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Author(s): Camila R. Cassano, Jos Barlow and Renata Pardini
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Large Mammals in an Agroforestry Mosaic in the Brazilian Atlantic Forest

Camila R. Cassano[1,2,5], **Jos Barlow**[3], and **Renata Pardini**[4]

[1] Departamento de Ecologia, Universidade de São Paulo, Rua do Matão, Travessa 14, n°101, São Paulo, SP, 05508-090, Brazil

[2] Instituto de Estudos Socioambientais do Sul da Bahia, Rua Araujo Pinho n°72, Ilhéus, BA, 45653-145, Brazil

[3] Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, U.K.

[4] Departamento de Zoologia, Universidade de São Paulo, Rua do Matão, Travessa 14, n°101, São Paulo, SP, 05508-090, Brazil

ABSTRACT

The forest-like characteristics of agroforestry systems create a unique opportunity to combine agricultural production with biodiversity conservation in human-modified tropical landscapes. The cacao-growing region in southern Bahia, Brazil, encompasses Atlantic forest remnants and large extensions of agroforests, locally known as *cabrucas*, and harbors several endemic large mammals. Based on the differences between *cabrucas* and forests, we hypothesized that: (1) non-native and non-arboreal mammals are more frequent, whereas exclusively arboreal and hunted mammals are less frequent in *cabrucas* than forests; (2) the two systems differ in mammal assemblage structure, but not in species richness; and (3) mammal assemblage structure is more variable among *cabrucas* than forests. We used camera-traps to sample mammals in nine pairs of *cabruca*-forest sites. The high conservation value of agroforests was supported by the presence of species of conservation concern in *cabrucas*, and similar species richness and composition between forests and *cabrucas*. Arboreal species were less frequently recorded, however, and a non-native and a terrestrial species adapted to open environments (*Cerdocyon thous*) were more frequently recorded in *cabrucas*. Factors that may overestimate the conservation value of *cabrucas* are: the high proportion of total forest cover in the study landscape, the impoverishment of large mammal fauna in forest, and uncertainty about the long-term maintenance of agroforestry systems. Our results highlight the importance of agroforests and forest remnants for providing connectivity in human-modified tropical forest landscapes, and the importance of controlling hunting and dogs to increase the value of agroforestry mosaics.

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

Key words: camera-trap; fragmentation; matrix; shade cacao plantation; *Theobroma cacao*; vertebrates.

PROTECTED AREAS ALONE DO NOT GUARANTEE THE MAINTENANCE OF ECOLOGICAL PROCESSES over large spatial and temporal scales, and are dependent on the long-term processes and dynamics of the surrounding landscape (Chazdon *et al.* 2009, Gardner *et al.* 2009). Most human-modified landscapes are composed of a mosaic of environments with different degrees of suitability for the occurrence and dispersal of individuals of native and non-native species (Daily *et al.* 2003, Harvey *et al.* 2006, Umetsu *et al.* 2008). Understanding changes in populations and communities between different environments and the linkages and dynamics across landscape mosaics are key research priorities for conservation planning in tropical forests (Chazdon *et al.* 2009, Gardner *et al.* 2009).

In tropical forest regions, agroforestry systems represent an opportunity for the development of multi-functional landscapes that combine agricultural production and biodiversity conservation as they retain more forest-like characteristics than any other agricultural land-use (Perfecto & Vandermeer 2008). Landscapes harboring large extensions of cacao (*Theobroma cacao*) and coffee (*Coffea arabica*) agroforests have raised special conservation interest, since they occur in areas originally occupied by biologically diverse tropical forest (Clough *et al.* 2009, Tscharntke *et al.* 2011). Species richness and abundance in cacao and coffee agroforests may parallel those of primary forest, but the structure of communities usually differs. As a general rule, these shaded plantations harbor more generalists and fewer forest-dwelling species than forests (Pardini *et al.* 2009, Waltert *et al.* 2011). Species richness and composition in agroforests, however, depend on the maintenance of forest cover at larger spatial scales (Bali *et al.* 2007, Faria *et al.* 2007), and on land-use intensification (*i.e.,* shade density and diversity, and agrochemical use; Perfecto *et al.* 2005, Gordon *et al.* 2007).

Large mammals play important roles in forest ecosystems directly through seed dispersal and predation (Tabarelli & Peres 2002, Terborgh *et al.* 2008) and prey population control (Terborgh *et al.* 2001), or indirectly by helping to maintain assemblages of other faunal groups (Nichols *et al.* 2009). Many large mammals are threatened by habitat loss and overhunting, that can extirpate species from apparently intact forests (Redford 1992, Morrison *et al.* 2007, Terborgh *et al.* 2008). The ease of access to forest remnants increases both hunting pressure (Cullen *et al.* 2000, Peres & Nascimento 2006, Michalski & Peres 2007), and the damage caused by invasive species (*e.g.,* domestic dogs; Fiorello *et al.* 2006). Furthermore, human-wildlife conflicts resulting from crop damage and predation of livestock often result in

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[5]Corresponding author; e-mail: cassanocami@hotmail.com

the persecution and death of mammals (Naughton-Treves *et al.* 2003, Michalski *et al.* 2006a). Studies of large mammal communities in agroforestry systems have shown that species differ in their sensitivity to the conversion of forest into agroforests, but species traits driving such responses are still poorly understood (Estrada *et al.* 1994, Harvey *et al.* 2006).

The Brazilian Atlantic forest has endured a long history of human influence, and current strategies for biodiversity conservation in this biome require the reestablishment of functional connectivity between forest remnants (Tabarelli *et al.* 2005, Ribeiro *et al.* 2009). The Atlantic forest in southeastern Bahia is recognized for its high species richness and endemism (Silva & Casteleti 2003). It also encompasses large extensions of agroforests, with approximately 6000 km^2 of land under cacao plantations shaded by native trees (Landau *et al.* 2008). These agroforests are known regionally as *cabrucas*, and their management is likely to be of major importance for biodiversity conservation (Cassano *et al.* 2009).

Like other agroforestry systems, *cabrucas* are structurally simpler than native forests; the canopy layer has lower tree diversity and density, the understory is exclusively composed of cacao trees and the undergrowth is periodically removed by mechanical and chemical means (Sambuichi 2002). These changes may have negative effects on large mammals that disperse and forage through the vegetation (*i.e.,* arboreal large mammals), as observed in studies on small arboreal rodents and marsupials and understory birds (Moura 1999, Faria *et al.* 2006), but may favor large mammals that forage mainly on the ground, since food resources may be easier to find in more open *cabrucas*. Other differences in large mammal assemblages between *cabrucas* and forests are expected to result from increased hunting activities and invasion by exotic species in managed agroforest compared to forest. Finally, the variation in the shade trees kept during the creation of the agroforests and in management practices (Sambuichi & Haridasan 2007) might produce greater among-site variation in resources and disturbances, and thus higher among-site variation in assemblage structure in *cabrucas* than in forests.

Few studies have been conducted on the use of *cabrucas* by large mammals, and these focused on single, endangered species (Raboy *et al.* 2004, 2008; Cassano *et al.* 2011, Oliveira *et al.* 2011). We used camera-traps and a paired design of *cabrucas* and forest remnants to sample large mammals across an agroforestry mosaic in southern Bahia, and to test the following hypotheses: (1) non-native and non-arboreal mammals use *cabrucas* more frequently, whereas exclusively arboreal and hunted mammals use these systems less frequently than forests; (2) consequently, the two systems differ in mammal assemblage structure, but not in richness (alpha diversity); and (3) mammal assemblage structure is more variable among *cabrucas* than forest. We use our results to critically examine the conservation value of *cabrucas*.

METHODS

Study area and sampling design.—This study was carried out in the cacao-growing region of southern Bahia, in a landscape encompassing part of the municipalities of Una and Arataca (~60 km^2; between 39°5′–39°22′ W and 15°4′–15°14′ S), largely covered by mature and late secondary forest (roughly 50% of the area—see Fig. S1). The original vegetation is Southern Bahian Wet Forest (Mori *et al.* 1983, Thomas 2003), which includes lowland rain forest over latisols, lowland rain forest over podzols and montane forest (above the 500 m asl) in a gradient from east to west in the study region (Thomas 2003). The mean annual temperature is 24°C, and rainfall is superior to 1800 mm/yr. The region lacks a distinct dry season, although a warmer and rainless period occasionally occurs between December and March (Mori *et al.* 1983, Thomas *et al.* 1998).

The study sites were located in farms around and between two protected areas: the Una Biological Reserve in the east, and the Serra das Lontras National Park in the west. Thirty-eight percent of the agroforestry mosaic outside the reserves is covered by old-growth forests that suffered different levels of selective logging in the past, and 21, 20, and 10 percent are covered by *cabruca*, pasture and permanent monocultures, respectively. The land-use is strongly related to edaphic and topographic conditions, and larger forest patches persist in areas that are less favorable for the development of cacao plantations (sandy soils in the East and the steeper slopes in the West).

We sampled 18 sites located in nine blocks, each composed of a *cabruca* site and an adjacent forest site, 200–450 m apart from each other. The criteria for block selection were: (1) cacao plantations were shaded mainly by native trees (excluding the more intensely managed plantations) and were adjacent to a forest remnant (used as a control); (2) blocks were at least 2.5 km from each other (distances varied from 2.5 to 6.2 km); and (3) there was a large variation in the amount of forest and *cabrucas* between blocks (Table S1). Within each block *cabruca* and forest sites were located to guarantee at least 200 m between them (distance varied from 200 to 450 m) while also maximizing the distance to other bordering environments (Table S1). Site locations were also dependent on suitable trees for placement of the understory trap stations. The block design increased the power of our analysis by helping control for the variable landscape context, soil, and topography. Although the block design limited our *cabruca* sites to areas near forest remnants, 70 percent of the area covered by *cabrucas* in the study landscape is < 200 m from forest edges.

Large mammal sampling.—Two camera-traps (analog Trapacamera—http://www.trapacamera.com) were placed in each site, one on the ground and one in the understory (3–4 m above ground level), 50–100 m apart from each other. Ground stations were baited with banana and sardine, and understory stations just with banana. The position of cameras and the types of bait were designed to sample terrestrial as well as arboreal and frugivorous as well as carnivorous mammals. Camera-traps are frequently used to sample terrestrial large mammals (Srbek-Araujo & Chiarello 2005, Tobler *et al.* 2008a, Espartosa *et al.* 2011) and have also proved effective for sampling arboreal species (Kierulff *et al.* 2004).

Data collection occurred during four sampling sessions when all sites were sampled, representing two times of the year in two different years (July–October of 2007 and 2008, and January–April of 2008 and 2009). This sampling procedure was adequate to take into account possible annual fluctuation in food resources, since the climate in the region is mostly aseasonal (Mori *et al.* 1983, Thomas *et al.* 1998), and cacao production extends from April to January, with higher yield in the second half of this period (Alvim & Rosário 1972). During each of the four sampling sessions, three *cabruca*-forest pairs were sampled simultaneously for four consecutive weeks and checked weekly to exchange film and re-bait (all nine pairs of sites sampled within 4 mo). Nevertheless, the malfunction of camera-traps and insufficient film on some occasions led to an unequal effort among sites and stations, which ranged from 90 to 127 trap-days in forest sites and from 100 to 128 trap-days in *cabruca* sites. The total sampling effort was 1895 and 2080 trap-days, respectively.

SPECIES CLASSIFICATION AND EXPECTED RESPONSES TO AGROFOREST.—The potential pool of 32 native large mammals occurring in the study region was identified following Moura (2003), excluding *Pseudalopex vetulus* which is not considered native to the region (Emmons & Feer 1999) and was not registered in our study. Species were classified as hunted or not following Cullen *et al.* (2000), Naughton-Treves *et al.* (2003), Peres and Nascimento (2006), Michalski *et al.* (2006a), and Whiteman *et al.* (2007). Hunted species included ungulates, armadillos, large primates, and large rodents hunted for meat, and felids, which are often persecuted to protect livestock. We also included *Didelphis aurita* as it is known to be heavily hunted in the study region (Santos 1999). Classification of species according to locomotion habit followed Fonseca *et al.* (1996), but was simplified as 'arboreal' or 'non-arboreal', this last class including the terrestrial, scansorial, semi-fossorial and semi-aquatic species. Of the 32 species, 14 were classified as hunted, 10 as arboreal and 21 as terrestrial (Table S2). Based on these classifications and our hypotheses, we expected 24 species to exhibit lower capture rates in *cabrucas* than forests and eight to exhibit the opposite trend (Table S2).

DATA ANALYSIS.—The capture rate was calculated for each species and site by dividing the total number of records by the total sampling effort. A single record was defined as the presence of at least one picture of one species in one station during a 24-h period (starting at 0000 h ending at 2400 h). To calculate sampling effort (trap-days) we only included days with no apparent camera-trap malfunction or film depletion. For arboreal and scansorial species we considered both ground-level and understory stations. We calculated capture rate by strata and then the average between them to prevent an uneven effort between stations from biasing capture rate. For terrestrial species, just the ground-level stations were considered. To compare the capture rate of each species between forests and *cabrucas*, we used a permutation test equivalent to a paired *t*-test, with 10,000 randomizations implemented in R 2.10.1 (R Development Core Team 2009). Only species recorded in at least four sites in one type of system (forests or *cabrucas*) were included in this particular analysis. This corresponds to approximately 25 percent of the number of sampling sites, and is here considered the minimum number required for a reliable comparison between the two systems.

We used non-metric multi-dimensional scaling (MDS) and analysis of similarity (ANOSIM) to summarize and test for differences in assemblage structure between forests and *cabrucas*. Analyses were run including all species, using both square-root transformed capture rates (a proxy of relative abundance) and presence-absence (*i.e.,* composition) data, and Bray-Curtis dissimilarity. A similarity percentage analysis (SIMPER) was used to identify the contribution of each species to the dissimilarity in assemblage structure between forests and *cabrucas* (Clarke 1993). The variation in assemblage structure among sites was tested using analyses of multivariate homogeneity of group dispersions and permutation tests (10,000 randomizations), which contrast the average dissimilarity from individual sites to their group centroid in multivariate space (Anderson *et al.* 2006). This analysis was run twice, first considering species capture rates and then considering species presence-absence. The MDS, ANOSIM and multivariate homogeneity of group dispersions analyses were implemented in R 2.10.1 (R Development Core Team 2009), using the Vegan package. SIMPER analysis was implemented in PRIMER 5.2.4 (Clarke & Gorley 2006).

Alpha diversity (*i.e.,* plot-level species richness) was estimated for each site using Jackknife1 (as suggested by Tobler *et al.* 2008a, b) using sampling day as the unit of effort, and considering only the days in which both camera-traps (ground and understory stations) were working (78–126 d among sites). We compared differences in alpha diversity between forests and *cabrucas* using the same randomization procedure as previously described for species capture rates using only native species. To examine gamma diversity (*i.e.,* total species richness within each environment), we constructed species accumulation curves with 95% CI, considering sites as the unit of effort. To standardize sampling effort per site we only used records of native species from the first 78 d in which camera-traps in both stations per site worked simultaneously. Mean number of species and the 95% CI were calculated by the Mao Tau method, using EstimateS 8.2.0 (Cowell 2006).

RESULTS

We recorded 19 native and three non-native large mammal species in trap stations. Fifteen native and two non-native species were registered in forest remnants (1010 and 22 records, respectively), whereas17 native and three non-native species were registered in *cabrucas* (460 and 76 records, respectively; Table S2). Four additional species that eluded the camera-trap stations were fortuitously detected once or twice in *cabrucas* (*Bradypus torquatus*, *Pecari tajacu* and *Tamandua tetradactyla*) and forest remnants (*Callicebus melanochir*) during the period of this study.

CAPTURE RATES IN FORESTS AND *CABRUCAS*.—*Didelphis aurita*, *Callithrix kuhlii*, *Leontopithecus chrysomelas*, *Dasypus novemcinctus*, *Na-*

sua nasua, *Eira barbara*, *Procyon cancrivorus*, *Cerdocyon thous*, and *Canis familiaris* were recorded in at least four forest or *cabruca* sites. Our expectation that capture rate would be lower in *cabrucas* was met for both arboreal species (*C. kuhlii* and *L. chrysomelas*) (Figs. 1A–B). Our expectation that capture rate would be higher in *cabrucas* was met for the only non-native (*C. familiars*) and one non-arboreal species (*C. thous*) (Figs. 1H–I). Two non-arboreal species (*P. cancrivorus* and *N. nasua*) and both hunted species (*D. aurita* and *D. novemcinctus*) had similar capture rates in forests and *cabrucas*, while one non-arboreal species (*E. barbara*) had higher capture rate in forests, contrary to our expectation for this group (Figs. 1C–G).

Assemblage metrics in forests and *cabrucas*.—The two-dimensional MDS and the ANOSIM tests show that large mammal assemblages in forests and *cabrucas* were significantly distinct in structure when species capture rates were considered (ANOSIM: $R = 0.23$, $P < 0.01$; Fig. 2A), but not when just presence-absence data were considered (ANOSIM: $R = -0.03$, $P = 0.66$; Fig. S2). Similarly, among-site variation in assemblage structure was higher in *cabrucas* than in forests when species capture rates were considered (permutation test, $P = 0.03$), but not when only presence-absence data were considered (permutation test, $P = 0.67$). The SIMPER analysis revealed that five species were responsible for 61 percent of the variation in assemblage structure between forests and *cabrucas* (Table S3). Capture rates of these species were superimposed on the two-dimensional MDS plot (Figs. 2B–F).

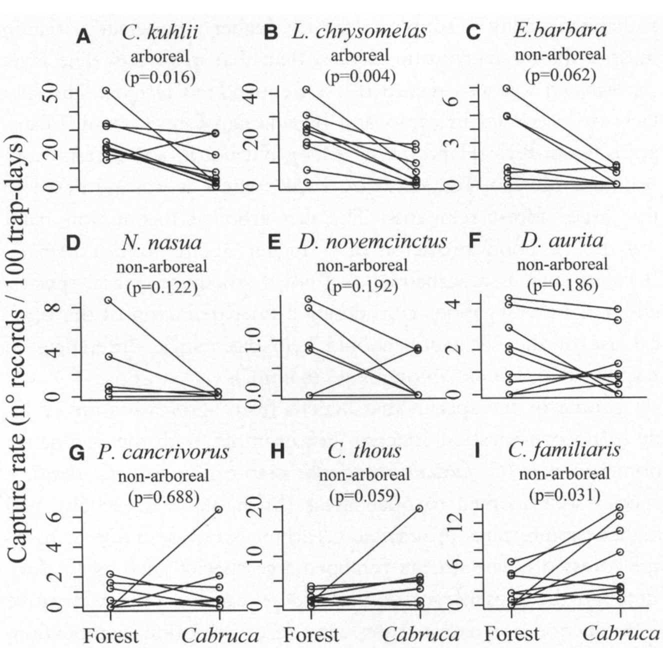

FIGURE 1. Capture rates of (A–H) eight native and (I) one non-native large mammal species in forest and *cabruca* sites. Locomotion habit: arboreal or non-arboreal, modified after Fonseca *et al.* (1996).

As expected, alpha diversity (*i.e.*, plot-level species richness estimated by Jackknife 1) was similar between the two systems (permutation test, $P = 0.44$), with an average of 7.6 (± 1.8 SD) species in forest and 7.2 (± 3.6 SD) species in *cabruca* sites (Fig. 3A). Gamma diversity was also similar, and species accumulation curves were approaching their asymptote after nine samples (Fig. 3B). Local species richness estimated by the abundance-based coverage (ACE) and the Chao1 estimators were also calculated and produced similar results to Jackknife 1, except for two

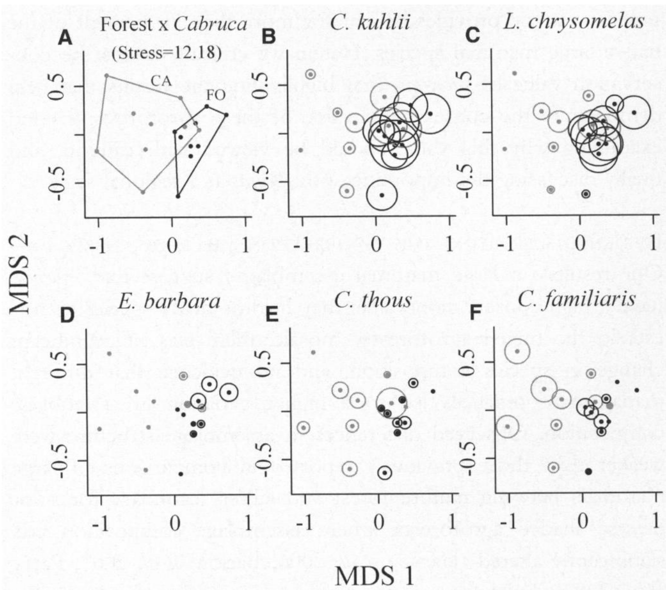

FIGURE 2. (A) Two-dimensional MDS plots on the similarity in assemblage structure among forest sites (FO) in black and *cabruca* sites (CA) in gray; (B–F) capture rates of species with significant differences between the two systems plotted over two-dimensional MDS (circle diameters are scaled according to square-root of the capture rate).

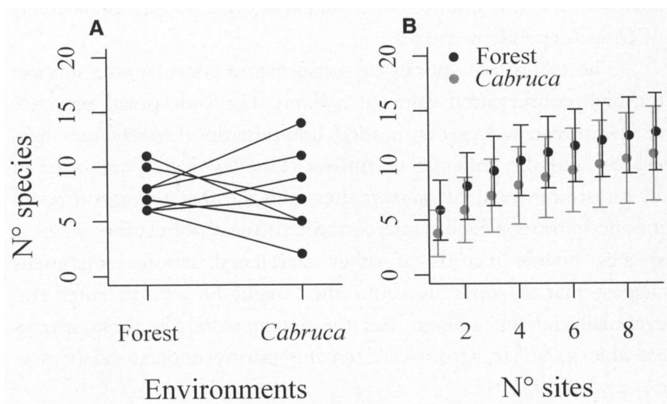

FIGURE 3. Comparisons of native large mammal richness in forest and *cabruca* sites. (A) Paired comparison of alpha diversity (*i.e.*, plot-level species richness estimated by Jackknife1) and (B) Comparison of gamma diversity (*i.e.*, total species richness) through species accumulation curves (mean ± 95% CI).

cabruca sites with a large number of rare species where estimation produced by ACE was 1.5 times larger than that found by the other estimators.

DISCUSSION

We recorded 23 species during the study (including the four species fortuitously detected) compared to the 32 species of large mammals that Moura (2003) reported to be present in the largest forest remnants (the current protected areas) in the region. A simplistic interpretation of these numbers indicates that this agroforestry mosaic provides habitat for more than 70 percent of the native large mammal species. Herein we critically assess the conservation value of *cabrucas*, first highlighting the results that help demonstrate the conservation value of these agroforests, second examining why this value should be viewed with caution, and finally discussing the importance of *cabrucas* at a regional scale.

EVIDENCE SUPPORTING THE CONSERVATION VALUE OF *CABRUCAS*.—Our results on large mammal assemblages suggest that *cabrucas* have a high conservation value: they held as many species as forests in the mixed agroforestry mosaic, there was no significant change in species composition, and no evidence that different management practices led to a higher variation in assemblage composition. Observed differences in assemblage structure were weaker than those previously reported in comparisons of large mammals between mature forest and either secondary forest or diverse shaded agroforests, where assemblage composition was significantly altered (Harvey *et al.* 2006, Barlow *et al.* 2007, Parry *et al.* 2007). Furthermore, the conservation value of *cabrucas* for large mammals was much higher than alternative anthropogenic land-uses such as urban areas (Crooks 2002), pastures (Daily *et al.* 2003), annual monocultures (Gehring & Swihart 2003), and banana (Harvey *et al.* 2006) and eucalyptus plantations (Barlow *et al.* 2007), all of which differ greatly from forests in terms of assemblage composition, and species richness. When compared to such land-uses, *cabrucas* are likely to increase both habitat availability and forest connectivity, increasing the population viability of forest-dependent species.

The records of species of conservation concern also support the high conservation value of *cabrucas*. The widespread presence of the threatened golden-headed lion-tamarin (*Leontopithecus chrysomelas*) and the endemic marmoset (*Callithix kuhlii*), recorded in all forest and most of *cabrucas* sites, indicate that the agroforestry mosaic harbors a highly interconnected (meta)population of these species. Sparse records of other threatened arboreal mammals suggest that in some situations they might be able to enter and eventually inhabit *cabrucas*, but the extent to which these species are able to utilize agroforests remains poorly understood (Cassano *et al.* 2009, 2011).

Hunting pressure could reduce the value of *cabrucas* for large mammals, but we did not find any evidence that the impact of hunting was significantly higher in agroforests than in the forest remnants from the agroforestry mosaic. The two game species analyzed (the opossum, *Didelphis aurita*, and the nine-banded armadillo, *Dasypus novemcinctus*) had similar capture rates in forest and *cabruca* sites, which suggests that they are adapted to changes in habitat and that hunting pressure does not decrease their use of the agroforests. Their low vulnerability to habitat changes is not surprising, as both species are well adapted to human-modified landscapes even when open environments are created (Crooks 2002, Michalski & Peres 2007). Regarding hunting pressure, the similar capture rates in the two systems indicate that hunting is not solely focused on *cabrucas* where humans are more active, but it might be widespread across land-uses (see further discussion below).

QUESTIONING THE CONSERVATION VALUE OF *CABRUCAS*.—A number of factors indicate that we should be cautious when interpreting our results regarding the high conservation value of *cabrucas*. The high proportion of forest in the study landscape is likely to improve local species richness and abundance. Furthermore, the paired nature of the study could complicate the extrapolation of our results to *cabrucas* isolated from forest patches.

Some species may still require forests, even if observed in *cabrucas*. For example, the capture rate of arboreal species (*C. kuhlii* e *L. chrysomelas*) was lower in *cabrucas* than that in forests, indicating that *cabrucas* can represent sub-optimal habitat for these species. In fact although *L. chrysomelas* has been previously shown to use agroforests, they are well adapted to *cabrucas* with a high density of canopy trees (Raboy *et al.* 2004) or a high abundance of key food resources (*e.g.,* jackfruit and bromeliads; Oliveira *et al.* 2011). Thus, *cabrucas* should be expected to provide habitat of variable quality for these primates due to the large variability of tree density and plant species diversity among them (Sambuichi 2002, Sambuichi & Haridasan 2007). In our study, this variability in habitat quality is supported by the higher among-site variation in assemblage structure in *cabrucas* than that in forests. The tayra (*E. barbara*) was also recorded less frequently in *cabrucas*. The species was recorded in cacao and banana agroforests from Talamanca, Costa Rica (Harvey *et al.* 2006), but not in agroforests from southern Mexico (Estrada *et al.* 1994), where it was restricted to the larger forest remnants. The non-arboreal locomotion habit was not a good predictor of a higher ability to use *cabrucas*. Because tayra is a scansorial and not a strictly terrestrial species, additional investigations considering a finer definition of the vertical use of the vegetation should help disentangle differences in responses to *cabrucas* among large mammals.

Some of the species that benefit from agroforests are of little or no conservation concern. For example, both the non-native domestic dog (*C. familiaris*) and the crab-eating fox (*C. thous*), a species well adapted to open areas (Michalski *et al.* 2006b), had higher capture rates in *cabrucas*. Clearly it is not desirable to manage forested environments for open-area species such as *C. thous*, although the presence of domestic dogs can have many negative consequences for native fauna because of predation, competition, and the spread of disease (Fiorello *et al.* 2006, Vanak & Gompper 2009). Domestic dogs are often recorded in forest fragments (Fiorello *et al.* 2006, Whiteman *et al.* 2007), and were present at all properties where the study was developed and frequently taken into *cabrucas* by the farm laborers (C. R. Cassano, pers. obs.). The widespread distribution of dogs through both forests and *cabrucas* certainly decreases the conservation value of the agroforestry mosaic for native fauna.

As in many tropical studies, our forest 'controls' harbor an impoverished fauna compared to the 'original' state of the forest. For example, many species commonly reported in camera-trap studies from mature forests (*e.g.*, Srbek-Araujo & Chiarello 2005, Tobler *et al.* 2008a) were rare or absent in our data. Most of these species are frequently hunted or persecuted, including the ungulates (*Pecari tajacu, Mazama* spp.), large-bodied rodents (*Cuniculus paca, Dasyprocta* sp.) and felids (*Leopardus* spp., *Puma yagouaroundi, Puma concolor*). Other hunted species that could occur in the area, such as the jaguar (*Panthera onca*), primates (*Alouatta guariba, Brachyteles hypoxanthus*), and ungulates (*Tayassu pecari* and *Tapirus terrestris;* Emmons & Feer 1999), have not been recorded recently even within the largest forest remnants (Moura 2003). The behavior of hunters provides additional evidence that populations of large-bodied mammals have already been reduced by hunting, as they now focus on small bodied species such as *D. aurita*, which is listed amongst the most hunted in the study region (Santos 1999). The decline of large-bodied animals has been previously explained by the local depletion of game stocks (Jerozolimski & Peres 2003), and has also been reported in other landscapes with a high proportion of agroforestry systems (Harvey *et al.* 2006, Bali *et al.* 2007). This 'shifted baseline' driven by hunting means we may overestimate the relative conservation value of the *cabrucas* because we cannot know if these now rare large-bodied species are vulnerable to land-use change. Recognition of such shifting baselines is important for interpreting observed results and setting conservation goals (Gardner *et al.* 2009).

Finally, it is important to remember that although our study provides a useful snapshot, conservation value should be assessed over a longer time frame. There is considerable uncertainty regarding the long-term future of *cabrucas* and the mosaic in which they lie. The management of agroforests strongly influences tree regeneration, resulting in increased dominance of fast growing native species (pioneers and species found in young secondary forests) and exotic tree species (Sambuichi & Haridasan 2007). Moreover, management intensification is a common process in cacao-growing regions (Clough *et al.* 2009). The cacao 'boom and bust' cycle described by Clough *et al.* (2009) has been occurring on a small scale in the southern Bahia if compared to other cacao-growing regions in the world, but remains as a potential threat (Schroth *et al.* 2011). Thus, the conservation value of *cabrucas* in the future depends crucially on avoiding management intensification and aiding regeneration in the agroforests.

IMPLICATIONS FOR THE CONSERVATION OF LARGE MAMMALS IN SOUTHERN BAHIA.—The forest-*cabruca* mosaic dominates the landscape between Una Biological Reserve and Serra das Lontras National Park, and potentially constitutes an important biodiversity corridor, increasing habitat availability and decreasing patch isolation for large mammals. The scarcity of game species in our study, however, indicates that the functionality of this corridor is severely impaired by past and present hunting pressure and the presence of domestic dogs in the *cabrucas* and forest remnants. Our results also help underline the importance of maintaining large forest remnants. The large areas of forest may provide the only habitat for species that are sensitive to the synergetic effects of forest fragmentation, overhunting, and the invasion of non-native species, whereas smaller forest remnants might represent higher quality habitat patches within the agroforestry mosaic for some species of conservation concern, such as *L. chrysomelas.* The importance of maintaining forest remnants in this landscape is even higher considering that *cabrucas* are agricultural environments, and economic pressures may lead to land-use intensification and change (Schroth *et al.* 2011).

CONCLUSION.—Given the increasing demand for food and other agricultural products, the implementation of large scale 'wildlife-friendly' but less productive agroforestry systems has been questioned (Balmford *et al.* 2005). In this article we demonstrate how cacao agroforests in a mixed forest and agroforestry landscape can be beneficial for large mammal conservation. Because biodiversity conservation in protected areas can be improved by increasing functional connectivity at broad scales, wildlife-friendly land-uses may benefit species that both reside in *cabruca* and use them as corridors. Moreover, diverse and highly shaded agroforests can confer higher resilience to ecosystems and help maintain environmental services (Tscharntke *et al.* 2005). Agroforests also deliver socio social-economic benefits to the rural poor (Perfecto & Vandermeer 2008) and provide income from secondary food and non-food resources (Tscharntke *et al.* 2011). In tropical regions dominated by agroforests, scientists and managers must work together to face the important challenge of how to increase productivity without losing the many environmental and social-economic benefits provided by these systems.

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SUPPORTING INFORMATION

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

TABLE S1. *Characteristics of the landscape surrounding sampling sites.*
TABLE S2. *Large mammals potentially occurring in the forest-agroforest mosaic. Showing: (1) species classification; (2) species recorded in the study and (3) responses to conversion of forest to* cabrucas.
TABLE S3. *Results from SIMPER analysis.*

FIGURE S1. Map of study area in southern Bahia.

FIGURE S2. Two-dimensional MDS plots showing similarity in assemblage composition between forest and *cabruca* sites.

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