Landscape context and scale differentially impact coffee leaf rust, coffee berry borer, and coffee root-knot nematodes

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Abstract. Crop pest and disease incidences at plot scale vary as a result of landscape effects. Two main effects can be distinguished. First, landscape context provides habitats of variable quality for pests, pathogens, and beneficial and vector organisms. Second, the movements of these organisms are dependent on the connectivity status of the landscape. Most of the studies focus on indirect effects of landscape context on pest abundance through their predators and parasitoids, and only a few on direct effects on pests and pathogens. Here we studied three coffee pests and pathogens, with limited or no pressure from host-specific natural enemies, and with widely varying life histories, to test their relationships with landscape context: a fungus, *Hemileia vastatrix*, causal agent of coffee leaf rust; an insect, the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Curculionidae); and root-knot nematodes, *Meloidogyne* spp. Their incidence was assessed in 29 coffee plots from Turrialba, Costa Rica. In addition, we characterized the landscape context around these coffee plots in 12 nested circular sectors ranging from 50 to 1500 m in radius. We then performed correlation analysis between proportions of different land uses at different scales and coffee pest and disease incidences. We obtained significant positive correlations, peaking at the 150 m radius, between coffee berry borer abundance and proportion of coffee in the landscape. We also found significant positive correlations between coffee leaf rust incidence and proportion of pasture, peaking at the 200 m radius. Even after accounting for plot level predictors of coffee leaf rust and coffee berry borer through covariance analysis, the significance of landscape structure was maintained. We hypothesized that connected coffee plots favored coffee berry borer movements and improved its survival. We also hypothesized that wind turbulence, produced by low-wind-resistance land uses such as pasture, favored removal of coffee leaf rust spore clusters from host surfaces, resulting in increased epidemics. In contrast, root-knot nematode population density was not correlated to landscape context, possibly because nematodes are almost immobile in the soil. We propose fragmenting coffee plots with forest corridors to control coffee berry borer movements between coffee plots without favoring coffee leaf rust dispersal.

Key words: Coffea arabica; connectivity; ecosystem service; fragmentation; Hemileia vastatrix; Hypothenemus hampei; *land use;* Meloidogyne arabicida; Meloidogyne exigua; *pathogen; pest; Turrialba, Costa Rica.*

Introduction

Injury levels caused by plant pests and pathogens at the plot level vary depending on the interactions between the host plant, the pest or pathogen, the physical and biological environment, and agricultural management (Zadoks and Schein 1979). Landscape context affects the functioning of this plot level system mainly through its effect on pest, pathogenic, beneficial, and vector organisms. Portions of the landscape may provide habitat or source patches for the maintenance and reproduction of these organisms outside the plot, and facilitate their immigration into adjacent plots (Altieri 1999, Thies and Tscharntke 1999, Zadoks 1999, Thies et al. 2003, Holdenrieder et al. 2004, Bianchi et al. 2006, Plantegenest et al. 2007, Werling and Gratton 2010). Immigration is facilitated in landscapes with greater functional connectivity, which depends on the distribution and density of the different land uses, on how these are perceived (hostile or not) by the organisms, and on their ability to move across non-habitat areas (D'Eon et al. 2002, Goodwin and Fahrig 2002, Werling and Gratton 2010). In a given landscape context, higher functional connectivity is therefore expected for generalist species with high dispersal abilities (Elzinga et al. 2007).

Whereas in conservation biology, metapopulation theory considers how source–sink dynamics maintain populations (Hanski and Gilpin 1991), particularly for species of conservation concern and species involved in biological control, agroecology asks how these dynamics can isolate, impede the spread, and reduce populations of noxious species to make their control easier (Zadoks 1999, Holdenrieder et al. 2004, Plantegenest et al. 2007). Therefore, limiting landscape connectivity may be useful when it hinders the movement of pest and pathogen populations, recognizing that what is permeable to one species can be a barrier to another. Fahrig et al. (2011) suggest that within this framework, a habitat matrix view can be replaced with a heterogeneous landscape view where land uses are classified as dangerous, neutral, or beneficial to organisms. While this classification helps to understand landscape contexts, a single land use can transition from beneficial, to neutral, to dangerous at different scales. These perceived changes are species specific (D'Eon et al. 2002, Steffan-Dewenter et al. 2002, Werling and Gratton 2010), providing additional challenges when trying to manage connectivity for ecological communities.

Landscape context may also affect injuries caused by pests and diseases through its effects on the physical environment of the plot. Landscape heterogeneity can alter air turbulence and flow, thereby affecting the direction, velocity, and distance moved by wind of dispersed pests and pathogens (Nathan et al. 2005, Plantegenest et al. 2007, Ricci et al. 2009), and modify local temperatures that act on the life cycles of both noxious and beneficial organisms. For example, forest edges can buffer temperatures and increase parasitoid longevity (Bianchi et al. 2006).

The information that exists on the effects of landscape context on pests is primarily documented from temperate landscapes (Altieri 1999, Thies and Tscharntke 1999, Thies et al. 2003, Bianchi et al. 2006, Sciarretta and Trematerra 2006, Ricci et al. 2009, Werling and Gratton 2010). Most of these studies focus on indirect effects of landscape context on pest abundance through their predators and parasitoids, with only a few on direct effects (Sciarretta and Trematerra 2006, Ricci et al. 2009, Parsa et al. 2011). Information on pathogens is globally scarce (Holdenrieder et al. 2004, Condeso and Meentemeyer 2007, Plantegenest et al. 2007), and even more limited for tropical pests and diseases (Parsa et al. 2011). Most studies focus on a single species, with few studies that consider multiple taxa.

In this study, we tested the relationships between landscape context and three highly differentiated focal coffee pests and pathogens: (1) a fungus, *Hemileia vastatrix*, causal agent of the coffee leaf rust; (2) an insect, the coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae: Scolytinae); and (3) root-knot nematodes, *Meloidogyne* spp. As a recently introduced pest in Costa Rica (officially detected in 2000 [Staver et al. 2001]), coffee berry borer can be considered as almost free of specialist parasitoids, despite some sporadic releases by local extension services. *Hemileia vastatrix* is also an introduced species, which was detected for the first time in Costa Rica in 1983 (Schieber and Zentmyer 1984). Specialist biocontrol agents of coffee rust and coffee root-knot nematodes are not known. However, two recognized generalist fungi *Beauveria bassiana* and *Lecanicillium lecanii* can parasitize the coffee berry borer and the coffee leaf rust, respectively, particularly under shaded conditions (Staver et al. 2001). Likewise, ants have been shown to be a generalist predator of the coffee berry borer (Perfecto and Vandermeer 2006, Armbrecht and Gallego 2007). These pests and pathogens, from three distinct phyla, differ in their host specificity and dispersal ability. Coffee leaf rust is a coffee obligate. Its urediospores can be spread by wind over great distances (Becker et al. 1975) and can even cross oceans (Bowden et al. 1971). The coffee berry borer is very specific to coffee. However, breeding individuals have been found in several alternate plant hosts (Damon 2000). The females are able to fly and probably can be transported by convection winds over a few hundred meters (Baker 1984), if not more. Root-knot nematodes are able to infect multiple plant species (Rich et al. 2009), and when not dispersed by planting infested seedlings, can be considered nearly immobile.

Our main goal was to test how these pests and pathogens interact with landscape context in the absence of specialist biocontrol agents. Our hypotheses were that coffee berry borer abundance increases with the coffee proportion in the landscape at fine spatial scales due to its poor dispersal ability; and that coffee rust and coffee root-knot nematodes are not influenced by landscape context at the scales of our study (50–1500 m), which seemed too large for nematodes and too fine for coffee rust.

METHODS

Agrobiological context of the study area

The study was conducted in the Central Volcanic-Talamanca Biological Corridor (CVTBC) with the town of Turrialba at its center (9°5′00″ N, 83°41′00″ W). The CVTBC is located in southeastern Costa Rica on the Caribbean slopes of the Central Cordillera (Fig. 1). This region has climatic characteristics that favor the development of the three studied pests and pathogens. Turrialba is a rainy region, with mean annual rainfall of 2700 mm, which is nearly evenly distributed throughout the year due to strong Caribbean influence. However, rainfall usually decreases between February and April, with 365 mm of rainfall on average during these three months. Most of the coffee plantations are located at low to medium altitudes (<1000 m). Mean annual temperature is 22°C with very little variation.

Costa Rican coffee cultivation is mostly intensive, with high crop densities (≥5000 coffee bushes/ha) and low shade tree cover, primarily provided by the

leguminous tree *Erythrina poeppigiana*, which is commonly pruned twice a year. Most farms make intensive use of inputs, especially fertilizers and herbicides, and elaborate coffee pruning systems. However, these techniques are often only partially applied by growers, depending on their knowledge, investment capacity, and environmental conditions, leading to a great diversity of cropping systems at the country level. The coffee grown in Turrialba is probably one of the least intensive systems within the country, and exhibits a greater reliance on shaded systems. As in many other low-elevation warm climates, the coffee quality of Turrialba is generally lower compared with high-altitude coffees (>1000 m). This results in lower prices, which limit grower investment capacity. Shade is often used as a management practice in these warm regions to increase the sustainability of the system. Shade regulates microclimate and yields, improves quality, controls weeds, and reduces fertilizer and herbicide use, while also increasing the life span of the coffee plants (Fernández and Muschler 1999).

The Central Volcanic-Talamanca Biological Corridor is a subcorridor of the Mesoamerican Biological Corridor (MBC), which links the Talamanca Mountains to the south to the Central Volcanic range to the north (Fig. 1). The MBC is an international effort to ensure biological connectivity throughout the five most southern states of Mexico, Central America, and Panama. Although the original concept was initiated in 1998 with a strong biological focus, the concept has evolved to include more interdisciplinary approaches to land use planning (DeClerck et al. 2010). These approaches often focus on managing landscapes for ecosystem services predominantly, including biological connectivity and conservation, carbon sequestration, hydrological services, and scenic value, and to a lesser extent, pollination services. The 114 000 ha of CVTBC are dominated by forest, which covers 51% of the area, particularly at the periphery. The center of the corridor is dominated by an agricultural matrix primarily made up of pastures (25%), coffee plantations (9%), and sugar cane (6%).

Data collection and studied variables

We conducted a 10-month survey on 29 georeferenced coffee plots embedded in commercial stands, starting in February 2009 (just after the 2008–2009 coffee harvest) through November 2009 (during the 2009–2010 harvest). These plots comprised eight rows of 15 coffee bushes (217 m^2 on average), and were selected to represent different degrees of landscape complexity, from coffee-dominated landscapes to localities where the coffee plantations were highly fragmented (Fig. 1). In addition, the presence of the three studied pests and pathogens in the chosen coffee stands was verified. We followed the methodological approach used by Thies and Tscharntke (1999), Steffan-Dewenter et al. (2002), and Thies et al. (2003) to study the relationships between the incidence of the studied species in these coffee plots and landscape context.

To describe the landscape context, we first classified a 1-m^2 resolution aerial image of the landscape taken in 2005 and ground-truthed in 2008. We assigned the land uses within a 1500 m radius from the center of each sampled coffee plot to one of these four uses: coffee, sugar cane, pasture, and forest. We then subdivided the 1500 m radius landscape into 12 nested circular areas: 50, 100, 150, 250, 300, 350, 400, 450, 500, 1000, and 1500 m radii. Within each of these nested circular areas, we calculated the proportion of each land use. We verified our classification by ground-truthing the 500 m radius areas. There was no overlap between landscapes below the 500 m radius scale. The 500 m radius circular sectors are therefore considered independent (Fig. 1).

Within each plot, we selected five coffee bushes, distributed in a cross shape, to quantify the incidence of the three studied pests and pathogens. We evaluated their incidence during a maximum of five evaluation periods, depending on the species. These periods were: (1) February–March, (2) May, (3) June–July, (4) September, and (5) October–November.

We measured coffee leaf rust incidence during all five periods by counting the number of diseased and healthy coffee leaves on three branches per coffee bush, for a total of 15 branches per plot (Avelino et al. 2006).

We estimated coffee berry borer abundance during four sampling periods, excluding the February–March period because no new coffee berries were available for sampling at this time. Although several methods exist for measuring the number of bored coffee berries, none is unanimously accepted (Rémond et al. 1993). Some authors calculate only the proportion of bored berries by sampling fruiting branches on several coffee bushes (Rémond et al. 1993, Feliz Matos et al. 2004, Trujillo E. et al. 2006), which seems appropriate for studying population dynamics in a single site. However, this method is inappropriate to compare the number of bored berries in different plots, as this number is dependent on fruit load, which can vary widely from one plot to another. Other authors prefer to conduct a full census of bored coffee berries in several coffee bushes (Soto-Pinto et al. 2002). However, this method is time intensive and not practical for evaluating numerous plots repeatedly (in our case, 29 plots counted four times). Because of these limitations, we developed an alternative method whereby we counted the number of bored coffee berries (BCB) on a sample of four fruiting branches, chosen in four strata in each of the five selected coffee bushes, for a total of 20 branches evaluated per plot. In addition we counted the total number of fruiting branches per coffee bush (FB). This method allowed us to estimate the total number of bored coffee berries for each selected coffee bush, and hence the mean number per coffee bush in each plot, by using the following equation. Estimated number of bored
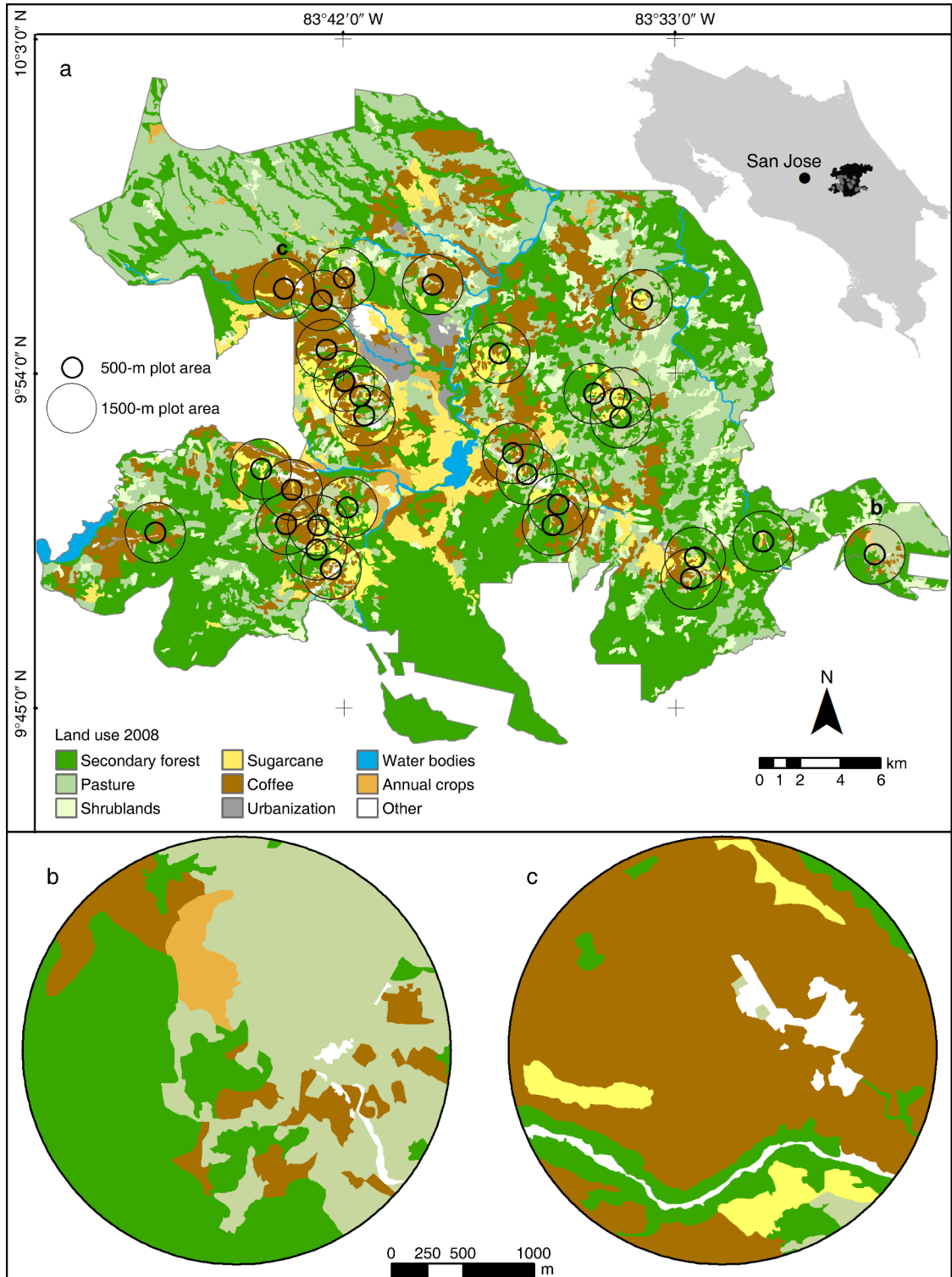
FIG. 1. (a) Landscape description within circular sectors of 500 and 1500 m radius centered on the 29 surveyed plots, and (b, c) two selected landscape contexts from (b) highly fragmented and (c) almost compact coffee areas, Turrialba, Costa Rica, 2009.

berries = (FB × BCB/4). See the Appendix for a validation of this methodology.

We assessed root-knot nematode population densities twice only, first in May, prior to the onset of the rainy season when nematode populations are thought to be most abundant (Souza et al. 2008), and a second time in September during the middle of the rainy season. We sampled coffee roots from four neighboring coffee bushes of each of the five selected coffee bushes for a total of 20 subsamples per plot (see Avelino et al. 2009). Nematodes were extracted from the plant tissue by the maceration sieving method (Taylor and Loegering 1953), which was modified according to Alvarado-Soto and López-Chaves (1981). Both nematodes and eggs were rinsed through and collected on nested 100 (0.15-mm openings) and 500 (0.025-mm openings) mesh sieves. We estimated their densities under a stereomicroscope. Species identification of nematodes belonging to the genus *Meloidogyne* was based on their perineal patterns (Franklin 1962, Taylor and Netscher 1974). We found *M. exigua* in 27 of the 29 plots, and additionally found *M. arabicida* in two of these plots.

We used the percentage of diseased coffee leaves at each sample date and the maximum percentage as descriptors of coffee leaf rust infection for our analysis. The coffee berry borer descriptors were the number of bored coffee berries estimated per coffee bush at each sample date, and the maximum number. For nematodes, we used the mean population density per 100 g of coffee roots found in May and September (*M. exigua* and *M. arabicida* together).

In addition, we assessed plot level predictors of the studied pests and pathogens. According to Avelino et al. (2006), the five most important plot level variables explaining coffee leaf rust epidemic intensities are: (1) the number of fruiting nodes per coffee bush where epidemics are more intense when fruit load is high; (2) the annual number of fertilizer applications where coffee bushes with good nutritional status and growth are better able to replace diseased leaves and appear healthy; (3) the percentage of shade cover where microclimatic conditions in shaded plantations favor coffee rust infection; (4) the elevation where low temperatures increase the latency period of the disease; and (5) soil pH where low soil pH is associated with high incidence of coffee rust. Concerning the coffee berry borer, two important plot level predictors are: (1) the number of bored coffee berries remaining on coffee bushes postharvest, where the abundance of bored berries in the following harvest is dependent on the population sheltered in these remaining berries; and (2) geographic elevation, where at high elevations, coffee berry borer populations are less abundant due to low temperatures (Baker 1984, Mathieu et al. 1997, Soto-Pinto et al. 2002). Three of the most important variables explaining the population densities of *M. exigua* in coffee roots are: (1) soil sand content where sandy soils favor nematode survival and reproduction; (2) soil

organic matter content where organic matter promotes beneficial organisms and saprophytic nematodes at the expense of plant parasitic nematodes; and (3) elevation where *M. exigua* populations are less important at high elevations due to low temperatures (Avelino et al. 2009). We performed different measurements to assess these previously mentioned variables. For each of the coffee plots we measured elevation by GPS. In addition, we collected a composite soil sample adjacent to the five selected coffee bushes in April, before the start of the rains, which was analyzed using the methods listed by Miranda Arauz (1989) for Central American coffee soils. We interviewed farmers who owned the coffee plantations to obtain information regarding the number of fertilizer applications made, including amendments. We determined the percentage of shade of the plots twice, first in April and again in September, over each of the five selected coffee bushes, with a spherical densiometer (Lemmon 1957) and used mean shade cover for the analysis. We counted the total number of fruiting nodes on the selected coffee bushes in July, before the harvest. Finally, we also counted the number of bored coffee berries per coffee bush remaining after the 2008–2009 harvest in each of the five selected coffee bushes at the beginning of the study, in February.

Statistical analyses

First, we examined the correlations between maximum coffee leaf rust incidence, maximum coffee berry borer abundance, mean root-knot nematode population density, and the percentage of the area occupied by the different land uses at each studied scale to determine whether landscape context impacted the studied pests and pathogens, and at what scales. Then, for each species, we focused our analysis on the most significant correlation (the lowest P value <0.05). We verified this correlation, obtained with specific land use and scale, at each assessment date to determine when the relationships with landscape were established. We applied an arcsine square-root transformation to coffee leaf rust incidence and a root-square transformation to the estimated abundance of bored coffee berries to normalize the data for each analysis. Distribution of nematode population density was normal and no transformation was needed.

Second, to confirm that these correlations reflect real effects of landscape context on the studied species, rather than a possible covariate effect associated to landscape, we performed an analysis of covariance using the general linear model, where the pest and pathogen descriptors were the response variables, the known plot scale predictors of these coffee pests and pathogens were the covariates, and the percentage of the area occupied by specific land use was the factor. To convert our continuous percentages to discrete values, we categorized the land use descriptors into three categories with similar number of plots (10 plots in two categories and 9 in the third one) and verified the assumption of
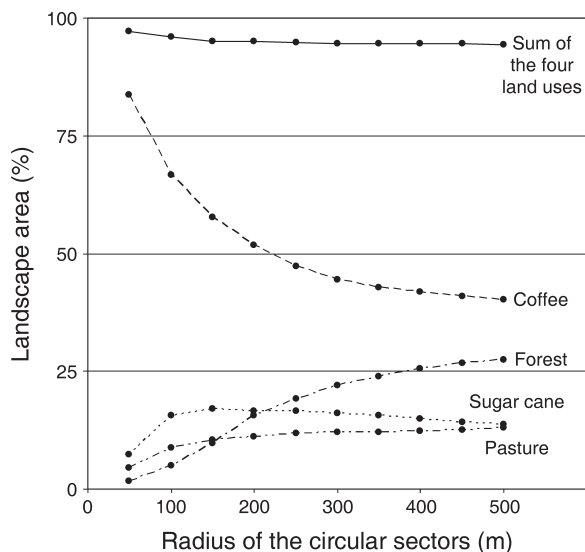
FIG. 2. Mean percentage of landscape area in coffee, forest, sugar cane, pasture, and the sum of these four land uses, in 10 nested circular areas centered on the surveyed coffee plots; data at the spatial scales of 1000 and 1500 m are not shown because circular sectors were not independent (see Fig. 1).

homoscedasticity for coffee pest and pathogen descriptors. We previously selected the covariates through a partial correlation analysis, and only retained the covariates correlated to coffee pest and pathogen descriptors at $P < 0.1$. Finally, we compared the adjusted means with the Bonferroni test by correcting for the effects of the covariates while holding the plot level predictors constant.

RESULTS

Data description

The combined value of coffee, forest, pasture, and sugar cane occupied >94% of the land at each studied spatial scale (Fig. 2; spatial scales >500 m were not considered because circular sectors were not independent). Logically, the landscape was almost exclusively occupied by coffee at fine scales (<100 m), because circular sectors were centered on coffee plots. At the 50 m radius scale, coffee occupied 84% of the area on average; at 100 m, the proportion fell to 67%, but was still quite high. In contrast, other land uses were poorly represented at fine scales. Proportions of forest and pasture increased with increasing spatial scales, while

proportions of coffee decreased. The proportion of sugar cane increased first, and then slightly decreased beyond the 150 m radius scale. Globally, proportions of different land uses were nearly stabilized beyond 250–300 m. At the 500 m radius scale, coffee, forest, sugar cane, and pasture represented 40%, 28%, 14%, and 13%, respectively (Fig. 2).

Our survey encompassed a wide range of incidence values for each of the studied species, with very low or even null incidences in some plots and very high incidences in other plots (Table 1). Coffee berry borer data showed the highest variability, with a coefficient of variation of 195%. Coefficients of variation for root-knot nematodes and coffee leaf rust were respectively 61% and 44%. This variability can partly be explained by the diversity of landscape contexts sampled, as demonstrated in the following section. We noted that the maximum number of bored coffee berries was reached in June–July for 52% of the plots and in September for 38% of them. The maximum percentage of rust-infected leaves was found in the October–November sampling period in 72% of the plots.

Relationships between coffee pests and pathogens and landscape context

We found diverse responses to landscape context for each of the study species. There were no correlations between landscape context and mean root-knot nematode population density. However, we found significant positive correlations between maximum coffee berry borer abundance and proportion of coffee in the landscape (Fig. 3a). The significance of this relationship peaked at the 150 m radius ($r = 0.43$, $P < 0.05$), and vanished after 200 m. Surprisingly, we found multiple significant positive correlations between maximum coffee leaf rust incidence and proportion of the landscape in pasture (Fig. 3b). In contrast to coffee berry borer, the significance of this relationship peaked at the 200 m radius ($r = 0.47$, $P < 0.01$), and vanished beyond 350 m. We also obtained multiple significant negative correlations for coffee berry borer with the proportion of the landscape in pasture; however, these were less significant than the positive correlations cited before. The significance peaked at 400 m ($r = -0.38$, $P < 0.05$; Fig. 3b) but was very similar between 300 m and 1000 m. In addition we found a significant negative correlation between the coffee berry borer and the proportion of the landscape in forest at the 150 m scale

TABLE 1. Maximum coffee berry borer abundances, maximum coffee rust incidence, and mean root knot nematode population densities observed in the survey.

Coffee pest and disease descriptors	Range	Mean (SD)
Maximum coffee berry borer abundance (number of bored coffee berries estimated per coffee bush)	0–533	56 (109)
Maximum coffee rust incidence, diseased leaves (%)	4–77	43 (19)
Mean population density of root knot nematodes (number of individuals per 100 g of coffee roots)	0–94 140	39 403 (23 965)

Correlation between the area devoted to four different land uses (%) and:
△ Maximum coffee borer abundance
◇ Maximum coffee rust incidence
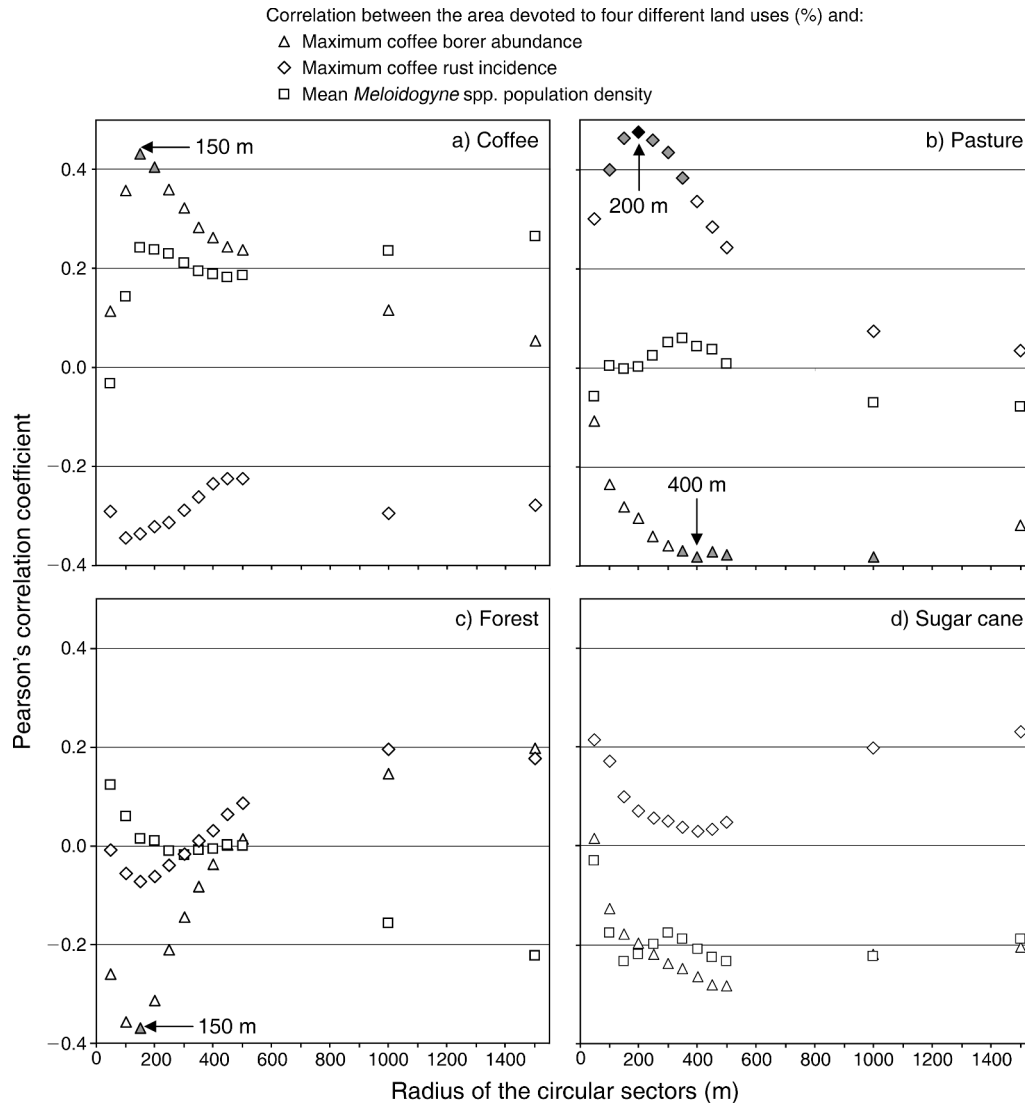□ Mean *Meloidogyne* spp. population density

FIG. 3. Correlation between the percentage of the area with (a) coffee, (b) pasture, (c) forest, and (d) sugar cane, and coffee berry borer, coffee leaf rust, and coffee root knot nematodes incidence at 12 spatial scales. Symbols: white, $P > 0.05$; gray, $P < 0.05$; black, $P < 0.01$. There are 12 data points across the x-axis, corresponding to the 12 distances studied; for clarity, the x-axis shows only seven distances. Arrows indicate the peaks when significant.

($r = -0.37$, $P < 0.05$; Fig. 3c). No significant relationships were found with the proportion of landscape in sugar cane and any of the study species (Fig. 3d). Only the best significant relationships ($P < 0.05$) were examined in the subsequent analytical stages. These relationships were positive and were obtained with coffee berry borer and coffee leaf rust only.

Considering the temporal distribution of these positive relationships, we found that the correlations were established at different times for coffee leaf rust and coffee berry borer (Table 2). For coffee berry borer, positive significant relationships with the proportion of coffee area were established earlier (June–July) and were nonexistent at the end of the year. On the contrary, for coffee leaf rust, positive significant relationships with the

proportion of pasture were established in September and were improved in October–November. The coffee berry borer correlations from the June–July and September sampling periods were better than those obtained with maximum coffee berry borer abundance. In contrast, the correlation obtained with maximum coffee leaf rust incidence was slightly better than those obtained with individual sampling dates.

Partial correlation analysis showed that maximum coffee berry borer abundance was negatively correlated to elevation ($P < 0.05$) and positively to the number of bored coffee berries remaining in the coffee bush after harvest ($P < 0.01$) as expected (Table 3). Similarly, maximum coffee leaf rust incidence was positively correlated to the number of fruiting nodes per coffee

TABLE 2. Correlations over time of bored coffee berry abundance vs. the percentage of coffee area at 150-m spatial scale, and of coffee rust incidence vs. the percentage of pasture at 200-m spatial scale.

| | Bored coffee berries abundance vs. percentage of coffee area, 150-m scale | | Coffee rust incidence vs. percentage of pasture, 200-m scale | |
Period	r	P	r	P
February–March			0.20	0.30
May	0.34	0.07	0.17	0.39
June–July	0.49	<0.01	0.11	0.58
September	0.50	<0.01	0.37	<0.05
October–November	0.26	0.17	0.45	0.02

Note: No data are available for coffee berry borer in February–March; r is Pearson's correlation coefficient with associated P.

tree and percentage of shade cover ($P < 0.1$), and negatively to the number of annual fertilizer applications and soil pH ($P < 0.05$). We found no linear relationship between maximum coffee leaf rust incidence and elevation (Table 3). As a consequence, this last variable was not retained in the following covariance analysis. Although we found no effect of landscape context on root-knot nematode population densities, we still performed a partial correlation analysis with potential plot level predictors. We did not find any significant effect of elevation and soil organic matter, but detected a very slightly positive relationship ($P < 0.15$) with soil sand content (Table 3). No covariance analysis was performed with mean root-knot nematode population density.

Our covariance analysis showed that even by removing the variability associated with plot level covariates explaining maximum coffee leaf rust incidence and maximum coffee berry borer abundance, landscape context retained a very significant effect ($P \leq 0.01$) on these pests and pathogens (Table 4). We found a maximum number of 81 bored berries per coffee bush in plots located in landscapes with >68% coffee at the 150-m scale. In contrast, on average 35 bored berries were found when the coffee area was between 9% and 42% at the same scale (Fig. 4a). Similarly, we found a maximum coffee rust incidence of 57% when the pasture

area ranged between 14% and 47% at the 200 m scale. Only 36% was found when pasture area was <12 % (Fig. 4b).

DISCUSSION

Our coffee leaf rust and coffee berry borer assessments appeared to be appropriate, as most of the known predictors at plot scale of these two pests and pathogens were correlated in the expected directions to maximum coffee leaf rust incidence and maximum coffee berry borer abundance (Baker 1984, Mathieu et al. 1997, Soto-Pinto et al. 2002, Avelino et al. 2006). Only elevation was not correlated to maximum coffee leaf rust incidence. However, elevation is typically not the strongest predictor of coffee leaf rust (Soto-Pinto et al. 2002, Avelino et al. 2006), and is not particularly surprising, since most of our plots were located at low to middle coffee-growing elevations. The lack of relationships between mean root-knot nematode population density and elevation or soil organic matter can be explained in the same way. Actually the negative effect of elevation on root-knot nematode populations has been detected above 1500 m in Costa Rica (Avelino et al. 2009), at higher elevations than those surveyed during this study. Similarly, the negative effect of soil organic matter on root-knot nematode populations has been particularly identified in soils with organic matter

TABLE 3. Partial correlation coefficients (r) between maximum coffee berry abundance, maximum coffee rust incidence, and some known predictors at plot level, and associated probabilities (P).

Response variable	Predictors	Range (SD)	r	P
Maximum coffee berry borer abundance	elevation (m)	619–1182 (134)	−0.42	0.03
	number of bored coffee berries remaining in coffee bush after harvest (February)	0–30 (5.6)	0.72	<0.01
Maximum coffee rust incidence	elevation (m)	619–1182 (134)	−0.04	0.85
	shade cover (%)	0–59 (18)	0.36	0.08
	annual number of fertilizer applications	0–5 (1.5)	−0.45	0.03
	soil pH	4.0–5.5 (0.4)	−0.46	0.02
	number of fruiting nodes per coffee bush	7–676 (202)	0.37	0.07
Mean population density of root knot nematodes	elevation (m)	619–1182 (134)	−0.08	0.70
	soil organic matter (% of dry mass)	0.6–3.1 (1.6)	0.03	0.88
	soil sand content (% of dry mass)	18–60 (8)	0.30	0.14

TABLE 4. Significance of landscape context effects on coffee berry borer abundance and coffee rust incidence, corrected by the effect of several significant covariates.

Response variable	Factor and covariates	F (df)	P
Maximum coffee berry borer abundance	coffee area at 150-m spatial scale (%) (factor)	5.2 (2, 24)	0.01
	elevation (covariate)	10.8 (1, 24)	<0.01
	number of bored coffee berries remaining in the coffee bush after harvest (covariate)	21.9 (1, 24)	<0.01
Maximum coffee rust incidence	pasture area at 200-m spatial scale (%) (factor)	6.1 (2, 22)	<0.01
	soil pH (covariate)	6.6 (1, 22)	0.02
	number of fruiting nodes per coffee bush (covariate)	9.2 (1, 22)	<0.01
	shade cover (%) (covariate)	7.7 (1, 22)	0.01
	annual number of fertilizer applications (covariate)	6.6 (1, 22)	0.02

contents above 12% of dry mass (Avelino et al. 2009), which are far higher than those found in the present research. On the contrary, the wide range of soil sand content we studied allowed us to find a relationship between soil sand content and root-knot nematode populations, which tends to be positive as expected (Avelino et al. 2009).

By removing the variability associated with coffee leaf rust and coffee berry borer plot level predictors, we still found strong landscape effects, supporting a real effect on both noxious species. Although local context strongly drives their incidence, probably even more so than regional context, as already demonstrated for coffee leaf rust (Avelino et al. 2006), our results indicate a strong effect at intermediate landscape scales on these pests and pathogens. Coffee leaf rust and coffee berry borer responses to landscape context were not the same, which can be explained by different dispersal strategies and life histories of these species. Coffee berry borer is a coffee specialist that perceives alternative land uses as dangerous (sensu Fahrig et al. 2011). On the contrary,

large extensions of connected coffee areas appeared to favor the coffee berry borer, probably by increasing the possibilities for flying individuals to find new coffee berries for colonization. This is especially important after the coffee harvest, when coffee berries are scarce. The consequence was an increased survival during this difficult period and higher infestations in the subsequent harvest. These results are compatible with those of Mathieu et al. (1999), who reported movements of coffee berry borer populations across several generations in a coffee plot. In addition, these authors mentioned that movements outside the coffee plot were practically nonexistent, as trapping of coffee berry borer in adjoining land use resulted in almost no catches. In contrast to coffee berry borer, fragmentation of coffee patches, specifically by pasture, surprisingly increased coffee leaf rust incidence. This is probably because coffee leaf rust is an airborne pathogen whose release and dispersal is favored by the presence of open spaces. Wind turbulence is important for the removal of urediospore clusters from host surfaces, before their
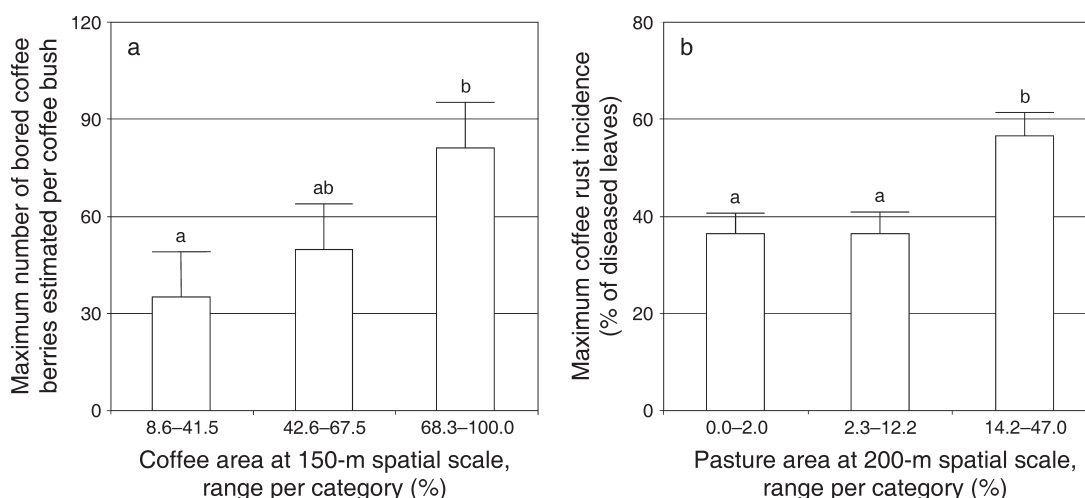

FIG. 4. Landscape context effect on (a) coffee berry borer, with adjusted means corrected by the effects of elevation and number of bored coffee berries remaining in the coffee bush after harvest, and (b) coffee rust incidence, with adjusted means corrected by the effects of soil pH, percentage of shade cover, number of fruiting nodes per coffee bush, and annual number of fertilizer applications. Categories with different letters are significantly different according to Bonferroni test at $P = 0.05$. Error bars show +SE.

dispersal at short and eventually long distances (Becker et al. 1975, Aylor 1990, 1999). Wind turbulence is amplified by gaps in the landscape (Nathan et al. 2005) like those that are produced by patches of pasture in coffee matrices. When removed as clusters, urediospores tend to be deposited at short distances from their source due to their increased settling speed (Aylor 1990, 1999), which could explain the high-intensity epidemics we found at plot level in coffee landscapes fragmented by pasture. This is an illustration of how landscape context could change the plot physical environment and enhance disease incidence.

The relationships of coffee leaf rust and coffee berry borer with landscape context were temporally explicit. The greatest correlation between coffee berry borer and the proportion of coffee in the landscape was found in June–July, just after peak dispersal occurred. It is known that the main dispersal period for this species is driven by limited availability of berries for females to colonize. Berry limitation, in turn, is driven by the coffee harvest. At this time, colonizing females abandon berries overlooked during the harvest to colonize the green berries of the new flowering (Baker 1984, Mathieu et al. 1997, Mathieu et al. 1999). In Turrialba's climatic conditions, this flight period occurs between February and May, depending on elevation (A. P. Olivas, *unpublished data*). At the end of the year, the relationship between coffee berry borer and landscape context disappeared because new harvest had begun, affecting the number of bored berries. This result is compatible with landscape effects on coffee berry borer dispersal and survival during the interseason, as suggested earlier. It also demonstrates that the effect of landscape structure is ephemeral, and driven by plot scale conditions. Concerning coffee leaf rust, significant correlations with landscape context were first found in September, when the epidemic grew enough to produce a great number of urediospores ready to be dispersed by wind. This result also supports our hypothesis that the landscape effect is on rust spore release and dispersal.

Other effects of landscape context on coffee leaf rust and coffee berry borer, particularly through temperature alterations, cannot be excluded. However, as coffee leaf rust and coffee berry borer have very similar temperature requirements, different responses to landscape context would not be expected. As a consequence, we believe that the hypothesis that temperature determines the observed patterns is less probable than those previously discussed. In addition, the landscape context effects we found cannot be explained through natural biological control. During our study, we did not find significant parasitism either of *H. vastatrix* by *L. lecanii*, nor of *H. hampei* by *B. bassiana*. Only one plot contained macroscopic indicators of coffee berry borer parasitism by *B. bassiana*. However, this plot also had the highest coffee berry borer infestation of any plot. Concerning coffee leaf rust, clear parasitism by *L. lecanii* was found in seven plots, but at low levels. Similarly,

PLATE 1. A coffee plantation close to the forest, Turrialba, Costa Rica. Photo credit: J. Avelino.

these seven plots had a higher coffee leaf rust incidence (maximum incidence of 51%, on average) compared to all other plots (maximum incidence of 40% on average).

Finally, root-knot nematodes, which are nearly immobile and sheltered in the soil, were not influenced by landscape context as expected, and possibly were much more dependent on plot scale factors, although we did not identify these factors in this study.

Before discussing the functional spatial scale at which coffee leaf rust and coffee berry borer respond to landscape context, two considerations must be taken into account. First, correlations calculated at very fine spatial scales (50 m) are not very reliable, because the spatial context was nearly uniformly dominated by coffee. Second, effects at large spatial scales necessarily included fine spatial scale effects, as landscape sectors of large radius included the areas of smaller radius. As a consequence, proportions of each land use at different spatial scales were correlated (Steffan-Dewenter et al. 2002).

Steffan-Dewenter et al. (2002) found that different pollinator guilds responded at different spatial scales to the proportion of landscape in seminatural habitats, in relation to their ability to fly and explore the environ-

ment. Species response to landscape context was correlated to larger distances when the dispersal ability of the species was greater (as a function of body size or social behavior). Werling and Gratton (2010) also found evidence that predation of different potato pests was influenced by landscape structure at different spatial scales, probably in relation to the dispersal ability of their specific natural enemies. For coffee berry borer, the relevant spatial scale depended on interpatch land use, which can be interpreted by analogy with the preceding reasoning in terms of permeability to coffee berry borer movements. We suggested that forest and pasture land uses limited coffee berry borer movements. However, forest presented greater friction compared to pasture, as seen by the different scale effects of each land use on the coffee berry borer. The negative correlation with forest peaked at the 150 m radius, and at 400 m for pasture. Although the correlation with sugar cane was not statistically significant, we found negative correlations peaking at 500 m, similar to the pasture scale, indicating a lower resistance to coffee berry borer movements. The peak correlation with coffee proportion at 150 m is compatible with known coffee berry borer dispersal distances (reported by Mathieu et al. 1999) of 110 m across generations within single coffee plantations over a 10-month period. Our results tend to confirm that the ability to move is determined by the landscape structure in addition to the dispersal ability of the species considered (Goodwin and Fahrig 2002). Concerning coffee leaf rust, we found a peak correlation with pasture proportion at the 200 m radius, indicating fairly fine-scale effects of landscape context on coffee leaf rust. However, coffee leaf rust, like many fungi (Aylor 1990, 1999) is able to spread to much larger distances (Bowden et al. 1971, Becker et al. 1975) and may also respond to larger landscape contexts that were beyond the scope of this study.

These results demonstrate that landscape structure can have direct effects on pests and diseases that differ from the indirect landscapes effects on pest and pathogen control through beneficial organisms generally reported (Altieri 1999, Thies and Tscharntke 1999, Thies et al. 2003, Bianchi et al. 2006, Werling and Gratton 2010). These effects depend on both the species in question and the scale (Goodwin and Fahrig 2002). Forest, pasture, and sugar cane offer differential resistances to coffee berry borer movement, but at different scales, with forests decreasing species abundance at the finest scale. The mechanisms underlying these differential resistances are not well known, but are most likely a combination of physical (barrier to wind current) and chemical ecology (attraction/repulsion). In contrast, coffee leaf rust incidence is increased with the presence of pastures adjacent to coffee at fine scales. Goodwin and Fahrig (2002), in testing for impact of landscape structure on landscape connectivity, found two generalizations. First, that increasing interpatch distance significantly decreased landscape connectivity,

which our coffee berry borer results support, although this distance varies depending on the land use type between adjacent coffee patches. Second, that the influence of matrix elements on landscape connectivity is small in comparison to the influence of habitat elements, which our results also support for the coffee berry borer. However, our results show that adjacency to nonhabitat land uses can also have favorable effects on some species; an example is the pasture matrix, which can increase coffee leaf rust incidence.

The results obtained indicate that fragmenting coffee farms at fine scales may help to significantly reduce coffee berry borer movements between coffee plots. The effect of connectivity of susceptible patches on pest and pathogen dispersal has already been suggested, mostly in temperate forests (Perkins and Matlack 2002, Holden-rieder et al. 2004, Condeso and Meentemeyer 2007). In those cases, landscape fragmentation with nonhost land uses was proposed to create barriers to pest and pathogen movement. In contrast, fragmentation of coffee landscapes, particularly by pasture, may increase coffee leaf rust epidemic intensity. These results provide evidence of the need to take into account the whole pest and pathogen complex for their efficient management. At the landscape scale, we hypothesize that interspersing forest corridors and coffee plots may help to control coffee berry borer movements between coffee plots without favoring coffee leaf rust dispersal. In addition, this strategy might complement other ecological mechanisms of coffee berry borer control such as predation by ants (Perfecto and Vandermeer 2006, Armbrecht and Gallego 2007), whose richness has been shown to decrease with distance from forest fragments (Perfecto and Vandermeer 2002, Armbrecht and Perfecto 2003), or even predation by birds (Kellermann et al. 2008), whose abundance is associated with the presence of trees. Such a strategy of fragmenting coffee-dominated landscapes with forest or tree cover may also increase structural connectivity for forest-dependent species, or provide other important ecosystem services such as pollination where needed (Ricketts 2004), presenting a potential win-win-win opportunity for pest and disease control, conservation, and coffee productivity.

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SUPPLEMENTAL MATERIAL

Appendix

Validation of the method for the assessment of the number of coffee berries bored by *Hypothenemus hampei* (*Ecological Archives* A022-036-A1).