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Research Article

Can community-protected areas conserve biodiversity in human-modified tropical landscapes? The case of terrestrial mammals in southern Mexico.

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Abstract

Scientists debate two alternative paradigms for tropical biodiversity conservation in human-modified landscapes (HML). Strict government-managed reserves (GMR) have many limitations, including little social support as they transfer conservation costs to local communities. Community-protected areas (CPA) retain control and benefits of biodiversity for local residents, but evidence of their ability to conserve biodiversity is scarce. To test the hypothesis that CPAs are effective in conserving biodiversity, we used camera-trap data to assess differences in abundance, taxonomic and functional (body size and trophic guild) diversity and composition of terrestrial mammal assemblages among CPAs, GMR, and open-access forests (OAF). CPA and OAF sites were located in a HML adjacent to Montes Azules Biosphere Reserve, which is representative of GMR. CPAs and OAFs did not differ in landscape context (forest cover, distance to towns and roads, patch size). Our results show that the HML retains all of the species in the regional pool. We found no difference in species diversity among protection conditions, but species composition was different among them. Abundance of medium-sized generalist species was higher in the HML than in GMR, while large species and small herbivores were scarcer. Abundance of omnivorous and insectivorous generalists was highest in OAF, where large predators were not detected. OAFs exhibited fewer functional groups. No evidence was found that landscape context affected these results. We conclude that CPAs can play an important role in biodiversity conservation. Spatial integration of conservation initiatives and training communities in wildlife management would increase the effectiveness of CPAs.

Keywords: Community conservation; Human-modified landscapes; Tropical mammals; Camera-trapping; Selva Lacandona.

Resumen

Dos paradigmas para conservar la biodiversidad tropical en paisajes modificados por humanos (PMH) contienden en el debate académico. Las reservas manejadas por el gobierno (RMG) transfieren el costo de la conservación a las comunidades locales. Las áreas protegidas comunitarias (APC) mantienen el control de la biodiversidad en los pobladores locales, pero existe poca evidencia de su capacidad para conservar la biodiversidad. Para probar la hipótesis de que las APC son efectivas conservando biodiversidad, usamos fototrampeo para evaluar la abundancia, diversidad y composición taxonómica y funcional de ensamblajes de mamíferos terrestres entre RMG, APC y bosques de acceso libre (BAL). APC y BAL están en un PMH adyacente a la Reserva de la Biósfera Montes Azules, representativa de las RMG. APC y BAL no difieren en cuanto a contexto de paisaje (cobertura de bosque, distancia a caminos y pueblos, área del parche). Nuestros resultados indican que el PMH mantiene todas las especies del pool regional. No encontramos diferencias en diversidad de especies entre condiciones de protección, pero sí en composición. Especies generalistas medianas fueron más abundantes en el PMH, mientras que especies grandes y herbívoros pequeños resultaron más escasos. Omnívoros e insectívoros fueron más abundantes en BAL, donde no detectamos carnívoros mayores. Los BAL presentaron menos grupos funcionales. No encontramos evidencia de que el contexto de paisaje afectara estos resultados. Concluimos que las APC pueden ser importantes para la conservación de la biodiversidad. La integración espacial de las APC y la capacitación en manejo de fauna silvestre incrementarían su eficiencia.

Palabras Clave: Conservación comunitaria; Paisajes modificados; Mamíferos tropicales; Fototrampeo; Selva Lacandona.

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Introduction

Tropical forests are the world´s most biodiverse terrestrial ecosystems [1] and face high deforestation rates [2]. As old-growth forests become scarcer [3], complex landscapes in which secondary and degraded forests coexist with productive land-cover types tend to be the most common scenario throughout the tropics. This reality has led to an academic debate on the potential of human-modified landscapes (HML) to conserve tropical biodiversity. Some authors emphasize the irreplaceability of large tracts of old-growth forest with little or no human presence, especially for species that face a higher extinction risk [4]. Others argue that the future of tropical biodiversity depends on our capability to preserve it in HMLs [5, 6]. Even as the latter opinion is gaining recognition in the scientific community [7], disagreement persists regarding the conservation model best applicable to HMLs.

The protectionist paradigm to conservation, based on the establishment of strict government-managed reserves (GMR), has resurged in the voice of some of the most renowned tropical ecologists [8, 9, 10, 11] who urge the allocation of the largest possible amount of tropical forest under this scheme. The limitations of this paradigm include not only the poor management of many reserves in developing countries [12], but also the fact that biodiversity inside reserves is affected by human-induced transformation processes occurring outside their limits [13, 14]. Most reserves are inhabited or used by local people, and the creation of new ones is not well accepted in most cases [12]. In practice, strictly protected reserves transfer conservation costs to local communities, economically, socially, and culturally, by displacing population or restricting access to natural resources [15].

The radically distinct community conservation paradigm keeps the control of natural areas and the benefits of biodiversity in the hands of local communities, by means of social norms that regulate access to natural resources [16]. Community-protected areas (CPA) have existed since ancient times, but their importance to biological conservation has only recently been recognized [17, 18]. Globally, land surface protected by local communities equals that of official reserves [17], and CPAs have proved their effectiveness in providing ecosystem goods and services [19] and preventing deforestation [20, 21], without the adverse social costs of official reserves.

The debate about the ability of local communities to preserve biodiversity in HMLs is sustained by the lack of robust evidence on the status of biodiversity in CPAs. Few studies have quantitatively compared the biodiversity conservation status in CPAs, GMRs and open-access forests (OAF) subject to unregulated resource use (see [22] for a review), and no studies have compared species assemblages in CPAs, GMRs and OAFs simultaneously. A rigorous assessment of the conservation effectiveness of CPAs should focus on the species of greater conservation concern, those that face a high extinction risk due to their vulnerability to habitat loss and fragmentation, or are subject to overexploitation. Terrestrial large mammals are a suitable indicator group to measure the impact of these processes on biodiversity [23], as they include species with large area requirements, naturally low abundances, and high habitat specialization, and species that are preferred prey for hunting. Large mammals are of paramount ecological importance, as they exert a strong influence on the ecosystem via such biotic interactions as predation [24], herbivory [25], seed dispersal [26], and seed predation [27]. The effects of the disappearance of large mammals on the structure and function of tropical ecosystems are well documented [28-30].

In this paper, we assessed the effectiveness of CPAs in retaining biodiversity by comparing species richness, species diversity, species composition, presence of endangered species, and functional diversity and composition of medium-to-large (>0.3 kg) terrestrial mammal assemblages among CPA, GMR and OAF protection conditions, with a case study in the Selva Lacandona, southeast Mexico. Also, we evaluated the effect of the landscape context of CPAs and OAFs on mammal assemblage attributes, given the well-established importance of landscape configuration for biodiversity in HMLs. [31, 32].

We test the hypothesis that CPAs sustain higher abundances and taxonomic and functional diversity than OAFs, and that assemblage attributes in CPAs are comparable to that of GMRs. If community conservation is effective, management practices and social norms regulating resource use should result in lower hunting pressure and reduced levels of other human-driven disturbances (e. g. timber extraction, land use change) inside CPAs. These conditions would enhance the probabilities for disturbance-sensitive mammal species to persist in CPAs in higher abundances, leading to a species-rich, functionally diverse terrestrial mammal assemblage similar to that in strictly protected GMRs. Higher levels of human disturbance in OAFs would benefit generalist species and affect large mammals, which play a critical regulating role in the food web (*e. g.*, top predators), modifying the composition of the assemblage and reducing abundance and taxonomic and functional diversity. We conclude by discussing current limitations of CPAs as a conservation strategy, and public policy issues that could enhance their performance in wildlife management and conservation.

Methods

Study Region

The study was conducted in the eastern part of the Selva Lacandona region, located in the state of Chiapas in southern Mexico (16°, 17° N and 90° 30´, 91° 30´ W). This region comprises the largest remaining tract of tropical rainforest in North America, is an important part of the Mesoamerican biodiversity hotspot [33], and has been identified as a priority for conservation at national [34] and international scales [33]. The climate of the region is hot (24-26°C) and humid, with a mean annual rainfall greater than 2,500 mm, 80% of which falls between June and November [35]. The vegetation is tropical rainforest, its structure and composition varying with soil, topographical, and hydrological features [36]. This region harbors the greatest mammalian richness of any area in Mexico, with about 115 species representing all the orders and 27 of the 33 families reported for the country [37]. Many severely threatened mammals, such as the Mesoamerican Tapir (*Tapirus bairdii*), the White Lipped Peccary (*Tayassu pecari*), and the Jaguar (*Panthera onca*) have important populations in the region.

Official conservation efforts in the Selva Lacandona have focused on the establishment of strict reserves, known in Mexico as Protected Natural Areas (PNAs), managed by the federal government with little or no participation of local communities [38]. The largest PNA in the region, with 331,200 ha, is the Montes Azules Biosphere Reserve (MABR), created in the late 1970s. Marqués de Comillas (MC), located in the easternmost part of the Selva Lacandona and adjacent to the MABR, presents an interesting opportunity to study new approaches to biodiversity conservation in HMLs. This region has undergone rapid deforestation since its government-induced colonization in the 1970s [39]. Today, the predominant land cover is pasture for cattle ranching, and additional deforestation is ongoing. However, old-growth tropical forest and second-growth forest cover approximately 47% of the region´s area, and maintain a high level of connectivity across the landscape, with large patches (500-9,900 ha) connected by remnant vegetation corridors [40]. Some of these large forest patches are CPAs with a legal community resolution to be preserved in the long term, with clearly established boundaries and a management plan. Although the Mexican government has a mechanism to certify CPAs and other social conservation schemes, this program lacks financial and human resources as well as clearly established incentives [41], and most CPAs in the region remain uncertified. The majority of the forest patches remaining in MC are OAFs, also in community tenure but without protection status, and are currently subject to selective logging, hunting and other extractive activities, or are being cleared for agriculture.

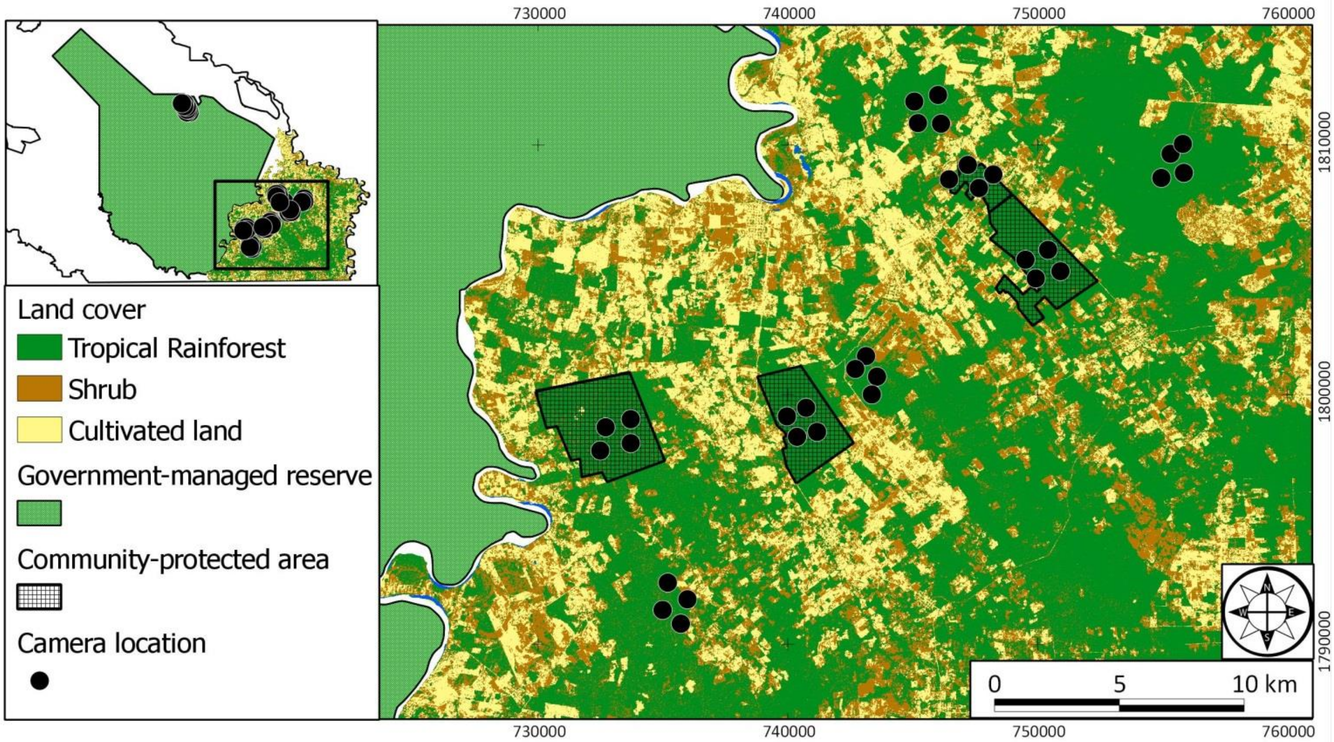


Fig. 1. Map of the sampling localities in the human-modified landscape of Marqués de Comillas. The upper panel includes the sampling localities inside the Montes Azules Biosphere Reserve and indicates the area enlarged in the main panel.

Study system and mammal sampling

For this study, we selected eight sites in MC, four corresponding to CPAs and four to OAFs (Fig. 1). Due to time and equipment limitations, only two sites were sampled inside the MABR, representing the GMR condition. The two GMR sampling sites were separated by 2km, while MC sites were separated by a minimum of 3km. Basic descriptive landscape measures were obtained for each of the eight MC study sites: percentage of forest cover in a circle of 2.5 km radius around the center of sampling sites, distance to the nearest road and town, and area of the forest patch (delimited according to Muench [40]).

We used digital camera traps (Bushnell Trophy Cam, Primos Truth Cam and Wild View Stealth Cam) for sampling mammals at each study site. Each sampling site consisted of four camera trap stations arranged in a square near the central part of each forest patch, with an approximate distance of 1 km between stations. Cameras were attached to trees 50-60 cm above ground in places with signs of animal presence, and no bait was used. In each site, half of the stations were placed near a stream or other water source. Cameras were active for 3-6 months between April 2012 and April 2014, with a CPA and an OAF site being sampled simultaneously at any time. GMR sites were also sampled simultaneously with a CPA and an OAF site. Sampling sites were visited every 40 days to check operation, retrieve images, and replace batteries.

We identified mammal images to the species level (except for the genus *Sciurus*) following Wilson and Reeder´s [42] nomenclature, and sorted images to independent capture events, considering as independent two images of the same species in the same site separated by more than 12 hours. This relatively long time span between independent captures was used to avoid overestimation of the abundance of species with small home ranges, where the same individual can be captured on several occasions during a single day. Although some arboreal and aquatic species were recorded, these captures can be considered fortuitous and do not reflect the species' incidence patterns or abundance in a sampling site; because this study was limited to terrestrial mammal assemblages, these records were omitted from our analyses.

Data analysis

To assess the completeness of our sampling, sample coverage was calculated for each of the ten study sites, using the C.hat estimator proposed by Chao and Jost [43]. We then compared several attributes (abundance, taxonomic and functional diversity and composition) of the terrestrial mammal assemblages among CPA, GMR and OAF conditions. We used capture rate as a proxy for abundance, quantified as the number of captures per unit time. Observed species richness and capture rate were calculated for each of the ten study sites, rarefying or extrapolating the results to a common sampling effort in trap-days (td). To do this, we used EstimateS v. 9.1.0 [44] to generate accumulation curves of captures and species as a function of cumulated sampling effort. To retain the maximum possible information from our samples, we established 400 td as the common sample size for comparisons. In four sites we rarefied abundance and species richness, as sampling effort was higher than 400 td. In the remaining six sites, where samples were smaller than the established criterion, we used rarefaction curves to extrapolate abundance and species richness to 400 td, following Colwell *et al.* [45]. Observed species richness was also obtained via rarefaction to a common number of individuals (the minimum recorded among all study sites). Total richness was estimated using the Chao2 non-parametric estimator. Diversity and evenness for each assemblage were calculated using the inversed Simpson and Simpson´s evenness indices, respectively. After transformation of the variables that did not adjust to a normal distribution, ANOVA tests were used to assess differences in assemblage attributes among protection conditions, using the R programing environment [46].

To compare the structure of assemblages among protection conditions, rank-abundance graphs were prepared following Magurran [47]. In these graphs, the y-axis values represent capture rates for each species and x-axis the species ranked by capture rate (from higher to lower values). Capture rates per species were calculated as $(n_{ij}/td_j)*100$, where n_{ij} is the number of captures of the species i in site j, td_j is the sampling effort accumulated in site j, and 100 is a conventional unit of time used to produce a standardized abundance index [48]. To avoid sampling effects of the fewer sites in the GMR condition, we elaborated a rank-abundance graph for each site, and then averaged the results to produce a single mean rank-abundance graph per protection condition.

Non-metric multidimensional scaling (NMDS) was used to evaluate similarity in species composition among protection conditions. This ordination analysis was based on a matrix of 10 columns (representing the study sites) and 24 rows (representing recorded terrestrial mammal species) with cells containing capture rates. The scores of the 10 sites in three NMDS dimensions were used to test for significance in compositional differences among protection conditions, using MANOVA and *a posteriori* Bonferroni test. We performed NMDS using Primer-E v.5 [49] and MANOVA using Data Desk [50]. Finally, we tested whether capture rate for each species differed between pairs of protection conditions, using Student´s *t* tests for samples with unequal variance.

Body mass (in kg) and general trophic guild (carnivore, insectivore, omnivore or herbivore) were used to classify recorded species into *a-posteriori* functional groups. Body mass was obtained from a global database [51], while trophic guild was defined according to Arita *et al.* [52]. A cluster analysis (using Ward´s method and Euclidean distance) was used for the classification. To quantify functional diversity for each site, we calculated functional group richness (FGR), which corresponds to the number of *a-posteriori* functional groups, and the functional evenness index (FEve), which ponders the distribution of abundances in a functional trait space [53], using the FD package for R [54]. Differences among protection conditions in functional diversity, as well as in the abundance of each functional group, were tested for using ANOVA. Functional similarity among sites in abundance of the functional groups was explored with a NMDS analysis based on a matrix with 10 columns (sites) and seven rows (functional groups). A MANOVA test was used to assess differences in functional composition among protection conditions, considering the scores of the sites in three NMDS dimensions.

We assessed to what extent landscape context varied between protection conditions in MC and affected mammal assemblages. For the former, we conducted Student´s *t* test comparing percentage of forest cover, distance to roads and towns, and patch area between CPA and OAF sites. GMR sites were not considered in these comparisons, as they were placed in a single forest patch of more than 300,000 ha with 100% forest cover and far away from roads or towns, and thus were evidently different from MC sites. Finally, to assess whether mammal species and functional diversity in MC sites were affected by landscape context, we used a MANOVA test.

Results

With an accumulated sampling effort of 3,479 effective trap-days, we obtained a total of 965 independent captures representing 29 mammalian species (Appendix 1). Of this total, 677 captures (70.2%) were obtained in CPA and OAF sites, with an accumulated effort of 2,702 td (77.7%), accounting for 28 species. In the GMR sites, with an effort of 777 td (22.3%), we recorded 288 captures (29.8%) corresponding to 18 species. A summary of the attained sampling effort, sample coverage, total number of captures, global capture rate, as well as observed and estimated species richness for each study site is presented in Appendix 2. Most sites attained a completeness level (C.hat) above 95%, except for one site that attained 90%. With the data from all sites grouped by protection condition, all conditions attained a coverage level of 99%. Four species were excluded from analyses, because they are almost strictly arboreal (Black Howler Monkey *Alouatta pigra*, Spider Monkey

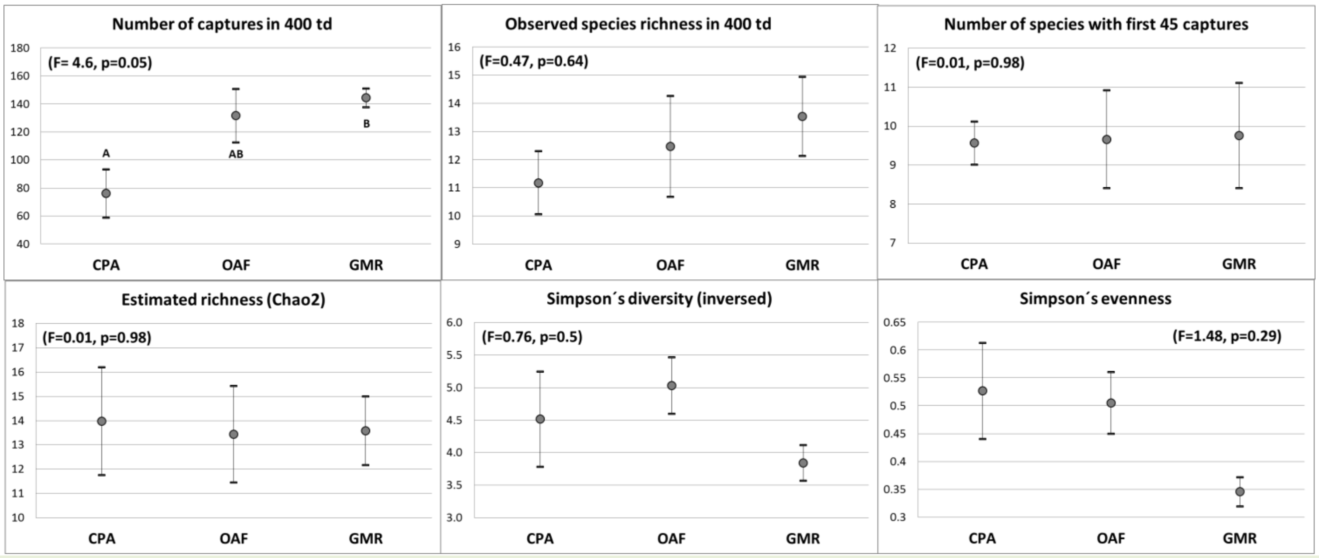
Ateles geoffroyi and Mexican Mouse Opossum *Marmosa mexicana*) or aquatic (Neotropical Otter *Lontra longicaudis*). We recorded a similar average number of endangered mammal species (according to the Mexican official norm NOM-059) in all protection conditions. Incidence data for these species are shown in Appendix 3.

Difference in taxonomic diversity among protection conditions

No significant differences were detected among conditions for species richness after both sample-based and individual-based rarefaction/extrapolation, or for Simpson´s diversity and evenness indices (Fig. 2). However, global mammalian abundance (i.e. number of captures at equal sampling effort) was significantly higher in GMR than in CPA (ANOVA F= 4.6, p= 0.05).

Difference in species dominance and species composition among protection conditions

Assemblage structure for sites under different protection conditions is presented as rank-abundance graphs in Fig. 3. The dominant species (i.e. the one with the highest capture rate) changed among protection conditions, although the Spotted Paca (*Cuniculus paca*) and the Red Brocket (*Mazama temama*) were consistently among the four most abundant species in all conditions. It is noteworthy that inter-site variation in capture rate per species was lower in the GMR condition.



Number of captures in 400 td

Observed species richness in 400 td

Number of species with first 45 captures

Estimated richness (Chao2)

Simpson´s diversity (inversed)

Simpson´s evenness

Fig. 2. Mean and standard error of species richness and diversity measures for the terrestrial mammal assemblage under different protection conditions in the Selva Lacandona, southern Mexico. CPA= Community-protected areas (n=4); OAF= Open-access forests (n=4); GMR= Government-managed reserve (n=2).

NMDS analysis (stress = 0.04, considering three dimensions) and MANOVA test indicated a significant difference (F = 4.5, P = 0.02) in species composition among CPA and GMR ($p<0.01$) and OAF ($p<0.05$), while GMR and OAF were not different ($p>0.05$; Fig. 4). Two species, the Spotted Paca and the Central American Agouti (*Dasyprocta punctata*), were significantly (Student´s *t* test $P<0.05$) more abundant in GMRs and OAFs than in CPAs (Appendix 4).

Difference in functional diversity and composition among protection conditions

Cluster analysis of species based on body mass and general trophic guild detected seven *a-posteriori* functional groups (Appendix 5). Functional group richness (FGR) was not significantly different between CPA and GMR conditions, while OAFs showed a significantly lower FGR (ANOVA F= 4.9, p= <0.05). No significant differences were detected among protection conditions for the functional evenness index (FEve; Appendix 6). Regarding functional composition, the NMDS ordination (stress = 0.04, considering three dimensions) and MANOVA test (F= 4.6, p= 0.02) showed that, along the dimension 1, CPA was different from GMR and OAF conditions (p<0.01; Fig. 5). These differences were mostly due to the fact that large carnivores were more abundant in GMR than in CPA and OAF (ANOVA F= 10.2, p< 0.01, Fig. 6), and that abundance of small herbivores was higher in GMR, medium in OAF and lower in CPA (ANOVA F= 77.4, p< 0.001, Fig. 6). Mean body mass of the mammal assemblage did not differ among CPA, GMR and OAF conditions (Fig. 6).

Landscape context and assemblage attributes

Landscape context varied widely among sites, but none of the variables we considered were significantly different between CPA and OAF protection conditions (Appendix 7). The results of MANOVA tests did not detect a significant effect of percentage forest cover, distance to roads and towns or patch area on any of the assemblage attributes (richness estimates, taxonomic and functional diversity indices) obtained for CPA and OAF sites.

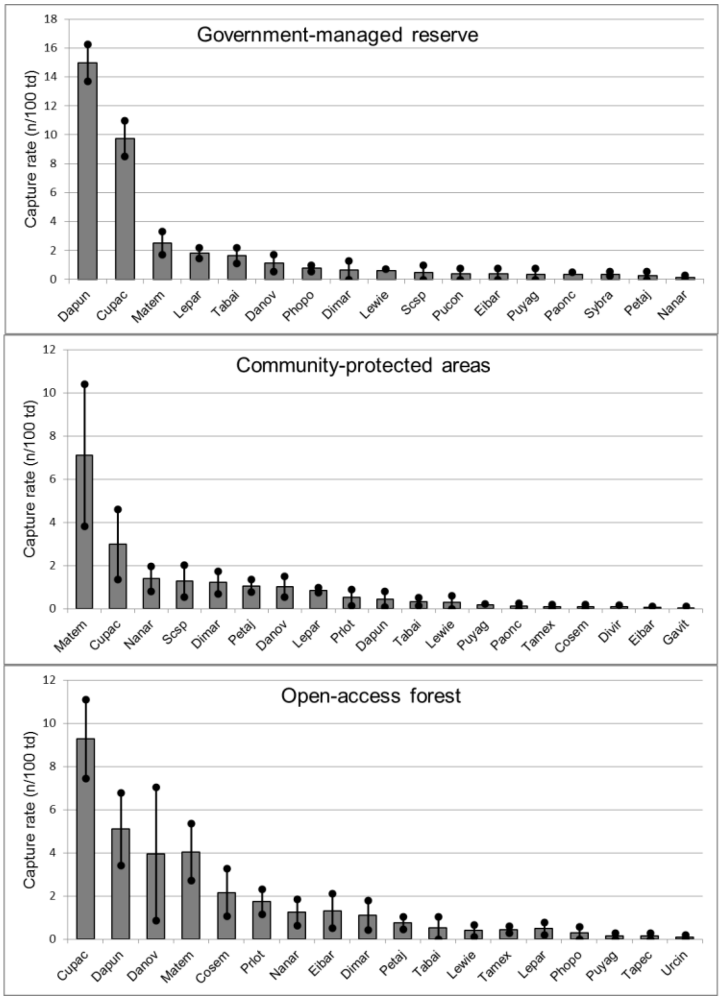


Fig. 3. Rank-abundance graphs for the mammal assemblage under three protection conditions in the Selva Lacandona, southern Mexico. Each panel shows mean capture rate (bars) and standard error (lines) values for each species recorded in a given protection condition. Identification codes for species are presented in Appendix 1.

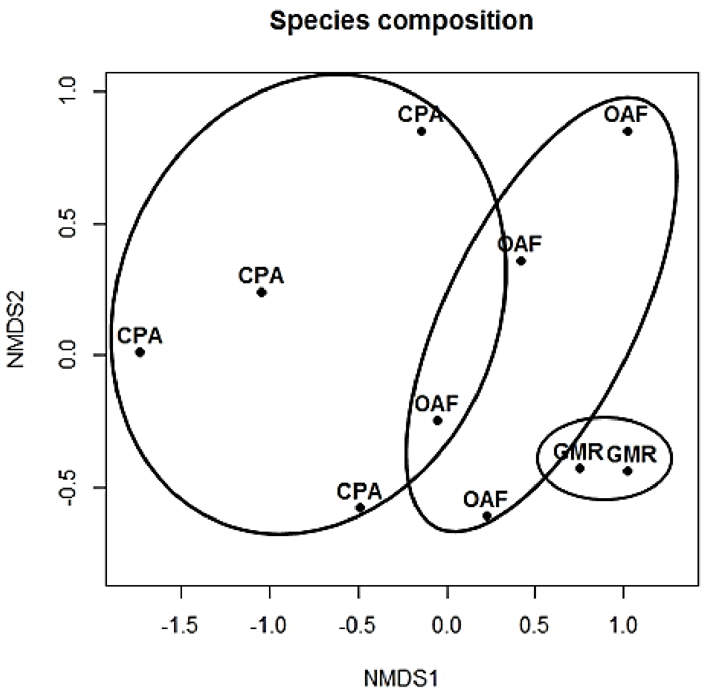


Fig. 4. Non-metric multidimensional scaling ordination of sampling sites based on capture rates of terrestrial mammal species in sites under different protection conditions in the Selva Lacandona, southern Mexico. Ellipses enclose sites under the same protection condition. CPA= Community-protected areas; OAF= Open-access forests; GMR= Government-managed reserve.

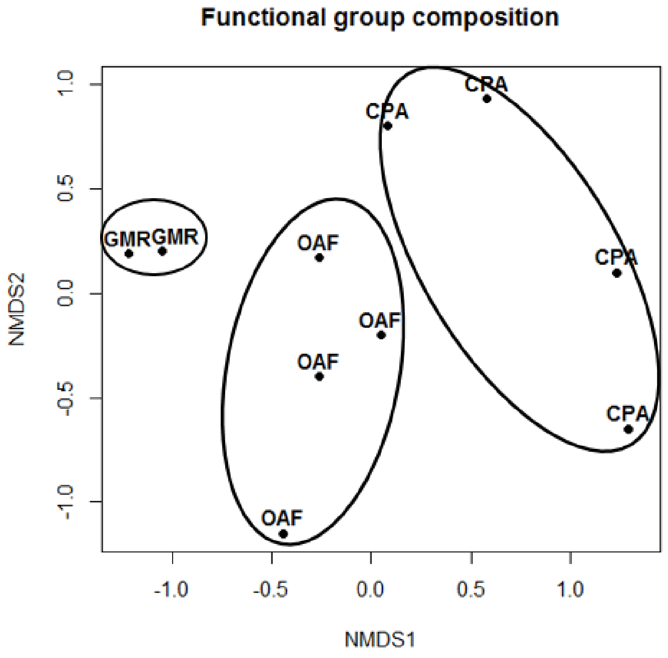


Fig. 5. Non-metric multidimensional scaling ordination of sampling sites based on abundance of terrestrial mammal functional groups in sites under different protection conditions in the Selva Lacandona, southern Mexico. Ellipses enclose sites under the same protection condition. CPA= Community-protected areas; OAF= Open-access forests; GMR= Government-managed reserve.

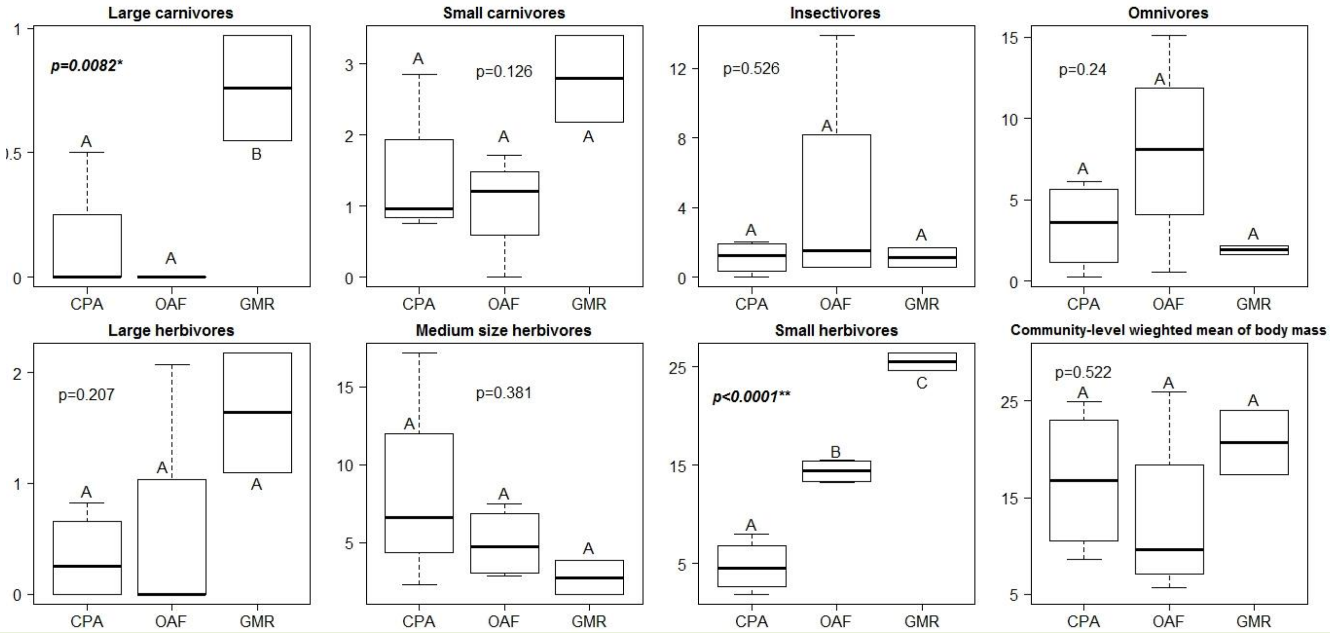


Fig. 6. Mean, range and standard error of the relative abundance (n/100 td) of functional groups of terrestrial mammals and community-level weighted mean of body mass (kg) for each protection condition in the Selva Lacandona, southern Mexico. CPA= Community-protected areas; OAF= Open-access forests; GMR= Government-managed reserve. Protection conditions with different capital letters are different (*p*<0.05); the *p* value obtained from ANOVA test is shown inside each panel.

Discussion

Our results show that a species-rich terrestrial mammal assemblage exists at the HML of Marqués de Comillas. We hypothesized that CPAs would sustain a mammal assemblage similar to GMRs and more diverse than OAFs. However, the three protection conditions showed similar species richness and diversity values, indicating that conservation effectiveness of both CPA and GMR conditions is not noticeable in terms of taxonomic diversity. Nonetheless, functional group richness did not differ between the CPA and GMR conditions, and was lower in the OAF condition, supporting our hypothesis of CPA effectiveness. In summary, our assessment of the effectiveness of CPAs as a conservation strategy shows that compared to OAFs, CPAs: (1) maintain healthier populations of large carnivores; (2) are less dominated by omnivorous and insectivorous generalist species; and (3) retain the same number of functional groups as our GMR protection condition. These results were independent of the landscape context variables we measured.

Sample coverage and species list of terrestrial mammals.

Our sampling attained a high completeness level, which enabled us to confidently assess the effects of protection condition on mammalian assemblages. Overall, we detected 24 terrestrial mammal species in MC. The White-tailed Deer (*Odocoileus virginianus*) and the Northern Naked-tail Armadillo (*Cabassous centralis*) have been captured by camera traps set by us in the region for a different purpose. We have observed the Coyote (*Canis latrans*) and the Brown Four-eyed Opossum (*Metachirus nudicaudus*) in MC, but they were not registered by our sampling protocol. Other species that may be present are the Spotted Skunk (*Spilogale angustifrons*) [55], the Long-tailed Weasel (*Mustela frenata*), the Eastern Cottontail (*Sylvilagus floridanus*) and the Red-bellied Squirrel (*Sciurus aureogaster*) [37]. Most of these species are associated with severely disturbed habitats, which may explain their absence from the forest sites we studied. Considering these species, the medium-to-large terrestrial mammal species list for MC should be 32 species, which is close to the upper limit predicted by our Chao2 richness estimate.

We registered several threatened mammal species in the studied HML. These include the White-lipped Peccary, an extremely space-demanding forest dweller [56] detected in one of the bigger OAF patches (7,560 ha). The Baird´s Tapir was recorded in several sites, both in CPA and OAF conditions. The Jaguar was photographed only in one CPA, but footprints were observed in other CPA sites. The Margay (*Leopardus wiedii*) was also present throughout our MC study sites. The Northern Tamandua (*Tamandua mexicana*) and the Striped Hog-nosed Skunk (*Conepatus semistriatus*) were more abundant in MC than in the GMR. The White-lipped Peccary, the Grey Fox (*Urocyon cinereoargenteus*) and the Greater Grison (*Galictis vittata*) were captured only in MC sites, but their detection occurred in unique capture events, and so may be attributed to chance rather than biological pattern. No effect of protection condition is apparent in the incidence of endangered mammals, thus we conclude that the GMR as well as the protected and unprotected patches in the HML play a role in the conservation of these species.

Effect of protection condition on species richness, diversity and composition

Our results show that species richness and species diversity did not differ among protection conditions, although inter-site variation in richness was high among OAF sites, with some sites showing a species-poor assemblage and others having a richness value similar to GMR sites. Such variation can result from a combination of landscape context [57, 58] and management factors [59, 60], as found in several studies. Although no effect of the landscape context variables we measured was found, other variables may be important. For example, low species richness was recorded in isolated forest patches, while patches connected by corridors showed higher richness (data not shown). Inter-site variation in species richness in the CPA condition was not higher than in GMR sites (Fig. 2, Appendix 2). It is likely that conservation efforts in CPAs result in the maintenance of several disturbance-sensitive mammals, contributing to high species richness.

In contrast to species richness and diversity, and contrary to our hypothesis, species composition of the terrestrial mammal assemblage was different between CPA and GMR conditions. Some species showed higher capture rates in CPA than in GMR sites, like the Red Brocket, which was dominant in CPAs. Other species showing increased abundance in CPAs (the White-nosed Coati, *Nasua narica,* and the Collared Peccary, *Pecari tajacu*) or present in CPAs and not detected in GMRs (e. g. the Northern Raccoon, *Procyon lotor*, and the Virginia Opossum, *Didelphis virginiana*) are medium-sized generalists that may benefit from supplementary resources provided by crops [61, 62]. Conversely, old-growth forest specialists like the Baird´s Tapir and the Ocelot (*Leopardus pardalis*) showed lower capture rates in CPAs than in GMR sites. However, the only significant differences in species abundance were detected for the Central American Agouti and the Spotted Paca, which had lower capture rates in CPA than in GMR. Overall, these results concur with those of Sahabuddin and Rao [22], who found no difference in species richness or diversity between CPAs and GMRs in several localities in the tropics, but identified consistent differences in species composition between the two protection conditions. Specialized and large bodied animals seem to be less abundant in CPAs, which tend to be smaller forest patches and more isolated than GMRs.

In OAF sites, a trend towards more generalist-dominated assemblages was notable, with species like the Nine-banded Armadillo (*Dasypus novemcinctus*), the Tayra (*Eira barbara*), the Striped Hog-nosed Skunk and the Northern Raccoon increasing their abundance even further. As these insectivores and carnivore-omnivores proliferate, specialized predators like the Ocelot were scarcer than in CPAs, and top predators like the Jaguar were not detected. Nevertheless, the Central American Agouti and the Spotted Paca were significantly more abundant in OAFs than in CPAs, determining a greater similarity between GMR and OAF sites, as these species are dominant in both conditions.

Effect of protection condition on functional diversity

The shift in species composition described above determines a decrease in functional diversity in OAFs relative to GMRs, measured as the number of functional groups present at each site, suggesting that CPAs are effective in retaining functional diversity of mammal assemblages. Large carnivores were not found in OAFs, and large herbivores tended to be scarce. Conservation of large mammals is a fundamental conservation goal, as they exert a strong influence on the ecosystem´s structure and function, and this is an important accomplishment of CPAs in our study region.

Large carnivores require large amounts of habitat, and this requirement is best met in the MABR, the largest tract of continuous old-growth forest in the Selva Lacandona, where our GMR sites were established. Prey availability does not explain the low abundance or absence of large carnivores, because both CPA and OAF sites had high capture rates for medium-sized herbivores. Perhaps even more important than habitat availability is the fact that large carnivores are hunted in MC as retaliation for cattle predation. The conflict between cattle ranching and large carnivores seems to be the main threat for these mammals in the region, and its effects may cascade down the trophic web [30]. Some of these cascade effects may be already evident: the increased abundance of medium-size herbivores outside GMR may indicate a deficient demographic regulation of these species by their natural predators.

The other significant functional difference between protection conditions was the scarcity of small herbivorous mammals in CPA compared to GMR sites. The Spotted Paca and the Central American Agouti were by far the most frequently captured species in all sites except for CPAs, a pattern that strongly influences the lower global capture rate at these sites. Low abundance of small herbivores may be related to hunting patterns, as these animals are preferred prey for traditional hunters. Hunting is not permitted in CPAs, but poaching endures and is perhaps the problem most frequently reported by CPA managers. Poachers may prefer smaller prey, which is easier to conceal, and this kind of selective harvest may cause a decline in small herbivore populations.

As stated by the mesopredator release hypothesis [63, 64], the loss of the large carnivores can open colonization opportunities for smaller, less specialized predators, which may in turn have strong impacts on small herbivore populations. Our data indicate that OAFs, where no large carnivore was detected, have the highest capture rates for carnivorous-omnivorous medium-sized mammals such as the Tayra, the Northern Raccoon and the Striped Hog-nosed Skunk (Appendix 4). Bottom–up effects caused by resource availability and habitat heterogeneity supplemented by anthropic land covers may also benefit generalist mesopredators. Strict carnivore medium-sized species like the Ocelot and the Margay do not appear to benefit from the absence of large predators, as their capture rates were lower in the HML than in the GMR.

Implications for conservation

Our results show that the forest patches in the HML that we studied have a high conservation value, maintaining species-rich terrestrial mammal assemblages. All endangered species with distribution in the Selva Lacandona are present in MC´s forest patches. Conservation of these patches most probably benefits many species inside the official reserves, not only providing a buffer against disturbance and resource extraction, but also enhancing landscape supplementation [61] and metapopulation dynamics [65].

The importance of CPAs for tropical mammal conservation in the region is straightforward, as community agreements guarantee persistence of forest cover in the long term. CPAs have great opportunities to grow as a conservation strategy in our study region. The larger remaining forest patches do not have community agreements to be destined to conservation, and many are being cleared for agriculture or degraded by mismanaged logging. Our results show that these patches (OAFs) retain a high conservation value, and even sustain populations of disturbance-sensitive forest specialists like the White-lipped Peccary. Supporting existing CPAs could encourage neighbor communities to preserve their biological heritage.

We found no effect of the landscape variables we measured on the mammal assemblage attributes of MC forest patches. MC maintains 47% of its area with forest cover (Muench, unpublished data), which is above the tipping-point (20-30%) of biodiversity collapse identified in HMLs of the Brazilian Atlantic Forest [31] and is enough to maintain high biodiversity levels [66]. MC also maintains a high landscape connectivity level, with large patches linked by corridors [40]. This situation may explain why protection condition seems to have a stronger effect than landscape context on the terrestrial mammal assemblage. Nevertheless, a spatially-explicit landscape perspective is critical for the performance of a community-based conservation strategy, especially for large mammals (e.g. Jaguar, Puma, Tapir, White-lipped Peccary), which can have home ranges larger than most CPAs. Large and well-connected patches can retain more species and greater abundances of large animals than small and isolated ones [32], and the conservation efficiency of the GMR in our study case is largely due to landscape integrity. In order to retain the ecological functions of these species, connectivity between CPAs, GMRs and other forest patches needs to be maintained. Regional integration of conservation initiatives should be encouraged, and remaining corridors that link CPAs should be important management units. This implies an organizational challenge, since congruent territorial management politics require agreements among communities.

CPA effectiveness can be enhanced by supporting these initiatives with capacity building. Training in wildlife management is recognized as a necessity by CPA managers. Our results suggest that species preferred for hunting, especially small herbivores, may be overexploited in CPAs, despite hunting prohibitions inside their limits. The cultural and economic importance of hunting for local communities hinders an inflexible banning policy, and sustainable use is feasible for some species. Sustainable harvest rates can be calculated from abundance and current harvest estimations [67], which communities could develop with proper training. Participative wildlife monitoring is made easy and robust with camera-trap methodology, but it usually requires financial and technical support. Keeping record of harvest rates is feasible for respected community members if the information is gathered for management purposes only. Killing large carnivores as retaliation for cattle predation is an important conservation problem in MC as well as in many rural areas of tropical Mexico [68]. Public policy addresses this problem with a predation insurance fund, but this policy is scarcely known and incorporates stipulations that are hard to meet for many peasants. This policy would be greatly enhanced by an effective communication strategy.

Evaluating costs and benefits of CPAs and GMRs should include social, economic, and environmental aspects, considering both benefits received from conservation and opportunity costs of not engaging in conventional productive activities [16]. Although such an evaluation is beyond the scope of this paper, it is useful to state some observations about this matter in our study region.

Economic benefits obtained by CPAs derive mainly from ecotourism and payment for ecosystem services. Some communities reinvest profits on CPA management, including monitoring, surveillance, fire control, species recovery, and restoration programs. Incomes are also used to improve social infrastructure [69]. Furthermore, capacity building may provide future benefits for the communities´ sustainable development, and certified CPAs achieve a legal status as PNAs [41], providing an opportunity for territorial defense against undesired activities such as mining or oil extraction [69].

People in communities with agrarian rights over GMRs obtain constant economic benefits from environmental institutions, and some are employed as park rangers. However, these benefits are not evenly distributed among communities [70], or among individuals living in benefited communities [71]. Many people with no access to land and excluded from official programs oppose GMRs and constantly threaten to open new croplands inside the reserves. Even for those favored by government institutions, official programs have not succeeded in creating long-term development opportunities based on alternative productive activities [71].

Community-protected areas have proved to be efficient in preventing deforestation [20, 21], providing ecosystem goods and services and, according to our results, conserving important components of functional diversity. Supporting CPAs from governmental and academic institutions could greatly increase their effectiveness in biological conservation, benefitting local communities and enhancing the viability of neighboring official reserves.

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Appendix 1. List of mammal species detected by camera trapping in Marqués de Comillas and the Montes Azules Biosphere Reserve, categorized by size, locomotion and conservation status in national and international lists of threatened species.

Order	Family	Species	Common name	Size	Locomotion	IUCN	NOM-059	Code
Marsupialia	Didelphidae	*Didelphis marsupialis*	Black-eared Opossum	L	T-Sc	LC		Dimar
Marsupialia	Didelphidae	*Didelphis virginiana*	Virginia Opossum	L	T-Sc	LC		Divir
Marsupialia	Didelphidae	*Marmosa mexicana**	Mexican Mouse Opossum	S	Ar-Sc	LC		Mamex
Marsupialia	Didelphidae	*Philander opossum*	Gray Four-eyed Opossum	M	T-Sc	LC		Phopo
Primates	Atelidae	*Alouatta pigra**	Black Howler Monkey	L	Ar	EN	P	Alpig
Primates	Atelidae	*Ateles geoffroyi**	Spider Monkey	L	Ar	EN	P	Atgeo
Pilosa	Myrmecophagidae	*Tamandua mexicana*	Northern Tamandua	L	Sc	LC	P	Tamex
Cingulata	Dasypodidae	*Dasypus novemcinctus*	Nine-banded Armadillo	L	T	LC		Danov
Carnivora	Canidae	*Urocyon cinereoargenteus*	Grey Fox	L	T	LC		Urcin
Carnivora	Felidae	*Panthera onca*	Jaguar	VL	T	NT	P	Paonc
Carnivora	Felidae	*Puma concolor*	Puma	VL	T	LC		Pucon
Carnivora	Felidae	*Puma yagouaroundi*	Jaguarundi	L	T	LC	A	Puyag
Carnivora	Felidae	*Leopardus pardalis*	Ocelot	VL	T	LC	P	Lepar
Carnivora	Felidae	*Leopardus wiedii*	Margay	L	T-Sc	NT	P	Lewie
Carnivora	Mephitidae	*Conepatus semistriatus*	Striped Hog-nosed Skunk	L	T	LC	Pr	Cosem
Carnivora	Mustelidae	*Eira barbara*	Tayra	L	T-Sc	LC	P	Eibar
Carnivora	Mustelidae	*Galictis vittata*	Greater Grison	L	T	LC	A	Gavit
Carnivora	Mustelidae	*Lontra longicaudis**	Neotropical Otter	L	Aq	DD-VU	A	Lolon
Carnivora	Procyonidae	*Procyon lotor*	Northern Raccoon	L	T	LC		Prlot
Carnivora	Procyonidae	*Nasua narica*	White-nosed Coati	L	T-Sc	LC		Nanar
Perissodactyla	Tapiridae	*Tapirus bairdii*	Baird´s Tapir	VL	T	EN	P	Tabai
Artiodactyla	Tayassuidae	*Pecari tajacu*	Collared Peccary	VL	T	LC		Petaj
Artiodactyla	Tayassuidae	*Tayassu pecari*	White-lipped Peccary	VL	T	VU	P	Tapec
Artiodactyla	Cervidae	*Mazama temama*	Central American Red Brocket	VL	T	DD		Matem
Rodentia	Sciuridae	*Sciurus deppei***	Deppe´s Squirrel	M	Sc-Ar	LC		Scsp
Rodentia	Sciuridae	*Sciurus yucatanensis***	Yucatan Squirrel	M	Sc-Ar	LC		Scsp
Rodentia	Dasyproctidae	*Dasyprocta punctata*	Central American Agouti	L	T	LC		Dapun
Rodentia	Cuniculidae	*Cuniculus paca*	Spotted Paca	L	T	LC		Cupac
Lagomorpha	Leporidae	*Sylvilagus brasiliensis*^{MA}	Tapeti	M	T	LC		Sybra

*Not considered in community analyses, due to their arboreal or aquatic habits. **Grouped as *Sciurus spp* in community analyses. ^{MA} Detected exclusively inside MABR. Size categories: S= Small (< 0.1 kg), M= Medium (0.1-1 kg), L= Large (1-10 kg), VL= Very large (>10 kg). Locomotion mode: T= Terrestrial, Sc= Scansorial, Ar= Arboreal, Fo= Forsorial, Aq= Aquatic. IUCN categories: LC= Least concern, DD= Data deficient, NT= Near threatened, VU= Vulnerable, EN= Endangered. NOM-059 categories: Pr= Subject to special protection, A= Threatened, P= Endangered.

Appendix 2. Sampling effort, sample coverage, observed number of species and captures, capture rate and estimated total richness for each study site under a given protection condition in the Selva Lacandona, southern Mexico.

Locality	**Protection condition**	**Sampling effort (td)**	**Sample coverage (C.hat)**	**Number of species**	**Number of captures**	**Capture rate (n/td)*100**	**Estimated richness (Chao2)**
MAS	GMR	412	0.99	15	159	38.6	15.00
MAN	GMR	365	0.98	12	126	34.5	12.16
RA	CPA	402	0.97	9	67	16.7	9.33
CO1	CPA	427	0.96	12	66	15.5	17.93*(ICE=14.9)
CO2	CPA	393	0.96	10	50	12.7	10.99
SIS	CPA	489	0.97	15	158	32.3	17.64*(ICE=18.7)
LM	OAF	252	0.99	13	118	46.8	13.00
PO	OAF	318	1	8	88	27.7	8.00
SLA	OAF	180	0.91	8	45	25.0	15.78*(ICE=20)
LV	OAF	241	0.95	15	79	32.8	16.96

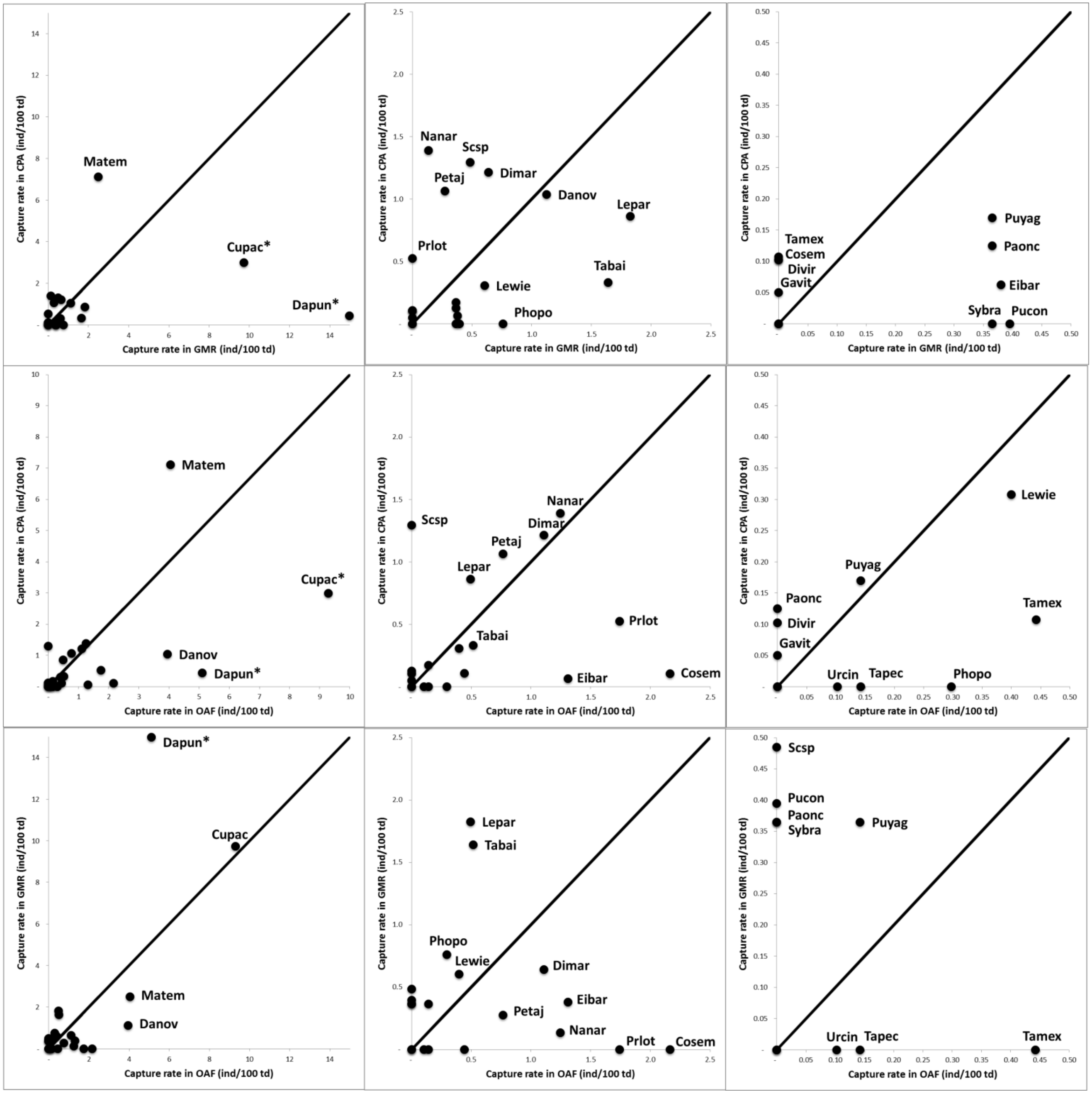
Acronyms for sampling locality: MAS= Montes Azules Biosphere Reserve South; MAN= Montes Azules Biosphere Reserve North; RA=Reforma Agraria; CO1=La Corona 1; CO2= La Corona 2; SIS=San Isidro; LM=Adolfo López Mateos; PO=Zamora Pico de Oro; SLA=San Lázaro; LV=La Victoria. CPA= Community-protected areas; OAF= Open-access forests; GMR= Government-managed reserve. *for these sites the Chao2 richness estimator shows a variation greater than 2 SD; ICE richness estimator is shown in parenthesis.

Appendix 3. Incidence matrix of species listed on the Mexican official norm for endangered species (NOM-059) in each sampling site and protection condition studied in the Selva Lacandona, southern Mexico.

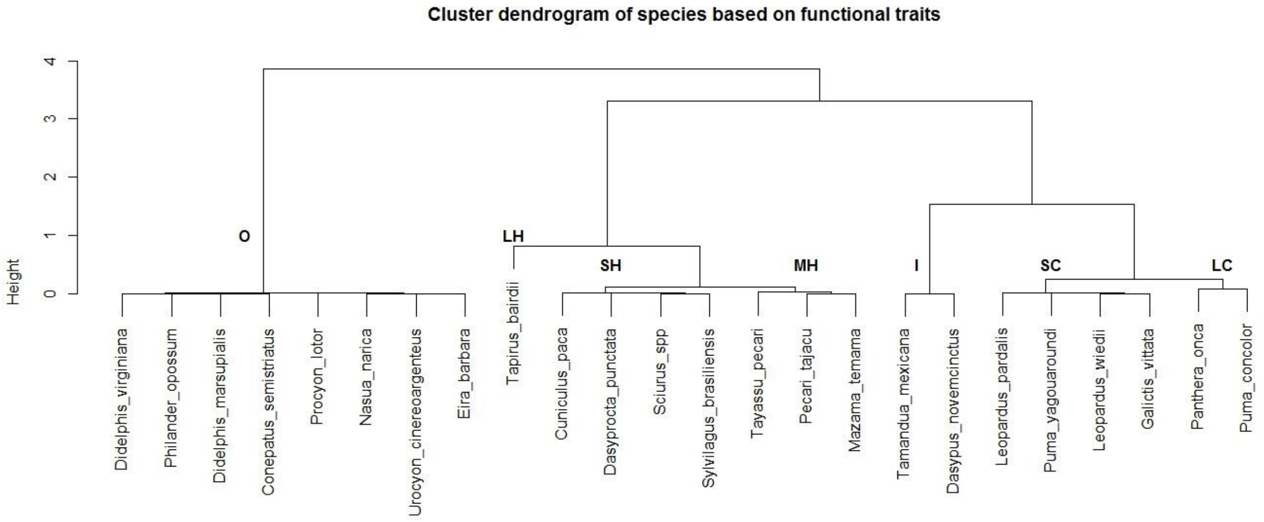
Species	**NOM-059**	**MAN**	**MAS**	**RA**	**SIS**	**CO1**	**CO2**	**LM**	**LV**	**PO**	**SLA**	**GMR**	**CPA**	**OAF**
Tamandua mexicana	P				1	1		1	1		1		1	1
Panthera onca	P (Priority)		1	1								1	1	
Puma yagouaroundi	A		1	1	1	1					1	1	1	1
Leopardus pardalis	P	1	1	1	1	1	1		1		1	1	1	1
Leopardus wiedii	P		1		1			1	1			1	1	1
Conepatus semistriatus	Pr				1			1	1	1	1		1	1
Eira barbara	P	1	1				1	1	1			1	1	1
Galictis vittata	A				1								1	
Tapirus bairdii	P (Priority)	1	1	1	1				1			1	1	1
Tayassu pecari	P (Priority)										1			1
Total/Average per site		3	6	4	7	3	2	4	6	1	5	6/4.5	9/4	8/4

NOM-059 categories: Pr= Subject to special protection, A= Threatened, P= Endangered. Species identified as priority by the endangered species conservation program (PROCER) are indicated in parenthesis. CPA= Community-protected areas (RA, SIS, CO1, CO2); OAF= Open-access forests (LM, LV, PO, SLA); GMR= Government-managed reserve (MAN and MAS).

Appendix 4. Pairwise comparisons of species capture rates between protection conditions. Left panels represent all species, and scale increases towards right panels for species with low capture rates. Top panel: CPA vs. GMR; Central panel: CPA vs. OAF; Bottom panel: GMR vs. OAF. Asterisks next to species codes indicate significant differences (Students *t* test p<0.05).



Appendix 5. Cluster dendrogram of species based on body mass and trophic guild, used to define functional groups of terrestrial mammals in the Selva Lacandona, southern Mexico. LC= Large carnivores; SC= Small carnivores; LH= Large herbivores; MH= Medium size herbivores; SH= Small herbivores; O= Omnivores; I= Insectivores.



Appendix 6. Values of functional diversity variables obtained for each study site in the Selva Lacandona, southern Mexico.

Locality	Protection condition	FGR	FEve
MAS	GMR	7	0.70
MAN	GMR	7	0.52
RA	CPA	6	0.44
CO1	CPA	5	0.74
CO2	CPA	5	0.70
SIS	CPA	6	0.75
LM	OAF	5	0.68
PO	OAF	4	0.69
SLA	OAF	5	0.69
LV	OAF	6	0.64

FGR=Functional group richness, FEve=Functional evenness index. Acronyms for sampling locality as in Appendix 2. CPA= Community-protected areas; OAF= Open-access forests; GMR= Government-managed reserve.

Appendix 7. Landscape context variables for the study sites in the human-modified landscape. Note that no significant difference was found between CPA and OAF conditions for any of the analyzed variables.

Locality	**Protection condition**	**Forest cover (%)**	**Distance to roads (m)**	**Distance to towns (m)**	**Patch area (ha)**
RA	CPA	85.2	2110	4010	2385
SIS	CPA	68.6	1180	1470	2094
CO1	CPA	53.1	680	880	1727
CO2	CPA	73.7	1110	3480	1727
Mean		**70.15**	**1270**	**2460**	**1983.25**
SD		**13.3**	**602.05**	**1518.71**	**318.85**
SLA	OAF	88.2	5490	6440	7564
PO	OAF	57.4	1460	3620	1784
LV	OAF	58	840	2840	1020
LM	OAF	69.2	1360	1700	7577
Mean		**68.2**	**2287.5**	**3650**	**4486.25**
SD		**14.4**	**2152.23**	**2020.20**	**3575.02**
t-test					
P value	**CPA vs OAF**	**0.87***	**0.43**	**0.35**	**0.41**

* Percentages were normalized using the angular transformation before conducting the test. Acronyms for sampling locality: RA=Reforma Agraria; SIS=San Isidro; CO1=La Corona 1; CO2= La Corona 2; SLA=San Lázaro; PO=Zamora Pico de Oro; LV=La Victoria; LM=Adolfo López Mateos. CPA= Community-protected areas; OAF= Open-access forests.