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Do Species Sorting and Mass Effects Drive Assembly in Tropical Agroecological Landscape Mosaics?

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ABSTRACT

Recent assessments of biodiversity in tropical agroecosystems have revealed surprisingly high functional and taxonomic diversity in systems with low management intensity. This biodiversity is the product of community assembly. Because agroecosystems are novel ecosystems and occur in landscape mosaics, the assembly processes generating communities in agroecosystems are poorly resolved. Broadly, two models have been proposed to explain landscape assembly: trade-offs in species performance across habitats (species sorting) and source-sink dynamics between habitats of differential quality (mass effects). These models are largely untested in tropical agroecosystems. We utilize an extensive data set on a tropical twig-nesting ant community from five microhabitat types in a shaded coffee agroecosystem to test for species sorting, mass effects, or a mixed model. To test among these models, we used community similarity and a variance decomposition on a focal microhabitat (a moderate-shade coffee farm) to partition community variance into spatial and environmental components. To identify the source habitat for mass effects and assess their strength, we measured dispersing alates (winged reproductives), artificial nests, and colony and nest size in shade trees and coffee. We found significant environmental and spatial signal and evidence for both species sorting and mass effects. We find sorting occurs among common species, but that mass effects are prevalent among rare species and likely originate in the shade trees. Our results indicate that both metacommunity models occur in tropical landscape mosaics, but they may not apply equally to all species in communities, habitat gradients, or timescales.

Abstract in Spanish is available in the online version of this article.

Key words: alates; biodiversity; dispersal; matrix; metacommunity; Mexico; shade coffee; twig-nesting ants.

BIODIVERSITY IN AGROECOSYSTEMS WITH LOW MANAGEMENT INTENSITY IS OFTEN HIGH AND SOMETIMES COMPARABLE WITH THAT OBSERVED IN UNMANAGED ECOSYSTEMS (Altieri 1999, Barlow *et al.* 2007). This is especially true for agroforestry systems where the structure of natural forest is maintained (McNeely 2004). The most extensive and well-studied agroforestry systems occur in the tropics. Across a diversity of taxa and crops, tropical agroforestry systems contain mean species richness values that exceed 60 percent of adjacent natural forest (Bhagwat *et al.* 2008). Although highly dependent on the agroforestry system examined (Perfecto & Vandermeer 2008), compositional similarity between forest and agroforest is more modest, averaging 48 percent across all taxa and systems (Bhagwat *et al.* 2008). Life history traits strongly influence community similarity with mean values ranging from 25 percent in plants to 65 percent in mammals and generally similarity increases with the mobility of the organisms considered (Bhagwat *et al.* 2008). In addition to systems with low management intensity, species richness and similarity to forest is high where the landscape was converted to agriculture more recently (*e.g.*, because extinction debts are unresolved) and the canopy cover of native trees is high (Beukema *et al.* 2007, Philpott *et al.* 2008). Most studies of agroforest biodiversity document static species richness, taxonomic composition, mobile species whose presence may be transient, or differences in trophic structure between habitats (*e.g.*, Tylianakis *et al.* 2007). In contrast, few examine the role of assembly processes, including species interactions, dispersal, and history, in determining the structure of agroecosystem communities (but see Hogg & Daane 2010). Although the assembly of communities within some agroecosystems is increasingly well studied (*e.g.*, Vandermeer *et al.* 2008), the general assembly processes that occur among agroecosystems and natural habitats and among different agroecosystems within a landscape are less well understood and are not integrated with theory. An understanding of community assembly processes is critical to understand the current conservation and management value of tropical landscapes and to predict the impacts of landscape change on biodiversity and ecosystem function (Chazdon *et al.* 2009, Gardner *et al.* 2009).

Assuming that an agroecological landscape can be characterized as a metacommunity (a set of local communities interacting via the dispersal of multiple interacting species), four basic assembly models are possible: neutral, patch dynamics, species sorting, and mass effects (Leibold *et al.* 2004). Neutral models remain contentious and are based on assumptions that are difficult to test (Purves & Turnbull 2010) and evaluating patch dynamics requires temporal data on communities in multiple different habitats that is typically not available in field systems. These

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limitations leave two models, species sorting and mass effects, as implicit assembly models in the literature on biodiversity and community structure in tropical agroecological landscapes. The first, species sorting, focuses on trade-offs in the way species respond to different landscape types. The occurrence of trade-offs in a metacommunity implies that: (1) species can disperse across the landscape (*i.e.*, there is no dispersal limitation) and (2) that species are differentially adapted to different habitats. Thus, species sorting is dispersal coupled with differential adaptation. Strict sorting occurs at the 'community-scale' (all species well adapted to the forest are poorly adapted to the agroecosystem and *vice versa*), although this scenario is unlikely to occur in most situations. This model fits with the general assumption that species found in natural forests of a given region will reproduce (Hatchwell *et al.* 1996), forage (Ricketts *et al.* 2001), and survive (Foppen *et al.* 2000, Vandermeer & Carvajal 2001) poorly, if at all in agricultural habitats of increasing management intensity (Ricketts *et al.* 2001). The second model, mass effects, proposes that constant dispersal from the forest into agroecosystems drives assembly. In this model, populations in forest fragments are considered sources from which dispersal maintains species survival in agroecosystems (Ricketts *et al.* 2001, Armbrecht & Perfecto 2003).

Species sorting and source-sink models fall at ends of a continuum from low to high inter-habitat patch dispersal rate in heterogeneous metacommunities, respectively (Mouquet & Loreau 2002, Leibold 2009), meaning both models may act on the same metacommunity. In addition, because dispersal rates and degree of habitat specialization may be highly unequal between species within the metacommunity, a mixture of sorting and mass effects can also occur where subsets of species follow each model (Pandit *et al.* 2009). Species sorting is thought to be the dominant metacommunity model in nature, but these two types of mixed models also occur (Cottenie 2005). Despite the presumption that these assembly models operate, we are aware of no studies explicitly testing for their occurrence in tropical landscapes that include agroecosystems.

We utilize a community of twig-nesting ants that occur across a gradient of microhabitat types in a coffee-producing region of southern Mexico to test three hypothesized landscape-scale assembly mechanisms: (1) species sorting, (2) mass effects, and (3) a mixed model. In this system, twig-nesting ants opportunistically colonize hollow twigs on coffee plants that occur in the understory (Philpott & Foster 2005), other understory shrubs, and the canopy of shaded coffee farms and also in trees and shrubs in forest fragments. Importantly, twig-nesting ant colonies are relatively sessile (compared with winged insects, *e.g.*, butterflies) and represent a guild of species that compete for similarly sized/structured and limiting nest sites (Livingston & Philpott 2010). This community is also important in regulating populations of the coffee leaf miner (*Leucoptera coffeella*) and the coffee berry borer (*Hypothenemus hampei*), key pests of coffee (De la Mora *et al.* 2008, Larsen & Philpott 2010, Philpott *et al.* 2012).

We utilize two interrelated approaches to test among assembly mechanisms. First, we surveyed community structure (species composition and colony abundance) from sampling sites in five microhabitats: coffee twigs under high, moderate, and low shade, understory plants of a natural forest, and twigs in the shade tree canopy of the moderate-shade farm. To test for sorting and mass effects, we used inter-microhabitat community-similarity analyses and supplemented this with a variance decomposition on a focal microhabitat (the moderate-shade farm) to partition community variance into spatial and environmental components. Second, to identify the source habitat and strength of mass effects, we directly measured dispersing alates in the coffee layer, compared colony and nest size between shade trees and nests in coffee, and examined colonization data by placing artificial nests in all microhabitats. Distinct ant communities occur across vertical strata in tropical forests, especially between the understory and canopy, but numerous species occur in both environments (Byrne 1994, Bruehl *et al.* 1998, Vasconcelos & Vilhena 2006). Assuming ants do not disperse solely through colony budding (Keller 1991), species are present in a microhabitat through mass effects only if they do not produce sufficient alates in that microhabitat to sustain a population. Larger colonies also produce more alates than smaller colonies (Shik 2008). We hypothesized larger nests and a greater diversity of woody plant species (and thus a greater diversity of nesting resources) in the shade tree canopy of the moderate-shade farm (Perfecto *et al.* 2003) would make the canopy a source habitat and coffee a candidate sink.

METHODS

Our study was conducted in the Soconusco region of Chiapas, Mexico (15° 10′ N and 92° 20′ W, 950–1220 m elevation, ~4500 mm rain annually; see Fig. S1) between 2006 and 2009. We conducted surveys of ant communities in natural (coffee and tree twigs) and artificial nests (bamboo twigs added to understory plants and shade trees). Artificial nests were initially placed to experimentally examine factors influencing colonization processes in twig-nesting ants (*e.g.*, Philpott 2010), but here, we use these data as a test of the response of ants in each microhabitat to a different nesting environment. Artificial nest sites differ from natural twig nest sites because they are open at one end (lacking a lateral entrance hole), have a thicker cavity wall, and thus differ in hardness, moisture content, and airflow (Cobb *et al.* 2006). Previous work in this system has established that ants inhabiting twigs on single or groups of coffee plants form local communities that link through dispersal to form a metacommunity at landscape (*e.g.*, entire farm) and inter-landscape scales (Livingston & Philpott 2010).

Surveys were conducted in three different coffee production environments: a shaded monoculture (Finca Hamburgo), a commercial polyculture (Finca Irlanda), and a traditional polyculture (Finca Irlanda Restoration) (Moguel & Toledo 1999, Philpott *et al.* 2008), hereafter referred to as low-, moderate-, and high-shade environments, respectively. Surveys and nest additions were conducted in the following five microhabitats (within or adjacent to the above three habitats): (1) coffee plants in the low-shade farm; (2) coffee plants in the moderate-shade farm; (3) coffee plants in the high-shade farm; (4) the subcanopy of a 15-hectare forest fragment bisecting the two farms (Armbrecht & Perfecto 2003); and (5) the shade tree canopy of the moderate-shade farm. With the exception of natural forest, each microhabitat type comprises a shade canopy and an understory of coffee plants. Each habitat is distinct and declines in canopy tree diversity from the forest to high-, medium-, and low-shade coffee (Perfecto *et al.* 2003, Philpott *et al.* 2008, see Table 1).

Ants were identified using a photographic guide to the ants of the region and other published guides for Neotropical ants (Fernández 2003, Longino 2007). We considered any number of queens, workers, or alates of a species inside a twig on a single coffee plant or shade tree to constitute a colony (McGlynn *et al.* 2009). Coffee plant surveys followed methodology detailed in Philpott and Foster (2005) and Livingston and Philpott (2010), and generally involved removing and opening all dry twigs from each coffee plant within a survey site (Appendix S1; Table S1) and recording the identity of ants in occupied twigs. Artificial nests (bamboo twigs) were attached to coffee plants with twist-ties between 0.5 and 2.0 m aboveground. Five artificial nests were attached per coffee plant and the spatial arrangement of plants to which bamboo twigs were attached varied with experiment (Appendix S1). The bamboo was cut between 10 and 20 cm long and had 3–8 mm diameter openings at one end. Although sampling effort varied among surveys and experimental nest site additions, all efforts are spatially and numerically extensive and have been shown to saturate species accumulation curves (Appendix S1; Table S1; Livingston & Philpott 2010). Accurate estimation of species abundances occurs before saturation of richness (Angermeier & Smogor 1995), indicating our abundance estimates are likely accurate. General patterns of twig-nesting ant proportional abundance have remained relatively constant since 2005 (*i.e.*, most and least abundant species have not reversed rank), indicating that the 3-yr window under which

TABLE 1. *Summary of environmental characteristics and twig-nesting ant communities in each microhabitat in coffee agroecosystems and forests in Chiapas, Mexico. LS, low-shade coffee; MS, moderate-shade coffee; HS, high-shade coffee.*

Microhabitat	Shade cover[a]	Tree richness[b]	Ant richness	Evenness[c]	Shared species[d]	Occupancy[e]	Dominant[f]	Subdominant
Natural nests in coffee, shade trees or forest								
LS	14	4 (0.37)	6	1.28	0.83	0.93	*Pseudomyrmex ejectus* (65)	*Pseudomyrmex simplex* (24)
MS	40	4.87 (0.44)	12	1.65	1	0.82	*Pseudomyrmex simplex* (29)	*Pseudomyrmex ejectus* (28)
HS	91.5	4.87 (0.44)	11	1.85	1	0.68	*Pseudomyrmex simplex* (31)	*Procryptocerus hylaeus* (25)
Tree	–	4.87 (0.44)	23	2.03	–	0.69	*Procryptocerus hylaeus* (19)	*Pseudomyrmex elongatus* (10)
Forest	100	14.33 (1.86)	13	2.02	–	0.35	*Procryptocerus hylaeus* (22)	*Myrmelachista #2* (19)
Artificial nests in coffee, shade trees or forest								
LS	14	4 (0.37)	30	1.84	0.8	0.37	*Dolichoderus lutosus* (16)	*Procryptocerus hylaeus* (14)
MS	40	4.87 (0.44)	21	1.79	0.81	0.29	*Procryptocerus hylaeus* (18)	*Pseudomyrmex simplex* (14)
HS	91.5	4.87 (0.44)	25	1.89	0.96	0.24	*Procryptocerus hylaeus* (26)	*Camponotus striatus* (11)
Tree	–	4.87 (0.44)	18	1.77	–	0.29	*Solenopsis picea* (26)	*Procryptocerus hylaeus* (19)
Forest	100	14.33 (1.86)	5	1.85	–	0.01	*Pachycondyla #1* (53)	*Wasmannia auropunctata* (20)

[a] Shade cover (percent) was estimated using convex spherical densitometer readings and fisheye lens photography.

[b] Tree richness (SE) is the average in 20 × 20 m plots in each habitat (Moorhead *et al.* 2010).

[c] Evenness is Pielou's evenness (Pielou 1966).

[d] Shared species is the proportion of species in each coffee microhabitat that also occurred in either natural or artificial nests in the forest or shade trees.

[e] Occupancy is the number of twigs occupied by ants over the total number of hollow twigs sampled in each microhabitat.

[f] Dominant species is the species with the most colonies and subdominant is the species with the second-largest colony count. Percent of relative dominance of total colonies in each community is shown in brackets.

these samples were taken does not confound sampling date with microhabitat (*e.g.*, Philpott & Foster 2005 to Livingston & Philpott 2010). Methods for survey of the shade tree canopy, forest fragment, and artificial nest surveys used variable sampling and blocking designs (Appendix S1; Table S1). Each microhabitat survey was conducted only once and not all surveys were conducted during the same year.

To examine ant dispersal, we utilized two Philadelphia style ultraviolet light traps (12W, range unobstructed of up to 1 km; Bioquip Inc., Rancho Dominguez, California, U.S.A.). We placed traps in open areas in the coffee layer along ridgelines within the moderate-shade area (>1 km distant from forest or other microhabitats) to maximize visibility to flying alates. Traps were run from dusk until dawn nightly for 8 wk between 31 May and 23 July 2009. This time period corresponds to the peak of alate production for many Neotropical species (Kaspari *et al.* 2001). Traps were moved on a weekly basis to different suitable locations 100 m distant from the previous location along a transect. Trap catches were collected once every 2–3 d (depending on rainfall) and alates were extracted from the catch. Alates were identified to species or morphospecies by comparing candidate ant queens against a reference library of male and female alates collected during 2009 and previous sampling periods. Capture rates were highly variable both spatially and temporally, and we use only the total number of captures here.

We summarize community compositional similarity among microhabitats by calculating Bray–Curtis dissimilarity and displaying the results using a cluster dendrogram implemented with the Vegan package (Oksanen *et al.* 2011) in R (R Development Core Team 2011). We also compute various summary statistics including evenness, shared species between coffee, forest, and shade trees, and we list the numerical dominant and subdominant species in each community. As we do not have high-resolution environmental data for all microhabitats, to test among our three assembly hypotheses, we used detailed environmental and spatial data from the moderate-shade coffee farm only to run a variance decomposition. We assume that if ant communities respond to the relatively narrow range of environmental variation (in *e.g.*, shade cover) within this single microhabitat, then they will respond to even greater variation in the same environmental factors between microhabitats. Data for this analysis come from 24 × 100 m^2 quadrats of coffee plants among six sites each 400 m^2 in size (4 quadrats per site) in the moderate-shade farm; detailed methods for environmental and spatial data collection are outlined in Appendix S1. The variance decomposition method partitions total variation in the community by site matrix into unique fractions that are explained purely by the spatial matrix (site coordinates) and purely by the environmental matrix and was implemented using the Vegan package. This uses a partial redundancy method and is a multivariate extension of linear regression computing R^2 values (Peres-Neto *et al.* 2006) that measure the amount of community variation (percent of total) that can be attributed exclusively either to the set of environmental or to the set of spatial variables. The spatial boundaries of local communities within each microhabitat are not well known; consequently, our spatial matrix is conservative and uses only linear information from site coordinates to avoid possible overfitting to random variation (Gilbert & Bennett 2010). In general, if a significant amount of variance is attributed to pure spatial components, then community assembly may follow a neutral model or patch dynamics model, whereas pure environmental components indicate species sorting, and a combination of spatial and environmental components indicates both mass effects and species sorting (Cottenie 2005). To distinguish between the two possible types of mixed model, we also ran a separate variance decomposition on common species (those with greater than ten total colonies, five species) and rare species (those with ten or less total colonies, seven species). Significance of fractions of variance explained was tested using ANOVA. We summarize the environmental factors using canonical correspondence analysis (CCA). An analysis of variation inflation factors (VIF) on the environmental variables showed sufficiently low co-linearity so that variable reduction was not necessary.

To identify the source and strength of mass effects, we used three approaches: (1) we correlated the colony abundance of each species in the moderate-shade farm with its abundance in the alate pool collected from the moderate-shade farm. If all species captured as alates are present with colonies in the moderate-shade farm, then a significant correlation indicates dispersal is primarily coming from within the microhabitat, whereas no correlation suggests that dispersal could be coming primarily from other microhabitats. (2) We compared mean colony (total number of individuals) and twig nest sizes (area of hollow circular opening at the center point of the cavity, Livingston & Philpott 2010) from a random subset of all colonies and occupied nests collected (logistical constrains meant not all colonies and nests could be measured) in the shade trees with those in coffee plants of the moderate-shade farm. Overall significantly larger colonies and nests in one microhabitat indicate a source-sink dynamic is possible because large colonies produce more alates (Shik 2008). (3) We compared the ratio of species richness in artificial nests to natural nests within all microhabitats. Greater species richness in artificial nests indicates recruitment to a microhabitat is limited by the characteristics of natural nest sites (*e.g.*, there are species found in the shade trees that can only establish in coffee using artificial but not natural nests). Under this situation of recruitment limitation due to natural nest-site characteristics, mass effects are likely because species arriving from other microhabitats (where they may be adapted to different nesting resources) are forced to colonize suboptimal natural nest sites. We used ANOVA for significance tests of (2) and (3).

RESULTS

Distinct communities occurred in each natural microhabitat (Table 1). The forest was the least similar to other communities, while similarity was high among low- and moderate-shade coffee and among the shade trees and high-shade coffee (Fig. 1A). Many communities shared the same numerically dominant or subdominant species and these species accounted for only four (12%) of the 33 species occurring in all natural microhabitats (Table 1). Consequently, dissimilarity among communities was driven both by changes in relative abundances of these dominant species and extensive turnover in rare species (Table S2).

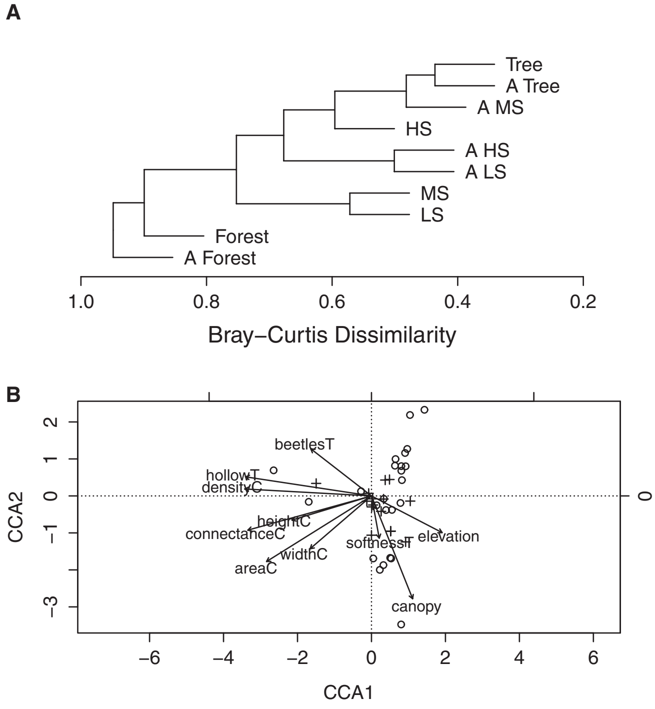

FIGURE 1. (A) Cluster dendrogram showing similarity in species composition among microhabitats. 'A' refers to artificial nests. (B) Canonical correspondence analysis of environmental variables for the moderate-shade microhabitat. Species are shown as crosses and sites as points. Environmental variables by site are elevation, mean canopy cover (canopy), connectance among coffee plants, mean width, height and area of coffee plants, density of coffee plants, number of hollow twigs, proportion of soft twigs, and the number of wood boring beetles inside twigs. 'C' indicates coffee plant variables while 'T' indicates twig variables.

The variance decomposition indicated that environmental and spatial factors together explained 24.5 percent of community variation in the moderate-shade microhabitat with 75.5 percent of the variation unexplained. Both space and environment, while controlling for the other, explained unique and significant fractions of variation (Table 2), suggesting both species sorting and mass effects are operating and providing no evidence for neutral or patch dynamics. Similar results occurred among common species, although space, controlling for environment, was marginally insignificant ($P = 0.055$). Among rare species, neither spatial nor environmental components explained significant fractions of variance, meaning we cannot evaluate assembly processes among these species using this method. The relationship between environmental factors, species, and sites are summarized with the first two components of a canonical correspondence analysis (Fig. 1B). Nest-site abundance, various coffee plant features, and canopy cover formed three clusters of explanatory factors.

Alate captures (totals listed by species in Table S2) in the moderate-shade microhabitat were highly significantly correlated with the abundance of each ant species in this microhabitat (Fig. 2, $N = 14$, $Y = -0.1x+0.82$, $R^2 = 0.63$, $F = 21.7$, df = 11, $P < 0.001$), suggesting microhabitats are dominated by internal dispersal. In addition, all species captured were a subset of those found in natural nests in the moderate-shade farm. The light trap catch was dominated by male alates by a 3:1 ratio.

Colony size and twig size were significantly larger (approximately double that of coffee) in the shade tree canopy (Fig. 3, $P < 0.0001$ in both cases, $F = 49.46$ and df = 1 for twig size and $F = 14.25$ and df = 1 for colony size, ANOVA). Nest-site occupancy rates were within a similar range among coffee microhabitats and the shade trees, but extremely low in the forest in

TABLE 2. *Variance decomposition output. (S+E) refers the total amount of variation explained by both space and environment, (E) and (S) are variation explained by environment and space, respectively, (E|S) is variation explained by environment controlling for space, and (S|E) is variation explained by space controlling for environment. Percent variation is the adjusted* R^2 *values of the model output.*

	Variance decomposition output	
Component	Percent variation	*P*-value
All species		
[S+E]	0.245	0.013^{*}
[E]	0.101	0.122
[S]	0.046	0.097
[E|S]	0.199	0.02^{*}
[S|E]	0.144	0.03^{*}
Common species		
[S+E]	0.318	0.022^{*}
[E]	0.155	0.107
[S]	0.015	0.302
[E|S]	0.302	0.029^{*}
[S|E]	0.162	0.055
Rare species		
[S+E]	0.17	0.0526
[E]	0.093	0.13
[S]	0.112	0.003^{**}
[E|S]	0.058	0.251
[S|E]	0.078	0.106

$^{*}P < 0.05$, $^{**}P < 0.01$.

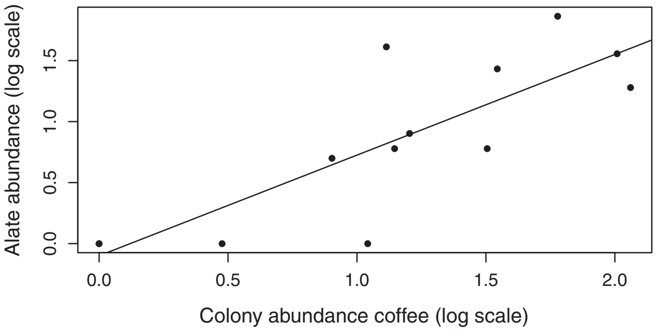

FIGURE 2. Correlation between colony abundance in moderate-shade coffee and total alates captured by species. A linear regression line is fitted. Each point represents one species.

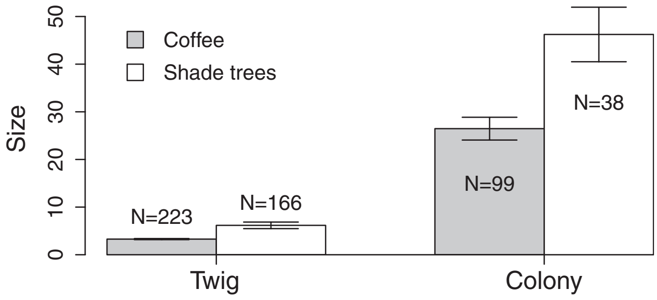

FIGURE 3. Twig and colony size in the moderate-shade coffee farm (coffee) and the shade tree canopy (shade trees). Twig size is the mean area in mm of the hollow circular opening at the center point (Livingston & Philpott 2010). Colony size is the mean number of individuals per colony. Both data sets come from a random subset of the community sampled in each habitat. Error bars show standard error. Twig and colony size are significantly correlated in coffee ($P < 0.0001$, $F = 1350$ and df = 1) but not in the shade trees ($P = 0.5$).

both natural and artificial nests (Table 1). Richness of ants in artificial nests was as much as five times higher than natural nests in a given coffee microhabitat, but in the shade trees and forest richness in artificial nests was reduced relative to natural nests (Fig. 4; Table 1). All species present in the moderate- and high-shade coffee microhabitats, and 83 percent of species found in low-shade coffee, were a nested subset of species present in the shade trees or forest (Table 1).

DISCUSSION

Our variance decomposition results support the hypothesis of a mixed model where both species sorting and mass effects occur. Although we only conducted this analysis within the moderate-shade microhabitat, high variation in the important environmental variables (*e.g.*, shade cover) between the coffee microhabitats and the shade tree canopy and forest mean that sorting is likely to be a primary driver of differences in ant communities across the gradient. Comparisons of the numerically dominant species across the microhabitats suggest that a small number of species drive the sorting process. Previous work in the moderate-shade system has shown that a numerically dominant species, *Pseudomyrmex simplex*, represents a core metapopulation that spatially aggregates less abundant satellite species into the remaining nest sites (Livingston & Philpott 2010). In our analysis, *Ps. simplex* again emerges as a dominant or subdominant ant species in all of the coffee microhabitats, suggesting that it and other dominant species (*e.g.*, *Pseudomyrmex ejectus* and *Procryptocerus hylaeus*) are responding to turnover in environmental conditions across microhabitats, whereas rare species remain rare or are absent entirely from some microhabitats.

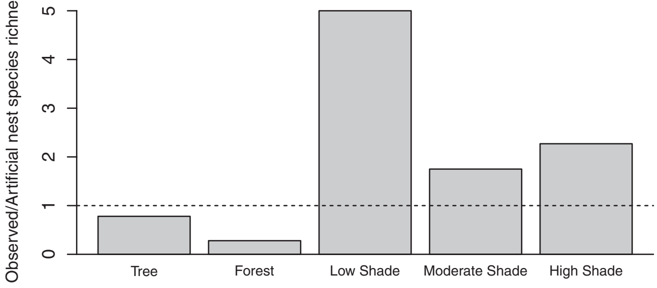

FIGURE 4. Ratio of observed total species richness in natural nests to richness in artificial nests in each microhabitat. The dashed line indicates the 1:1 line. Artificial nests in the shade trees and forest captured less species than were observed in natural nests, whereas the reverse occurred in the coffee microhabitats.

The significant correlation we observed between alate captures and colony abundance in the moderate-shade microhabitat is the first correlation reported between dispersing propagules and population abundance for an ant community. It suggests dispersal within a microhabitat is primarily driven by internal dynamics and not by a heavy 'propagule rain' from another microhabitat. The spatial signal in our variance decomposition suggests mass effects are occurring alongside sorting within the moderate-shade microhabitat. For common species, these mass effects are likely to be occurring among sites with different environmental conditions within the coffee microhabitat. These observations do not, however, negate the likelihood of mass effects between microhabitats because some rare species were absent entirely from the alate captures and a proportion of alates for more common species may have originated in other microhabitats.

In fact, for rare species, we hypothesize that our variance decomposition is uninformative because the analysis did not include their probable source microhabitat: the shade trees. For rare species, the origin of these mass effects is more likely to be the shade tree canopy than source environments within the coffee layer or the forest. This is because the environmental differences between the shade trees and coffee are much greater than that among sites in the relatively homogenous coffee layer. The significantly larger twig and colony sizes in the shade trees and the diversity of shade tree species (total tree diversity may be as high as 200 species in the moderate-shade farm, Perfecto *et al.* 2004) indicate the shade trees are both a more productive and heterogeneous environment than coffee. Although the forest is more heterogeneous still, extremely low occupancy rates in both natural and artificial nests suggest that productivity of twig-nesting ant biomass is low or restricted to the high canopy. The forest is also less likely to drive mass effects because it is small in size (~15 ha) and because it is spatially disjoint from the coffee layer, whereas the shade tree canopy extends over the entire area of coffee production (300 ha for the moderate-shade farm).

The enhanced species richness in artificial nests in coffee, but not in the shade trees or forest, provides an important experimental confirmation that natural nest-site characteristics, including possibly their number, structure, or spatial arrangement, limit recruitment of certain ant species to the coffee layer. This suggests that natural nest sites in coffee may be a suboptimal resource for some species that occur in the shade trees or forest and establishes the environmental differences necessary for mass effects. This observation coupled with higher evenness in the forest and shade trees (Table 1) suggests ant communities in the forest and shade trees may inhabit a diverse and stable (less source-sink dynamics) niche space relative to coffee. This may be especially true for the forest microhabitat, where many species we recorded nesting in twigs in coffee may occupy different micro-environments. For example, *Crematogaster carinata* was found on the myrmecophytic plant *Cordia alliodora* at La Selva Biological Station in Costa Rica (Trager & Bruna 2006) and *Dolichoderus lutosus* nested in epiphytes in the canopy of the Atlantic rain forest of Brazil (Majer & Delabie 1999).

Overall, our results indicate that a set of dominant species drive sorting across the microhabitat gradient we considered, whereas rare species may be present or not in coffee depending on the strength of mass effects from the shade tree canopy. The forest could be important in this landscape as a long-term source pool of species that colonize or recolonize the coffee layer or shade trees as management changes in the surrounding agroecological matrix. Uncovering this dynamic, however, would require long-term data that is not yet available for tropical systems. Further research elucidating environmental and behavioral factors that modulate the permeability of agroecosystems to dispersal (both short term source-sink and long-term colonization) from candidate source habitats (shade trees, remnant, or fallow forest) will ground a mechanistic understanding of metacommunity assembly in tropical landscape mosaics. This is crucial to determine whether agroecosystems act as a high-quality matrix that supports the conservation of species dispersing among fragments (Vandermeer & Perfecto 2007), as a sink environment, or as a novel environment dominated by internal assembly dynamics (Gardner *et al.* 2009).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1.*Summary of sampling efforts by microhabitat.*
TABLE S2. *Colony counts by species and microhabitat.*
FIGURE S1. Map of the study region.
APPENDIX S1. Additional sampling details.

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