Landscape patterns influence communities of medium- to large-bodied vertebrates in undisturbed terra firme forests of French Guiana

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Abstract: Whereas broad-scale Amazonian forest types have been shown to influence the structure of the communities of medium- to large-bodied vertebrates, their natural heterogeneity at smaller scale or within the terra firme forests remains poorly described and understood. Diversity indices of such communities and the relative abundance of the 21 most commonly observed species were compared from standardized line-transect data across 25 study sites distributed in undisturbed forests in French Guiana. We first assessed the relevance of a forest typology based on geomorphological landscapes to explain the observed heterogeneity. As previously found for tree beta-diversity patterns, this new typology proved to be a non-negligible factor underlying the beta diversity of the communities of medium- to large bodied vertebrates in French Guianan terra firme forests. Although the species studied are almost ubiquitous across the region, they exhibited habitat preferences through significant variation in abundance and in their association index with the different landscape types. As terra firme forests represent more than 90% of the Amazon basin, characterizing their heterogeneity – including faunal communities – is a major challenge in neotropical forest ecology.

Key Words: animal communities, diversity, environmental heterogeneity, French Guiana, landscape ecology, species-habitat association

INTRODUCTION

Although they are often iconic and well known to forest dwellers, precise information is lacking on the distribution and ecological preferences of most vertebrate species in neotropical forests. In central Amazonia, previous studies revealed that the structure of communities of medium- to large-bodied vertebrates varies according to the two major forest types: seasonally inundated forests (várzea) and terra firme forests (Haugaasen & Peres 2005a, b, 2008). According to these studies, seasonally inundated forests appeared to be less diverse but carry higher densities and biomass of primates compared with the well-drained uplands (terra firme). However, at finer geographic scale (i.e. within each category), the inherent heterogeneity of these faunal communities remains poorly documented, with the exception of some mainly descriptive studies focused on primate communities (Buchanan-Smith *et al.* 2000, Freese *et al.* 1982, Heymann *et al.* 2002, Sussman

& Phillips-Conroy 1995), and a more recent and detailed analysis in western Amazonia (Palminteri *et al.* 2011). According to these authors, although hunting pressure and/or human impact are often the best predictors of primate community structure, biogeographic and environmental factors also drive community structure. The main descriptive parameter for forest types was still flooded vs. unflooded areas, but this parameter was refined as gradient. The same authors also pointed out that the drivers may be more a combination of environmental factors rather than any one factor.

In French Guiana, the whole territory was until recently considered as apparently homogeneous terra firme forest. However, recent research demonstrated the existence of several types of terra firme forest across Amazonia (Anderson *et al.* 2009) or within the Guiana Shield (Fayad *et al.* 2014, Gond *et al.* 2011). Even in a regional context where environmental gradients are quite weak, as is the case of the Guiana Shield, the hyper-diversified tropical rain forest shows a significant gradient of tree composition and strong subregional patterns (Guitet *et al.* 2015). The best factor identified

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to explain these broad-scale patterns in the floristic and structural diversity of the terra firme rain forest was the geomorphological landscape type (Guitet *et al.* 2013). In the Amazon region, other studies have also linked geomorphological landscape type with forest physiognomy (Anderson *et al.* 2009) and/or biological diversity or community structure (Deichmann *et al.* 2011, Figueiredo *et al.* 2014, Sombroek 2000). Such an integrative variable is thus a good candidate to combine local ecological conditions and to approximate forest structure and composition, but its influence on vertebrate communities has never been tested to date.

In French Guiana, abundance data on medium- to large-bodied vertebrates revealed strong differences across undisturbed forest sites (Richard-Hansen 2006). This study scale is below that typically used for turnover in most Amazonian large-vertebrate species, thereby focusing the analysis of community heterogeneity on niche differentiation and community structure (abundances) rather than dispersal limitation and species replacement (http://www.iucnredlist.org/mammals/data_types; Patterson *et al.* 2005). We therefore hypothesized that environmental parameters and forest types can partially explain this heterogeneity in French Guiana, as documented in other forested environments of Amazonia. The influence of the landscape type on the forest structure has been proved (Guitet *et al.* 2015), and the aim of the present study was to assess the relevance of this classification as an underlying driver of the distribution patterns of the communities of medium- to large-bodied vertebrates, with respect to its ability to describe the combination of local environmental factors.

METHODS

Study area: French Guiana

French Guiana covers about $85\,000\,km^2$ in the east of the Guiana shield between Suriname and the Brazilian state of Amapa (4°N, 53°W). Altitude generally ranges between 0 and 200 m asl (mean 140 m asl) with few mountain peaks exceeding 800 m. The climate is equatorial with annual rainfall ranging from 3600 mm in the north-east to 2000 mm in the south and the west, with a mean annual temperature of about 26°C. The number of consecutive months with less than 100 mm precipitation (dry season) ranges from two in the north to three in the south with high interannual variation (Sombroek 2001). Savannas and mangroves occur only in the coastal sedimentary plain, while the evergreen rain forest covers more than 90% of French Guiana (http://www.fao.org, Guitet *et al.* 2015). Natural habitats show slight variability and high species diversity, with a complex tree community and

often more than 150–200 species ha^{-1} (Sabatier *et al.* 1997).

Overall human density is below 3 inhabitants km^{-2}, and 75% of the population is restricted to the five major towns, with the remaining population living in a few small villages and settlements (http://www.insee.fr) mainly along the two main rivers that form the borders with Suriname and Brazil (Figure 1). A National Park covers 34 million ha, 20 million ha of which comprise the core area where only the resident population is allowed to hunt for subsistence. Roads are limited to a less than 50 km-wide northern coastal strip, while the rest of the country is accessible only by boat or by small airplane from Cayenne to a few main settlements. Timber harvesting and agriculture are contained in subcoastal areas, covering currently around 2 million ha, close to the biggest towns and main roads. Consequently, most of the hunting pressure is applied on the northern coastal strip, along main rivers and streams and around the scattered villages.

Animal abundance

Standardized line transect surveys (Buckland *et al.* 1993) were conducted at 25 different study sites across French Guiana. The study sites are very isolated and most can be accessed only by helicopter or several days walking, so we consider that there was no strong or recent hunting pressure, even by autochthonous populations. The same field design was implemented at each site, consisting of four 3-km long trails radiating from a central place (campsite). This design makes it possible to account for small local variations in the environment, including topographic features or scattered resources (fruiting trees), within a single global abundance index, characterizing a similar area for each site surveyed. Transects were walked at less than 1 km h^{-1} every morning (7h00–11h00) and afternoon (14h30–18h00) by only one observer per trail, systematically alternating transects on consecutive days to avoid observer bias. All encounters with focal species and their localization on the trail were systematically recorded and the perpendicular distance between the animal and the transect was measured to the nearest metre with a laser range finder. Transects were surveyed an average ± SD of 13.7 ± 1.9 times each, during an 8-d field session. Total survey effort per site ranged from 140 to 210 km (average ± SD = 163 ± 17.7 km), with a cumulative survey effort of 4073 km across 99 individual transects at 25 sites. The minimum effort required for reliable estimates of abundance and richness in this environment was estimated at 100 km (de Thoisy *et al.* 2008). The surveys were all conducted during the dry season (September–December) to avoid interference with potential seasonal variation.
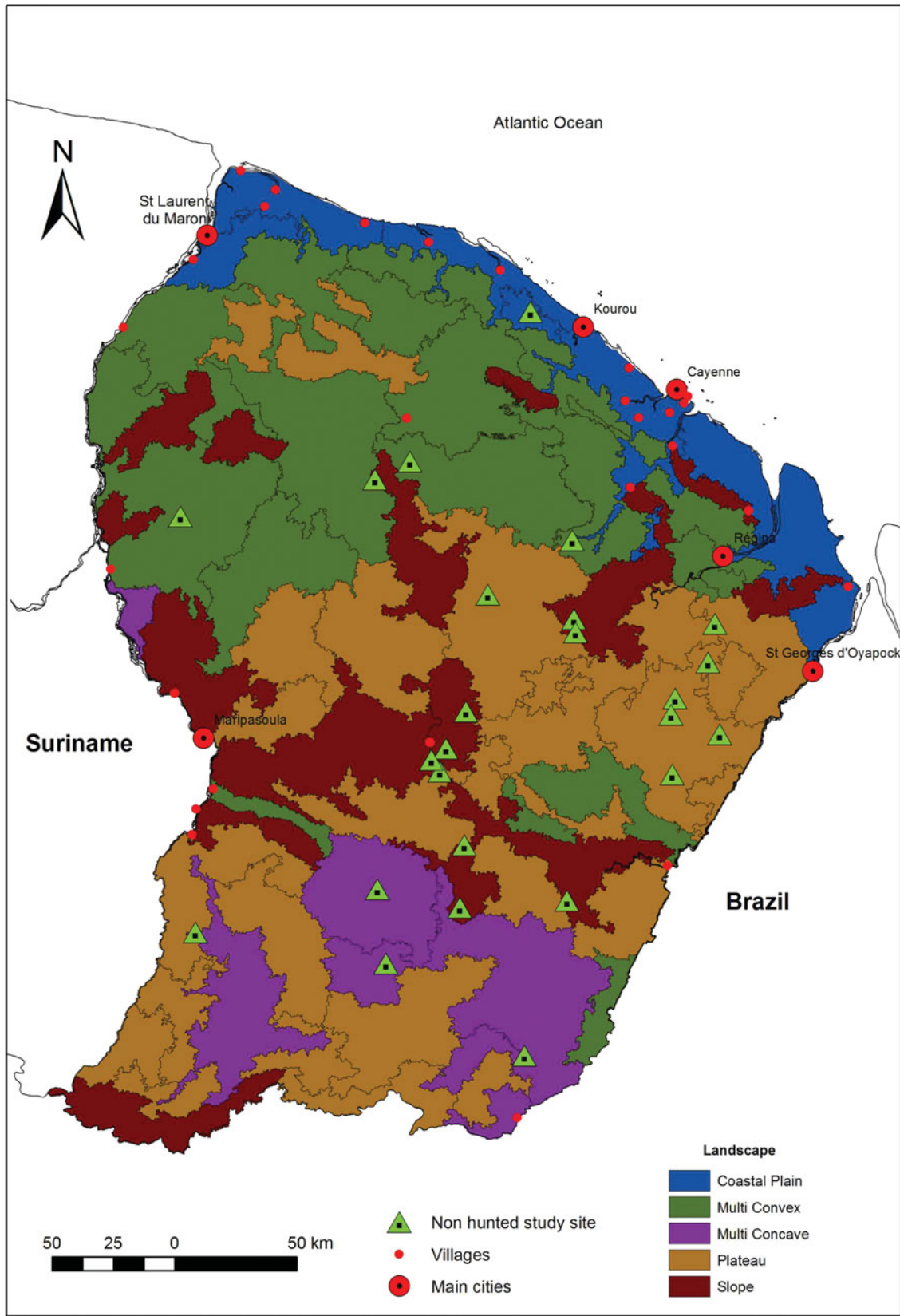
Figure 1. Location of 25 undisturbed study sites in French Guiana, and their distribution within the five landscape types, characterized from a geomorphological analysis based on a digital elevation model.

Thirty-seven species were recorded (mammals weighing > 0.5 kg and large terrestrial birds), and diversity estimates were based on this pool of species. For abundance comparisons, we focused on the 21 most frequent species, including primates, ungulates, caviomorph rodents, large terrestrial birds (cracids, tinamous, trumpeters, guans) and tortoises, for which a reliable index of abundance could be calculated. Tinamidae species (*Crypturellus* spp. and *Tinamus major*) were grouped because many observations lacked clear identification.

Environmental characteristics of the study sites

The environment was characterized by the geomorphological landscape type defined by Guitet *et al.* (2013). This typology was developed from a multi-scale geomorphological diversity analysis based on a digital elevation model computed from a fine Shuttle Radar Topography Mission images (SRTM, 30 m resolution). Variations in micro-relief defined 12 landform types whose spatial distribution drew 82 different patches classified in 10 landscape types that can be grouped under five main categories: (1) coastal plain, (2) plateau, (3) mountain, (4) multi-convex and (5) multi-concave landscape. The joint-valleys are considered with the multi-convex category (Guitet *et al.* 2013). Recent results showed that the structure and composition of the forest is clearly influenced by these landscape types (Guitet *et al.* 2015). Coastal plains (N = 2 sites in this study), located in the northern part of French Guiana, are lowland forests on Quaternary marine sediments. They are characterized by a relatively low canopy (28 m in height), high density of small trees, and relative high abundance of Clusiaceae, Caesalpinioideae and Lecythidaceae. The plateau category (N = 8 sites) includes several types of relatively flat relief of moderate elevation dissected to a varying extent by rivers, exclusively covered by well-drained ferralsols with very localized hydromorphic soils. Burseraceae, Mimosoideae and Caesalpinioideae are dominant tree families, but high abundances of palms are also found. Small inselbergs are also frequent. Sloping areas (N = 9 sites), locally called mountains despite their modest altitudes (<840 m asl), are characterized by higher relief with many slopes. The dominant forest type is characterized by a high canopy (35–40 m), high basal-area values and the abundance of very large trees, with high diversity and much more infrequent families such as Vochysiaceae, Malvaceae and Annonaceae being more abundant compared with other forest types. The multi-convex landscape (N = 3 sites) is dominated by more or less regular hills with a dense hydrographic network, and dominance of Lecythidaceae and Caesalpinioideae. The soil cover is more diversified mixing clayic ferralsols with more sandy or loamy soils acrisols. The multi-

concave landscape (N = 3 sites) corresponds to large peneplains in the south, characterized by very flat relief, covered by leached and partially inundated soils during the wet season, although the water levels never rise as high as in the Amazonian várzea forests. The canopy is low (30 m high) and discontinuous, and vegetation is characterized by the dominance of Burseraceae, Mimosoideae and Myristicaceae with relatively few large trees and dense understorey with few palms. Finding undisturbed sites was harder in some landscapes types because of proximity of human settlements (coastal plain) or difficult access (multi-concave landscape), thus explaining the unbalanced sampling.

Six other broad-scale environmental variables were also tested: the biogeographic region (Paget 1999), the vegetation type based on remotely sensed landscape classes (RSLC) from the VEGETATION sensor of the SPOT-4 satellite (Gond *et al.* 2011), annual rainfall (Meteo France, unpubl. data), the proportion of hydromorphic soils, the mean slope and the mean differences in altitude for the area. The last three variables were extracted from a digital elevation model computed from fine-resolution Shuttle Radar Topography Mission images (SRTM, 30 m resolution). All these data were computed for a circle with a 4-km radius encompassing the survey transects.

Data analysis

An index of abundance of groups encountered per 10 km walked (elsewhere referred to as encounter rate, sensu Buckland *et al.* 1993) was calculated to control for overall differences in sampling effort (Peres 1997). Perpendicular distances (PD) were recorded, but not enough observations of each species were made at each site to correctly estimate the detection function for all of them and hence to calculate densities. However, we assumed that this index of abundance (hereafter, abundance) of different species could be compared between sites because, except for agouti (*Dasyprocta leporina*), the distributions of the distances of observation were not statistically different (ANOVA on log(PD), P > 0.5).

The dissimilarity between faunal communities in different landscape types was first tested by permutational multivariate analysis of variance on the site × species tables of raw counts of the 21 most common species, using chi^2 distance matrices. The Adonis test was selected because it is more robust and less sensitive to dispersion effects (within-group variation) than some of its alternatives (ANOSIM, etc.) (Anderson 2001). We also tested the pertinence of the landscape typology as a potential explanatory variable in this variation using a between-class correspondence analysis (BCA), which is a particular case of correspondence analysis

on instrumental variable (i.e. canonical correspondence analysis) with only one categorical variable (Dolédec & Chessel 1989, Dray & Dufour 2007, Dray *et al.* 2012, Pélissier *et al.* 2003). A correspondence analysis was first performed on the site × species tables of raw counts of the 21 most common species, and between-class analysis was then performed on the results (site coordinates), with the landscape type of each site as categorical variable. From this analysis, the between-class inertia is the proportion of total inertia of the table explained by the landscape variable, while the within-class inertia is the proportion of total inertia not explained by this variable. The statistical significance of this portion of initial variance captured by this instrumental variable was tested with Monte Carlo row permutation tests against the null hypothesis of no relation between species assemblage and landscape type (Couteron *et al.* 2003). The same analysis was made for the six other variables. These analyses were performed with the ade4 (Dray & Dufour 2007) and vegan-packages in R.

Diversity of communities and meta-communities. Crude richness of a study site is the number of species recorded during the survey, within the fixed maximum of 37 focal species. We calculated the diversity profile for each site community, and for each meta-community created by pooling the sites belonging to the same landscape type. The diversity profile plots the value of Hill numbers (Hill 1973) against the order of diversity q (Kindt *et al.* 2006, Patil & Taillie 1982). Hill numbers are the transformation of Tsallis entropy values into an effective number of species, i.e. the number of species of equal frequency that would yield the same diversity as real data (Jost 2006). Tsallis entropy ^qH (Tsallis 1988) generalizes the classical indices of diversity in a parameterized measure, where the choice of the parameter gives more or less importance to rare species: ^0H is the number of species minus 1, ^1H is Shannon entropy (Shannon 1948) and ^2H is Simpson index (Simpson 1949). All values of diversity were corrected for estimation bias (Marcon *et al.* 2014): the Chao & Shen (2003) estimator applies to small values of q, that of Grassberger (1988) to high values.

We tested the relevance of landscape type as a diversity predictor. We first pooled sites within one landscape type, and then pooled all landscape types together, allowing the measurement of β diversity across both levels (Marcon *et al.* 2012). We tested the observed ratio of β diversity between landscapes over β diversity within landscapes against its distribution under the null hypothesis of independence between sites and landscapes: we shuffled sites among landscapes and calculated the ratio of β diversity 1000 times. A result of the test was considered significant if the actual ratio was in the last five percentiles of the distribution of the simulated values, showing

that β diversity between landscapes was higher (relative to β diversity within landscapes) than under the null hypothesis. An alternative, more intuitive test would address the ratio of β entropies. Although it is more similar to a classical analysis of variance (since the total β entropy is the sum of within and between landscape β entropies), it suffers from the drawbacks discussed by Jost (2008). β entropy is constrained by the value of α entropy, thereby invalidating the test. Diversity estimates and comparison were made with R package entropart (Marcon & Hérault 2015).

Finally, we looked for species-landscape associations using the set of indices initially proposed by Dufrêne & Legendre (1997) to study species assemblages and habitat types. Our aim here focused on the relative abundance of the 21 most common species occurring in most sites rather than that of rare or indicative species. Following De Caceres & Legendre (2009), we thus selected the point-biserial correlation coefficient (r_{pb}), which is the Pearson correlation computed between a quantitative vector (i.e. the vector containing the species abundance values at the various sites) and a binary vector (i.e. the vector of site membership values) rather than the better known indicator value index (IndVal). To account for the unequal number of sites in the different landscape types, we used the corrected group-equalized index (r^g_{pb}), (De Caceres & Legendre 2009). The significance of these associations was tested by Monte Carlo permutation tests. We also tested the difference in species abundance in sites belonging to one particular landscape compared with sites located in different landscapes by permutation tests, after Sidak's correction for multiple testing. We then considered whether combining basic landscape types would better match species preferences (De Caceres *et al.* 2010). It may also happen that a particular site group has no indicator or associated species even if its sites have a community composition that is clearly distinct from the sites of other site groups (De Caceres *et al.* 2012). In these cases, the joint occurrence of two or more species has a higher positive predictive value for the site group than the two species taken independently, so we also explored correlation values for combinations of species (De Caceres *et al.* 2012). All analyses mentioned in this section were computed with the R package indicspecies.

RESULTS

Abundances of common species varied greatly across French Guiana, even in areas with no strong or recent human influence of hunting, logging or gold mining (Table 1). Nine out of 21 species were present in each of the 25 sites, 15 were present in at least 90% of sites (more than 21) and 12 showed a null abundance at least once. These 12 species may be totally absent from the site

Table 1. Index of abundance (number of observations per 10 km) recorded for 21 species in 25 undisturbed sites in French Guiana, and according to the different landscape types (MCV: multi-concave; MCX: multi-convex; PLA: plateau; PLN: coastal plains; SLO: sloping areas). Abundance significantly higher or lower compared with all other sites: * P $\leq$ 0.05; abundance significantly higher or lower compared with other landscapes : †P $\leq$ 0.05 (permutation test, corrected P-value for multiple comparisons).

| | General mean ± SD | Landscape | | | | |
		MCV	MCX	PLA	PLN	SLO
Primates						
Alouatta macconnelli (Linnaeus, 1976)	0.56 ± 0.30	0.71	0.42	0.61	0.45	0.52
Ateles paniscus (Linnaeus, 1758)	1.19 ± 0.76	0.81	1.31	0.96	0.36	†1.66*
Cebus apella (Linnaeus, 1758)	0.85 ± 0.46	0.96	1.04	0.61	1.69*	0.79
Cebus olivaceus (Schomburgk, 1848)	0.24 ± 0.24	0.19	†0.45	0.21	†0.00*	0.25
Pithecia pithecia (Linnaeus, 1766)	0.06 ± 0.08	0.16	0.00	0.06	0.07	0.04
Saguinus midas (Linnaeus, 1758)	0.41 ± 0.31	0.53	0.55	0.32	0.92	0.30
Saimiri sciureus (Linnaeus, 1758)	0.04 ± 0.09	0.15	0.00	0.00	0.10	0.03
Ungulates						
Mazama americana (Erxleben, 1777)	0.43 ± 0.29	0.33	0.32	0.53	0.30	0.43
Mazama nemorivaga (F.Cuvier, 1817)	0.44 ± 0.29	0.39	0.34	0.51	0.59	0.39
Pecari tajacu (Linné, 1758)	0.29 ± 0.20	0.34	0.07	0.41	0.41	0.22
Tayassu pecari (Link, 1795)	0.03 ± 0.06	0.02	0.00	0.02	0.00	0.05
Tapirus terrestris (Linnaeus, 1758)	0.05 ± 0.07	0.00	0.06	0.04	0.07	0.06
Rodents						
Dasyprocta leporina (Linné, 1758)	1.48 ± 0.75	1.66	2.26	1.27	2.50	††1.11
Myoprocta acouchy (Erxleben, 1777)	0.57 ± 0.33	0.72	0.50	0.52	0.65	0.57
Birds						
Crax alector (Linnaeus, 1776)	0.57 ± 0.33	0.33	0.48	0.60	0.49	0.66
Odontophorus gujanensis (J.F. Gmelin, 1789)	0.31 ± 0.31	0.54	0.04	0.42	0.00	0.30
Ortalis motmot (Linnaeus, 1766)	0.02 ± 0.07	0.13	0.02	0.01	0.00	0.00
Penelope marail (S. Müller, 1776)	0.33 ± 0.17	†0.59*	0.11*	0.32	0.42	0.31
Psophia crepitans (Linnaeus, 1758)	1.05 ± 0.66	1.44	0.87	0.97	1.29	1.01
Tinamidae	2.20 ± 0.89	3.33*	2.11	2.12	2.29	1.92
Reptile						
Chelonoidis denticulata (Linnaeus, 1766)	0.19 ± 0.17	0.45*	0.20	0.12	0.24	0.16

or present in densities that were too low to be detected with our sampling protocol.

Structure of animal communities in various landscapes

The permutational multivariate analysis of variance (Adonis test) on animal communities according to the various environmental variables showed that the proportion of variance explained by the landscape variable was the highest ($R^2 = 0.24$), and significant according to permutation test (Table 2). The between-class analysis also revealed that 24.3% of the total inertia of the data was explained by the instrumental variable of landscape typology. The Monte Carlo row permutation test for this unique environmental variable was significant (P = 0.007). Moreover, the graphic representation of the results of this between-class analysis showed that multi-convex and multi-concave landscapes presented the most distinct vertebrate assemblages, while plateau and mountain communities were less clearly distinguished (Figure 2). The main structuring species are shown on the graph, and their affinities with the various landscapes were tested subsequently with the

correlation index. All the other environmental variables tested explained a smaller proportion of total inertia with both analyses (Table 2).

Diversity of landscape communities

For each individual site community, Simpson diversity varied from eight to 16 effective species, and richness (q = 0) estimated with Chao and Shen's bias correction (approximately equal to the Jackknife 1 or Chao 1 estimators) was between 18 and 31 (Table 3). With a few exceptions, the highest richness values corresponded to sites in multi-concave landscapes and the lowest richness values to sites in multi-convex ones, with values for plains and mountainous sites between the two. Considering Simpson diversity, however, mountain sites were among the lowest values. The beta diversity between landscape meta-communities was significantly different (P < 0.05) from the β diversity between random meta-communities for q values of between 0.2 and 1.9. Common species were more evenly distributed in the various landscapes, and were present everywhere: less common species made the difference between landscapes; ignoring them (choosing

Table 2. Analysis of variance between the communities of medium- to large-bodied vertebrates in 25 study sites in French Guiana, according to seven environmental variables. Partial R-square from permutational multivariate analysis of variance (Adonis test), tested with permutation test with pseudo-F. Between-class inertia from a principal component analysis with respect to the instrumental variable (PCAIV) performed on the coordinates of a correspondence analysis, tested by Monte Carlo test. * $P < 0.05$; ** $P < 0.01$; ***$P < 0.001$.

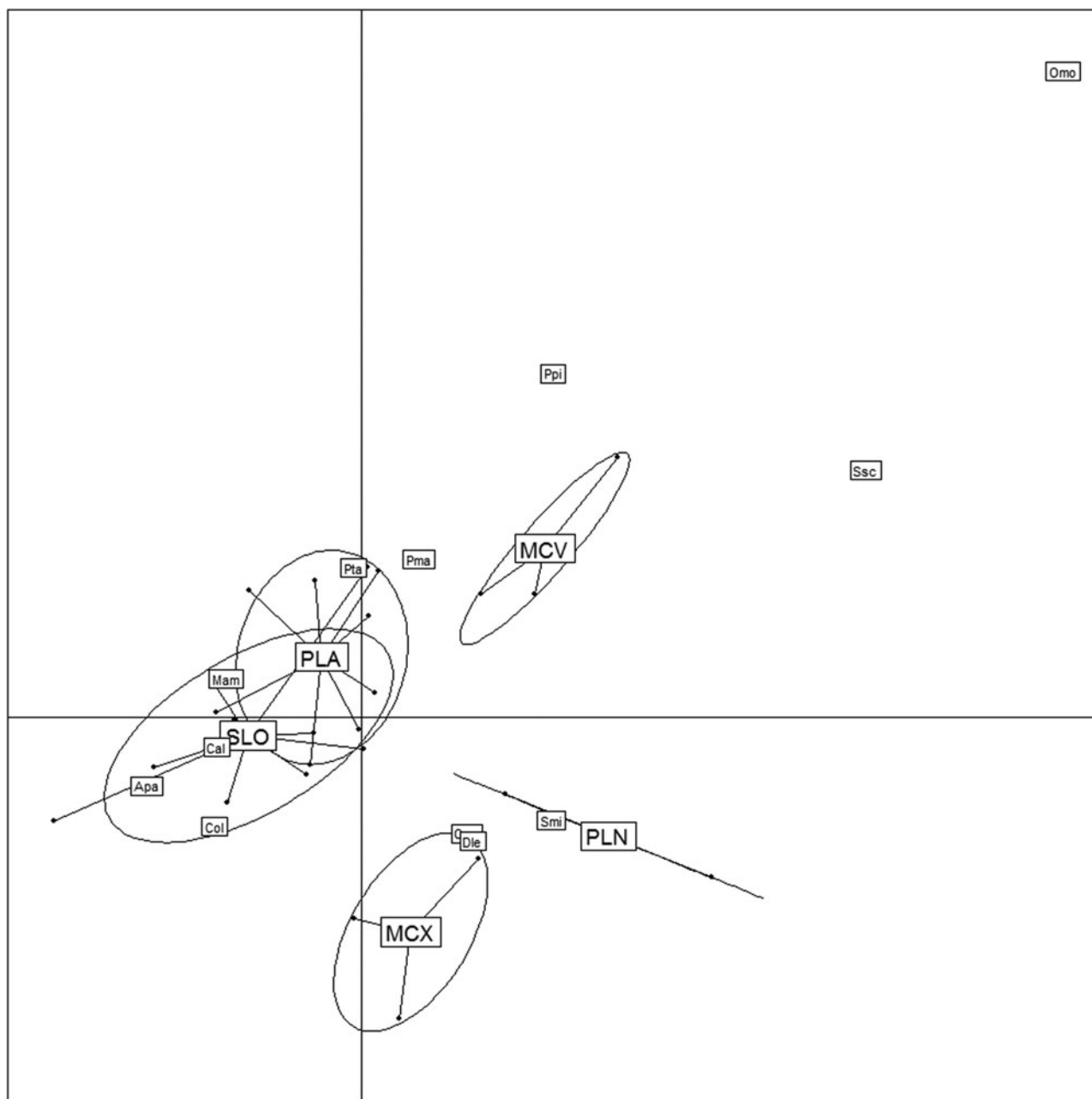|	Landscape	Vegetation type	Biogeography	% Hydromorphic soil	Mean Slope	Difference in altitude	Annual rainfall
Partial R^2 (Adonis test)	0.24**	0.17	0.15**	0.16***	0.14**	0.13*	0.12*
% between-class inertia	0.24**	0.20*	0.15***	0.15**	0.14*	0.13*	0.13*

Figure 2. Between-class analysis of the communities of medium- to large-bodied vertebrates in 25 study sites in five landscapes types in terra firme forests of French Guiana. The ellipses graphically sum up each landscape type (MCX = multi-convex; MCV = multi-concave; PLA = plateau; SLO = sloping areas; PLN = coastal plain) by covering 67% of the sites belonging to the landscape type; the centre of each ellipse is the centre of gravity of these sites. Main structuring species are indicated (Omo: *Ortalis motmot*, Ssc: *Saimiri sciureus*, Ppi: *Pithecia pithecia*, Pma: *Penelope marail*, Pta: *Pecari tajacu*, Mam: *Mazama americana*, Cal: *Crax alector*, Apa: *Ateles paniscus*, Col: *Cebus olivaceus*, Smi: *Saguinus midas*, Dle: *Dasyprocta leporina*).

Table 3. Main diversity indices, corresponding to three entropy values (q), for the medium- to large-bodied vertebrate communities in 25 study sites in terra firme forests of French Guiana, according to their landscape type. Values correspond to effective number of species. Landscape types : MCV = multi-concave, three sites; MCX = multi-convex, three sites; PLA = plateau, eight sites; PLN = coastal plains, two sites; SLO = sloping areas, nine sites.

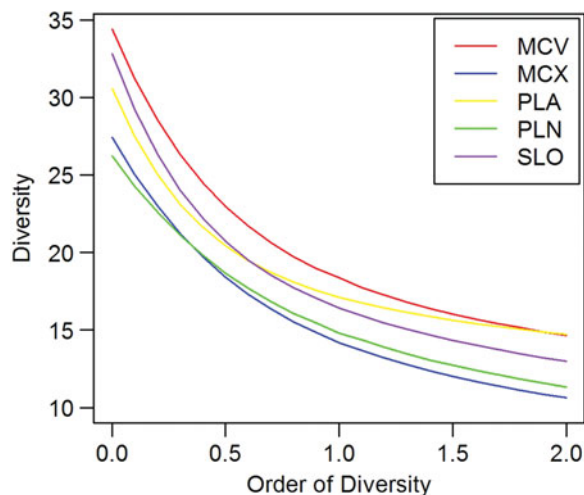| Site | Diversity index | | |
	Richness (q = 0)	Shannon (q = 1)	Simpson (q = 2)
MCV.1	31.3	18.1	14.1
MCV.2	21.7	13.8	11.0
MCV.3	26.3	18.2	15.3
MCX.1	22.4	13.6	10.1
MCX.2	22.6	11.9	09.0
MCX.3	23.5	14.1	11.1
PLA.1	20.9	14.9	12.3
PLA.2	25.7	16.5	12.7
PLA.3	22.6	14.2	11.3
PLA.4	23.7	15.5	12.3
PLA.5	22.0	15.0	13.1
PLA.6	24.0	17.6	15.4
PLA.7	26.6	19.0	16.3
PLA.8	18.9	13.8	10.8
PLN.1	23.3	12.8	08.6
PLN.2	17.8	14.6	12.2
SLO.1	23.3	12.2	07.9
SLO.2	19.7	13.9	11.5
SLO.3	23.8	13.8	09.3
SLO.4	23.7	15.2	12.4
SLO.5	23.3	13.5	09.5
SLO.6	24.6	16.2	13.7
SLO.7	22.9	16.9	14.6
SLO.8	20.2	14.7	13.0
SLO.9	23.6	15.1	11.6

Figure 3. Gamma diversity profiles of the communities of medium- to large-bodied vertebrates in the five landscape types (MCV = multi-concave; MCX = multi-convex; PLA = plateau; PLN = coastal plain; SLO = sloping areas), as estimated by diurnal line-transects conducted in 25 non-disturbed study sites in terra firme forest in French Guiana.

high values of q) made the test inconclusive. For small values of q, a lack of power of the test was involved: bias correction was more important, and so was the variance of the estimator of diversity.

The diversity profiles of the five meta-communities (γ diversity) corresponding to the five landscape types differed, whatever the order of entropy considered (0 $\leq$ q $\leq$ 2, i.e. from the number of species to Simpson diversity, Figure 3). The most diverse meta-community is encountered in the multi-concave landscape, despite the small sample size in this category, and the least diverse in the plain and multi-convex landscapes. Plateaux and mountainous areas were intermediate in terms of diversity, the steeper-sloped areas were more diverse than plateaux when rare species were considered (q = 0), and the reverse when only common species were considered (q = 2).

Characterization of landscape communities

The multi-concave landscape was positively associated with the largest number of species (Table 4). Six

species had a correlation coefficient $r^g_{pb} \geq 0.5$ for this landscape category. *Penelope marail*, *Ortalis motmot*, Tinamidae and the tortoise *Chelonoidis denticulata* were the most characteristic species, and *Saimiri sciureus* and *Pithecia pithecia* were the most typically associated primates. Moreover, despite lower scores and no statistical significance, four more species had their maximum correlation coefficient in multi-concave landscapes (*Alouatta macconnelli*, *Psophia crepitans*, *Odontophorus guyanensis* and *Myoprocta acouchi*). These results on association tendencies between species and landscapes are confirmed by comparisons of abundance. The abundance of *S. sciureus*, *O. guyanensis*, *O. motmot*, *P. marail*, *C. denticulata* and tinamidae were significantly higher in multi-concave landscapes than in other landscapes and/or other sites combined (Table 1). In contrast, two species had negative r^g_{pb} in these areas: *Tapirus terrestris* and *Crax alector* ($r^g_{pb} = -0.4$ and -0.3 respectively) (Table 4). Finally, two of the three top-ranked sites in terms of crude richness were also located in a multi-concave landscape, and they also belonged to the three top-ranked sites regarding total abundance (total abundance, all species combined).

Cebus apella was clearly associated with coastal plains ($r^g_{pb} = 0.7$, P < 0.05, Table 4). The abundance of this species was significantly higher there than at all the other sites combined (Table 1) (P < 0.05). *Saguinus midas* also reached its maximum levels in this plain landscape. In contrast, *Ateles paniscus* and *Cebus olivaceus* had their lowest and negative coefficient there ($r^g_{pb} = -0.5$), and the abundance of *C. olivaceus* was significantly lower than in other landscape types.

Table 4. Association of 21 medium- to large-bodied vertebrate species with five landscape types in French Guianan pristine rainforest, as estimated by point-biserial correlation coefficient, corrected for unequal sampling in different landscapes (r^g_{pb}). MCV: Multi-concave; MCX: Multi-convex; PLA: Plateau; PLN: Coastal plains; SLO: sloping area. Monte Carlo Permutation test: *: $P \leq 0.05$; **: $P \leq 0.01$.

	Landscape				
	MCV	MCX	PLA	PLN	SLO
Primates					
Alouatta macconnelli	0.3	− 0.2	0.1	− 0.2	0
Ateles paniscus	− 0.2	0.2	0	− 0.5	0.5
Cebus apella	− 0.1	0	− 0.4	0.7**	− 0.2
Cebus olivaceus	− 0.1	0.5	0	− 0.5	0.1
Pithecia pithecia	0.5	− 0.3	0	0	− 0.1
Saguinus midas	0	0	− 0.3	0.5	− 0.3
Saimiri sciureus	0.5	− 0.3	− 0.3	0.2	− 0.1
Ungulates					
Mazama americana	− 0.1	− 0.1	0.3	− 0.2	0.1
Mazama nemorivaga	− 0.1	− 0.2	0.1	0.3	− 0.1
Pecari tajacu	0.1	− 0.6	0.3	0.3	− 0.2
Tayassu pecari	0	− 0.2	0	− 0.2	0.4
Tapirus terrestris	− 0.4	0.1	0	0.2	0.1
Rodents					
Dasyprocta leporina	− 0.1	0.3	− 0.3	0.4	− 0.4
Myoprocta acouchy	0.2	− 0.1	− 0.1	0.1	0
Birds					
Crax alector	− 0.3	− 0.1	0.2	− 0.1	0.3
Odontophorus guyanensis	0.4	− 0.3	0.2	− 0.4	0.1
Ortalis motmot	0.6	− 0.1	− 0.1	− 0.2	− 0.2
Penelope marail	0.6**	− 0.6	− 0.1	0.2	− 0.1
Psophia crepitans	0.3	− 0.2	− 0.1	0.1	− 0.1
Tinamidae	0.5	− 0.1	− 0.1	0	− 0.2
Reptiles					
Chelonoidis denticulata	0.6	− 0.1	− 0.3	0	− 0.2

The associations between all species and the multi-convex, mountainous or plateau landscapes were all weaker ($r^g_{pb} \leq 0.5$), and none was statistically significant. *Cebus olivaceus* was the only species showing some association with multi-convex areas ($r^g_{pb} = 0.5$) and a higher abundance than in other landscapes, while nine species showed a negative association with this landscape, among which most conspicuously *Pecari tajacu* and *Penelope marail* ($r^g_{pb} = -0.6$) (Table 1). *Ateles paniscus* tended to show a maximum association with the mountainous landscape ($r^g_{pb} = 0.5$; abundance significantly higher than in other landscapes and other sites ($P < 0.05$)), whereas *Dasyprocta leporina* and the small primate *Saguinus midas* showed their minimum and negative values in this landscape type (Table 1). The abundance of *D. leporina* was significantly lower in mountainous landscapes than in other landscapes ($P < 0.05$) (Table 1). *Mazama americana* was the species most associated with plateaux ($r^g_{pb} = 0.3$) and *Cebus apella* the least ($r^g_{pb} = -0.4$, Table 4).

Another analysis considered if combining landscapes matched species preferences better. Whereas several species remained more strongly associated with a single landscape type, some species turned out to be more strongly associated with a combination of landscapes. For example, *Penelope marail* appeared to be associated with the combination of smoothed landscapes, i.e. multi-concave + plain ($r^g_{pb} = 0.7$, $P < 0.05$).

Finally, another analysis looked for associations between combinations of two or more species and various landscapes. Multi-concave landscape appeared to be characterized by a large multi-species community, mainly comprising birds (*Odontophorus guyanensis*, *Penelope marail*, *Ortalis motmot*, Tinamidae), the small primate *Saimiri sciureus* and the tortoise *Chelonoidis denticulata*; the plateau landscape by the simultaneous abundance of *Pecari tajacu* and *Mazama americana*, and the multi-convex landscape by the combined high abundance of *Cebus olivaceus* and *Dasyprocta leporina*.

DISCUSSION

We found that the geomorphological typology of landscapes is a non-negligible factor driving the structure and the beta-diversity patterns of medium- to

large-bodied vertebrate communities in terra firme forests in French Guiana. The geomorphological landscapes combine effects of geology, climate, relief and history in one descriptive variable. As previously found for tree beta-diversity patterns, this integrated parameter better explains the differences between animal communities than some simple environmental parameters separately.

Habitat preference results in the disproportionate use of some resources and/or conditions over others. Habitat selection can be considered at various scales, previously defined as four selection orders (Johnson 1980). At small spatial and temporal scales, animals select different local resources or conditions. As both scales increase, these individual behavioural decisions result in survival and reproductive performances at the levels of individuals and populations. Over evolutionary time, these habitat choices contribute to the species' environmental niche or functional habitat (Gaillard *et al.* 2010). In the same way, De Caceres & Legendre (2009) stated that the r^g_{pb} value, computed from relative abundance, indicates the degree of preference of species for a target landscape compared with the other landscapes, and that 'negative correlation values tell us when a species "avoids" the target site group' (also referred to as 'negative fidelity' by phytosociologists). Following these assumptions, we interpreted the higher abundance of species in a particular habitat as a preference of this species for this habitat, resulting in higher abundance.

Some species, such as the howler monkey *Alouatta macconnelli*, appeared to be generalists or ubiquitous, and were not associated with any particular landscapes. This is consistent with other studies generally considering howler monkey as a generalist plastic species, with a varied diet (Julliot & Sabatier 1993, Simmen *et al.* 2001) and few particular requirements (Lehman 2004, Schwarzkopf & Rylands 1989). Some other species appear to have more restricted distribution: *Saimiri sciureus* were only detected in three study sites and *Pithecia pithecia* in 12. This may be related to very special habitat requirements leading to a true patchy distribution, or to very low densities in the other sites, in both cases denoting some habitat preferences although no significant results were highlighted in this study. In contrast, *Cebus apella* is a very common species encountered all over the country, but our results showed a clear preference for plain landscape type, in which they are particularly abundant. Among birds, the smallest species are characteristic of the low-altitude southern area, while *Penelope marail* is more generally associated with all the flat relief areas (northern plains and southern multi-concave area). On the other hand, *Crax alector* appears to favour steeper areas. In French Guiana, the distribution of *Crax alector* in various habitats and with respect to environmental parameters has been analysed more precisely, showing a clear positive relationship between *C. alector* densities and the mean slope of the prospected site (Denis 2012).

Few species appeared really specialized, but although most species taken separately do not demonstrate strong habitat preferences, their assemblages produced typical communities in the various landscapes types.

Landscape communities characteristics

The multi-concave forest type appears to be the preferred habitat of a large set of species. These relatively low-elevation forests also host higher diversities of both rare and common species. We hypothesize that the lower and fragmented canopy provides a better-lit environment, with vertical strata and a greater diversity of niches. The flat environment at lower elevations can also be considered as less constraining. However one site appears to be quite different from the others with respect to most of the parameters considered, in particular for its much lower diversity. However, this site (the Waki basin) is also considered to be a very particular forest habitat type, and should probably be considered and characterized separately (Guitet *et al.* 2013, 2015).

In contrast, the other landscapes were the preferred habitat of only one or two species, and the α diversities of these sites were also lower. For example, the correlation coefficients of all animal species with montane environments were generally low, and very often negative, and only two species tended to be associated (*Ateles paniscus* and *Crax alector*). The α richness (q = 0) of each mountainous site was rather low (20–24), even if the estimated richness of the meta-community of whole mountainous landscape (γ diversity) was among the highest, and was similar to that of the multi-concave meta-community (32.8). These two results may indicate that our mountain sample is rather heterogeneous (greater turnover), or that many less abundant species are present in these environments, but were difficult to detect and hence only randomly detected by our sampling method. However, the larger number of study sites in this category may also explain this higher γ diversity. *Cebus olivaceus* and *Dasyprocta leporina* were the only species to be positively associated with multi-convex landscapes. These areas are generally characterized by high abundance of the tree families Lecythidaceae and Caesalpinioideae, and of several species of palm tree (>200 ha^{-1}), which could explain the high abundance of this rodent (Cid *et al.* 2013). As for mountainous or multi-convex areas, few animal species clearly showed preference for plateaux, but the combined abundance of red brocket deer *Mazama americana* and the collared peccary *Pecari tajacu* is nevertheless characteristic of these environments. Like for mountainous areas, the mean α diversity was relatively low whereas the global γ diversity was higher (for q = 0), which could also be linked with

the large sample size in this category. Moreover, the definition of 'plateau' used in this study was probably too broad, and combined habitats that were too dissimilar. A finer-scale landscape typology identified three different types of plateaux (Guitet *et al.* 2013), but we lacked sufficient replicates to analyse the potential differences in the vertebrate community in these subcategories. In the same way, the two study sites considered in this study in the 'plain' category are in fact quite different and belonged to different types in the finer typology (Guitet *et al.* 2013). The coastal plain is the most extensively inhabited and consequently hunted area (de Thoisy *et al.* 2010), so finding replicates in undisturbed localities is challenging.

In all cases, it should be kept in mind that the diversity values estimated here depend on the methodology used, which mainly concerns the large diurnal species potentially detected during line transects. Some taxa may be underrepresented by this method, particularly nocturnal species and felids.

Relevance of the landscape typology for communities of medium- to large-bodied vertebrates

Our results highlight the influence of broad habitat categories on medium- to large-sized vertebrate communities in upland terra firme forests of French Guiana. An integrative parameter, the geomorphological landscapes proposed by Guitet *et al.* (2013), explains this heterogeneity better than most of the single parameters related to it. This is congruent with the conclusions drawn by Palminteri *et al.* (2011) that each environmental variable examined appeared to contribute to some component of the heterogeneity in primate communities in Peru, none of them being an outstanding contributor. In some cases, however, the geographic scale inherent to this classification (and used in this study) may not match field reality. For example, a medium-sized valley within a larger sloping environment was included in the mountain landscape category, whereas its faunal community was not characteristic of this landscape type (low to medium abundances of *Ateles* and *Crax*, for example). However, the overall floristic composition of this particular site matched the expected one better, according to the classification, than the faunal community (Guitet *et al.* 2015). It is likely that the temporal and geographic scales of these two biodiversity components differ. The vegetation reflects long-term climatic and geomorphological influences, whereas the large-fauna community should react more rapidly to local conditions and present filter-effects. On the other hand, some species presented affinities with two different landscapes, which for them, probably share key environmental features. For example, *Penelope marail* and *Saimiri sciureus* were associated with both the multi-concave

landscapes located in the southern part of French Guiana and with the plains located in the northern part. The common pertinent parameter may be flat relief and low elevations, independently of other parameters. The landscape classification used here permitted sufficient replicates within each type. A finer classification exists, identifying 12 different landscape types instead of five (Guitet *et al.* 2013), including three different forms of plateau, and three types of forest in the coastal plains, but additional sampling is needed to correctly analyse vertebrate assemblages at this finer scale.

A priori classifications of structural habitats do not focus on the meaning of the species distributions, with respect to active habitat selection or to environmental parameter selection by the different species. However, it corresponds to the approach used when designing legislation or policy to manage species in geographic space. Although still rough, our results may help guide territorial management of highly sensitive species, and help analyse the impacts of hunting while accounting for natural variation in abundance in various environments. More generally, the geomorphological-based typology of landscapes could be used in other countries and/or regions to characterize and predict animal community distribution throughout their territory. Coblentz & Riitters (2004) already pointed out that topography plays a primary role in regional to continental-scale biodiversity, and the landscape level is becoming more and more popular in analysis and/or resource management (Arroyo-Rodriguez & Fahrig 2014, Bonnot *et al.* 2013, Clark & Clark 2000, Hawes *et al.* 2012, Melo *et al.* 2013, Mockrin *et al.* 2011, Priego-Santander *et al.* 2013). The terra firme forests are generally known as oligotrophic forests typically sustaining low biomass densities of primates and other medium-sized to large-sized vertebrates (Emmons 1984, Haugaasen & Peres 2005a, Palacios & Peres 2005). However, they represent approximately 95% of the Amazon basin (Palacios & Peres 2005), so it is a major challenge to be able to characterize their heterogeneity, including the faunal assemblages with which they are associated.

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