Tropical Forest Fragments Enhance Pollinator Activity in Nearby Coffee Crops

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Abstract: *Crop pollination by wild bees is an ecosystem service of enormous value, but it is under increasing threat from agricultural intensification. As with many ecosystem services, the mechanisms, scales, and species through which crop pollination is provided are too poorly understood to inform land-use decisions. I investigated the role of tropical forest remnants as sources of pollinators to surrounding coffee crops in Costa Rica. In 2001 and 2002 I observed bee activity and pollen deposition rates at coffee flowers along distance gradients from two fragments and one narrow riparian strip of forest. Eleven eusocial species were the most common visitors: 10 species of native meliponines and the introduced honeybee,* Apis mellifera *(hereafter* Apis*). Bee richness, overall visitation rate, and pollen deposition rate were all significantly higher in sites within approximately 100 m of forest fragments than in sites farther away (maximum distance of 1.6 km).* Apis *visitation rates were constant across the distance gradient, however, and* Apis *accounted for >90% of all floral visits in distant sites. The gradient from the riparian strip showed a similar drop in bee species richness with distance, but visitation rates were uniformly low along the gradient. Throughout the study area,* Apis *abundances declined sharply from 2001 to 2002, reducing visitation rates by over 50% in distant sites (where* Apis *was almost the only pollinator). In near sites, however, overall visitation rates dropped only 9% because native species almost entirely compensated for the* Apis *decline. Forest fragments (more so than the riparian strip) thus provided nearby coffee with a diversity of bees that increased both the amount and stability of pollination services by reducing dependence on a single introduced pollinator. Exploring the economic links between forest preservation and coffee cultivation may help align the goals of conservation and agriculture within many regions of global conservation priority.*

Key Words: bees, coffee, ecosystem services, fragmentation, landscape, pollination

Fragmentos de Bosque Tropical Incrementan la Actividad de Polinizadores en Cultivos de Café Cercanos

Resumen: *La polinización de cultivos por abejas es un servicio del ecosistema de gran valor, pero está bajo amenaza creciente por la intensificación agrícola. Como sucede con muchos servicios del ecosistema, se conoce muy poco de los mecanismos, escalas y especies por medio de los que proporciona la polinización de cultivos para informar decisiones sobre uso de suelo. Investigué el papel de los remanentes de bosque tropical como fuente de polinizadores en plantaciones de café circundantes en Costa Rica. En 2001 y 2002 observé la actividad de abejas y la tasa de deposición de polen en flores de café a lo largo de gradientes de distancia de dos fragmentos y una franja angosta de bosque ripario. Once especies eusosiales fueron los visitantes más comunes: 10 especies de meliponines nativos y la abeja introducida* Apis mellifera *(*Apis *de ahora en adelante). La riqueza de abejas, la tasa de visitación y la tasa de deposición de polen fueron significativamente mayores en sitios a menos de 100 m de fragmentos de bosque que en sitios más lejanos (distancia máxima 1.6 km). Sin embargo, las tasas de visitación de* Apis *fueron constantes a lo largo del gradiente de distancia y* Apis *dio cuenta de >90% del total de visitas florales en sitios distantes. El gradiente a partir de la franja riparia mostró un descenso*

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similar en riqueza de especies de aves con la distancia, pero las tasas de visitación fueron uniformemente bajas a lo largo del gradiente. Las abundancias de Apis *declinaron drásticamente de 2001 a 2002 en toda la zona de estudio, con reducciones de más de 50% en las tasas de visitación en sitios distantes (donde* Apis *casi fue el único polinizador). Sin embargo, las tasas de visitación en sitios cercanos solo disminuyeron 9% porque las especies nativas compensaron la declinación de* Apis *casi totalmente. Por tanto, los fragmentos de bosque (más que la franja riparia) proporcionaron a los cafetales cercanos una diversidad de abejas que incrementó tanto la cantidad como la estabilidad de los servicios de polinización al reducir la dependencia en un solo polinizador introducido. La exploración de los vínculos económicos entre la preservación del bosque y el cultivo de café puede ayudar a alinear las metas de la conservación y la agricultura dentro de muchas regiones prioritarias para la conservación global.*

Palabras Clave: abejas, fragmentación, miel, paisaje, polinización, servicios del ecosistema

Introduction

Ecosystem services are those natural processes through which ecosystems sustain and fulfill human life. Examples include water purification and flood control by wetlands, crop pollination by wild bees, and spiritual fulfillment derived from natural areas (for general review, see Daily 1997). Because these services are central to human welfare, their economic value, although difficult to estimate exactly, is clearly enormous (e.g., Costanza et al. 1997; Heal 2000). As a result, ecosystem services have the potential to form an economic basis for ecosystem conservation and to clarify the trade-offs decision makers often face in managing landscapes for both nature conservation and economic development (e.g., Chichilnisky & Heal 1998; Balvanera et al. 2001).

Although the economic value of these services is generally recognized, the important specifics about the ways in which ecosystems provide them remain poorly understood (Daily et al. 2000). At what scales do ecosystems provide different services? Which particular species or guilds are most important? Does a diverse system provide higher or more stable levels of a service than a depauperate one (Chapin et al. 2000)? Answers to these questions and others at this level of detail will be essential to managing landscapes for sustained provision of important services.

Crop pollination is a particularly clear example of an ecosystem service with enormous value (Allen-Wardell et al. 1998). Cultivars of approximately two-thirds of the world's crop species require pollination by bees or other animals (Roubik 1995). Although estimating the economic value of pollination services is problematic, they are likely worth billions of dollars per year globally (Southwick & Southwick 1992; Nabhan & Buchmann 1997). Throughout the world, farmers have relied on managed pollinators, particularly honeybees (e.g., *Apis mellifera*, *A. cerana*) to ensure sufficient crop pollination (Levin 1986; Free 1993; Allen-Wardell et al. 1998). However, both feral and managed honeybee populations have undergone severe declines in some regions, as a result of parasitic mites, pesticides, and other factors (Watanabe 1994; Allen-Wardell et al. 1998).

These declines in honeybee populations have sparked renewed interest in the capacity of wild species to provide crop pollination services. Native bees pollinate a variety of crops effectively, at times with greater efficiency than managed species (e.g., Tepedino 1981; Kevan et al. 1990; Freitas & Paxton 1998; Heard 1999). In addition, maintaining a diversity of pollinators may stabilize pollination services over time, buffering against declines in any individual species (McCann 2000; Kremen et al. 2002). As agricultural intensification continues, however (Tilman et al. 2001), there is increasing evidence that wild pollinators are threatened by human land-use practices, exotic species, and other factors (Kearns et al. 1998; Kremen & Ricketts 2000; Richards 2001). Loss of native habitats within agricultural landscapes may be of particular importance, because crop pollination by wild species is provided locally, constrained by the foraging ranges of bees.

Several recent studies have shown that the diversity and abundance of several taxa in agricultural landscapes decline significantly with increasing distance from native habitats. In the Neotropics, for example, Ricketts et al. (2001) found such a decline in moths, Perfecto and Vandermeer (2002) in ants, and Luck and Daily (2003) in birds. To date, however, few studies have linked these patterns to pollination (or any other) services by specifically investigating crop-pollinating (or other service-providing) guilds (e.g., Heard & Exley 1994; Steffan-Dewenter & Tscharntke 1999; Thies & Tscharntke 1999; Kremen et al. 2002). Although these declines in diversity and abundance with distance from forest might be intuitive and expected from theory (MacArthur & Wilson 1967; Hanski 1998), the reported scales of decline differ widely among taxa (Ricketts et al. 2001; Perfecto & Vandermeer 2002; Luck & Daily 2003). Understanding the relevant scales for service-providing taxa is crucial, therefore, to assessing the delivery of ecosystem services in agricultural landscapes (Balvanera et al. 2001).

I investigated tropical forest remnants in Costa Rica as sources of wild pollinators for surrounding coffee crops

and asked whether crops near forest receive higher levels of pollination services than those farther away. I chose coffee because of its importance to both the economies and land-use patterns of many developing countries. Coffee (*Coffea arabica* and *C. canephora*) is one of the most valuable export commodities from developing nations, and coffee production employs over 25 million people worldwide (O'Brien & Kinnaird 2003). Almost 11 million ha worldwide are planted in coffee, typically replacing lower- and middle-elevation tropical forests in some of the world's most biodiverse regions (Olson & Dinerstein 1998; Myers et al. 2000; Roubik 2002). *Coffea arabica*, the species normally grown in Costa Rica, is autogamous (i.e., self-compatible), and thus can set fruit without cross-pollination. Several field experiments have shown, however, that yields decrease 15% to 50% when bee visitation is prevented (Raw & Free 1977; Badilla & Ramirez B. 1991; Free 1993; Roubik 2002).

To investigate whether forest fragments enhance pollination services to nearby coffee farms, I asked three specific questions. (1) Are the diversity and activity (i.e., visitation rate, pollen deposition rate) of coffee pollinators higher in sites near forests than in sites further away? (2) Are distance gradients of pollinator diversity and activity similar from narrow riparian forest strips and large forest fragments? (3) If pollinators are more diverse near forests, does this diversity lead to more stable provision of pollination services over time?

Methods

Study Sites

The ideal landscape for addressing these questions would allow establishment of long, simple, replicated distance gradients from more than one forest patch, with other important variables held constant. This design is difficult to achieve because coffee-producing landscapes are typically composed of many small farms that vary in plant age, variety, shade density, and management regime. The complexity of these landscapes also makes it difficult to measure distance from forest with confidence.

After surveying the coffee-growing regions of Costa Rica, I selected a landscape near San Isidro del General that avoids most of these difficulties. The landscape is dominated by two relatively large forest patches (111 and 46 ha, respectively) and a large coffee farm (Finca Santa Fe, approximately 1100 ha) that extends between them (Fig. 1). Throughout its extent, Finca Santa Fe is managed with similar weed- and pest-control methods, planting and harvest practices, and shade-tree species (*Eucalyptus deglupta*) and density. In addition, the point of maximum distance from forest (1.6 km) exceeds the typical foraging ranges of most local bees (Heard 1999). The finca was converted to coffee from cattle pasture and secondary forest over approximately the last 15 years. No honeybees are currently managed in the area, but feral, Africanized honeybees (*Apis mellifera*, hereafter *Apis*) are abundant (Butz Huryn 1997; Roubik 2002).

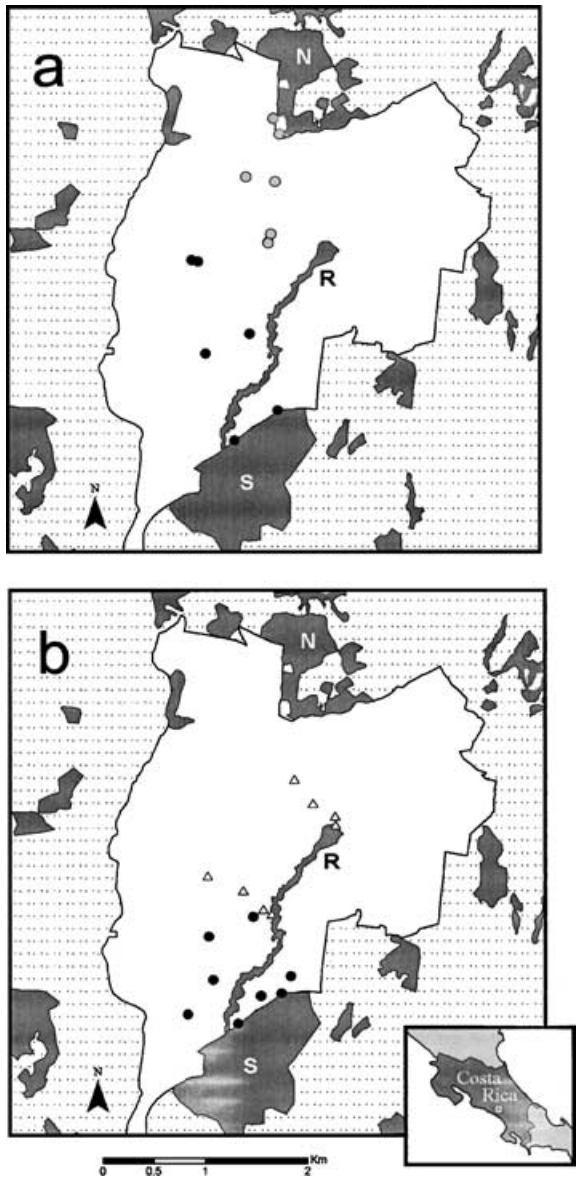

Figure 1. Map of study area near San Isidro del General, Costa Rica, and study sites from (a) 2001 and (b) 2002. In both panels, white area is Finca Santa Fe, planted homogeneously in coffee; stippled area is a mix of coffee, pasture, and sugar cane; and dark gray areas are forest. The three focal forest areas for this study are S, south patch, N, north patch, and R, the riparian forest strip within the farm. Black circles represent sites along the distance gradient from the south patch (note the four sites used in both years), gray circles represent sites along the distance gradient from the north patch, and triangles represent sites along the distance gradient from the riparian strip.

The two forest patches bordering Finca Santa Fe represent tropical/premontane moist forests (Janzen 1983), with typical canopy heights of 20–25 m (J. Florez, unpublished data). The southern patch is held as a forest reserve by a local timber company, and the northern patch is owned by a private individual. Both have been subjected to moderate levels of selective timber harvest but otherwise appear relatively well-conserved. In addition to the two patches, a riparian strip of forest extends 2.5 km into the farm and typically varies in width from 30 to 70 m (Fig. 1). This strip retains a high diversity of native forest tree species and is similar to the forest along most of its length in terms of canopy height, tree density, and age structure (J. Florez, unpublished data). The understory, however, is often more open than that of the forest patches, and edge effects almost certainly affect microclimates and light environments in the narrow strip.

In 2001 I observed bee activity in 12 sites, arranged in three distance classes along transects from both the north and south forest patches (Fig. 1a). The three distance classes corresponded to the maximum possible distance from forest (approximately 1600 m), half of that distance (approximately 800 m), and near the forest edge (approximately 50 m). All sites contained coffee plants of the same variety ("Caturra") and age (8–10 years).

In 2002 I observed bee activity in 16 sites (Fig. 1b). I selected these sites, based on results from 2001, to focus on nearer distance classes and to compare the patches to the riparian strip as sources of pollinators. I placed eight sites to resample the 2001 southern transect, at the existing 50-m and 800-m distance classes and at two new, intermediate classes (100 m and 300 m; Fig. 1b). I placed eight additional sites along two transects extending from a narrow riparian forest strip, at distances that matched those of the 2002 southern transect. Again, all sites contained 8- to 10-year-old Caturra plants.

Bee Activity and Pollen Deposition

Assistants and I observed bee activity throughout the flowering seasons of both 2001 and 2002. In this region, coffee flowers between January and April, typically in three or four flushes ("floreas") lasting 3 days each. Every site was sampled between 1000 and 1400 hours every day during a florea, and sampling order was shuffled daily to avoid biases in environmental factors.

At each site, a portion of a coffee plant composed of approximately 250 flowers was selected, and bee activity at these flowers was observed for 10 minutes (Kearns & Inouye 1993). Every visitor and the number of flowers it visited were recorded. (I define a "visit" as a bee landing on a flower and collecting resources from it.) For each site, two such 10-minute observations were conducted simultaneously on different plants and the counts pooled for analysis.

Visiting bees were identified to morphospecies in the field, with a reference collection to maintain consistency among sites and observers. Individuals that eluded morphospecies assignment in the field were coded as "unknown" and were assumed to be native because *Apis* was the only known exotic bee in the area. Morphospecies were later specifically identified by C. Michener and R. Brooks (University of Kansas).

To measure pollen-deposition rates, in each of the 12 sites I collected stigmas from 10 coffee flowers 24 hours after they opened, during a single florea in 2001. Following Kearns and Inouye (1993), I mounted stigmas on slides with fuchsin jelly and counted pollen grains under a compound microscope.

Environmental Data and Floral Resources

For each 10-minute observation period, five environmental variables that may affect bee activity were recorded (Kearns & Inouye 1993): time of day, percent sun (percentage of 10-minute period consisting of full sun, as opposed to cloud or haze cover), wind strength (categorical scale from 0, no wind, to 3, wind at approximately 15 km/hour), temperature, and relative humidity (both recorded with a HOBO data logger, Onset Computer Corporation, Bourne, Massachusetts).

In addition, the flower densities of coffee, weeds, and shade trees were estimated in the immediate vicinity of each site. The density of surrounding flowers could either increase observed visitation rates (by attracting more visitors to the area) or decrease them (by competing with coffee flowers for the same visitors). For coffee, flower density within a 10-m radius was recorded on a scale of 0 (no flowers) to 3 (all plants in full flower), for each observation period in both years. For weeds, the same scale was used to estimate the density of flowers for each weed species within a 40-m radius. I then summed scores across species for an overall measure of weed flower density, which was recorded once per florea, only in 2002. I used the same scale to record the density of flowers on every *Eucalyptus deglupta* individual within a 50-m radius and summed scores across trees for an overall measure of flower density in shade trees. Tree flower densities were recorded once per florea, only in 2001. Several of these measures are visual categorizations and subject to observer bias. To minimize this potential problem, observers standardized their techniques before collecting data, and, whenever possible, variables were measured by the same observers in every site.

Data Analysis

I used SYSTAT 10.0 for data analysis and ln(richness), ln(visitation rate + 0.1), ln(pollen grains), and ln(weed flower density) to improve normality in statistical tests.

Table 1. Common bee species observed at coffee flowers and their abundances in 2001 and 2002.

Species[a]	*2001*	*2002*
Melipona fasciata	4	1
Nannotrigona mellaria	24	9
Meliponini spp.[b]	15	0
Plebeia jatiformis	81	128
Plebeia frontalis	28	65
Trigona (Tetragona) clavipes	3	0
Trigona (Tetragonisca) angustula	17	17
Trigona dorsalis	12	5
Trigona fulviventris	45	2
Trigonisca spp.	12	64
Apis mellifera	290	133
Miscellaneous native species[c]	38	45

[a] *All species are in the tribe Meliponini except for* Apis mellifera *(tribe Apini) and miscellaneous native species (mixed tribes).*
[b] *Found, when later identified, to be composed of three species:* Partamona cupira, Trigona fuscipennis, *and* T. corvina.
[c] *Includes 29 rare morphospecies and individuals that eluded morphospecies assignment in the field (i.e., "unknowns" from Methods section).*

Results

Over the 2 years, 1041 individual bees representing 40 morphospecies were observed. Of these 40, the 11 most common visitors to coffee flowers were eusocial species, including 10 members of the tribe Meliponini (Apidae) and *Apis* (Table 1).

In all analyses of 2001 data, I found neither significant differences between the north and south transects (Fig. 1a) nor any significant interactions involving a north-south transect term. Therefore, I pooled the two transects for all analyses that follow.

Bee morphospecies richness (i.e., total number of species) was significantly higher in sites near forest than in sites farther away (Fig. 2a). In 2001 the 50-m sites were significantly richer than the 800- and 1600-m sites, which did not differ from each other (analysis of variance [ANOVA]: $F_{2,9} = 13.36$, $p = 0.002$). In 2002 richness declined steadily between 50 and 800 m from the south patch, although the differences were not significant (ANOVA: $F_{3,4} = 2.17$, $p = 0.234$).

Rates of bee visitation to coffee flowers (calculated as the number of visits per 100 flowers per 20-minute sample) were also significantly higher in near sites than in more distant sites (Fig. 2b). In 2001 the visitation rate in 50-m sites was roughly double that of the 800- and 1600-m sites, which did not differ from each other (ANOVA: $F_{2,119} = 15.24$, $p < 0.001$). Data from 2002 confirmed this result and showed that visitation rates actually dropped within 100 m of the forest edge and remained relatively constant thereafter (ANOVA: $F_{3,51} = 6.13$, $p = 0.001$).

Results for pollen deposition, which is likely the most informative measure of pollinator activity, were similar to

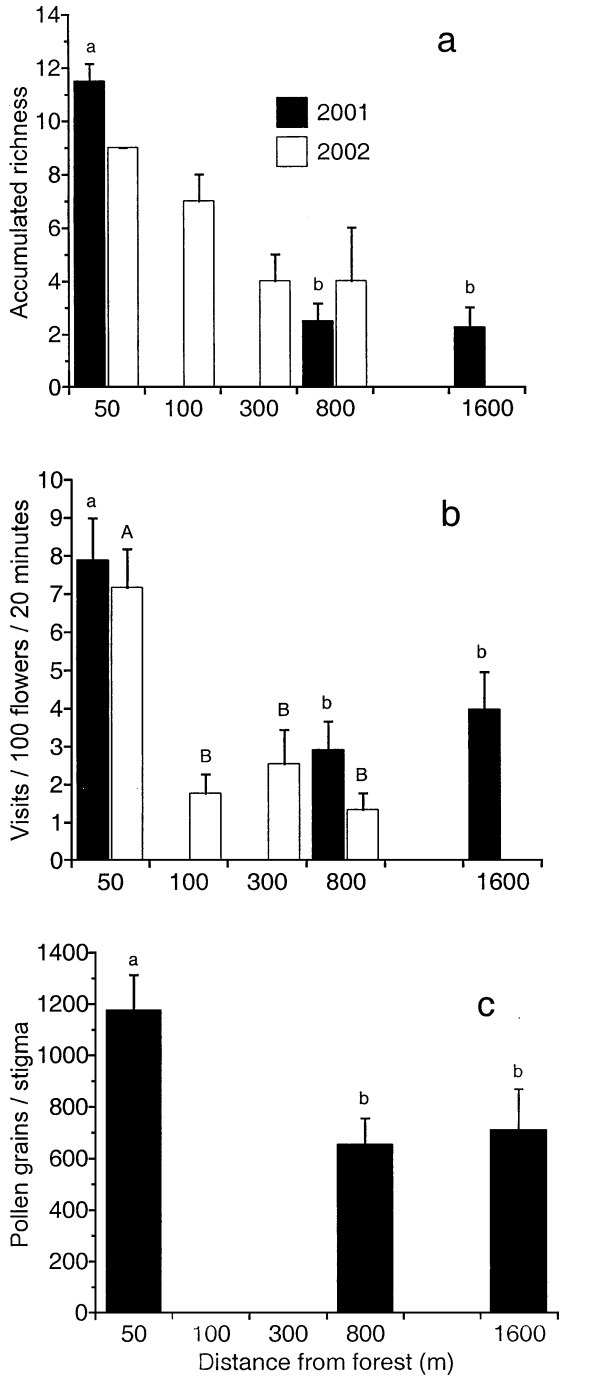

Figure 2. Measures of bee activity and pollen deposition (mean ± SE) along distance gradients from the forest patches: (a) accumulated bee richness (i.e., all samples per site pooled); (b) rate of bee visitation to coffee flowers; and (c) pollen grains deposited per stigma. Letters above bars reflect results of post hoc pairwise comparisons (Bonferroni, p < 0.05) (2001, lower case; 2002, upper case). The 2002 data include patch gradient only (Fig. 1b).

Table 2. Mean visitation rate for *Apis* to coffee flowers and proportion of total visitation rate from *Apis* for each distance class and both years.

	2001		2002[c]	
Distance[a] (m)	visit rate (SE)[b]	% of total	visit rate (SE)[b]	% of total
50	4.06 (0.90)	51.5	0.73 (0.44)	10.2
100	—	—	0.67 (0.32)	38.1
300	—	—	2.35 (0.92)	92.9
800	2.81 (0.74)	96.9	1.19 (0.44)	90.2
1600	3.94 (0.98)	99.5	—	—

[a] *Distance class from nearest forest patch.*
[b] *Mean visitation rate for* Apis *(units are the same as in Fig. 2b: number of visits/100 flowers/20 minutes).*
[c] *Only sites in south-patch gradient are included (Fig. 1b).*

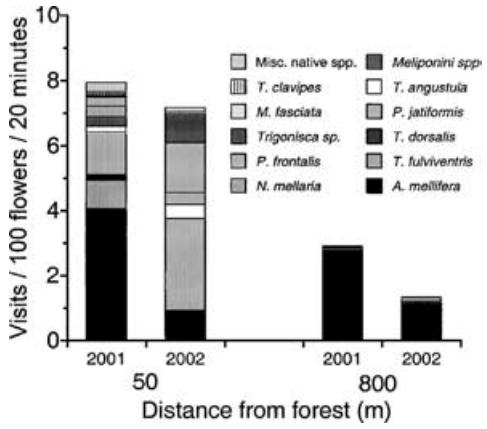

Figure 3. Rate of bee visitation to coffee flowers at 50- and 800-m distance classes from the south patch in 2001 and 2002. Each bar segment represents the mean visitation rate for the corresponding species (error bars are omitted for clarity). Species appear in the stacked bars in the same order as in the legend. Full names are provided in Table 1.

those for overall visitation rates (Fig. 2c). Sites near forest received roughly twice the number of pollen grains as the 800- and 1600-m sites, which did not differ from each other (ANOVA: $F_{2,116} = 7.10$, $p = 0.001$).

Apis contributed an increasing proportion of all visits as distance from forest increased (Table 2). Within 100 m of forest, *Apis* accounted for half or fewer of all floral visits, whereas in more distant sites over 90% of visits were from *Apis*. In fact, *Apis* visitation rates did not differ significantly among distance classes in either year (Table 2; ANOVA: both years $p > 0.65$). The higher overall visitation rate near the two forest patches was therefore due to native species.

Throughout the farm, *Apis* visitation rates declined sharply between 2001 and 2002 (72% decline overall, $t_{116} = 3.88$, $p < 0.001$). At near (50-m) sites, however, several native species increased in visitation rate over the same period, such that overall visitation rates declined only 9% (Fig. 3). In contrast, at the 800-m sites, where *Apis* was almost the sole pollinator, overall visitation rates dropped 54%. (To ensure the closest comparison between years, these results are based only on data from the four sites sampled in both years; Fig. 1.)

Bee richness declined similarly with increasing distance from both the riparian strip and the south forest patch (Fig. 4a; two-way ANOVA: distance, $F_{3,8} = 13.38$, $p = 0.002$; source [i.e., patch vs. strip], $F_{1,8} = 3.58$, $p = 0.095$; distance × source, $F_{3,8} = 3.26$, $p = 0.081$). Rates of bee visitation to flowers, however, showed contrasting patterns. Although visitation rates were significantly elevated in sites nearest the forest patch, they were low at all distance classes from the riparian strip (Fig. 4b; two-way ANOVA: distance, $F_{3,89} = 2.42$, $p = 0.072$; source, $F_{1,89} = 0.26$, $p > 0.60$; distance × source, $F_{3,89} = 6.51$, $p < 0.001$).

Almost none of the environmental variables differed significantly among distance classes, transects (i.e., north vs. south), or sources (i.e., south patch vs. riparian strip). In 2001 (two-factor ANOVAs with distance and transect as factors) only time of day differed significantly among transects ($F_{1,116} = 5.37$, $p = 0.022$). In 2002 (two-factor ANOVAs with distance and source as factors) wind speed was significantly related to distance × source interaction ($F_{3,135} = 4.47$, $p = 0.005$), and abundance of weed flowers differed between sources ($F_{1,36} = 13.52$, $p = 0.001$) and with distance × source interaction ($F_{3,36} = 5.77$, $p = 0.003$). With a Type I error rate (α) of 0.05 and 42 total comparisons, one would expect two significant results by chance alone. I found four.

Discussion

These results suggest that forest remnants enhance pollinator activity in surrounding agricultural fields. Coffee plants within 100 m of forest received more visits by more bee species and experienced higher pollen-deposition rates than plants at greater distances (Fig. 2). These increases were from native bees, which were primarily in sites nearest the forest patches. Plants farther than 300 m from forest appeared to rely almost exclusively on introduced *Apis* for pollination (Table 2).

In addition to augmenting pollinator activity in a single year, bee diversity near forest appeared to help stabilize levels of pollinator activity over time. The sharp decline in *Apis* from 2001 to 2002 greatly reduced overall visitation rates in sites far from forest (800 m), whereas in sites near forest, native species almost entirely compensated for this decline (Fig. 3). Large fluctuations in insect populations are common, including those of important pollinators (Wolda 1978; Roubik 2001). Bee diversity therefore may stabilize pollination services over time through an averaging effect, whereby fluctuations in the abundance

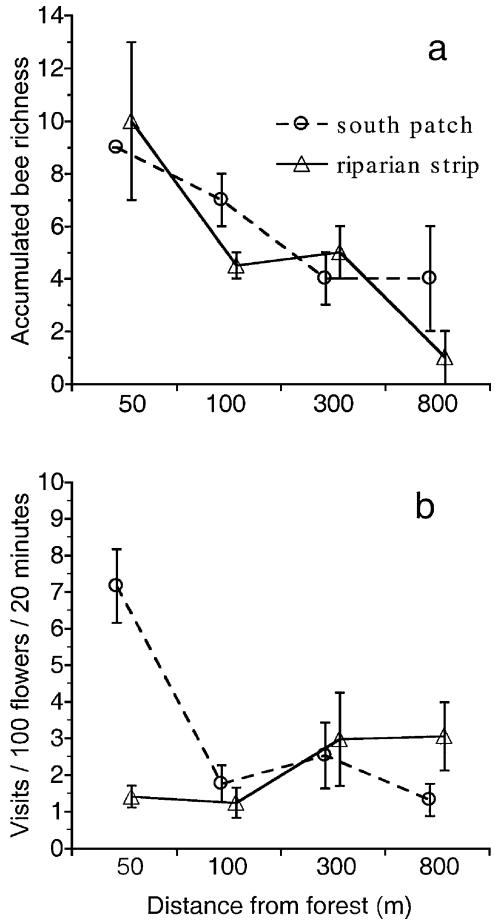

Figure 4. Measures of 2002 bee activity (mean ± SE) along distance gradients from south patch and from riparian strip (Fig. 1b): (a) accumulated bee richness (i.e., all samples per site pooled) and (b) rate of bee visitation (all species) to coffee flowers (for definition, see Results section).

of one population are compensated for by asynchronous dynamics of others (McCann 2000).

Riparian strips of forest are often preserved in agricultural landscapes either by law or by default in areas too steep or flood-prone for cultivation (de Lima & Gascon 1999). Because they are more common than large forest remnants and less threatened by competing land use, these strips potentially represent a convenient and inexpensive source of pollination (and other) services. In my study, however, the riparian strip of forest did not enhance pollinator activity at nearby coffee plants to nearly the same degree as the larger forest patches did (Fig. 4). Although the riparian strip harbored bee richness similar to that of the south forest patch, these species occurred at lower abundances (data not shown); therefore, visitation rates to coffee flowers were not elevated near the riparian strip as they were near the forest patch. The riparian strip clearly contained a diversity of flowering tree species and potential nesting sites (personal observation). Reduced bee abundances there may reflect smaller area or edge effects (e.g., a hotter, dryer microclimate) that reduce its suitability for nesting (Bierregaard et al. 2001).

Although not all bees depend on natural habitats (Michener 2000), both meliponines and *Apis* are thought to require forest habitats for two reasons. First, they prefer to nest in tree cavities (Wille & Michener 1973; Griswold et al. 1995), which are more available in forest than in the managed shade trees on this farm. Second, the diversity of plants (and flowering phenologies) in forests likely provides year-round floral resources for these continually active social species (Roubik 1989; Allen-Wardell et al. 1998; Kevan 1999).

Among native species, the Meliponini were the most common visitors to coffee. The eusocial behavior of these species, and thus their ability to recruit nestmates quickly to resources, may explain their dominance among natives on this flush-flowering crop (Heard 1999). The restriction of the Meliponini to sites nearest coffee is consistent with published studies of their flight ranges. Effective foraging ranges for the majority of meliponines are typically 100–400 m (reviewed in Heard 1999), although maximum observed flights range from 1 to 2 km (e.g., Roubik & Aluja 1983). Given the abundance of coffee flowers open simultaneously throughout the farm, one would expect foraging radii during a florea to be smaller than the maxima observed in native habitats.

If native species are found primarily near forest, why were *Apis* workers equally abundant at all distance classes (Table 2)? This result suggests that *Apis* have either larger foraging distances, less specific nesting preferences, or both. *Apis* are known to forage over greater distances than the native bees found in this study, often ranging to several kilometers (Seeley 1985). In addition, managers destroy *Apis* nests within Finca Santa Fe because these Africanized "killer bees" are dangerous to personnel (farm manager M. Jimenez, personal communication). Together, these two points suggest that *Apis* individuals I observed, even in the study sites farthest from forest, were from nests in surrounding forest patches. Mark-recapture studies (Roubik 1999) and more careful surveys for nests within the farm may help clarify this issue.

Few of the measured environmental factors differed among sample sites in either year. Furthermore, those variables that showed differences did not vary in ways that would appear to influence the bee activity results. For example, although the mean time of sampling differed significantly between transects in 2001, bee activity did not. In addition, the significant distance × source interaction for wind strength and weeds in 2002 (data not shown) did not reflect the pattern of bee visitation rates shown in Fig. 4b.

Although the size and homogeneity of Finca Santa Fe alleviated many design difficulties common to landscape-level studies, nonindependence of sites may still be a potential concern for two reasons (Hargrove & Pickering

1992). First, in 2001 some sites in the same distance class had to be placed within 200 m of each other to keep variety and age of plants constant (Fig. 1a). However, the similarity of results between the two transects, which extended from different forest patches and were oriented in opposite directions, suggests that my findings were not strongly affected by nonindependence of sites. Second, the gradients from the forest patch and riparian strip were somewhat intertwined in 2002; for example, a site in the 800-m distance class from the south patch was within 250 m of the riparian strip (Fig. 1b). Because the observed declines in bee activity usually occurred within 100 m, however, this design is unlikely to have affected the results. Indeed, the site mentioned above showed no evidence of higher bee activity than others in its 800-m distance class.

A few recent studies have begun to illustrate the role of natural habitats as sources of pollinators of surrounding crops. Kremen et al. (2002) found that watermelon farms near natural habitats in California had higher pollinator richness and pollen-deposition rates than those with little or no natural habitat nearby. Heard and Exley (1994) found that the abundance of native bees (primarily *Trigona carbonaria*, a meliponine) at macadamia flowers was strongly correlated with the amount of native vegetation within 1 km, whereas the abundance of *Apis* was not. Finally, in a heavily managed agricultural landscape in Germany, Steffan-Dewenter and Tsharntke (1999) showed that the abundance and richness of flower-visiting bees declined along a 1000-m distance gradient from seminatural grasslands. This decline led to a reduction in seed set for two self-incompatible plants experimentally positioned in the landscape.

Although my results indicate that forest patches are potentially valuable sources of crop pollinators, clear management recommendations will require careful consideration of at least three important issues. First, it is unclear what minimum patch sizes are necessary to support pollinator populations. If forest patches larger than 46 ha supply high bee abundances to nearby coffee but narrow riparian strips do not (Fig. 4b), is there a critical size threshold between these two? Second, although studies of individual ecosystem services are valuable, management options will be best informed through integrated assessments of the bundles of services that forests provide. It appears that the forest patches I studied support both crop pollinators and low-intensity timber production, because each patch was selectively logged (see also Rincon et al. 1999). What other services can forests confer without reducing levels of pollination services? Third, the trade-offs faced by farmers must be carefully considered. For example, the potential benefits of nearby forest must be weighed against the cost of forgone production in those forested areas. If the zone of enhanced pollination services extends only 100 m from the forest edge (Fig. 2), the required area and density of forest patches may be substantial. These options must also be compared to the establishment of managed bee colonies or artificial nests in coffee fields far from forest. *Apis* management, once common in the San Isidro region, was abandoned when *Apis* colonies became "africanized" (M. Jimenez, personal communication), but several Meliponini have been domesticated with varying success (Parker et al. 1987; Heard 1999).

A complementary alternative to maintaining natural habitats near farms may be to manage the farms themselves for pollinator conservation. Coffee is grown under a wide range of shade-management regimes, from intensively managed monocultures with no shade to "rustic" farms planted under the original (typically thinned) forest canopy (Perfecto et al. 1997). Several researchers have shown that less intensively managed farms harbor greater diversity of many taxa, including social bees (Greenberg et al. 1997; Perfecto et al. 1997; Klein et al. 2002). A variety of native shade trees would likely provide nesting sites and year-round floral resources to allow pollinators to persist in the farm itself.

The next step in evaluating the economic value of forests to nearby coffee will require yield experiments along an isolation gradient from forest. Such experiments have begun in this system. Although coffee is self-compatible, yields do increase with higher bee visitation (Raw & Free 1977; Badilla & Ramirez B. 1991; Free 1993; Roubik 2002). Coffee flowers contain only two ovules (Free 1993), so relief from pollen limitation (i.e., too few pollen grains deposited on the stigma) is unlikely to be the mechanism for this observed increase, especially if the pollen loads observed here are typical (Fig. 2c). Instead, the observed increase in yields is likely from higher rates of outcrossing, leading to larger and more robust fruit (Free 1993). Raw and Free (1977) also suggest that coffee individuals may be amphicarpic, with some flowers self-compatible and others requiring cross-fertilization. In addition to yield experiments, studies of the relative pollination efficiency of common bee species would be informative because species are known to differ in their effectiveness as pollinators (Freitas & Paxton 1998; Thomson & Goodell 2001; Kremen et al. 2002).

Despite these remaining uncertainties, my findings suggest that forests may provide a valuable service to surrounding agriculture. As declines in European honeybees worry farmers elsewhere in the world (Watanabe 1994; Allen-Wardell et al. 1998), conserving a diversity of native pollinators may be considered especially valuable as a form of insurance against such declines (McCann 2000; Kremen et al. 2002). Exploring such economic links between forest preservation and coffee cultivation may help align the often-conflicting goals of conservation and agriculture within many tropical regions of global conservation priority (Balvanera et al. 2001).

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