Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems

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Abstract. In agroecosystems, biodiversity correlates with ecosystem function, yet mechanisms driving these relationships are often unknown. Examining traits and functional classifications of organisms providing ecosystem functions may provide insight into the mechanisms. Birds are important predators of insects, including pests. However, biological simplification of agroforests may decrease provisioning of this pest removal service by reducing bird taxonomic and functional diversity. A recent meta-analysis of bird exclosure studies from a range of agroecosystems in Central America concluded that higher bird richness is associated with significantly greater arthropod removal, yet the mechanism remains unclear. We conducted a meta-analysis of the same data to examine whether birds demonstrate functional complementarity in tropical agroforests. We classified birds according to relevant traits (body mass, foraging strategy, foraging strata, and diet) and then examined how design of functional classification, including trait selection, classification methods, and the functional diversity metric used affect the suitability of different classifications as predictors of ecosystem services. We determined that vegetation characteristics are not likely drivers of arthropod removal by birds. For some functional classifications, functional richness positively correlated with arthropod removal, indicating that species complementarity may be an important mechanism behind this ecosystem function. The predictive ability of functional classifications increased with the number of traits included in the classification. For the two best classifications examined, functional group richness was a better predictor of arthropod reduction than other metrics of functional diversity (FD and Rao's *Q*). However, no functional classification predicted arthropod removal better than simple species richness; thus other factors may be important. Our analysis indicates that the sampling effect may also play a role, as one species and two functional groups were responsible for disproportionate effects of arthropod removal.

Key words: agroforest; biodiversity; birds; Central America; ecosystem function; exclosure experiment; functional richness; insects; meta-analysis; predation; species complementarity; species trait.

INTRODUCTION

Agroecosystems varying in management intensity and vegetation complexity create outdoor laboratories for studying how biodiversity loss affects ecosystem services. Because agroecosystems are managed primarily for productivity, it is useful to examine the manner and mechanism by which biodiversity affects production. In particular, sustainable production and conservation measures might enhance production of agricultural crops. Gradients of coffee and cacao agroforests, ranging from those with diverse, dense, complex shade canopies to those with few or no shade trees are important areas in which to study biodiversity loss (e.g., Perfecto et al. 2007) and to examine associated changes in ecosystem services such as pollination (Klein et al. 2008) and pest control (Perfecto et al. 2004). Birds are important predators in such agroecosystems and play important roles in pest control (e.g., Greenberg et al. 2000, Mols and Visser 2002, Perfecto et al. 2004, Kellermann et al. 2008). Many have speculated that species loss or changes in species composition of birds may result in impaired ecosystem functioning.

Although patterns demonstrating linkages between biodiversity and ecosystem services are striking in pattern, the mechanisms driving the observed relationships often remain elusive. For example, a recent meta-analysis examined impacts of predatory birds on arthropods across a range of agroforest sites differing in both shade canopy complexity and bird diversity and

abundance (Van Bael et al. 2008). They found that the magnitude of predatory effects did not correlate with the abundance or density of birds, but did correlate with richness of insectivorous birds; where bird richness, particularly of migratory species, was greater, birds reduced arthropod densities to a greater extent. But what factors drive this pattern? First, bird and insect richness is often correlated with vegetation complexity (Greenberg et al. 1997, Mas and Dietsch 2003, Philpott et al. 2008), and vegetation complexity may affect predator efficiency (Grabowski 2004). Thus, observed relationships between bird richness and predatory effects could reflect influences of habitat or vegetation differences rather than top-down control (Hunter and Price 1992). Bird richness may also influence ecosystem function via several mechanisms, including sampling effects or species complementarity (Hooper et al. 2005). The sampling effect is the increase in ecosystem function due to the increased probability of more diverse communities containing one or more species that are highly effective at performing a given ecosystem function (Aarssen 1997, Huston 1997, Tilman et al. 1997). Broadly defined, complementarity is any positive interaction among species (Loreau and Hector 2001, Cardinale et al. 2002). This may include: (1) facilitation, whereby the presence of one species makes another more efficient (Bruno et al. 2003), and (2) niche differentiation, whereby niche partitioning reduces interspecific competition and increases the proportion of total available resources utilized (Tilman et al. 1997, Loreau 1998, 2000). It is likely that facilitation, niche differentiation, and sampling effects are all relevant, to some extent, in most systems (Hooper et al. 2005).

In contrast to simply assessing species richness, functional group richness has been invoked as a better predictor of ecosystem service since it is directly related to traits rather than to an evolutionarily based taxonomic classification that may not relate to the capacity of the organism in question to provide a particular service (Tilman et al. 1997, Díaz and Cabido 2001). A functional group is a grouping of species based on behavioral, morphological, physiological, or resource use traits. Although other definitions exist (e.g., Mason et al. 2005), we define functional richness as the number of functional groups present in a community. Functional richness explicitly describes hypotheses of niche differentiation in groups of co-occurring species. Nevertheless, little quantitative data from natural or managed systems has linked functional richness to ecosystem services in agroecosystems. If assessed appropriately, functional richness can clarify the causes underlying observed relationships between species richness and ecosystem functioning, especially if the functional classification includes traits directly tied to the function of interest. For one well-studied ecosystem process, biomass accumulation, a priori functional classifications may be surprisingly poor predictors of ecosystem functioning (Wright et al. 2006). Yet for ecosystem functions that have received less attention, such as arthropod removal, there is still a need to consider all possible combinations and numbers of relevant traits as well as continuous metrics of functional richness.

There is an increased interest in using continuous metrics of functional diversity, which summarize the variation in species traits within a particular community (Petchey and Gaston 2006). Dendrogram-based measures, such as the functional diversity index FD (Petchey et al. 2004) account for the relative functional distinctiveness of each species, although several methodological choices need to be carefully considered (Podani and Schmera 2006, Mouchet et al. 2008). Abundance-weighted measures, such as Rao's quadratic entropy (Q; Botta-Dukat 2005), additionally incorporate information on the abundances of species present in a community. In all indices, the choice and number of traits, the particulars of the multivariate distance calculations, and the resolution of the trait data are all important considerations. While functional diversity can provide greater explanatory power for the relationship between diversity and ecosystem functioning than functional group richness (Petchey et al. 2004), it is less well known how general this observation is. In particular, no studies have to date used these metrics to assess the contribution of bird diversity to ecosystem functioning or have used these metrics in agroecological studies.

We investigated potential relationships between functional richness and ecosystem services in Mesoamerican agroforests. Specifically, for a group of exclosure studies that examined the top-down effects of birds as predators in agroforests, we aggregated data on vegetation and habitat characteristics, bird abundance and diversity, and arthropod removal. We then conducted a meta-analysis to examine relationships between species and functional richness, habitat characteristics, and ecosystem services provided by birds. We tested multiple functional classifications based on bird traits most relevant to insectivory: body size, diet, foraging strata, and foraging strategy. We categorized birds according to individual traits and created functional classifications based on a single trait (e.g., body size) and combinations of two to four traits (e.g., body size and foraging strategy or body size and foraging strata and diet). We then asked: (1) whether environmental characteristics of farms correlate with changes in bird function, (2) whether functional richness of bird species correlates with total bird richness or richness of insectivorous birds, (3) whether the number of species with particular traits corresponded to increased arthropod removal, (4) whether functional richness correlated with increases in arthropod removal, (5) which functional classification best predicted the ecosystem service provided by birds, and finally, (6) whether considering continuous metrics of functional diversity had improved explanatory power compared to functional group richness.

METHODS

Data sources

For our meta-analysis, we used data from nine bird exclosure studies conducted across a range of coffee and cacao agroforests in Central America between 2000 and 2005. The data for each study was compiled by Van Bael et al. (2008), and a full description of the habitats and studies can be found in Appendix B of that publication. For each study, the database includes information on: (1) the percentage of arthropods removed during exclosure experiments in which birds were experimentally removed from canopy trees or understory (i.e., coffee or cacao); and (2) total abundance and richness of birds based on 10-min, 25 m radius point counts. The data on bird richness and abundance and thus our functional classification were limited to only insectivores and omnivores observed in the foraging strata (canopy or understory) where exclosures were placed (Van Bael et al. 2008). In the original studies, arthropods were sampled with two different methods. For five studies, including all canopy exclosures, individual branches were bagged and clipped to collect arthropods (Greenberg and Ortiz 1994, Greenberg et al. 2000, Philpott et al. 2004, Van Bael et al. 2007). For the three studies with coffee plant exclosures, arthropods were aspirated from branches (I. Perfecto et al., *unpublished manuscript*). We complemented the database by obtaining data on vegetation and elevation in each site from the authors of the nine experiments.

Vegetation complexity and arthropod removal

We examined whether differences in arthropod removal relate to changes in vegetation complexity across agroforests studied in order to determine whether some component of the habitat, rather than of the bird assemblage per se, correlated with increased arthropod removal. Although some studies collected more data than others, all of them measured elevation, tree richness, tree density, and percentage of canopy cover within 25 m radius plots. The number of plots in each study varied from 16 to 206. We examined the influence of elevation using a simple linear regression. We used multiple regressions with stepwise deletions to examine the influence of canopy cover, tree richness, and tree density on arthropod removal.

Functional classification

To examine the relationships between functional richness of the bird communities and arthropod reduction, we first categorized 106 bird species (33 migrants and 73 residents) in the database according to relevant traits and then classified birds into distinct functional groups. We based our functional classifications on four different bird traits: primary foraging strata, foraging strategy, diet, and body mass. We chose these traits based on (1) their perceived relevance to a particular function of arthropod removal, (2) reliability

and consistency of information in available literature, and (3) examples in the literature of similar groupings being used for functional classification of birds (Holmes et al. 1979, Henderson et al. 2000). For example, the foraging strata and strategies used by birds may influence their ability to capture arthropods. Differences in body size may lead to resource partitioning of prey sizes. For example, during the breeding season, preferences for larger prey items may become relevant, increasing prey size separation for small- and large-bird species (Greenberg 1995). Finally, differences in the relative proportion of arthropods consumed by insectivorous or omnivorous birds may influence their effects on lower trophic levels.

Bird strata classifications were based primarily on foraging data gathered in Xalapa, Mexico, from R. Greenberg, A. Cruz-Angon, and P. Bichier (*unpublished data*), Howell and Webb (1995), and *personal communications* (R. Greenberg). Those bird species that reportedly forage primarily on the ground or in the understory were categorized as understory foragers, those that forage primarily in the mid to upper canopy were categorized as canopy foragers, and those that are aerial foragers or forage across understory and canopy strata were included as both strata foragers. We classified foraging strategies according to six categories: foliage glean, bark glean, ground glean, hover and glean (or sally-hover), hawks, and multiple strategies following the terminology of Remsen and Robinson (1990). Information on foraging strategy was taken mainly from Ehrlich et al. (1988), and for birds not found in this reference, we collected information on foraging strategy from Stiles and Skutch (1990) and Stotz et al. (1996). Where it was clear from information provided in those texts that birds foraged only or primarily using one strategy, birds were assigned in one individual category. Where birds clearly used multiple foraging strategies or where their main foraging strategy was somewhat ambiguous, birds were designated as multiple foragers. Finally, using the same sources, we classified birds into three diet categories based on diet items listed for each species. Strict insectivores included birds that feed exclusively on insects. Insectivores are birds that feed mainly on insects and were described as (1) obtaining <25–30% of their diet from non-insect items, (2) feeding mostly or mainly insects, or (3) feeding on insects and few berries or seeds. All other birds were classified as omnivores. Birds were classified into five body mass size classes: tiny (<15 g), small (15 to <30 g), medium (30 to <60 g), large (60 to <120 g), and extra large (≥120 g) based on data from Dunning (1993).

We created 15 functional classifications based on individual traits, pairs of traits, and groups of three or four traits (Tables 2, 4). Four classifications were based on each of the four traits included where only differences in bird size, diet, foraging strata, or foraging strategy were used to classify distinct groups. Six functional classifications were based on pairs of traits (e.g., size plus

diet) in which birds were classified according to both traits (e.g., large omnivores, small strict insectivores). Four classifications resulted from dividing birds into groups based on three different traits (e.g., size plus strata plus strategy), and the final functional classification included all four traits. Except for the multiple foraging strategy, all other categories within traits are mutually exclusive, and traits themselves are not necessarily correlated. For a list of bird species and assigned traits see the Appendix.

Relationships between species richness, functional richness, and percentage of reduction in arthropods

We began each analysis by standardizing for differences in bird census sampling effort across studies, because the number of point counts varied from 38 to 410 and the number of individual birds recorded ranged from 132 to 1070. We compared across studies using rarefied species and functional richness. To determine both the number of species with each trait and functional richness for each functional classification, we calculated rarefied species richness values using the same algorithms as in EstimateS (Colwell 2005). We rescaled the species or functional richness to the number of individuals found in the site with the lowest abundance (132 individuals).

We were interested in examining whether species richness of birds related to richness of insectivores and whether insectivore richness correlated with functional richness. In other words, did species richness of insectivores correlate with the number of functional groups present in a site, and did this relationship vary with the number of traits in the classification? We examined relationships between rarefied richness of all birds and of insectivorous birds with simple linear regressions. To examine relationships between insectivore richness and the number of functional groups present we carried out individual regressions for each of four classifications, based on one, two, three, or four traits. Each regression included rarefied species richness of insectivores as the dependent variable and values of functional richness for all classifications including that number of traits as independent variables.

In determining which aspect of the bird assemblage may relate to the ecosystem service provided by birds, we were interested in two aspects of functional classifications: (1) whether the number of bird species in an assemblage with a particular trait relates to arthropod removal and (2) whether the number of functional groups represented (i.e., functional richness) in the bird assemblage relates to arthropod removal. From a methodological standpoint, we were also interested in examining the effectiveness of particular functional classifications in predicting this ecosystem service. To determine whether the number of bird species with a particular trait (e.g., foliage gleaners) was important, we separately regressed rarefied richness of birds with each of the 17 traits (canopy forager,

understory forager, both strata forager, foliage gleaner, bark gleaner, ground gleaner, hover and gleaner, hawker, and combined strategy forager, strict insectivore, insectivore, omnivore, tiny, small, medium, large, and extra large) against the percentage of arthropods removed by birds. In other words, we conducted a total of 17 comparisons, one for each of the individual traits across the four functional groups. To examine whether functional richness of the bird assemblage was important, we examined each of the 15 functional classifications (i.e., one, two, three, and four trait classifications) separately, regressing the number of functional groups present in a site vs. percentage of arthropods removed, where each point in the regression represented a single site. We then asked which classification better predicted arthropod removal and whether any classification predicted arthropod removal better than species richness alone by comparing R^2 values ($R^2 = 0.6008$ in Van Bael et al. [2008]; Fig. 2a).

Finally, we explored whether any of the common metrics used to assess functional diversity predicted our ecosystem service better than simple functional richness. For functional classifications including all traits and that best predicted ecosystem function (based on the number of functional groups represented), we also calculated Petchey and Gaston's FD index (Petchey and Gaston 2002) and Rao's quadratic entropy, Q (Rao 1982). Because sampling intensity varied between sites, we estimated rarefied FD and Q by bootstrapping our sample data to the lowest common sample intensity (38 samples) and calculating the expected values. This approach is analogous to that used by EstimateS for species richness prior to the work of Colwell et al. (2004) and is equivalent to the approach independently derived by Walker et al. (2008) for rarefying FD. We did not, however, utilize their analytical approach for calculating Q, choosing instead to apply the same numerical approach as for FD. We then used simple linear regressions to examine the relationships with percentage of arthropods removed of our rarefied estimates of functional richness, FD, Q, and the species richness of those birds that prey on insects. All calculations and analyses were done using the statistical programming package R (R Development Core Team 2008).

For all regressions described (species richness vs. functional richness, functional classifications vs. arthropod removal, and functional diversity metrics vs. arthropod removal), we were primarily interested in examining which factors explained the greatest amount of the variation in our response variables. We thus focused on comparing goodness of fit, as represented by R^2 values, and not examining the significance of the slopes of different relationships. For this reason, we did not apply any multiple comparison corrections to adjust P values and present only the R^2 values for the regressions. We also applied an Akaike's Information Criterion (AIC) approach to our data to examine goodness of fit of different relationships. The rankings

TABLE 1. Influences of habitat on differences in arthropod removal by birds in agroforests that vary in vegetation characteristics and elevation.

Habitat characteristic	Slope	R^2	df	P
Elevation	−0.0389	0.156	1, 7	0.333
Multivariate		0.686	3, 7	0.164
Tree richness	−3.959		1, 7	0.270
Cover	1.241		1, 7	0.213
Tree density	−0.956		1, 7	0.075

Note: For the meta-analysis, data came from nine bird exclosure studies conducted across a range of coffee and cacao agroforests in Central America between 2000 and 2005.

of model goodness of fit by AIC or R^2 were identical for the best-fitting models, meaning that in this case, R^2 is an intuitive metric that allowed us to pick out the trait classifications that best explain arthropod removal for our data set.

Relationships between individual species, functional groups, and percentage of reduction in arthropods

We used linear regressions to examine whether sampling effects could explain observed arthropod removal. We individually regressed the abundance of each species against arthropod reduction, as well as regressed the abundance of birds within specific functional groups against arthropod reduction. We do not correct for multiple comparisons here, as our main intent was to examine whether reasons other than niche differentiation might explain our observed function.

RESULTS

Bird exclosure sites differed in terms of vegetation characteristics and elevation, yet such differences did not relate to differences in arthropod reduction. Within 25 m radius plots, the mean number of tree species ranged from 2.7 to 13.5 species, percentage of canopy cover from 5% to 54%, and tree density from 57 to 158 trees. However, neither vegetation characteristics in a site nor elevation were significant predictors of arthropod removal by birds (Table 1). Thus, it is unlikely that changes in the vegetation or elevation are the primary drivers behind increased or decreased bird predation on arthropods in the study sites included in this meta-analysis.

Species richness of all birds was an important predictor of richness of insectivorous (including omnivore) birds ($y = 0.49x + 1.60$, $R^2 = 0.736$, $P = 0.003$). The relationship between both total bird richness and insectivore richness and functional richness depended on the number of traits included in the classification. The relationship between rarefied species richness and functional richness was not significant for two of the four single-trait classifications, but was significant for all two-, three-, or four-trait classifications (Table 2). Similarly, the relationship between rarefied insectivore

richness and number of functional groups was not significant for two of the four single-trait classifications, but was significant for all two-, three-, or four-trait classifications (Table 2, Fig. 1).

We examined whether the rarefied species richness of birds with particular traits was associated with higher arthropod reduction. The species richness of birds that forage in both the canopy and understory strata, richness of foliage gleaners, richness of omnivores, and richness of tiny birds were all positively correlated with increases in arthropod reduction (Table 3). The number of bird species with other individual traits was not related to predatory function of birds in these studies.

For the functional classification based on all four traits (bird size, diet, foraging strata, and foraging strategy), there was a total of 270 possible functional groups. We observed 64 of these groups across all exclosure study sites. Of these 64 groups, 39 included one bird species, 15 included two species, seven included three species, and there was one group each with four, five, or six species. Based on the functional classification including all four traits, the number of functional groups present was positively correlated with arthropod reduction (Table 4). Likewise, for each of the four different functional classifications based on three traits, functional richness was significantly positively correlated with arthropod reduction (Table 4). Of the six two-trait functional classifications, three showed positive relationships between functional richness and arthropod reduction (Table 3). Of the four single-trait classifications (body size, diet, foraging strata, and foraging strategy), only that of body size was positively correlated with arthropod reduction ($R^2 = 0.6$, $F_{1,7} = 10$, $P = 0.015$).

TABLE 2. Regression summary showing relationships between rarefied richness of all birds and rarefied richness of insectivorous birds and rarefied functional richness for functional classifications including one, two, three, or four traits.

No. traits	Traits included	R^2 for bird richness	R^2 for insectivore richness
1	size	**0.456**	**0.624**
1	diet	0.004	0.002
1	strata	0.021	0.004
1	strategy	**0.552**	**0.609**
2	size, diet	**0.739**	**0.903**
2	size, strata	**0.668**	**0.83**
2	size, strategy	**0.584**	**0.872**
2	diet, strata	**0.777**	**0.837**
2	diet, strategy	**0.569**	**0.825**
2	strata, strategy	**0.721**	**0.792**
3	size, diet, strata	**0.721**	**0.861**
3	size, diet, strategy	**0.611**	**0.911**
3	size, strata, strategy	**0.796**	**0.951**
3	diet, strata, strategy	**0.674**	**0.956**
4	size, diet, strata, strategy	**0.746**	**0.971**

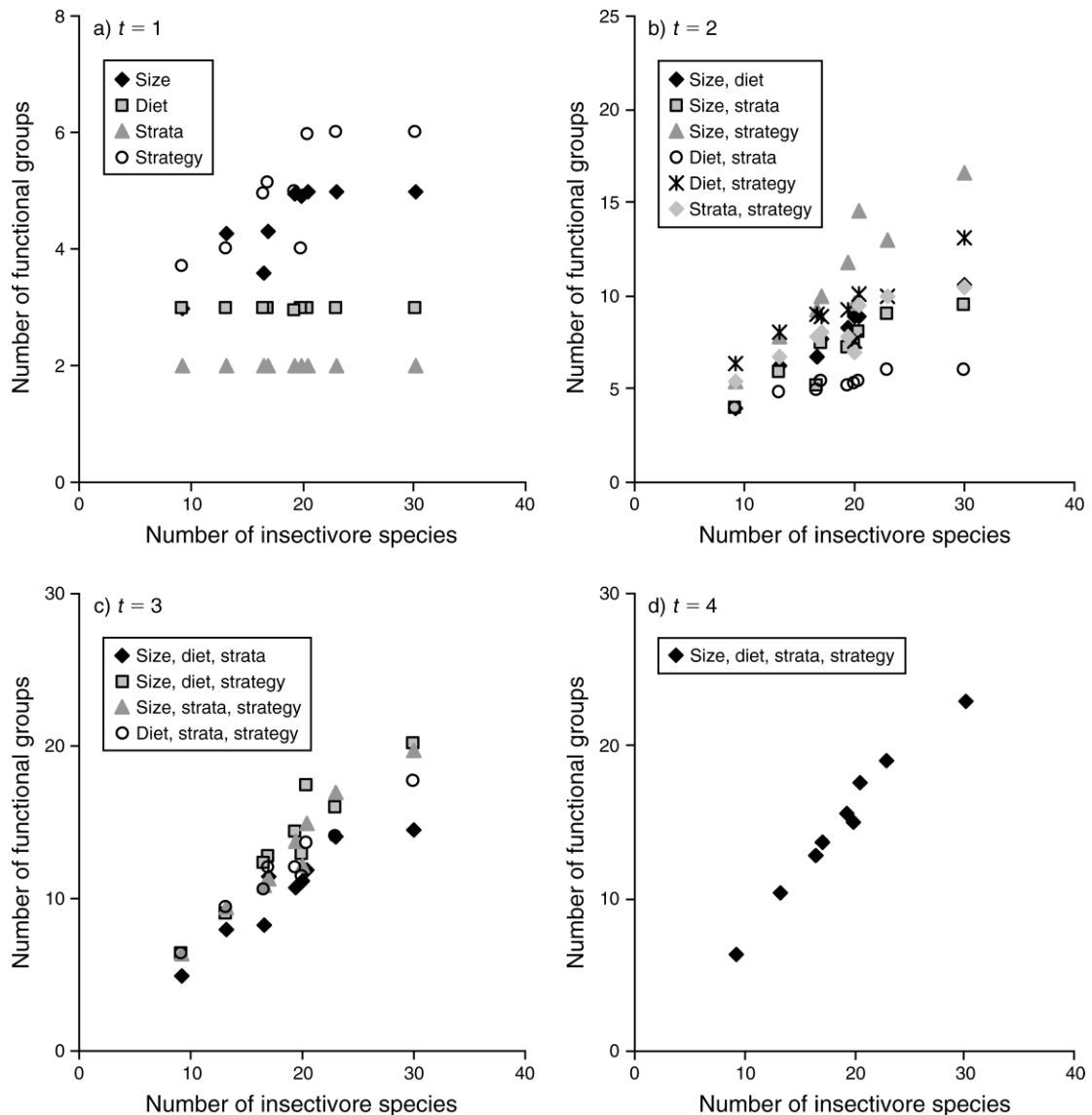*Note:* Where regressions are significant ($P < 0.05$), R^2 values appear in boldface.

FIG. 1.   Relationships between species richness of insectivorous birds and functional richness depending on number of traits (t) included in the classification. Two of the four single-trait classifications were significant ($P < 0.05$), as were all regressions including two-, three-, and four-trait classifications. For the meta-analysis, data came from nine bird exclosure studies conducted across a range of coffee and cacao agroforests in Central America between 2000 and 2005.

We examined which of the common metrics used to evaluate functional richness better predicted arthropod removal. We examined the relative power of functional group richness for the classification including all four traits, Petchey and Gaston's FD, and Rao's Q to predict arthropod reduction. For this classification, functional group richness was a better predictor ($R^2 = 0.492$, $F_{1,7} = 6.782$, $P = 0.035$) than FD ($R^2 = 0.375$, $F_{1,7} = 4.206$, $P = 0.079$) or Rao's Q ($R^2 = 0.350$, $F_{1,7} = 3.765$, $P = 0.093$), which both had similar predictive power. Overall, the best classification based on R^2 was the classification including body size plus foraging strata. For that classification, functional group richness (Fig. 2b, $F_{1,7}$ = 8.7, $P = 0.022$) and FD (Fig. 2c, $F_{1,7} = 8.5$, $P = 0.022$) were better predictors of arthropod reduction. Rao's Q ($F_{1,7} = 4.7$, $P = 0.066$) did not predict ecosystem function as well as functional group richness or FD (Fig. 2d).

Finally, with linear regressions, we singled out one bird species (Tennessee Warbler, *Vermivora peregrina*, Parulidae; $R^2 = 0.455$, $y = -0.328x + 54.884$, $P = 0.030$) and two functional groups (small, understory, foliage-gleaning strict insectivores [$R^2 = 0.461$, $y = -3.43x + 47.478$, $P = 0.030$] and tiny, both strata, foliage-gleaning omnivores [$R^2 = 0.455$, $y = -0.328x + 54.884$, $P = 0.030$]) as candidates for a sampling effect.

TABLE 3. Relationships between rarefied species richness of birds with particular traits and percentage of arthropods removed by birds in exclosure experiments.

Trait	No. birds in group	R^2
Foraging strata		
Canopy	37	0.26
Understory	40	0.084
Both strata	28	**0.62**
Foraging strategy		
Foliage gleaner	44	**0.8**
Bark gleaner	6	0.24
Ground gleaner	10	0.1
Hover and glean	7	0.2
Hawks	10	0.033
Multiple strategies	28	0.034
Diet		
Strict insectivore	26	0.21
Insectivore	33	0.13
Omnivore	46	**0.63**
Size		
Tiny (<15 g)	35	**0.53**
Small (15 to <30 g)	27	0.21
Medium (30 to <60 g)	22	0.15
Large (60 to <120 g)	15	0.38
Extra large (≥120 g)	6	0.056

Note: Where regressions are significant ($P < 0.05$), R^2 values appear in boldface.

Discussion

The results of this study indicate that vegetation characteristics and elevation of agroforests are not good predictors of changes in bird predatory effect on arthropods. Thus it may be somewhat difficult to make data-backed recommendations to farmers regarding the density or diversity of shade trees they may need to maintain bird-provided ecosystem services. In contrast, several aspects of the bird assemblage correlate with increased predatory function in agroforests. The species richness of birds with particular functional traits correlated with arthropod removal, perhaps indicating special relevance or importance of those traits to the arthropod removal effects. Specifically, the number of species of foliage gleaners, tiny birds, birds foraging in both agroforest strata, and the number of omnivores significantly correlated with increased arthropod reduction. The richness of foliage gleaners is particularly relevant here, as all arthropods collected from exclosures on either crop plants or shade trees were those found on foliage. The arthropod sampling method differed with study and thus may affect our ability to assess bird impacts on certain groups of arthropods. In general, there do appear to be certain traits that associate certain bird assemblages with increased provisioning of ecosystem services or function.

For several functional classifications, functional richness of birds significantly and positively correlated with arthropod reduction (Table 4). Overall, for six of 15 functional classifications, the functional richness correlated with arthropod removal, and three of 15 functional classifications were marginally significant correlates of

arthropod reduction ($0.05 < P < 0.08$). However, none of the functional classifications provided better fits for arthropod removal than did the simple species richness ($R^2 = 0.6008$ in Van Bael et al. [2008]; Fig. 2a). Because species richness of all birds and of insectivores correlated with bird functional richness, and species richness predicts arthropod removal, we might also expect that functional richness predicts arthropod removal, and for many cases it did. The interesting question then is why functional richness does not do as well. It is possible, given the specific traits included, that species richness may better approximate the true diversity of guilds and niches in the bird communities. For example, the functional classification may identify particular groups (i.e., ground gleaners) that would not necessarily be expected to influence crop or canopy arthropods. However, the species identified as ground gleaners may in reality actually forage (albeit rarely) in the strata from which arthropods were sampled. Thus even with careful selection of traits, functional classifications may not adequately represent the real assemblages and we may expect a sampling effect at the functional group level. For this service in particular, the presence and abundance of small foliage-gleaning insectivores may be more important than community diversity, species or otherwise. That said, the relationship between FD and arthropod removal appeared to be the steepest of all, and with the outlier (especially visible in Fig. 2c) removed, the R^2 value for the regression increased to 0.946, a near-perfect relationship in explaining arthropod removal and better than other measures. Removing the outlier altered the R^2 for species richness to 0.815, for number of functional groups to 0.733, and for Q to 0.548, making FD the best predictor in this scenario. The outlier data came from a sun coffee plantation, the only of the nine sites devoid of trees, and thus may have some biological meaning, but we felt it was important to

TABLE 4. Regression summary showing relationships between rarefied functional richness of insectivorous birds for 15 different functional classifications and percentage of arthropod removal.

No. traits	Traits included	R^2
1	size	**0.53**
1	diet	0.00059
1	strata	0.0021
1	strategy	0.23
2	size, diet	**0.52**
2	size, strata	**0.55**
2	size, strategy	0.35
2	diet, strata	0.44
2	diet, strategy	0.29
2	strata, strategy	0.33
3	size, diet, strata	**0.48**
3	size, diet, strategy	0.41
3	size, strata, strategy	0.38
3	diet, strata, strategy	**0.49**
4	size, diet, strata, strategy	**0.49**

Note: Where regressions are significant ($P < 0.05$), R^2 values appear in boldface.
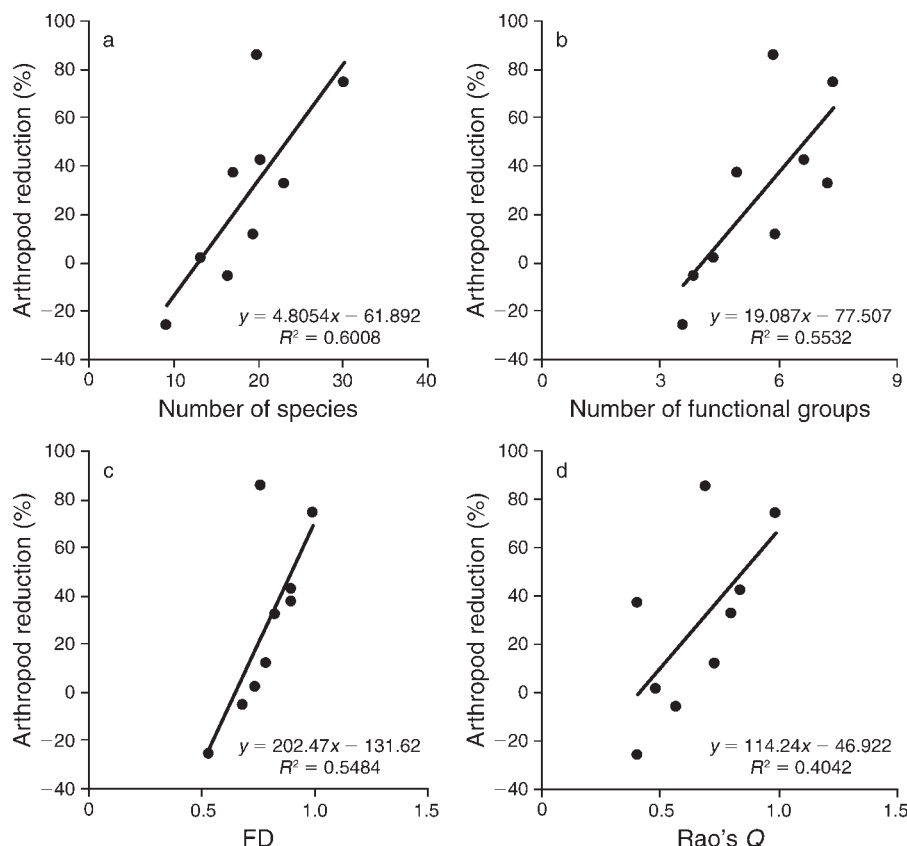
FIG. 2. Relationships between percentage of reduction of arthropods and (a) rarefied species richness of insectivores, (b) functional richness, (c) Petchey and Gaston's functional diversity index (FD), and (d) Rao's quadratic entropy (Q). Functional richness, FD, and Rao's Q use the two traits from the best functional classification, body size and diet.

keep all points to best explain the originally observed relationship. For the best classification (size and foraging strata), functional richness, FD, and Q all were worse predictors of ecosystem function than simple species richness. This was also true for the functional classification including all traits. Yet, for the best functional classification, functional group richness and FD better predicted arthropod removal than Q. Thus the results demonstrate overall that differences among habitats do not contribute to the biodiversity ecosystem services relationship described, but that at some level, niche differentiation may be important. Yet, because species richness was still a better predictor of this ecosystem service than any functional classification, these results are somewhat equivocal.

With more traits included in the functional classification, positive correlations between arthropod removal and functional richness were more likely. All classifications including two, three, or four traits correlated with arthropod removal, but only half of the single-trait classifications were significant. The number of traits included in the classification tended to increase the chances that functional richness would predict the ecosystem service provided ($y = 0.22x + 0.085$, $R^2 = 0.840$, $P = 0.080$). Thus, as we included more traits, we

had increasingly finer functional group classifications, to the point that with enough traits, each species falls into its own group. This should not be surprising, however, since as we add traits, the number of functional groups converges on species richness, which in this case is a good predictor of ecosystem function. More generally, this result highlights how the choices of which traits to include and the number of traits to include in functional classifications can highly influence the results. Furthermore, the specific traits included in the analysis may have a strong impact on the predictive ability of the relationship. Those classifications that include size tended to be more relevant than those including foraging strategy, for example. The relative abundance of different foraging strategies was relatively constant across size groups, but perhaps bird size can be an important correlate of arthropod prey size (e.g., Rotenberry 1980).

Although this paper focuses on the relationships between niche differentiation as described by functional classification and ecosystem services, the presence of particular bird species (i.e., sampling effect) or particular functional groups may still drive the observed relationship between species richness and arthropod removal. This is especially notable given that none of the

functional classifications better predicted arthropod removal rates than did simple species richness. Given our specific data set, however, it is extremely difficult to partition relative contributions of the sampling effect and complementarity. Nearly all available methods require monoculture data to (1) calculate the relative yield increase due to presence of a particular species (e.g., Hector 1998) or (2) partition the total effect into species complementarity and the sampling effect (Loreau and Hector 2001). We do not have data for the isolated effects of particular bird species (i.e., bird "monoculture"), nor would gathering these data be practical. Putting birds into enclosures to measure their individual effects, for example, would likely result in significant behavioral changes. However, we found, using linear regressions, that the abundance of one bird species and two functional groups was correlated with arthropod removal, signaling these three groups as candidates for the sampling effect. The residuals from these regressions are not significantly correlated with any of our measures of diversity, suggesting that, if the Tennessee Warbler or the two functional groups are indeed affecting arthropod reduction to the degree suggested by the regression, then there is no statistically significant effect of diversity on residual ecosystem function.

In summary, we demonstrate that functional classifications of birds can contribute to our understanding of an observed biodiversity ecosystem function relationship and provide some evidence that niche differentiation may contribute to this relationship, although species richness remains a better predictor of the pest removal function examined here. We also find that this particular type of data does not lend itself well to methods for partitioning the sampling and complementarity effect (Loreau and Hector 2001). Alternatively, carefully controlled experimental studies or new analytical methods will be required to examine the relative importance of sampling and complementarity effects in studies of species richness, functional richness, and the provisioning of ecosystem services in managed landscapes. Of those methods used to examine mechanisms driving biodiversity ecosystem function relationships for plants, most are nearly impossible to apply to ecosystem services provided by highly mobile organisms (e.g., birds, bees, or bats) that would be difficult to maintain in monocultures and appropriate species mixtures. Sufficient evidence exists that altering biological communities impacts the capacity of such systems to provide services. However, in order for these observations to have practical applications in managed systems, a better understanding of both the top-down and bottom-up mechanisms that drive these multitrophic ecosystem services is critically needed.

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APPENDIX

Functional classification of bird species found in nine exclosure sites (*Ecological Archives* A019-077-A1).