

## Competition and Facilitation in the Capuchin–Squirrel Monkey Relationship

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### ABSTRACT

In Guyana, the range of the brown capuchin, *Cebus apella*, meets the range of its congener, the wedge-capped capuchin, *C. olivaceus*, with the two species exhibiting a mutually exclusive patchy distribution. Squirrel monkeys, *Saimiri sciureus*, and *C. apella* form ubiquitous interspecific associations, but the reason remains debatable. With a large biogeographic field study, we tested the degree to which the distribution and abundance of *Cebus* and *S. sciureus* is determined by habitat type, fruit availability, and geography (*i.e.*, determinants of the fundamental niche) relative to interspecific interactions, such as competition and facilitation (*i.e.*, the realized niche). We used the competition between the two capuchin monkeys as a natural experiment that subjected *S. sciureus* to *C. apella* and *C. olivaceus* ‘treatments’. Using spatial regression models and principal components analysis, we found that *S. sciureus* was associated with seasonally flooded forests, and was correlated with fruit abundance and diversity (fundamental niche), but was also correlated with *C. apella* density even when accounting for habitat and fruit availability (realized niche). *Saimiri sciureus* density was unrelated to *C. olivaceus* density. *Cebus apella* was associated with a variety of forest types, but particularly included disturbed and edge habitats such as logged forests, seasonally flooded forests, and upland savanna, in addition to mature forest. *Cebus apella* was also positively correlated with *S. sciureus* density and negatively correlated with the density of *C. olivaceus*. In contrast, *C. olivaceus* avoided riparian areas and was associated with mixed-height forests on sloped mountainous terrain. In sum, interspecific interactions such as competition between species of *Cebus* and facilitation between *C. apella* and *S. sciureus* were as important as habitat and fruit availability in determining the distribution and abundance of these primates.

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

**Key words:** biogeography; *Cebus*; fundamental niche; Guyana; mutualism; realized niche; *Saimiri*; *Sapajus*.

NEOTROPICAL FORESTS CAN ACCOMMODATE UP TO FOURTEEN SYMPATRIC primate species (Peres 1997). Previous work has suggested that primate diversity can be maintained when species partition habitat types, food resources, and vertical canopy structure (Mittermeier & van Roosmalen 1981) in accordance with the classic paradigm of the fundamental niche (Grinnell 1917, Elton 1927). The fact that congeners seldom coexist in primate communities supports the role of strict partitioning. Hutchinson emphasized that species are often restricted to a narrower realized niche by negative interactions such as competition and predation (Hutchinson 1957). A growing body of evidence, however, suggests that facilitation, or positive interactions among species, also plays an important role in the structure of ecological communities (Brooker *et al.* 2008, Bulleri *et al.* 2008). While facilitation may improve the fitness of one or more species, examples of direct facilitation determining community structure (*i.e.*, presence, absence, or abundance of species) are rare. Competition for resources

certainly impacts primate community structure, but the role of facilitation has received little attention given the frequency of stable interspecific associations among primates (Terborgh 1983, Boinski 1989, Podolsky 1990, Chapman & Chapman 2000, Haugaasen & Peres 2009, Leonardi *et al.* 2010).

Stable associations among primates are prominent in many tropical forests where multiple species feed and travel together. One ubiquitous primate association is the semi-permanent interspecific foraging groups formed between brown capuchin monkeys, *Cebus apella*, and squirrel monkeys, *Saimiri sciureus*, throughout South America. This mixed-species association is particularly intriguing because *Cebus* is three times larger than *S. sciureus* and regularly preys on similarly sized mammals such as squirrels, coati (*Nasua nasua*) young, bats, and even other monkeys (Fedigan 1990, Carretero-Pinzon *et al.* 2008). Nevertheless, these species have been observed to feed and travel together up to 90 percent of the time (Terborgh 1983).

The lack of generality in the *Cebus*–*Saimiri* relationship is perplexing—while *C. apella* and *S. sciureus* consistently form mixed-species groups, similar congeners do not. *Saimiri sciureus*

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does associate with *Cebus albifrons*, but to a far lesser extent, and *Saimiri oerstedii* rarely associates with *Cebus capucinus* in Central America (Boinski 1989). Any observations of an association between *S. sciureus* and *Cebus olivaceus* have received little attention in the literature, but the two have been observed feeding together in Guyana, although much less frequently than with *C. apella* (Lehman *et al.* 2006).

The benefit of the association with each species is debated. The larger group sizes under mixed-species association likely decrease predation risk, which benefits both species, but is particularly important for squirrel monkeys, which are susceptible to predation by a greater diversity of raptors (Ferrari 2009). It is uncertain, however, whether the association increases feeding competition for both species; improves the foraging efficiency of squirrel monkeys, which are able to exploit resources found by capuchins or feed on their messy remains; or improves the foraging efficiency of capuchin monkeys, which can quickly dominate fruit resources discovered by squirrel monkeys (Terborgh 1983, Podolsky 1990, Haugaasen & Peres 2009). While it is known that these species consistently associate, the impact of this association on the distribution and abundance of each species remains unknown. One method to infer the role of the association on the success of each species (measured as realized population density, or advantage over competitors) is to sample many sites at sufficiently large spatial scales to capture species occurrence with and without association, while controlling for differences in habitat characteristics and food availability.

*Cebus olivaceus* is more widespread than *C. apella* in Guyana despite being otherwise restricted to northern South America (Lehman 2000). Mittermeier and Roosmalen (1981) found that in Suriname *C. apella* is a habitat generalist that occupied forest edge habitats, while *C. olivaceus* is largely restricted to upland forest types. Contrary to this observation, Lehman (2004) found that in neighboring Guyana, *C. olivaceus* is a widely distributed habitat generalist, while *C. apella* is the habitat specialist. These apparently contradictory results suggest that geography and niche partitioning based on habitat or food type are not sufficient to explain patterns of primate community structure. Interspecific interactions, such as competition or facilitation, may influence the local persistence of species, thus determining community structure. Indeed, the absence of one or the other capuchin species at sites in Guyana has previously been explained by competitive exclusion (Lehman *et al.* 2006). The semi-permanent association between *S. sciureus* and *C. apella* in a situation of sympatry with two potentially competing *Cebus* species provides an opportunity to test the relative role of facilitation and competition in community structure.

In Guyana, *S. sciureus* is sympatric with both capuchin species. *Cebus apella* and *C. olivaceus* are sometimes sympatric, but are competitors that frequently exclude each other and have non-overlapping home ranges (Lehman 2000). We used a large-scale biodiversity field study in Guyana to assess the degree to which the abundance of each primate is determined by competition between *C. apella* and *C. olivaceus* and facilitation between *C. apella* and *S. sciureus*, relative to determinants of the fundamental niche such as geography, forest type, fruit abundance, and fruit diversity. If facilitation is strong enough to impact primate community

structure, we would expect to see the distribution and abundance of *S. sciureus* largely influenced by the distribution and abundance of the two capuchin monkeys. In particular, *S. sciureus* should be less abundant at sites dominated by *C. olivaceus*, and be more abundant at sites dominated by *C. apella* when controlling for variation in habitat type, fruit availability, and geography. In our analysis, we use spatial autoregressive models to account for spatial processes.

## METHODS

**STUDY AREA.**—This research is part of a larger study on the interactions among indigenous livelihoods, biodiversity dynamics, and environmental constraints, that was conducted in Guyana, South America within the Guiana Shield geographic region between May 2007 and June 2010 (Luzar *et al.* 2011). The study area encompassed approximately 48,000 km<sup>2</sup> in both the Amazon and Essequibo river watersheds. The region experiences one wet season with most precipitation falling from May to September. Mean annual rainfall across the area varies from 1400 to 4450 mm (Bovolo *et al.* 2011). Extensive flooding of lowlands including forest and savanna ecosystems occurs between the months of May and August.

Vegetation within the study region varies considerably, including lowland and highland rain forest, and lowland and highland savanna (Fig. 1). In many areas, vegetation forms mosaics of forest and savanna, with both upland and wetland hydrologies. Topography also varies within the study region, including lowland (150 m asl) forest and savanna in the center of the study region and mountainous terrain ranges to the east, north, and south reaching about 1000 m asl.

**SURVEY METHODOLOGY.**—The study region is occupied by Amerindian communities, predominantly of the Makushi and Wapishana ethnic groups. Transect arrays were installed around 23 Makushi and Wapishana villages and four non-village control sites (Luzar *et al.* 2011). Each settlement-based transect array was centered on the approximate geographic center of villages. Control arrays were located from 15 to 40 km from the center of the nearest village. Primates are not hunted in the region; their populations would therefore not be directly affected by hunting at either village-centered or control sites. All arrays were divided into two concentric zones, *near* (0–6 km) and *far* (6–12 km), with four transects, each 4 km in length, within each zone. Transect positions and bearings were randomly generated, but placement was stratified by a minimum of 3 km distance between adjacent transects. In the larger study, data were collected on all large and medium-sized vertebrates on the transects; because we focus here on arboreal species, we use the subset of total transects that have at least 90 percent forest cover (Fig. 1; 94 transects in total). In rare situations, barriers were encountered that could not safely or effectively be surveyed (*e.g.*, cliffs). In these instances, a transect turned to the right at a 90° angle, and continued until the 4 km end point. Transect placement was also stratified to avoid placement in areas where concentric 12 km sample areas of adjacent villages overlap.

Observation sampling was conducted monthly for a minimum of 2 and up to 3 years on each transect by trained village

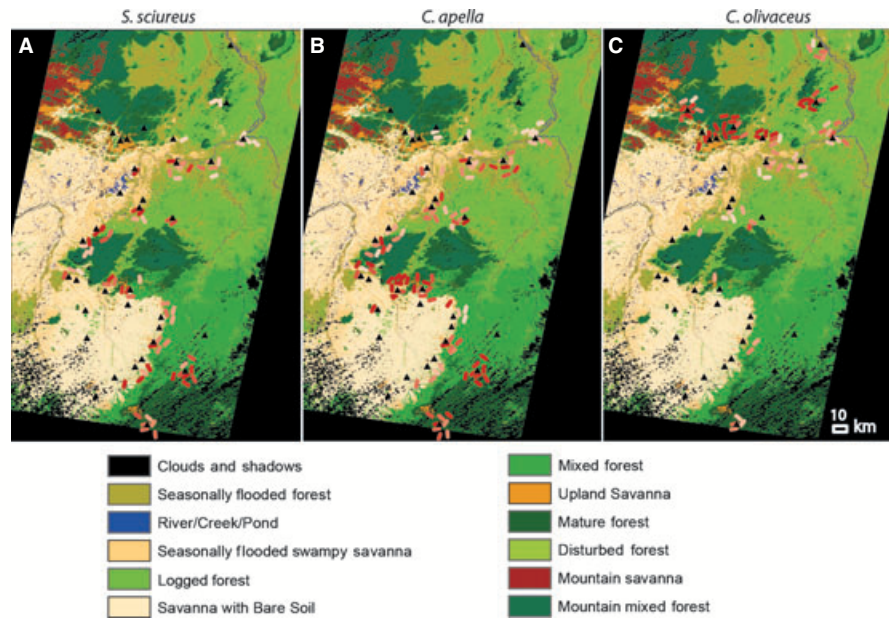


FIGURE 1. The distribution and abundance of *S. sciureus*, *C. apella*, and *C. olivaceus* over the 94 transects in the Rupununi study area of Southern Guyana with at least 90 percent forest cover. Villages are denoted by black triangles. Transects are denoted by a colored line with darker red indicating higher population density.

technicians with expert detection capabilities of local wildlife, using a standardized distance sampling methodology (Buckland *et al.* 1993). Over this period, there was an average of 96 km of census effort per transect (range 32–140 km walked per transect). We recorded 219 records of squirrel monkey groups, 764 records of brown capuchin groups, and 500 records of wedge-capped capuchin groups, which ensured a robust sample size. During each survey, two technicians walked slowly and quietly (approx. 1 km/hour) and recorded observations of species, number of individuals, distance to animal, location on transect, and bearing to animal. In cases where a group of animals was observed, the center of the group was recorded as the location of the group. When the number of individuals in a group was uncertain, which is common for large groups of primates, the technicians estimated the number of animals within the group. In this analysis, we calculate density with the more robust estimate of average group size across the study region (hereafter called ‘global mean group sizes’) rather than local group size records, which are more uncertain (See *Density Estimation* below).

In addition to wildlife observation, technicians collected fruit abundance and diversity data along all the same transects monthly during a separate sampling period from that of animal surveys. All patches (clusters of fruit fallen from a single tree) of fleshy fruited species known to be edible to mammals within a 1 m wide band on the centerline of the wildlife transects were identified to species and recorded by the technicians (see Luzar *et al.* 2011). This method has the advantage of efficiently censusing a relatively large area of forest. We used the mean number of fruit patches encountered on each transect over the course of the study period as a measure of fruit abundance, and the number of unique fruit species encountered as a measure of fruit diversity.

We additionally recorded the proportion of each transect within each of eight Landsat-derived habitat types (Fig. 1). Habitat classification on transects included percent cover of six forest types, three savanna types, water bodies, and topography (Table 1). Vegetation classes were developed through a ‘mixed’ methods classification process. Clouds, cloud shadows, and forest shadows were removed from the 2005 Landsat ETM through a classification and masking process. The resulting imagery was combined with an ASTER DEM of the study area. The image was then separated into 50 spectral classes through an unsupervised classification. The 50 spectral classes were labeled with a vegetation cover description based on vegetation cover type field data collected on all eight 4-km long transects across 28 study sites on the Rupununi landscape.

**DENSITY ESTIMATION.**—We converted encounter rate data to density estimates (in  $\text{km}^2$ ) with distance sampling (Buckland *et al.* 1993). Density,  $D$ , is related to the group size,  $GS$ , and group encounter rate (per km),  $ER$ , by an empirically derived effective strip width,  $ESW$ , which accounts for the decreasing probability of observing animals farther from the trail. Density is thus given by  $D = ER/ESW * GS$ .  $ESW$  is typically determined by the global dataset to maximize sample size, but either a local (*i.e.*, transect scale) or global (*i.e.*, across all transects) group size can be used depending on the goal of the study. We used global group size estimates so that density estimates are simply scaled group encounter rates, which are an appropriate measure of animal abundance. Thus, our density estimates are not quantitatively different from group encounter rates, but serve as a more intuitive and comparable metric of animal abundance.

TABLE 1. *A description of the habitats encountered along transects within the study region.*

Habitat Type	Description
Mixed Forest	Mixed-height terra firme forest with areas of low density small trees mixed with stands of larger trees at higher density
Mountain Mixed Forest	Mixed-height terra firme forest at an elevation above 400 m
River/Creek/Pond	Semi-permanent water bodies. Surrounding vegetation is dominated by herbaceous (grasses) plants and is distinct from seasonally flooded forest.
Seasonally Flooded Forest	Seasonally flooded forest of varying composition. Includes <i>Mauritia flexuosa</i> palm-dominated seasonal wetlands.
Seasonally Flooded Swampy Savanna	Seasonally flooded grasslands with occasional small trees
Disturbed Forest	Upland terra firme forest <15 m in height including secondary regrowth from old farms and active slash and burn agriculture
Mature Forest	Upland terra firme forest >20 m height
Upland Savanna	Terra firme grasslands with occasional small trees

STATISTICAL ANALYSIS.—We first inspected patterns of interspecific relationships consistent with: (1) a positive relationship between *C. apella* and *S. sciureus*; and (2) with competitive exclusion among the two species of *Cebus*. We used logistic regression to estimate the probability that one species of *Cebus* was present as a function of the abundance of the other species.

We then used simultaneous autoregressive models to account for spatial autocorrelation (*spdep* package; R statistical software v. 2.15.1) to make inferences about the importance of interspecific relationships among *C. apella*, *C. olivaceus*, and *S. sciureus* (i.e., determinant of the realized niche) relative to the importance of determinants of the fundamental niche such as habitat type, fruit availability, and geography. We logit transformed all proportions (i.e., percentage of habitat type on transect), and log transformed all other predictors. Because some of our predictors are correlated (e.g., fruit abundance and fruit diversity), we used principal compo-

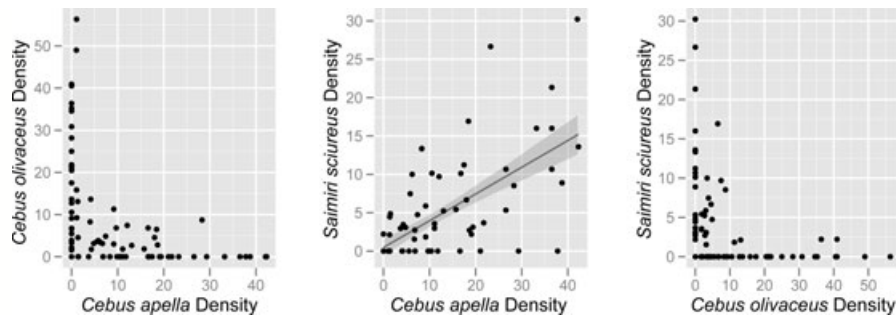
nents analysis on three classes of predictors—those associated with fruit, geography, and habitat. We retained one PCA axis for our measures of fruit abundance and diversity, which explained 93 percent of the variance, one PCA axis for our measures of slope, aspect, and elevation, which explained 82 percent of the variance, and three PCA axes for our eight habitat types, which explained 97 percent of the variance. We used these five PCA variables in our spatial regression model along with the densities of the other primate species. For each regression, we compared the effect size of the PCA variables to determine their relative importance in determining the distribution and abundance of each primate species.

To complement the regressions using PCA axes, we additionally used a simultaneous autoregressive model with the full set of predictors including interspecific interactions, the frequency of fruit patch encounters, the diversity of fruit patches (derived from the diversity of species of fruit encountered on transects), the elevation, slope and aspect of the transect, and the fraction of the transect within each habitat type (Table 1; Fig. 3). To select the most parsimonious models, we used stepwise model selection with Akaike Information Criterion (AIC; Burnham & Anderson 2002).

## RESULTS

NONSPATIAL MODELS OF INTERSPECIFIC RELATIONSHIPS.—Visual inspection of spatial patterns demonstrates increasing dominance of *C. olivaceus* in the northern part of the study region, and of *C. apella* and *S. sciureus* in the southern part of the study region (Fig. 1). Simple correlations across transects indicate a positive relationship between the densities of *C. apella* and *S. sciureus* ( $R^2 = 0.21$ ,  $P < 0.001$ ). *Saimiri sciureus* was not only positively correlated with the abundance of *C. apella*, but *S. sciureus* was also rare or absent at transects without *C. apella* (Fig. 2). *Cebus apella* was at times abundant in the absence of *S. sciureus*, but this was uncommon (*C. apella* above 15 per km<sup>2</sup> without *S. sciureus* on only four transects).

The relationships between the density of *C. olivaceus* and *C. apella* was highly nonlinear and by inspection consistent with competition leading to competitive exclusion (Fig. 2; logistic regression of *C. olivaceus* presence/absence as a function of *C. apella* density:  $\beta = -0.13 \pm 0.03$ ,  $P < 0.0001$ ). Similarly, squirrel monkeys rarely occurred on transects where *C. olivaceus* was

FIGURE 2. Relationship between the densities of the *S. sciureus*, *C. apella*, and *C. olivaceus* across 94 transects.



abundant (Fig. 2; logistic regression of *S. sciureus* presence/absence as a function of *C. olivaceus* density:  $\beta = -0.08 \pm 0.03$ ,  $P < 0.01$ ). *C. olivaceus* was never abundant ( $>15$  per km<sup>2</sup>) at the same transects as *C. apella* or *S. sciureus*, and at most transects either the mixed-species pair was observed, or *C. olivaceus*, but not both (Figs. 1 and 2).

When accounting for the positive relationship between *C. apella* and *S. sciureus*, *C. olivaceus* did not have a significant negative effect on the distribution and abundance of *S. sciureus* (linear regression:  $P = 0.38$ ; logistic regression:  $\beta = -0.03 \pm 0.03$ ,  $P = 0.26$ ). Similarly, when controlling for the negative effect of *C. apella* on *C. olivaceus*, *S. sciureus* did not have a significant negative effect on *C. olivaceus* (linear regression:  $P = 0.38$ ; logistic regression:  $\beta = -0.05 \pm 0.04$ ,  $P = 0.26$ ). In contrast, *C. apella* significantly interacted with both species (linear regression:  $P < 0.001$  for both species; logistic regression:  $\beta_{C.olivaceus} = -0.05 \pm 0.02$ ,  $P < 0.05$ ;  $\beta_{S.sciureus} = 1.03 \pm 0.36$ ,  $P < 0.01$ ). These results suggest that the competitive interaction between *Cebus* genera largely determines which capuchin species successfully occupies each site, and that *S. sciureus* is benefited by the presence of *C. apella*, but is not affected by *C. olivaceus*. These correlations, however, could be driven by shared habitat needs, fruit availability, geography, or unobserved spatial processes. To explore the relative importance of species interactions driving the distribution and abundance of these species, we used a series of spatial multiple linear regressions (see below).

**SPATIAL MODELS.—*Saimiri sciureus*.**—Multiple regression using principal components of the habitat, fruit, and geography covariates (Fig. 3) revealed that *S. sciureus* is: (1) associated with the fruit principal component, associated with high fruit abundance and diversity ( $P = 0.005$ ); (2) and negatively correlated with the third habitat principal component ( $P = 0.017$ ), confirming an association with seasonally flooded forest and negative relationship with upland low forest; and (3) no dependence on geography ( $P = 0.73$ ). In this regression that accounted for habitat type, fruit, availability, and geography, *S. sciureus* retained a significant correlation with the density of *C. apella* ( $P < 10^{-5}$ ).

*Saimiri sciureus* density was highly correlated with *C. apella* density ( $\beta = 0.51$ ,  $P < 7E-10$ ) and 46.4 percent of *S. sciureus* density was explained by this one variable. There was no significant spatial autocorrelation in this relationship ( $\lambda = 0.55$ ,  $P = 0.14$ ; Moran's I test:  $P = 0.34$ ). Adding *C. olivaceus* density did not improve the model fit ( $R^2$  increased from 0.464 to 0.467). The most parsimonious model selected with stepwise AIC from the complete set of covariates improved model fit to explain 57.9 percent of the variance in *S. sciureus* density (Table 2). The most important explanatory variables for *S. sciureus* indicated a preference for seasonally flooded and low elevation habitat with high fruit diversity (Table 2). Very little variance was explained by spatial autocorrelation, with a nonspatial version of the same model still explaining 56.8 percent of the variance in squirrel

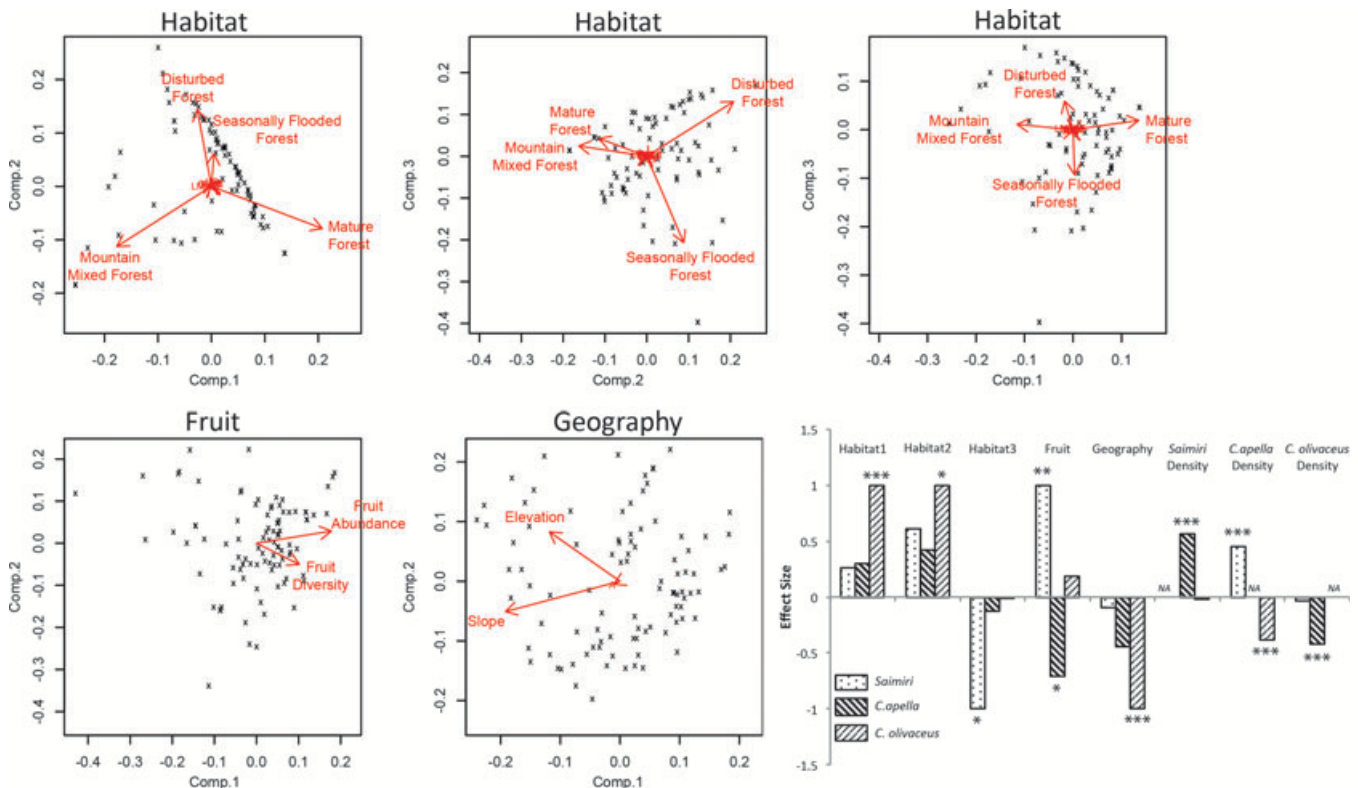


FIGURE 3. The principal components of the habitat, fruit, and geography predictors, and a bar graph of their effect sizes in regressions for the density of *S. sciureus*, *C. apella*, and *C. olivaceus*. Significant effects are indicated with \*, \*\*, and \*\*\* for  $P < 0.05$ ,  $P < 0.01$ , and  $P < 0.001$ , respectively.

TABLE 2. Primate distribution and abundance explained by interspecific interactions, and by the most parsimonious model from the full set of predictors.

	<i>S. sciureus</i>				<i>C. apella</i>				<i>C. olivaceus</i>			
	Interspecific		AIC		Interspecific		AIC		Interspecific		AIC	
	$\beta$	$p$	$\beta$	$p$	$\beta$	$p$	$\beta$	$p$	$\beta$	$p$	$\beta$	$p$
<i>S. sciureus</i>	NA				0.35	6.2E-05	0.34	0.0004	-0.06	0.62		
<i>C. apella</i>	0.48	10 <sup>-6</sup>	0.48	10 <sup>-6</sup>	NA				-0.36	0.003	-0.42	7.7E-06
<i>C. olivaceus</i>	-0.06	0.54			-0.06	0.54	-0.27	0.005	NA			
%Disturbed Forest							0.11	0.07				
%Upland Savanna							0.44	0.08				
%River/Creek/Pond											-0.64	0.05
%Seasonally Flooded Forest			0.17	0.004			0.14	0.1				
%Seasonally Flooded Swampy Savanna			0.98	0.04								
%Mature Forest							0.09	0.07				
%Mountain Mixed Forest											-0.21	7.8E-05
%Mountain Savanna												
%Lowland High Logged Forest												
Elevation												
Slope							0.32	0.02			0.62	2.6E-06
Aspect												
Fruit Patch Frequency							0.32	0.03				
Fruit Diversity			0.50	0.002			-0.86	0.0001				
$\lambda$	0.54	0.14	0.79	0.01	0.95	10 <sup>-6</sup>	0.95	10 <sup>-6</sup>	0.92	10 <sup>-5</sup>	0.90	10 <sup>-4</sup>
AIC	242.73		228.54		227.8		215.7		263.85		240.24	
Variance Explained ( $R^2$ )	0.47		0.56		0.68		0.76		0.50		0.63	

monkey density. This is evidence that unobserved environmental drivers, which are typically autocorrelated, are not driving the spatial pattern of *S. sciureus* distribution and abundance. However, part of the variation is still unexplained.

*Cebus apella*.—Using principal component axes as covariates in multiple regressions found that the density of *C. apella* was negatively correlated with the fruit principal component (opposite of *S. sciureus*), which is associated with lower fruit abundance and diversity ( $P = 0.04$ ). *Cebus apella* was not significantly correlated (at  $P = 0.05$  threshold) with any other principal component, but had a marginally significant negative relationship with the geography principal component ( $P = 0.06$ ), which indicates preference for higher elevation and sloping terrain. In this analysis, *C. apella* was most clearly associated with *S. sciureus* ( $P < 10^{-4}$ ) and negatively associated with *C. olivaceus* ( $P < 0.001$ ).

A regression using only interspecific interaction variables explained much of the distribution and abundance of *C. apella* ( $R^2 = 0.68$ ), which was positively correlated with *S. sciureus* ( $\beta = 0.35$ ,  $P < 7E-5$ ) and negatively correlated with *C. olivaceus* ( $\beta = -0.24$ ,  $P < 0.004$ ). There was significant spatial autocorrelation in this relationship ( $\lambda = 0.95$ ,  $P < 10^{-6}$ ; Moran's I test:  $P < 10^{-6}$ ), which we accounted for in our model. The most parsimonious model (by stepwise AIC) from the complete set of covariates further improved model fit ( $R^2$  increased from 0.68 to 0.76). The most important explanatory variables for *C. apella* (in addition to interspecific interactions) indicated a wide habitat

preference for mature *terra firme* forest, disturbed forest, upland savanna, and seasonally flooded forest, as well as a preference for sites with low fruit diversity, but high fruit abundance (Table 2).

*Cebus olivaceus*.—In contrast to the other two species, *C. olivaceus* was significantly correlated with the first two habitat covariates ( $P < 0.001$ ,  $P < 0.01$  for axes 1 and 2, respectively), which indicated greater preference for mature forest than the other two species. *Cebus olivaceus* was also negatively correlated with the geography principal component, indicating preference for higher elevation and sloped habitat.

In an interspecific interaction model, the distribution and abundance of *C. olivaceus* was negatively correlated with *C. apella* ( $\beta = -0.36$ ,  $P < 0.003$ ), but not significantly correlated with *S. sciureus* ( $\beta = -0.06$ ,  $P = 0.62$ ). There was significant spatial autocorrelation in the interspecific model ( $\lambda = 0.92$ ,  $P < 10^{-5}$ ; Moran's I test:  $P < 10^{-4}$ ). The most parsimonious model indicated that *C. olivaceus* avoids *C. apella*, riparian areas, and mixed-height *terra firme* forest on mountainous terrain, and is more abundant on sloping terrain (Table 2).

## DISCUSSION

Several observational studies have attempted to explain why *Saimiri* and *Cebus* form stable interspecific associations with arguments based on foraging efficiency and predator avoidance (Boinski 1989, Podolsky 1990, Terborgh 1990). It has been

difficult, however, to assess the actual impact of these associations on primate distribution and abundance. Using a large field study, we were able to collect species abundance and biogeographic data on 94 transects distributed over a 48,000 km<sup>2</sup> area to infer the consequence of the conspicuous mixed-species groups formed by *C. apella* and *S. sciureus*. We used competitive exclusion due to the competition between *C. apella* and *C. olivaceus* as a type of natural experiment in which squirrel monkeys were subject to two *Cebus* ‘treatments’. In one treatment, *C. apella* is available to forage in association with *S. sciureus*, and in the other treatment *C. apella* is either rare or absent due to competition with *C. olivaceus*.

Squirrel monkeys were more abundant at sites where *C. apella* was abundant, and were conspicuously absent at sites without *C. apella*. When accounting for the positive relationship between *C. apella* and *S. sciureus*, *C. olivaceus* did not have a significant negative effect on the distribution and abundance of *S. sciureus*. Thus, it appears that *S. sciureus* benefits from the presence of *C. apella* by reaching higher densities, but is not directly negatively impacted by *C. olivaceus*. Although it remains unclear what life history parameters (*i.e.*, survival and fecundity) might be most affected. In addition, these correlative relationships could be caused by external drivers such as habitat or food availability.

To account for this possibility, we included fruit, habitat, and geography into our statistical models. Across all three species and using both model formulations (*i.e.*, with PCA and with all covariates included individually), interspecific interactions remained significantly correlated with the density of each primate species. Our results support the hypothesis that competitive exclusion determines the distribution of *Cebus*, which may explain why the range of *C. apella* does not extend into central and northern Guiana. Squirrel monkeys persist without *C. apella* at other sites throughout Guyana (Lehman *et al.* 2006), but their distribution is highly patchy and they are conspicuously absent from large areas (Sussman & Phillips-Conroy 1995). Our results suggest that this patchy distribution could be partially explained by the absence of *C. apella*.

Guiana Shield forests have poor soils, low forest productivity, and low fruit abundance relative to other tropical forests (Terborgh & Andresen 1998, Lehman 2000). The relationship between the densities of *S. sciureus* and *C. apella* occurred despite this low productivity, which is expected to deter associations due to the increased cost of feeding competition. While we did not measure invertebrate abundance, a potentially important food source for both *Cebus* and *Saimiri*, the densities of *C. apella* and *S. sciureus* were associated with disturbed forest and seasonally flooded forest (but *C. apella* was also associated with mature forests). Disturbed forests and those with edge habitats contain abundant pioneer plant species that are relatively fast growing with less investment in leaf defense, which may support orthopterans and other folivorous insects on which these monkeys feed (Coley & Barone 1996). Thus, habitat plays an important role in the distribution and abundance of these species, but our results suggest that facilitation is also important.

In contrast, *C. olivaceus* was not associated with any particular habitat types, using mature *terra firme* forest as well as seasonally

flooded or disturbed forest (PCA habitat axes 1 and 2, negatively correlated with axis 3), but avoiding mixed-height *terra firme* forest on mountainous terrain. The density of *C. olivaceus* was unrelated to fruit abundance and diversity. The lack of clear habitat or fruit associations is difficult to explain due to poor understanding of *C. olivaceus* diet.

While our analysis cannot tease out causal relationships, it does suggest that interspecific interactions are important in determining the distribution and abundance of *Cebus* and *Saimiri*. When controlling for fruit availability and habitat type, *S. sciureus* was able to thrive with *C. apella* present. However, these results could also have been obtained if some crucial predictors were excluded from the model. One reason that this is less likely to be the case for *S. sciureus* is that there is no residual spatial autocorrelation in a model with *C. apella* as a predictor, and the spatial model did not outperform a simple nonspatial model. Because predictors are inherently spatially autocorrelated due to Tobler’s law of geography (Tobler 1970), we would expect to see residual spatial autocorrelation if an important driver of *S. sciureus* distribution and abundance was missing from our analysis.

One hypothesis to explain our results is that *C. apella* and *S. sciureus* benefit from antipredator defenses of a larger group size. Due to their small size and conspicuous presence in trees, *S. sciureus* are particularly susceptible to predation by raptors (Hart 2007, Ferrari 2009). Raptor diversity is very high in the Neotropics, and at our site we recorded 19 diurnal raptor species. Unlike other raptor prey species, *S. sciureus* retains the slow life history characteristic of primates; including delayed sexual maturity and low fecundity. Neotropical primates are highly social and cooperate to deter predators many times their size (Ferrari 2009). Here, it is plausible that interspecific cooperation aids in predator avoidance to increase the population density of both species. One advantage to forming mixed-species groups is that a larger group size is obtained with less feeding competition than in a conspecific group, which has complete dietary overlap, and without increasing mate competition. It is also possible that *C. apella* uses *S. sciureus* to find fruit that it can then quickly dominate (Podolsky 1990), which allows *C. apella* to dominate sites with the most abundant fruit resources, but the opposite has also been suggested (Terborgh 1983). Further field studies are needed, but without experimentally removing *S. sciureus* and measuring the response in the feeding rate, predation rate, or density of the two sympatric capuchins, it is difficult to imagine experimental corroboration of these observations. The ubiquity of the *C. apella*–*S. sciureus* association relative to other species of *Cebus* and *Saimiri*, coupled with the correlation in their densities, and their ability to coexist in captivity (Leonardi *et al.* 2010) despite the often predatory nature of capuchin monkeys, suggests that this interaction is an evolved mutualism. It is unknown whether *C. olivaceus* and *S. sciureus* can similarly coexist in captivity, but this can be experimentally tested in the future to determine whether long-term associations between these species are possible, or whether aggressive interactions are prevalent.

The *Cebus*–*Saimiri* species interactions highlight the complexities of primate community structure. Where experimental manipula-

tions are not feasible, large-scale observational studies that account for differences in habitats and explicitly measure resource availability can identify patterns. Our biogeographic data suggest that in Guyana, a *C. apella*–*S. sciureus* mutualism works to make both species more abundant, and to exclude *C. olivaceus*, such that primate communities at our field site are generally structured to include the *C. apella*–*S. sciureus* pair or the regionally dominant species, *C. olivaceus*.

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## SUPPORTING INFORMATION

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

TABLE S1. *Primate distribution and abundance explained by interspecific interactions, and by the most parsimonious model from the full set of predictors.*

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