypha semirufa intercedens*	I
Scarlet-Chested Sunbird	*Nectarinia senegalensis lamperti*	N
Siffling Cisticola	*Cisticola brachypterus*	I
Singing Cisticola	*Cisticola cantans pictipennis*	I
Speckled Mousebird	*Colius striatus kikuyuensis*	F
Spectacled Weaver	*Ploceus ocularis suahelicus*	I
Speke's Weaver	*Ploceus spekei*	O
Streaky Seedeater	*Serinus s. striolatus*	G
Tambourine Dove	*Turtur typanistria*	G
Tawny-Flanked Prinia	*Prinia subflava melanorhyncha*	I
Thick-Billed Seedeater	*Serinus burtoni*	O
Tree Pipit	*Anthus trivialis*	I

Species	Latin Name	Guild
Variable Sunbird	*Nectarinia venusta*	O
White-Bellied Tit	*Parus albiventris*	I
White-Browed Scrub Robin	*Cercotrichas leucophrys*	I
White-Eyed Slaty Flycatcher*	*Melaenornis f. fischeri*	I
White-Starred Robin	*Pogonocichla stellata intensa*	O
Willow Warbler	*Phylloscopus trochilus*	I
Yellow Bishop	*Euplectes capensis crassirostris*	O
Yellow Wagtail	*Motacilla flava*	I
Yellow-Bellied Waxbill	*Estrilda quartinia kilimensis*	G
Yellow-Breasted Apalis	*Apalis flavida*	I
Yellow-Crowned Canary	*Serinus canicollis flavivertex*	G
Yellow-Rumped Seedeater	*Serinus reichenowi*	G
Yellow-Rumped Tinkerbird	*Pogoniulus bilineatus*	O
Yellow-Whiskered Greenbul	*Andropadus l. latirostris*	O

Bird data per site for sun and shade coffee obtained using mist-nets.

Parameter	Sun Coffee Mean	Sun Coffee SD	Shade Coffee Mean	Shade Coffee SD
Total Abundance	93.73	58.16	53.10	28.70
Species Richness	17.32	9.44	11.00	2.59
Insectivore Abundance	13.91	11.17	14.50	8.13
Preferential Predator Abundance[a]	1.55	1.57	4.10	3.84
Cape Robin-chat Abundance	1.18	1.60	1.70	1.70
Common Bulbul Abundance	10.45	12.61	3.00	3.44
White-eyed Slaty Flycatcher Abundance	0.36	0.92	2.40	2.67

[a]Abundance of Cape Robin-chats, Common Bulbuls, and White-eyed Slaty Flycatchers

APPENDIX C

Model averaged parameter estimates (β), unconditional standard errors (SE), and lower and upper 95% confidence intervals (LCI and UCI, respectively) from the final models included in the distance analysis.

Parameter	β	SE	95% LCI	95% UCI
Canopy Cover	0.0168	0.0084	0.0003	0.0333*
Volume of Midstory Vegetation	-0.2425	0.1603	-0.5567	0.0716
Trunk	-0.1769	0.1184	-0.4090	0.0552
Tree Density	-3.3737	2.1976	-7.6809	0.9335
Total Abundance	0.0028	0.0015	-0.0020	0.0059
Species Richness	-0.5404	0.2348	-1.0006	-0.0802*
Insectivore Abundance	-0.0410	0.0821	-0.2019	0.1199
Preferential Predator Abundance[a]	-0.0202	0.0744	-0.1660	0.1256
Distance	-0.0254	0.0077	-0.0405	-0.0103*

*95% CI does not overlap zero
[a]Abundance of Cape Robin-chats, Common Bulbuls, and White-eyed Slaty Flycatchers

Model averaged parameter estimates (β), unconditional standard errors (SE), and lower and upper 95% confidence intervals (LCI and UCI, respectively) from the final models included in the farm type analysis.

Parameter	β	SE	95% LCI	95% UCI
Canopy Cover	0.0157	0.0054	0.0051	0.0262*
Coffee Density	-0.0227	0.0098	-0.0418	-0.0035*
Shade Tree Diversity	-0.7596	0.4944	-1.7286	0.2094
Total Abundance	0.0006	0.0016	-0.0026	0.0038
Species Richness	0.0373	0.0253	-0.0124	0.0870
Insectivore Abundance	-0.1166	0.0700	-0.2538	0.0205
Preferential Predator Abundance[a]	0.0222	0.0358	-0.0479	0.0923

*95% CI does not overlap zero
[a]Abundance of Cape Robin-chats, Common Bulbuls and White-eyed Slaty Flycatchers

Model averaged parameter estimates (β), unconditional standard errors (SE), and lower and upper 95% confidence intervals (LCI and UCI, respectively) from the final models included in the arthropod analysis.

Parameter	β	SE	95% LCI	95% UCI
Canopy Cover	0.0211	0.0059	0.0096	0.0326*
Shade Tree Diversity	-0.8966	0.5125	-1.9010	0.1078
Arthropod Abundance	-0.0016	0.0009	-0.0034	0.0002
Arthropod Size	0.2708	0.0937	0.0871	0.4544*
Ant Abundance	0.0012	0.0008	-0.0003	0.0027
Bird Abundance	-0.0040	0.0029	-0.0096	0.0015
Bird Species Richness	0.0562	0.0397	-0.0216	0.1340
Insectivore Abundance	-0.0815	0.0715	-0.2217	0.0587
Preferential Predator Abundance[a]	0.0104	0.0448	-0.0773	0.0982

*95% CI does not overlap zero
[a]Abundance of Cape Robin-chats, Common Bulbuls, and White-eyed Slaty Flycatchers

Model averaged parameter estimates (β), unconditional standard errors (SE), and lower and upper 95% confidence intervals (LCI and UCI, respectively) from the final models included in the bird predation analysis.

Parameter	β	SE	95% LCI	95% UCI
Canopy Cover	0.0003	0.0093	-0.0178	0.0185
Volume of Midstory Vegetation	-0.5600	0.3067	-1.1610	0.0411
Tree Density	3.6112	1.9164	-0.1450	7.3673
Trunk Height	-0.0535	0.0374	-0.1268	0.0199
Shade Tree Diversity	-1.8408	0.8282	-3.4640	-0.2176*
Total Abundance	0.0051	0.0023	-0.0006	0.0095*
Species Richness	0.0614	0.0272	0.0081	0.1147*
Insectivore Abundance	-0.2778	0.1422	-0.5565	0.0010
Preferential Predator Abundance[a]	0.0637	0.0389	-0.0125	0.1399

*95% CI does not overlap zero
[a]Abundance of Cape Robin-chats, Common Bulbuls, and White-eyed Slaty Flycatchers

Model averaged parameter estimates (β), unconditional standard errors (SE), and lower and upper 95% confidence intervals (LCI and UCI, respectively) from the final models included in the ant predation analysis.

Effect	β	SE	95% LCI	95% UCI
Volume of Midstory Vegetation	-0.2572	0.2262	-0.7007	0.1862
Tree Density	4.7616	3.1519	-1.4160	10.9392
Ant Abundance	0.0022	0.0017	-0.0012	0.0055