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ORIGINAL PAPER

Rapid evaluation of threats to biodiversity: human footprint score and large vertebrate species responses in French Guiana

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Abstract Although there is an extensive literature demonstrating the impact of human activities on both species extinction risk and local ecological processes, the methodological tools that allow for the visualization and quantification of the intensity of the observed and forthcoming impacts are lacking. Here we propose a Footprint index for French Guiana, (northern Atlantic coast of South America) which sums up the expected and proven disturbances on biodiversity. The index was developed by superimposing geographical and human data, including human population densities, land use, settlements and camps, mining and forest activities, tracks, roads and rivers. The relevance of the index as a general measure of anthropic impact on large terrestrial fauna was estimated by investigating the structure of the large terrestrial vertebrate assemblages, including primates, large frugivorous birds, rodents and ungulates, in relation to the extent of disturbances. The abundance of large terrestrial fauna was assessed using the line-transect sampling method in 34 forest sites facing different disturbance levels, including hunting, logging and

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fragmentation, and consequently different footprint scores. A Self Organizing Map was used to combine species abundances and disturbance scores. It allowed us to rank species in accordance to their sensitivity towards disturbances, identifying the response of fauna to different concomitant threats. The index provided correct identification of sites with similar threats which proves it is a relevant estimator of human disturbance. In addition, the richness of animal communities and abundances of several seed dispersers and predators were negatively correlated to the index (e.g. large monkeys and frugivorous birds, $r^2 = 0.49$, $P < 0.0001$ and $r^2 = 0.48$, $P < 0.0001$, respectively), indicating its reliability in identifying areas where animal communities are disturbed. The index could, therefore, constitute a useful tool to identify areas where ecological processes supported by those species are expected to be disrupted, and where they are already disrupted. Furthermore, the footprint index can deal with lack of field data or with only partially valid information, and so may directly help land managers forecast and, hopefully, mitigate forthcoming impacts resulting from the development of human activities.

Keywords Vertebrates · Threats · Management · Footprint · Self organizing maps · Ecological processes

Introduction

The role of habitat suitability, heterogeneity and connectivity between patches in sustaining species diversity and abundance has been demonstrated for a wide range of ecosystems and organisms. Matching environmental patterns and species requirement is therefore one of the main objectives of conservation programs (Meffe and Carroll 1997). These objectives need to be carefully shaped to match the compromise between maintaining species diversity and ecosystem processes, and land developments. The use of distribution, abundances, and population trends of well identified focus species is a commonly used approach to assess conservation priorities (Redford et al. 2003); however the choice of the target species remains a challenge. A wide variety of criteria are used for this purpose, including endemism, rarity (Tognelli 2005), size and heterogeneity of area requirements, vulnerability, ecological functions (Coppolillo et al. 2004), range-restricted distribution area (Larsen et al. 2007) and Red List classification (Keller and Bollmann 2004). However, drawing conservation plans developed on the basis of lessons from a restricted part of the community provides an incomplete assessment of ecosystem status. Hence, searching for indicator groups in areas of the highest richness (e.g., Manne and Williams 2003; Tognelli 2005) can miss important conservation concerns, since richness may be unequally distributed among taxa (Prendergast et al. 1999). Similarly, the use of rare and threatened species as indicators may miss areas of high diversity, since rare species may have particular habitat requirements that may not fit with overall patterns of ecological diversity (Orme et al. 2005). Finally, focussing conservation indices on species richness may not provide relevant indicators of the sustainability of ecological processes. For such purposes, key species groups (e.g. seed predators, disseminators, predators) should be preferred as surrogates for the overall community, providing more complete and more objective information (Pearman and Weber 2007).

The ability to monitor diversity and abundance of target indicator species with a short term effort compatible with field requirements, management plans and funding was recently demonstrated in French Guiana (de Thoisy et al. 2008). Compared to other neotropical countries, the forest conservation status of French Guiana is still favourable, with a single continuous forest block representing more than one third of the remaining neotropical rainforest (Hammond 2005). However, current increases of demographic pressure and a recent gold rush (Hammond et al. 2007), induce widespread disturbances and often unsustainable hunting pressure (Richard-Hansen and Hansen 2004; de Thoisy et al. 2005, 2009) that seriously threaten terrestrial and freshwater biodiversity.

Our aims were therefore: (i) To map the human pressures on natural resources by building a human footprint index (Sanderson et al. 2002a; Kareiva et al. 2007) integrating various expected impacts on biodiversity; (ii) To establish the distribution of a target species assemblage that incorporates diverse seed predators and dispersers; (iii) To compare the environmental disturbance summarized in the footprint index to the spatial distribution of target species in order to measure how faithfully the range of disturbance affecting the target vertebrate community is summarized by the footprint index.

Materials and methods

The country

French Guiana is a French administrative unit of 84,000 km^2. The population size is rather small but the demographic pressure has increased during the last decade, with 157,000 inhabitants in 1998, and 220,000 inhabitants estimated in 2008. Most of the population is concentrated in the coastal area and along the Maroni river, which constitutes the boundary with Suriname. The climate is equatorial, with a short dry season in March and a longer one from August to December. The average annual rainfall increases from West to East, from 1,500 to more than 4,000 mm.

Survey of target species

The structure of large terrestrial vertebrate assemblages was investigated using line-transect sampling in 34 forest sites dispersed throughout the country, according to technical opportunities for field work implementation (Fig. 1). The line-transect method is commonly used to measure richness and abundance of large diurnal mammals, and consists of walking slowly (1–1.3 km/h), on a single linear forest track 4–5 km long, in a homogeneous habitat in terms of forest structure and observed human-induced disturbances. Species were identified and counted along the census walk, the census was replicated daily on a site until a large enough cumulated distance had been covered (102 $\pm$ 10 km). That sampling effort has been recognised as valid to estimate large vertebrate richness and the abundance of a set of target species identified as sensitive to habitat disturbance (de Thoisy et al. 2008): monkeys, large frugivorous birds, ungulates and large diurnal rodents. The characteristics of the sites, including sources of disturbance and species and/or habitats and forest type were measured in each site (Table 1). Four major causes of disturbance that are current threats to large vertebrate species in the region (de Thoisy et al. 2005) were measured using a semi-quantitative scale with four grades from no impact to strong disturbance. The disturbances considered and associated grades are: (i) *Logging*: 0 = no logging; 1 = ancient logging (>10 years prior to the survey); 2 = recent and short (<1 year period) logging; 3 = recent and long logging period. (ii) *Hunting*: 0 = no hunting; 1 = light hunting pressure; 2 = medium hunting pressure; 3 = heavy hunting pressure. These levels were defined according to numbers of hunters met during the survey, the density of hunting tracks, and the presence of used cartridges. (iii) *Fragmentation*: 0 = no fragmentation; 1 = one forest track close (<3 km) to the surveyed site;

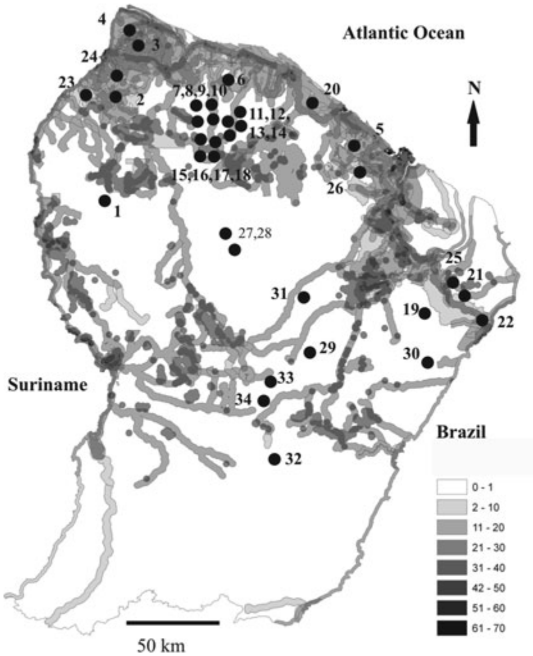


Fig. 1 Map of French Guyana showing the locations of the sites surveyed for large vertebrate communities, and associated human footprint

2 = several tracks in the immediate vicinity of the site; 3 = site isolated from the continuous forest block. (iv) *Access* by motorized engine (boat or car): 0 = site located more than 10 km from the closest access; 1 = closest access 5–10 km away; 2 = closest access 2–5 km away; 3 = closest access less than 2 km from the survey site. Additionally, the *forest type* was used to describe the natural environment of each site. It was derived from remote-sensing analysis VEGETATION time series data from SPOT 4 satellite (1-km spatial resolution from blue to middle infra-red wavelength); low resolution time series data were used to identify large vegetation types (Gond et al. 2009). All sites were covered by upland moist forest types, and the following subtypes were identified: forest with discontinuous canopy on hydromorphic soils (Table 1, class A); hyperwet forest with continuous canopy (class B); forest with continuous and dense canopy (class C); and subwet forest with continuous canopy (class D).

The footprint index

The footprint index for French Guiana was derived from the Human Footprint approach (Sanderson et al. 2002a) that aims to sum up the strength of proven and potential disturbances on biodiversity. The index was based on scores describing human activities. Buffer zones were then defined depending on the nature and intensity of the activities. It is based on GIS superimpositions of geographical and human data, including human population densities (data source: INSEE "French Institute for Statistical and Economic studies", unpublished data, 2005), land use (data source: Direction départementale de l'Agriculture et de la Foret, unpublished data, 2005), forest settlements and camps, forest activities and forest tracks (data source: ONF "National Forest Agency", unpublished data, 2005), roads and rivers (data source: DDE "Regional Equipment, Habitat and Planning Authority", unpublished data, 2005), and mining. Data sources for mining camps were derived from

Table 1 Survey sites, strength of direct pressure, habitat type, and associated footprint index

Sites (N° refers to Fig. 1)	Hunting	Logging	Access	Fragmentation	Habitat	Index
Lucifer (1)	0	0	0	0	B	0
Cr. Maurice (2)	2	0	2	1	B	17
Charvein (3)	3	0	3	3	D	16
Coswine (4)	1	0	3	0	B	14
Matiti (5)	3	1	3	3	D	9
Patagaïe (6)	3	1	3	3	B	17
Counami A, 1998 (7)	1	0	2	1	B	4
Counami A, 2000 (8)	2	0	3	2	B	8
Counami A, 2001 (9)	3	2	3	2	B	12
Counami A, 2003 (10)	3	3	3	2	B	17
Counami B, 1998 (11)	1	0	2	1	A	4
Counami B, 2000 (12)	2	0	3	2	A	4
Counami B, 2001 (13)	3	0	3	2	A	8
Counami B, 2003 (14)	3	1	3	2	A	17
Counami T, 1998 (15)	0	0	1	0	A	0
Counami T, 2000 (16)	0	0	1	1	A	0
Counami T, 2001 (17)	1	0	1	1	A	8
Counami T, 2003 (18)	1	0	1	1	A	17
RNT (19)	0	0	1	0	B	0
CSG (20)	2	1	2	3	B	13
RN2 (21)	1	0	3	1	B	4
RN3 (22)	3	0	3	2	B	24
Apatou (23)	3	0	3	2	D	14
Balaté (24)	3	1	3	2	D	18
RN1 (25)	1	0	2	1	A	4
Balata (26)	2	0	2	1	B	8
Trinité Leblond (27)	1	0	0	0	B	4
Trinité Aimara (28)	0	0	0	0	B	0
Croissant (29)	0	0	0	0	B	0
Armontabo (30)	0	0	0	0	B	0
Nouragues (31)	0	0	0	0	B	0
Piton Baron (32)	0	0	0	0	B	0
Matecho (33)	0	0	0	0	B	0
Limonade (34)	0	0	0	0	C	0

(i) *Logging*: 0 = no logging; 1 = ancient logging (>10 years prior to the survey); 2 = recent and short (<1 year period) logging; 3 = recent and long logging period

(ii) *Hunting*: 0 = no hunting; 1 = light hunting pressure; 2 = medium hunting pressure; 3 = heavy hunting pressure

(iii) *Fragmentation*: 0 = no fragmentation; 1 = one forest track close to the surveyed site; 2 = several tracks in the immediate vicinity of the site; 3 = site isolated

(iv) *Access* by motorized engine (boat or car): 0 = site located more than 10 km from the closest access; 1 = closest access 5–10 km away; 2 = closest access 2–5 km away; 3 = closest access at less

(v) Forest classes are given according to Gond et al. (2009). A = forest with discontinuous canopy on hydromorphic soils; B = hyperwet forest with continuous canopy; C = forest with continuous and dense canopy; D = subwet forest with continuous canopy

(vi) Index values: see "Materials and methods" section

Table 2 Variables and scores used to map the footprint index in French Guiana

Variable	Intensity	Associated score
Human population density	>10 inhab./km^2 (urban areas)	10
	50 km around inhabited areas (widespread settlements)	5
Land use	Urban	12
	Industrial agriculture	8
	Subsistence agriculture	4
Camps	Mining camp	8
	Tourist camp	8
	Other forest camp	4
Roads and tracks	2 km buffer along primary roads	12
	2 km buffer along secondary roads	8
	2 km buffer along trails	4
Rivers	2 km buffer along lower parts (to 50 km from the mouth)	8
	2 km buffer 50 km upstream and downstream of all settlements and camps	4
Mines	Illegal	10
	Legal	8
Logged areas	Without management plan	10
	With management plan	4

remote sensing analysis for location of both legal and illegal activities (Hammond et al. 2007). For each source of disturbance, a buffering area of influence and an associated score were attributed according to the expected intensity in relation to the impact on target species (Table 2). To do this, we used information from previous research and field projects. First, most target species are game species, and we have shown that most game is bagged within 2 km of a point of motorized access, river or track (de Thoisy et al. 2005). Consequently, navigable rivers and forest tracks were considered as a direct disturbance source, and are illustrated by a buffer of potential threat for the overall target community. Regarding land use, a median disturbance score was ascribed to legally logged areas, tourist camps, subsistence slash and burn agriculture, as the direct impacts are restricted in time and/or space. These areas were therefore considered as less disturbed than those where unmanaged uses occur. We also considered mining activities that have been proven detrimental to the fauna (Hammond et al. 2007). A high disturbance score was therefore assigned to mining areas. The resulting map, for the entire country, is the sum of the scores. Once the map was built, a focus on each of the 34 study sites defined their respective human footprint index (Table 1).

Data analysis

In the first step, the correlation between fauna richness and site variables (logging, hunting, access, fragmentation and forest type) was investigated with linear regression; the strength of the relationships between the abundance of each target species (mean number of individuals sighted by km) and the characteristics of associated survey sites were investigated with variance analysis (ANOVA; Xlstat©). Relationships between richness, abundance of target species, and footprint index were investigated with a linear regression (Xlstat©).

Secondly, abundances of the target species were used as input data to pattern the 34 sites using unsupervised artificial neural networks, also called Kohonen self-organizing maps (SOM; Kohonen 2001). SOM are known to provide an objective picture of the ecological structure in a data set, because they are not influenced by preconceived notions regarding the samples or the environment (Blayo and Demartines 1991; Chon et al. 1996; Giraudel and Lek 2001; Reyjol et al. 2005). Here we applied this multispecies approach in order to ordinate the sampling sites according to their target species composition. This permitted us to assess the degree of confidence we can have in our footprint index as a surrogate of the status of a target community. In the SOM model, input samples can be considered as a vector of 34 dimensions (i.e. sites) in n-dimensional space Rn. The SOM reduces the dimensionality of these data to a two-dimensional map (i.e. the Kohonen map) while preserving the spatial relationships of the original samples. Hence, sites with similar species assemblage structures map together on the two-dimensional grid (i.e. in the same or a neighbouring cell); conversely, samples with very different assemblage structures (i.e. different species compositions) should map far apart, depending of the degree of difference. The learning process of the SOM is as follows. Each neuron of the output layer comprises one virtual unit (i.e. virtual sampling site). The virtual units of the Kohonen map are initialised by random sampling from the input data set (i.e. real sampling sites, hereafter called sample units). The virtual units are then updated in an iterative way: a sample unit is randomly chosen in the input data set (initial unit) and the Euclidian distance between that sample and every virtual unit is computed. The virtual unit that has the lowest Euclidian distance from the initial virtual unit is then selected as the best matching unit (the winner) and placed adjacent to the initial unit. A weighting vector is produced for this pair of units using the SOM learning rule and the process continues iteratively, with the weighting vector updated during each iteration, until all sample units are located on the SOM. The SOM was performed using the toolbox developed by Alhoniemi et al. (2003) for Matlab. Full details on the method can be found in Kohonen (2001) and Lek et al. (2005). The form of the SOM map is a hexagonal lattice (Kohonen 2001) and the SOM consists of two layers (i.e. one input layer and one output layer), connected to each vector of the data set. The output layer corresponds to the SOM map of 20 neurons organised in an array of 4 cell-rows and 5 cell-columns, a configuration that yields the clearest representation of the data (Lek et al. 2005). This ordination method is recognized as a powerful tool due to its ability to deal with both linear and nonlinear data (Chon et al. 1996; Park et al. 2003; Lek et al. 2005; Brosse et al. 2007). Once the final SOM map was obtained, we identified groups of sites on it using the weight vector of each virtual unit (i.e. cell) in a hierarchical cluster analysis (Ward linkage method). Results of the cluster analysis were validated using discriminant function analysis (DFA) and Monte-Carlo tests (1,000 permutations) in R with the ADE4 package (Thioulouse et al. 1997). Then, the probability of occurrence of a species in a group of samples was calculated and displayed on the SOM map as shades of grey: the darker the color, the higher the probability (Park et al. 2003). Lastly, the mean values of each environmental variable and of the footprint index were calculated in each node of the trained SOM map to understand the relationships between the biological and environmental variables. These mean values assigned to the SOM map were visualised using a grey scale, and then compared to maps of sampling sites as well as to biological attributes. Such a procedure is commonly used in SOM analyses (e.g. Park et al. 2003; Solidoro et al. 2007) and provides the opportunity to make visual comparisons between the probability of presence of the species, the disturbances and the footprint index. Those relationships between the species abundance and the index were then statistically tested using linear regressions. In the same way we also tested the relationship between the index and the species richness as well as between the index and assemblage indicators (e.g. abundance of monkeys and abundance of birds).

Results

Responses of species to disturbances

The species richness of the large vertebrate species recorded ranged from 6 to 22 according to the sites, and the richness of the monkey community ranged from 2 to 6 species per site. Among disturbances, most of the variation of the overall diversity of the large vertebrate community was explained by the hunting pressure (ANOVA, $P = 0.04$) and to a lesser extent by the logging pressure (ANOVA, $P = 0.06$). Primate richness was significantly related to hunting pressure only (ANOVA, $P = 0.003$). The diversity of species was not related to the forest type (ANOVA, $P > 0.5$).

SOM of sites ordination according to their species abundance (Fig. 2) revealed four distinct clusters (AFD, Monte Carlo test, $P = 0.009$). Mapping the probability of presence of each species on the SOM map (Fig. 3) shows how the abundances of the different

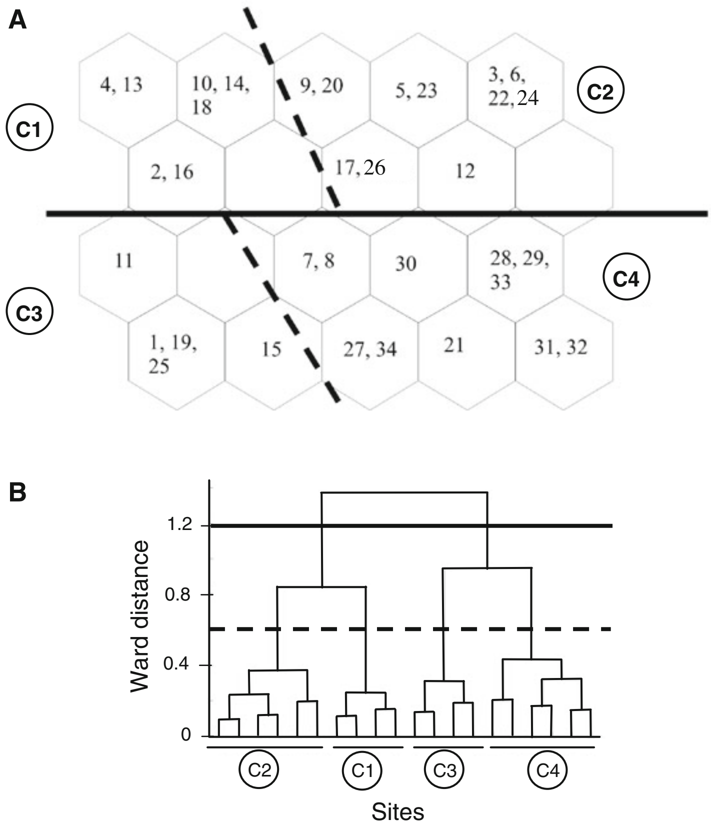


Fig. 2 The self-organizing map (SOM) site ordination according to species abundance. **a** The SOM map with the 34 sites represented on the 5 × 4 cell output map (see Fig. 1 for sites codes). Then the 20 cells were classified into four clusters (C1, C2, C3, C4) based on a hierarchical cluster analysis. The clusters were delineated with continuous and dashed bold lines according to the similarity level considered. **b** Hierarchical classification of the 20 SOM cells (Ward method)

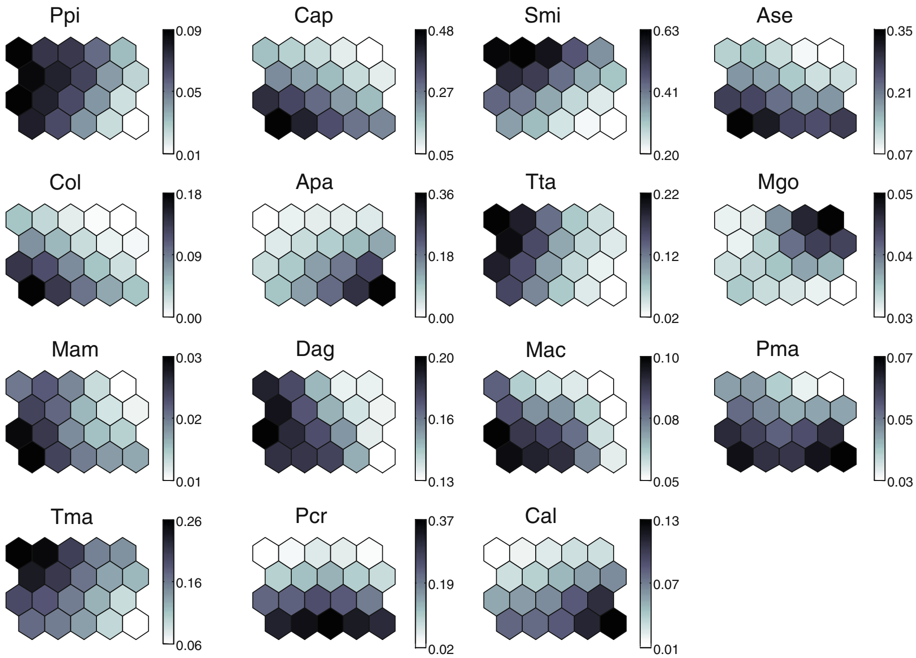


Fig. 3 Probability of presence of species on the self-organizing map (SOM). *Darker shades* represent higher probabilities of occurrence, although *lighter shades* indicate lower probabilities. Ppi, *Pithecia pithecia*; Cap, *Cebus apella*; Smi, *Saguinus midas*; Ase, *Alouatta seniculus*; Col, *Cebus olivaceus*; Apa, *Ateles paniscus*; Tta, *Tayassu tajacu*; Mgo, *Mazama gouazoubira*; Mam, *Mazama americana*; Dag, *Dasyprocta agouti*; Mac, *Myoprocta acouchi*; Pma, *Penelope marail*; Tma, *Tinamus major*; Pcr, *Psophia crepitans*; Cal, *Crax alector*

species contributed to the ordination of the sites. For instance, high densities of the tamarin, *Saguinus midas*, and of the great tinamou *Tinamus major*, and low abundances of the spider monkey, *Ateles paniscus*, and of the black curassow, *Crax alector*, contributed to the patterning of the cluster 1. High densities of frugivorous birds (black curassow, grey-winged trumpeter, marail guan) and of large Cebids (spider and howler monkeys, capuchins), discriminate clusters 3 and 4 from clusters 1 and 2. Then, the mean values of each environmental variable were calculated, and visualized in the SOM map (Fig. 4). Clusters 1 and 2, as defined in Fig. 2, gather sites subjected to strong human disturbance: high hunting pressure, fragmentation, logging, and high accessibility level (Fig. 4). Cluster 3 is characterized by medium hunting pressure, and a medium level of fragmentation and accessibility. Finally, cluster 4 is free of most of disturbances, and hence identifies reference sites. In contrast, habitat structure (Fig. 4) does not show any relation with site patterning, suggesting that the abundance of focal species is not related to habitat structure.

By combining species abundances and potential threats on the SOM map we were able to rank species in accordance to their sensitivity of disturbances. The spider monkey and the black currassow for instance were restricted to areas free of human pressure (cluster 4; Figs. 2 and 4). In contrast, trumpeters, guans, howler monkeys and brown capuchins were found in sites ordinated in clusters 3 and 4 indicating that they withstand moderate hunting

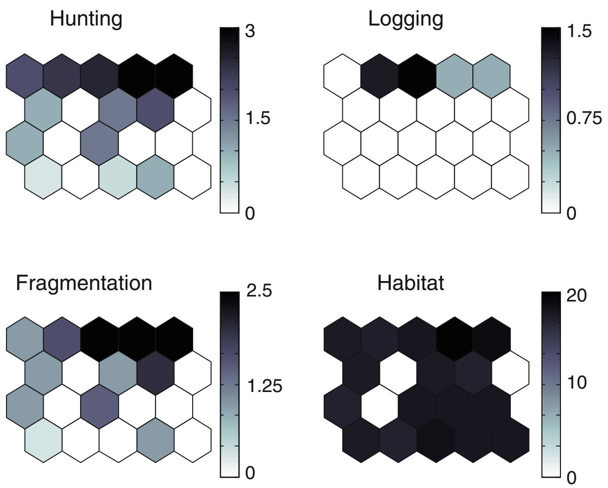


Fig. 4 Visualization of environmental disturbances (hunting; fragmentation, logging, accessibility) and habitat structure on the self-organizing map (SOM) trained with large vertebrate assemblages. *Dark* represents high values and *light* represents low values

pressure, and persist in areas with low to medium fragmentation and accessibility (Figs. 2 and 4). The abundance of ungulates was not segregated by the level of disturbances, a high variability being recorded both within and among site characterization classes. Lastly, some opportunistic species such as the tamarin or the great tinamou may benefit from the decrease of larger competitors in disturbed sites, and are thus found in highest densities in the sites clustered in groups 1 and 2.

Human footprint

The human footprint index calculated for French Guiana (Fig. 1) highlights the areas where disturbances and associated impacts on fauna are expected to be highest. Unambiguously, most potentially threatened areas are in the northern part of the country, which is the most populated and hence disturbed by roads, logging areas, hunting, and gold mining activities. The richness of animal communities was negatively correlated with the human footprint index (linear regression, $r^2 = 0.367$, $P = 0.001$ for all vertebrates (Fig. 5), and $r^2 = 0.482$, $P < 0.0001$ for monkeys only). Abundances of several indicator species were also negatively correlated to the index: the spider monkey (linear regression, $r^2 = 0.18$, $P = 0.01$); the brown capuchin ($r^2 = 0.289$, $P = 0.001$); the red howler monkey ($r^2 = 0.286$, $P = 0.001$); the marail guan ($r^2 = 0.149$, $P = 0.024$), the great tinamou ($r^2 = 0.244$, $P = 0.005$), the grey-winged trumpeter ($r^2 = 0.313$, $P = 0.001$) and the black currassow ($r^2 = 0.408$, $P < 0.0001$). Summed abundances of communities of (i) large monkeys, including capuchins, howlers and spider monkeys, and of (ii) frugivorous birds (currassows, trumpeters and marail guan), both known to have a key trophic role and hence expected to be efficient surrogates of ecological processes, are also negatively correlated to the index (Fig. 5, $r^2 = 0.49$, $P < 0.0001$ and $r^2 = 0.48$, $P < 0.0001$, respectively). In contrast, the abundance of tamarins is positively correlated to the index ($P = 0.008$). The abundances of the remaining species are not related to the index.

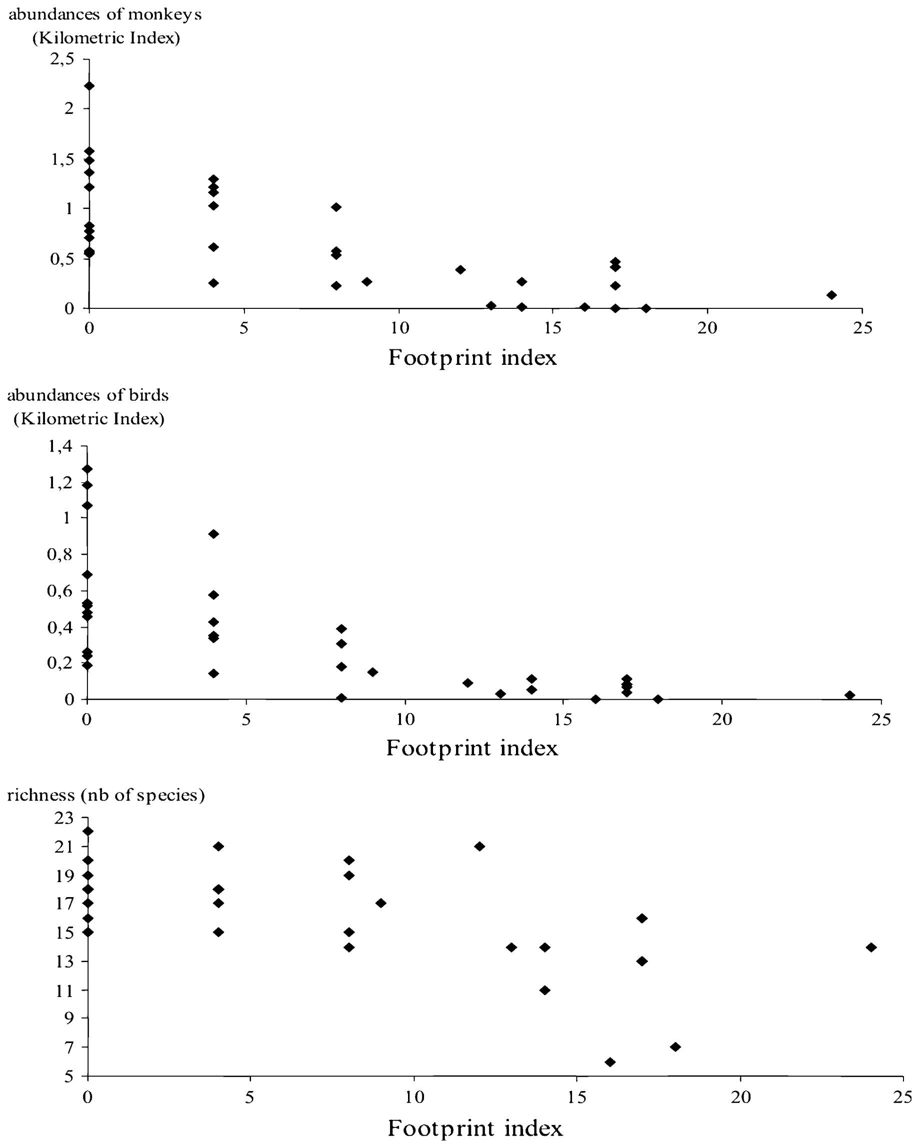
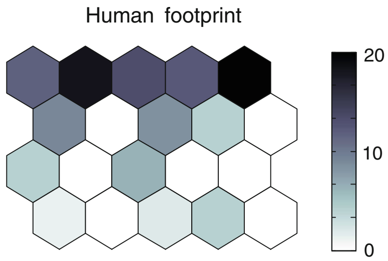


Fig. 5 Relationships between the footprint index and **a** abundance of large monkeys (capuchins, howlers and spider monkeys), **b** abundances of frugivorous birds (currassows, trumpeters and marail guan), **c** the richness of animal communities. Abundances are expressed with a kilometric index, i.e. number of records per km of transect (see de Thoisy et al. 2008 for further details)

Visualizing the footprint index on the SOM map (Fig. 6) showed that areas with high index values are mainly located in the clusters characterizing disturbed sites (clusters 1 and 2), although the lowest index values are located in clusters 3 and 4 indicating medium to low human disturbances. There is, however, no way to discriminate between clusters 3 and 4 using the footprint index.

Fig. 6 Visualization of the human footprint on the self-organizing map (SOM) trained with the large vertebrate assemblages. *Dark* represents high values and *light* represents low ones



Discussion

Identification of vertebrate assemblages in relation to human disturbances

The Guianas are covered by a unique continuous forest block in the Neotropics, with a low rate of habitat loss and fragmentation (FAO 2005). It also hosts high levels of endemism, estimated at 35% for vascular plants, 47% for amphibians, 27% for reptiles. The geographic distribution of this endemism has led to priorities being mapped and conservation strategies promoted (CI 2002). The area is also recognized as a major refuge for large vertebrate populations, such as the Jaguar, *Panthera onca* (Sanderson et al. 2002b), the Lowland tapir, *Tapirus terrestris*, the white-lipped peccary, *Tayassu pecari* (Taber et al. 2008) or the Giant otter, *Pteronura brasiliensis* (Groenendijk 1998). In addition to these flagship species, assessing the conservation status of more common and widespread species can efficiently complement ecosystem conservation strategies, as these species support most ecological processes (Pearman and Weber 2007). Such a community approach was achieved using SOM. Unlike most analytical tools, the SOM has the direct advantage of being able to deal with noisy quantitative data that are not linear- or normal-shaped (Bessa-Gomes and Petrucci-Fonseca 2003; Lek et al. 2005). Although we originally analysed our data using traditional multivariate methods (e.g. CCA, PCA, MDS) the results are not presented because they were less interpretable than those of the SOM; a conclusion similar to that of previous papers comparing SOM and traditional multivariate statistics (Blayo and Demartines 1991; Brosse et al. 2001; Giraudel and Lek 2001; Lee et al. 2006, Zhang et al. 2008).

Site ordination by the SOM on the basis of vertebrate species abundance was consistent with both field records (Table 1) and disturbance distribution throughout French Guiana (Fig. 4). This confirms that clusters 1 and 2 gather the most disturbed sites, whereas clusters 3 and 4 gather sites with no or low anthropic pressure (all undisturbed sites and three sites with low anthropic pressure). In addition, the strength of disturbances recorded in the field is known to be higher in cluster 2 sites than in cluster 1 sites, which suffer lower fragmentation and are more remote than in those of cluster 2. On the other hand, no contrast of pressures can explain the patterning of sites in cluster 3 versus those of cluster 4. These two clusters may have different natural habitats, but since a crude remote-sensing classification of habitats, based on canopy structure only (Gond et al. 2009) was the unique feature included, we are not able to provide a precise characterisation of the natural habitat potentially influencing the faunal community structure. Characterizing habitats and vegetation types more precisely would probably be a further step towards a better characterisation of the interactions between natural environment and the response of animal communities to human disturbances.

The prominent role of human disturbances, and particularly hunting pressure, in determining community richness and abundances of large species, including most monkeys, and frugivorous birds, is consistent with previous studies. Indeed, the impact of unmanaged hunting has been widely demonstrated on large bird species in the Neotropics (Silva and Strahl 1991; Begazo and Bodmer 1998; Ohl-Schacherer et al. 2007). Population declines and local extinctions of South American monkeys in relation to direct human exploitation have also been widely reported in Guyana (Lehman 2000), Venezuela (Urbani 2006), Peru and Bolivia (Freese et al. 1982), and lowland Amazonia (Lopes and Ferrari 2000; Haugaasen and Peres 2005; Peres and Palacios 2007). However, the main challenge related to fauna management and resource use remains the ability to distinguish between the effects of direct pressures (e.g., hunting) and indirect pressures (e.g. mining, logging, fragmentation). Indeed, the response of species to hunting may differ between and within species, with often a non-linearly between hunting pressure and species abundance (Hill et al. 2003; Milner et al. 2007). Those relationships are also complicated by temporal variations (Carillo et al. 2000), and by a potential variation in species detectability according to hunting pressure in non-remote areas, possibly influencing survey success (e.g., Johns 1985). Similarly, responses of a single species to different disturbances (e.g., hunting, logging, fragmentation) cumulated in a single place may not follow similar patterns (Peres and Lake 2003). These statistical problems are partly overcome by the ability of SOM to deal with noisy and non-linear data. It provides an opportunity to better identify the responses of fauna to different disturbance sources that are commonly linked in the field. For instance, spider monkeys and black currassows have high abundances as soon as no pressure is recorded at the survey sites (Fig. 3, high densities in the bottom left corner only, which is also the region of the map where the nil levels of all disturbances are recorded), although howlers, capuchins, guans and trumpeters are affected by hunting only, but not by fragmentation and logging (Fig. 3, high densities in all the bottom). For some species, SOM analysis revealed that declines are related much more closely to hunting than to logging per se. Most previous studies were unable to highlight such differences (de Thoisy et al. 2005) which have direct conservation implications (see below).

Human footprint summarizes both pressures and responses of species

The real-time identification of areas where biodiversity is threatened in response to most human disturbances should then be a valuable tool for management planning. The human footprint is a "global map of human influence" (Sanderson et al. 2002a). The main idea of the footprint score is not to identify biodiversity hotspot areas, but to highlight areas where the local biodiversity is expected to face disturbances, with either potential and already observed impacts on animal populations (Kareiva et al. 2007). Together with other strategies including demographic sustainability and sustainable use, ecological integrity as assessed by the footprint index may contribute to saving some animal populations (Sanderson et al. 2008). To reach this goal efficiently, two stages have to be completed. First, it should be verified that the index is a reliable surrogate to disturbances directly recorded in the field. The human footprint map of French Guiana resulting from the work of Sanderson et al. (2002a) (http://www.ciesin.columbia.edu/wildareas/), roughly identified the same threatened areas as we did. Our approach nevertheless used more detailed GIS layers, and provides a much better sensitivity of the geographic distribution of threats. The second step is then to measure how species responses to disturbances fit the footprint index. As shown in mountains in tropical Africa (Burgess et al. 2007) and in North America for carnivores and ungulates (Laliberte and Ripple 2004), both richness of animal communities and abundances of most of the target species show significant decline associated with high levels of statistical confidence as footprint indexes increase. Although the footprint index was not able to distinguish between low and no disturbance (Figs. 2 and 6), it clearly identifies highly disturbed areas and their associated animal communities. Further surveys in French Guiana in more heavily impacted areas (index c.a. 35) showed a total richness of 6 species (B. de Thoisy, obs. pers.), increasing the determination coefficient of the relationships between index and richness from 0.367 (see results) to 0.559.

As for the global approach of Sanderson et al. (2002) who used human population density, land transformation, access and electrical power infrastructures to score human influence, the footprint index we developed in this work was built with a priori pressures, and a priori scoring of the extent of the associated disturbances. The simplified GIS procedure used to define the human footprint index, which is highly dependent on the resolution of the GIS information, also allows rapid and efficient adaptation, as soon as further data are acquired on species' sensitivity to disturbances. Buffer areas around sources of disturbances and scores given to the different disturbances, according to their known impacts, may be easily modified, and adapted to targeted indicators. Large species, for example, may have benefited from higher scores given to hunting pressures (e.g., size of buffer along rivers and tracks). Moreover, continuous scoring rather than threshold values could help to increase the biological and consequently conservation value of the index. A further important topic is the balance between the score of a given point and the scores of the surrounding areas. Indeed the index in its current form accords little importance to population dynamics: source-sink systems (Pulliam 1988) were not considered which reduces the efficiency of the footprint at providing a long-term view of dynamics. This limited consideration for landscape continuity, with potentially negative conservation issues, has been pointed out in more heavily impacted regions (Levin et al. 2007). Also, the footprint gave similar scores to areas facing a similar level of pressure, but did not consider the temporal extent of the disturbance. Obviously, faunal community structure in areas experiencing high scores of human pressures for years, is different to those with a recent score increase (e.g., road opening). These differences become clear from the site ordination of surveys 10, 14 and 18 (cluster 1), that are opposed to 3, 6, 22, and 26 (cluster 2): sites in cluster 1 had a recent increase in human pressure and hence footprint index, while the sites in cluster 2 have been under pressure for decades. Despite these differences, all these sites share a similar footprint index (Fig. 6, darker cells above), but show distinct community patterns (see Fig. 2), confirming the need to consider the temporal extent of disturbances in the footprint index calculation.

Human footprint: A management tool for wild species and their associated ecological roles?

In countries with high levels of ecosystem remoteness but also recent economic development and/or demographic increase, methodological tools are urgently needed to guide sustainable land management considering both human needs and biodiversity conservation. Although extensive studies describe the impacts of human activities on large vertebrate communities (Haugaasen and Peres 2005), the responses of species to local disturbances are nevertheless rarely crossed with the requirements of land managers. Knowledge of species' ability to face disturbance is needed as a first step to guide forest management, but more proactive tools are also necessary. As the footprint index identifies the most threatened areas, but also the wildest habitats, there are direct implications for preservation, conservation and restoration planning of ecosystems (Noss 1983; Sanderson et al. 2002a) and species (Dinerstein et al. 2007; Sanderson et al. 2008). Excluding the 15% of coastal area that is no longer covered by forest habitat, Fig. 1 shows that 50% of the forest habitat has an index = 0, almost 20% has an index ranging from 1 to 10, 15% of the forest habitat has an index ranging from 11 to 20, and 15% has a score >20. Although both index and richness, and index and large species abundance correlations exhibit a significant negative linear trend, Fig. 6 suggests that in sites with a footprint index below 10, the animal communities remain close to values recorded in the most remote sites, providing both conservation and land management lessons. Ecological processes such as seed-dispersal (Russo et al. 2006; Stoner et al. 2007) are indeed expected to be maintained over 70% of the country. These processes are also maintained in areas facing low levels of disturbance, such as selective and low-impact logging that could be implemented with limited impact on fauna communities, as soon as other indirect impacts are mitigated. In contrast, a significant decrease of key seed-dispersal agents in the remaining 30% likely limit the extent of seed deposition patterns (Nuñez-Iturri and Howe 2007), resulting in lower levels of seedling recruitment (Peres and van Roosmalen 2002) and consequently altering forest dynamics. The identification of potential ecological breaks and/or corridors, refuges, source-sink systems may help forest management, forecasting and hopefully mitigating the forthcoming impacts of planned activities such as logging and road building.

The human footprint index also identifies areas where conservation costs will be higher, due to the strength of existing pressure. Areas with limited scores could be easily restored, as soon as the extent of threats is controlled, with limited costs. In contrast, restoration of high-scoring areas will require both time and money, since most ecological flows are expected to be disrupted following depletion of key species. For such purposes, the importance of considering the entire region of interest has to be underlined. For instance, the areas in white in Fig. 1 in the north-west of the country may only have a limited effect and poor long-term efficiency in maintaining biodiversity and ecological processes, if connections with the green blocks in the south are not restored.

Implementation of biodiversity conservation plans may also face socioeconomic constraints, compounding difficulties. For instance, despite their biogeographic unity, Guyana, Suriname, French Guiana and the Brazilian Amapa face extremely different policy contexts and extremely divergent opportunities to investigate and monitor wildlife, leading to considerable discrepancies in the ability of countries to implement monitoring and to provide reliable data to mangers and/or politics for land settlement (CI 2002). As soon as its limits are well understood, and once the relationships between certain target species and scores validated in the areas of interest, the use of the footprint index should enable relevant conservation priorities to be established. Previous studies have pointed out the importance of real-time pressure and biodiversity data to get reliable mapping on a fine scale (Burgess et al. 2007). To fill the gap in these limiting factors, the use of complementary tools may be useful. Remote sensing may help to fill geographical gaps, as recently done with success to locate illegal and unrecorded mining camps in the Guianas (Hammond et al. 2007). Both human footprint and efficient surrogate species may be useful tools to handle this challenging dilemma for policymakers and conservationists: maintenance of ecological processes and biodiversity conservation across a gradient of human influences (Miller and Hobbs 2002).

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