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## Human impact gradient on mammalian biodiversity

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## ABSTRACT

Drastic changes have been caused by human influence in natural landscapes, which may exert an intensive effect on species loss. However, species loss from human pressure is not random but depends on a series of environmentally associated factors. Linking species traits to environmental attributes may allow us to detect the ecological impacts of habitat so that meaningful habitat degradation gradients can be identified. The relationships between environmental factors and species traits provide the basis for identifying those biological traits that make species more sensitive to disturbance. These relationships are also helpful to detect the geographic distribution of latent risk to reveal areas where biodiversity is threatened. Here, we identify a “Human Impact Gradient for Biodiversity (HIGB)” based on a three-table ordination method (RLQ analysis) and fourth-corner analysis to identify key species traits that are associated with environmental gradient. Species distribution and environmental geographic data were gathered nationwide to analyze 68 localities, which represent 27% of Mexico's surface, including 211 species of mammals. Nine environmental variables (including biophysical, geophysical and land-use impacts) were analyzed by using the Geographic Information System. Three types of species' traits were evaluated: locomotion, trophic habit and body size. We identified a human impact gradient, which was mainly determined by the percentage of the area that was covered by seedlings, the plant richness, the understory coverage percentage and the human settlement index. The most important species traits that are associated with non-human-impacted sites were carnivores, frugivores–herbivores and a body size that was greater than 17.8 kg; 25 species were selected by the decision criteria framework for species that were sensitive to degradation based on ecological function information. Conversely, granivores, fossorial and semifossorial traits were associated with highly impacted sites. The environmental attributes were mapped to highlight the spatial patterns of human risk for species. Finally, we highlighted the need to apply science-based monitoring to future research based on the decision criteria framework for selecting species that are sensitive to degradation.

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## 1. Introduction

Species evolve ecological traits when adapting to natural conditions. Biotic or abiotic forces act as environmental filters to constrain certain traits within their limits ([Woodward and Diament, 1991](#), [Keddy, 1992](#)). However, current human activities

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alter some of these conditions through land transformation, and some traits may be “filtered out”, whereas other traits may appear in the resulting communities. Therefore, changing conditions may filter traits when species re-assemble a community after a human impact (Towsend and Hildrew, 1994; Díaz et al., 1998).

Analyzing human impacts on biodiversity has been mostly performed at the species diversity level (e.g., according to the intermediate disturbance hypothesis on diversity, which states that local species diversity is maximized at an intermediate level of disturbance; see Grime, 1973; Connell, 1978; Huston, 1979; Wilkinson, 1999). However, this approach does not consider functional changes that alter ecosystems' integrity or provide opportunities to link the functional attributes of biological diversity and environmental change (Hausner et al., 2003). Currently, species functional traits have gained greater relevance (i.e., components of an organism's phenotype that influence ecosystem-level processes; see Hillebrand and Matthiessen, 2009) because they can link species diversity to ecosystem functioning (Díaz and Cabido, 2001; Lavorel and Garnier, 2002; Naeem et al., 2009; Luck et al., 2012). Therefore, knowledge regarding the linkages between species traits and environmental attributes is more essential than species richness to predict the responses of species groups (i.e., assemblages) to human impacts because several functions in ecosystems can be associated with particular traits (Sekercioğlu et al., 2004). For example, many of the functional roles that are played by carnivores in ecosystems depend on traits that are associated with their trophic group habits (Duffy, 2002; Casula et al., 2006; Farias and Jaksic, 2009, 2011).

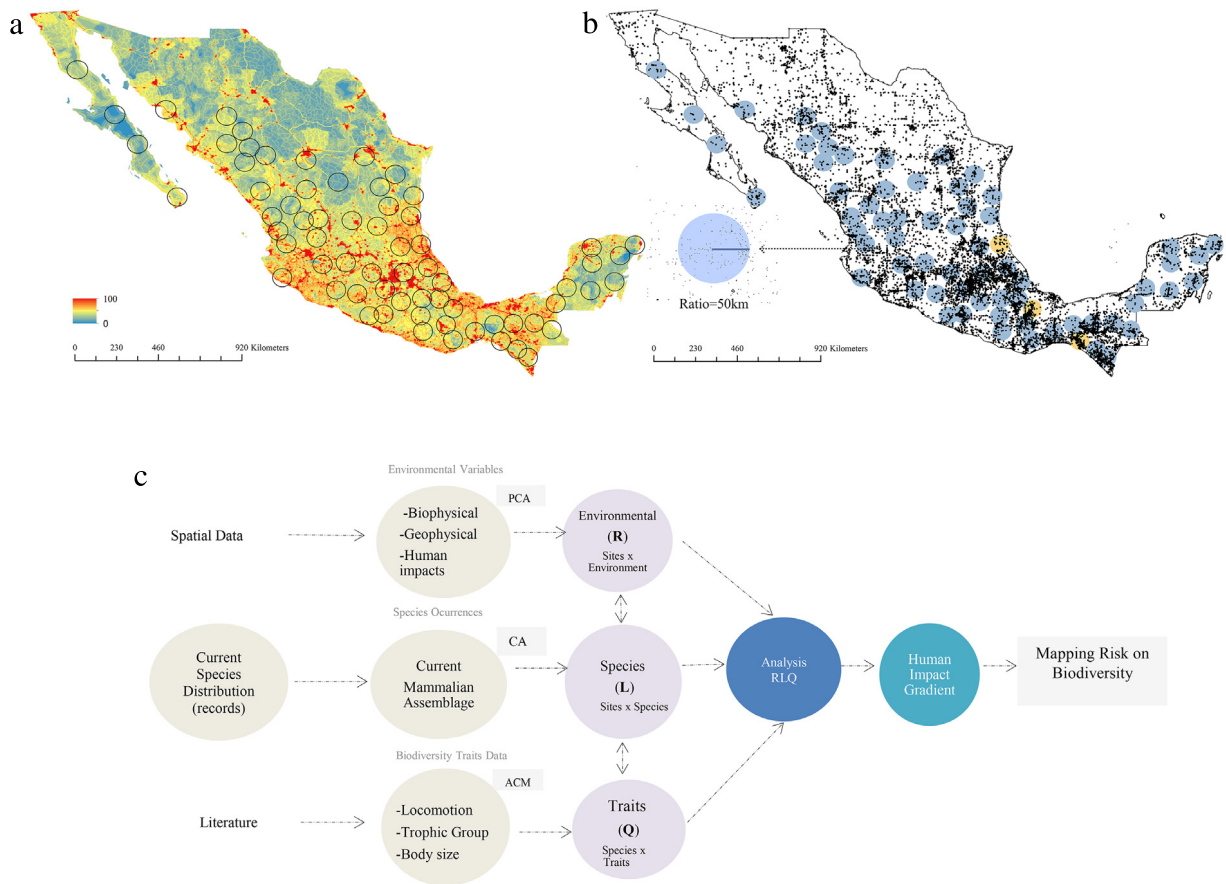
Biodiversity is subject to natural spatial variations in environmental natural conditions and impacts from human activities (e.g., roads and human settlements; Tilman et al., 1997; Chapin et al., 2000; Bellemare et al., 2002). Thus, complex interactions between species traits and the environment emerge from the regular environmental variations to which organisms are more or less adapted and to episodic and catastrophic disturbances, which lead to extensive mortality and local species extinction (Cooper-Ellis et al., 1999; Lugo, 2008). Unfortunately, human impacts are usually intense and permanent, without any opportunity for recovery (Connell, 1978). The current and rapid conversion of land is considered a key factor in global environmental change and a major biodiversity threat (Dale et al., 2001; Schmidt et al., 2001). Currently, we are losing biodiversity at unprecedented rates (Levin, 2005; Steffen et al., 2011; Barnosky et al., 2011). Given that numerous species are exposed to these changes, predicting the effects on biodiversity is almost impossible. In addition, the extinction of ecological functions may frequently precede the complete disappearance of species (Redford, 1992; Janzen, 2001; Wilkie et al., 2011; Galetti et al., 2013; Säterberg et al., 2013), that is, when a species' abundance is so reduced as to represent its functional extinction. Then, biodiversity attributes like traits are important because biodiversity loss has been largely assessed at the species level, apparently without success, given the high current extinction rates (Barnosky et al., 2011). Because traits are associated with many functional aspects of an ecosystem that closely depend on biotic interactions (e.g., frugivores represent a key function such as seed dispersal, nectarivores represent pollination, and carnivores represent predator–prey interactions), they are a major but often neglected component of biodiversity that must be considered to define critical indicators (Gámez-Virués et al., 2015) and provide an early diagnosis of environmental problems (Tylianakis et al., 2010; Aizen et al., 2012; Dirzo et al., 2014; Valiente-Banuet et al., 2015).

In this manner, species loss from assemblages under human pressure is not random but depends on the traits of organisms (Duffy, 2003). We can predict the consequences that are associated with ecosystem functions (Sekercioğlu et al., 2004) that are good indicators of the integrity of the ecosystem (Stotz et al., 1996) by detecting which species traits are more sensitive. A human impact gradient on biodiversity (HIGB) would include variables that describe abiotic and biotic factors in which different species and traits interact and could not only identify a particular HIGB but also would help identify biological traits that make species particularly sensitive to disturbances and provide environmental indicators. In general, we expect that an HIGB would be driven by different environmental attributes, particularly those with high values, which are associated with more transformed habitats (such as countryside areas near major cities and metropolitan villages), and would impact remote rural villages or more isolated areas less (e.g., mountains or low-human-accessibility regions), where traits in species assemblages show differential associations with different types of human impacts (Antrop, 2004).

This study involves mammal species that represent various taxa and life histories and could be considered for national conservation diagnosis and monitoring. We analyze functional traits through the environmental gradient to detect factors that are more vulnerable and detect unknown correlations among mammals that have not yet been assessed in conservation national strategies. Here, we identified (1) an HIGB for mammals and their major ecological impacts because of human influence at the national scale, (2) the biological traits that make these mammals particularly sensitive to disturbance, (3) a decision criteria framework to identify potential indicators of ecological integrity with a particular emphasis on traits and species levels, and (4) a map of the geographic distribution of current risk areas where mammal fauna are highly threatened by human impacts in Mexico.

## 2. Materials and methods

To evaluate how traits and single species respond to an environmental gradient of human impact, RLQ analysis was applied (Kleyer et al., 2012) to obtain an HIGB, which integrates three main factors: the current species distribution (L), the species biological traits (Q) and environmental variables, which include human impacts (R) (Fig. 1). The R component is the baseline for the environmental gradient impact, which was evaluated throughout spatial information. Then, several traits can be associated with those variables that form the environmental gradient. For this analysis, the current biodiversity data distribution of mammals and information on the literature of species traits was used.



**Fig. 1.** Sampling and method (a) distribution of 68 localities along the human footprint in Mexico (Sanderson et al., 2002); (b) systematic sampling scheme of the mammal assemblages with mammalian records in a locality in Mexico (1970–2005), localities with high completeness are marked in blue (100%) and beige (>80%); and (c) the general method. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

## 2.1. Current species distribution data (L)

We used 85 087 geographic records for terrestrial (volant and non-volant) mammal species with geographic validation from the “Sistema Nacional de Información sobre la Biodiversidad” of the “Comisión Nacional para Uso y Conservación de la Biodiversidad” in Mexico (CONABIO, 2012). We retained localities from 1970 to 2005 to ensure that the mammal records represent the most probable current distribution that is associated with land transformation and human impact trends because the Government of Mexico’s data show that forest and woodland cover have decreased since the 1970s at a rate of 747 000 ha or 1.36% per year (FAO 2005).

Species record data represent a proxy of the current distribution of mammal assemblages. However, selecting an adequate spatial scale for the sampling is crucial to properly represent the mammal assemblages on plots because regional areas contain more knowledge than local areas (Colín et al., 2006; Soberón et al., 2007; Meyer et al., 2015), but local areas would generalize the environmental information less. We detect the scale with the best chance to obtain localities with high completeness and representativeness in Mexico. We sampled species records by assigning the “presence” of species for each locality with the neighboring spatial analysis procedure, which is available in the Spatial Analysis tool (Proximity-Point distance, ESRI, 2014), by using spatial circle buffers with a radius of 50 km (Fig. 1(b)). In total, we obtained 2761 localities according to the National Forest Inventory of Mexico (Comisión Nacional Forestal, 2009).

To select only well-sampled localities for the 2761 localities by using 85 087 records of terrestrial mammals, we calculated species-accumulation curves (Estimates, 9.1.0) to estimating species richness through a method that is based on estimating the proportion of assemblage richness, which is represented by a set of replicated incidence samples (ICE; Chao et al., 2005). From observed and estimated richness of 925 localities we identify those with high completeness (>80%), of which we excluded those with more than 5% of their buffer areas overlapping among localities, by using independent species data, we also exclude sites with less than 5 species.

**Table 1**  
Species traits in the RLQ analysis. The parenthesis is the percentage of species.

	Traits	Code	Species number
Trophic	Myrmecophage	M	1(0.47) <sup>a</sup>
	Carnivore	C	4(1.89)
	Granivore	G	50(23.6)
	Insectivore Aereal	IA	44(20.8)
	Ground insect eater	IS	15(7.1)
	Omnivore insect eater	IO	21(9.9)
	Sanguinivore	S	2(0.9)
	Frugivore–Granivore	FrG	13(6.1)
	Frugivore	Fr	17(8)
	Frugivore–Omnivore	FrO	15(7.1)
	Frugivore–Herbivore	FrH	7(3.3)
	Herbivore–Grazer	HP	10(4.7)
	Nectarivore	N	8(3.8)
	Carnivore–Omnivore	CO	3(1.4)
	Herbivore–Browser	HR	2(0.9)
	Terrestrial	T	58(27.4)
	Locomotion	Fossorial	F
Semifossorial		SF	37(17.5)
Semiaquatic		SQ	6(2.8)
Volant		V	79(37.3)
Arboreal		A	9(4.3)
Semiarboreal		SC	17(8.5)
> 17.78		L	5(2.4)
Body mass	17.78–1.78 kg	B	18(8.5)
	1.78–0.17 kg	M	25(11.8)
	0.17–0.02 kg	SM	85(40.1)
	0.02–0.002 kg	S	78(36.8)

<sup>a</sup> This trait was not used in the statistical analyses.

## 2.2. Species trait information (Q)

Three main types of traits were analyzed. These traits were associated with trophic habit classification (16 groups), locomotion (7 groups), and body mass (5 groups) (Arita and Rodríguez, 2004; Table 1 and Table A.4). The body mass was log-10-transformed (Table A.2) to fit data into 5 classes following Smith et al. (2004). Trait information for each species was obtained from the scientific literature (Fleming, 1973; Eisenberg, 1989; Robinson and Redford, 1973; Chapman and Feldhamer, 1982; Nowak, 1991; Choate and Fleharty, 1974; Armstrong and Jones, 1972; Baker and Greer, 1962; Owen and Hoffman, 1983; Arita and Medellín, 1985; Gardener, 1977).

## 2.3. Environmental data (R)

Environmental spatial data sources include three geophysical variables (slope (Slp), aspect (As) and terrain elevation (Te)), which were derived from the 50-m resolution ASTERGDEM (Advanced Spaceborne Thermal Emission and Reflection Radiometer, 2011). Five biophysical attributes of the remnant habitats represent the natural regeneration of forest, which is measured as the percentage of the area that is covered by seedlings (See), and the structural complexity, i.e., tree richness (Plr), understory coverage percentage (Ucp) and herb percentage (Hper). Biophysical variables were obtained from the National Forest Inventory for sample units (Comisión Nacional Forestal, 2009). The habitat connectivity (Hc) was derived from a connectivity analysis of natural areas and remnant forest (resolution of 250 m), which was derived from the application of remote sensing techniques based on a map of the North American Land Cover (CEC, 2005).

Furthermore, we used four variables of human impacts that are associated with land transformation and human accessibility (Table 2). The human settlement index (Hsi), which was derived from satellite maps of stable night lights, provides an additional source of information on the spatial extent of human development (NOAA/NESDIS/NCEI, 2011). Human accessibility and remoteness were obtained by calculating the distance to natural features. The human settlement distance (Had), which was obtained from population center maps (INEGI, 2010) and road distances from main roads (IMT, 2001), was created in raster layers at 1 ha resolution. The forest damage index (Fdi) was calculated from observations of the following variables: shepherding, mining, tree pests, electric lines, fire, land cover change, human settlements, forestry management and roads, which were obtained from INF-CONAFOR (Comisión Nacional Forestal, 2009). Variables of the Fdi were weighted by their recorded categorical degree: non-perceptible, minor, median and high. This particular index can adequately represent the human footprint, in which land transformation, accessibility, electrical power infrastructure and population density are incorporated into an anthropic damage measure (Sanderson et al., 2002). These recent spatial sources (2004–2011) were integrated into a Geographic Information System (ESRI, 2014) to build a cartographic model to establish a set of environmental variables that are currently associated with human influence at 1 ha resolution (R).

**Table 2**

Environmental variables in Mexico. Environmental variables that were not significant to any trait in the fourth-corner analysis were not used in the final statistical analyses.

Type	Environmental variable	Id	Measure description	Units	Range of localities (range in Mexico)	Year	Source
Geophysical	Slope	Slp	Measure of change in elevation, from 50-m resolution.	Degrees	1.77–39.18(0–134)	2011	ASTERGDEM (Advanced Spaceborne Thermal Emission and Reflection Radiometer, 2011)
	Aspect <sup>a</sup>	As	Direction that the slope faces, from 50-m resolution.	Degrees	143.5–237.5(0–359)	2011	ASTERGDEM (Advanced Spaceborne Thermal Emission and Reflection Radiometer, 2011)
	Terrain elevation	Te	Height above sea level, from 50-m resolution.	Meters	16.33–3975(0–3975)	2011	ASTERGDEM (Advanced Spaceborne Thermal Emission and Reflection Radiometer, 2011)
Biophysical	Natural regeneration of forests	See	Percentage of area covered by seedlings	Percentage	0–41.14(0–70)	2004–2009	National Forest Inventory (Comisión Nacional Forestal, 2009)
	Tree richness	Plr	Number of tree species	Number of species	0–25(0–49)	2004–2009	National Forest Inventory (Comisión Nacional Forestal, 2009)
	Understory coverage	Ucp	Understory coverage percentage	Percentage	0–30.9(0–52)	2004–2009	National Forest Inventory (Comisión Nacional Forestal, 2009)
	Herb coverage <sup>a</sup>	Hper	Herb percentage	Percentage	0–29.9(0–71)	2004–2009	National Forest Inventory (Comisión Nacional Forestal, 2009)
	Habitat connectivity	Hc	Connectivity analysis of natural areas and remnant forest (resolution of 250 m)	Percentage	0.5–1(0–1)	2005	Remote sensing techniques based on a map of the North American Land Cover (CEC, 2005)
Human impact	Human settlement index	Hsi	DMSP-OLS night light data	Index units	0.15–0.6(0.1–1.79)	2011	NOAA/NESDIS/NCEI
	Human settlement distance	Had	A measure of natural sites to populations	Meters	9614.02–119 876.1(0–138 924)	2010	Instituto Nacional de Estadística y Geografía, 2010
	Road distance <sup>a</sup>	Rd	Accessibility measure	Meters	1036.9–16 116.1(0–37 901)	2001	Instituto Mexicano del Transporte 2001
	Forest damage index	Fdi	These variables include shepherding, mining, plagues, electric lines, fire, land cover change, human settlements, forestry management and roads, weighted by their categorical degree recorded: non-perceptible, minor, median and high	Index units	0–0.15(0–0.33)	2009	National Forest Inventory (Comisión Nacional Forestal, 2009)

<sup>a</sup> These variables were not used in the statistical analyses.



Due to the size of each plot (7853.98 km<sup>2</sup>) and the different resolution on environmental variables, the average of all them for each locality was calculated. Furthermore, we explored the environmental gradient representation on all 68 localities (plots) through the frequency values along the localities (Fig. A.1) and by comparing differences between the maximum and minimum environmental values in the analyzed localities and for Mexico (Table 2). Additionally, we showed the geographical representativeness of the sampling method for the human footprint in the country (Sanderson et al., 2002) with a representation of several human activities that were recorded at the satellite scale (Fig. 1(a)). Each environmental variable has different units, so the variables were standardized before the ordination analysis was performed by subtracting its mean from that variable and dividing it by its standard deviation to achieve equal weight in the analysis.

Although the temporal scope of biophysical data (2004–2009) and spatial human impacts data (2009–2011) do not coincide with species data (1970–2005), we assume that the later remained stable in non-impacted sites. In addition, it is well known that the local extinction of species can occur long after habitat loss or degradation (i.e. species do not disappear immediately). Thus, the most reliable information corresponds to pristine areas and their species.

#### 2.4. Human impact gradient on biodiversity

The human impact gradient on biodiversity (HIGB) is produced through a co-inertia analysis of the interaction between traits and the environment. This approach is symmetrical, which allows the use of various methods to model the structure in each environmental data set, including the R-environment, information of species distribution (L-species), and species traits (Q-traits) (Dolédec and Chessel, 1994; Dolédec et al., 1996; Dray et al., 2002). RLQ analysis computes the covariance matrix with the sum of squared covariance, which results from the total co-inertia. Three separate ordinations of the R, L and Q data sets were performed. The first step was determining the presence of species. The point locations (i.e., geographic sample units) (L) were analyzed by a correspondence analysis (CA). The point locations and taxon scores were used to link the R and Q data sets as point locations that were shared by R and L, and species were shared by Q and L. In total, 68 locations and 212 species were included in this analysis. The second step was to investigate the relationship between locations and 12 environmental variables (R).

A principal component analysis (PCA) was used to detect patterns of the variations in environmental quantitative data by using weights from the result of the CA, thereby linking R to the L matrix. Then, co-inertia analysis explored the covariance between the PCA and CA (Culhane et al., 2003), i.e., between the L and R tables. Finally, we applied a multiple correspondence analysis (ACM) in the Q table of species and qualitative data on traits, weighting rows (species) by a CA analysis of the L matrix (Fig. 1(c)). The RLQ analysis then combined these three separate analyses and maximized the covariation between the environmental variables and taxonomic traits. The locations scores in the R table constrained the sample unit scores and taxon scores in the L table. Considering these constraints, a co-inertia analysis selected axes that maximized the covariance between the R and Q tables. The environmental variables were related to the functional traits. The significance of the relationship between R and the functional traits Q was investigated with a Monte Carlo test (999 permutations). The null hypothesis was independent between the R and Q tables, and the alternative hypothesis was that they were related (Dolédec et al., 1996). All of the analyses were performed by using the ade4 software package within the R statistical package 3.1.0 (R Development Core Team, 2014).

To test the relationships between traits and environmental variables, we performed a fourth-corner analysis (Kleyer et al., 2012) through the link that is provided by the presence of taxa (Dray and Legendre, 2008). While RLQ provides the ordination score, the fourth-corner method mainly tests individual traits and their environmental relationship; both methods are complementary (Dray et al., 2014). This analysis allows statistical tests of the significance of links between all combinations of functional traits and environmental variables in a correlation type analysis. The analysis relates the R table of environmental variables to the Q table of functional traits by way of the L table of taxon occurrences. Five different ecological hypotheses that were tested by permutations were described by Dray and Legendre (2008). These authors recommended a combination of permutation tests to reduce type I errors. We used their model 2 to test the null hypothesis that the taxon and environmental variables were unrelated. Then, we tested model 4, which states the null hypothesis that taxon abundance and traits are unrelated. If both permutation tests were significant, we could reject the null hypothesis that the functional traits were unrelated to the environmental characteristics.

#### 2.5. Mapping the risk index from the human impact gradient on biodiversity

We established a risk index for biodiversity (RIB) with all human impact variables that were included for the analyses. The variables were weighted by using the ordination scores as defined by the HGIB by the first axis of the RLQ analysis. We summed all 3 variables (Table 2) within a spatial analysis system (ESRI, 2014), and reclassify from 1 ha to obtain a map at a 1 km × 1 km resolution. We use natural break methods to obtain 10 classes, resulting in values between 1 and 10.

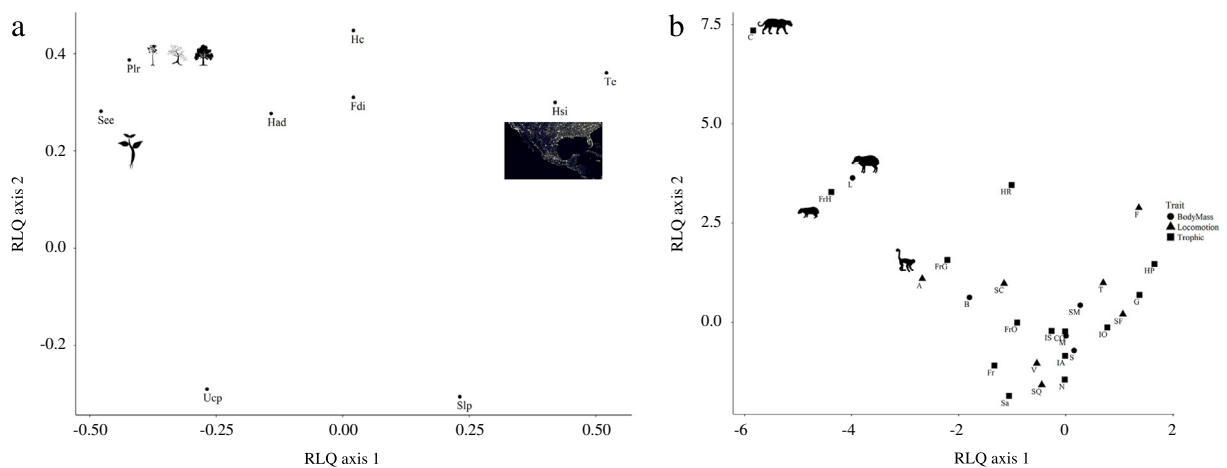
### 3. Results

We used a final data set of 68 localities that comprised 211 mammal species with completeness above 80% within the country. The mean observed taxon richness was 10.5 and the estimated value was 10.6, with a minimum richness of 5

**Table 3**

Results of multivariate analyses. (a) Separate analysis, eigenvalues and percentages of the total inertia for axes 1 and 2. Ordinations included a principal component analysis (PCA) of table R (environmental variables), a correspondence analysis (CA) of table L (taxon composition), and a multivariate correspondence analysis (ACM) of table Q (functional traits). (b) Summary of the RLQ analysis that shows the eigenvalues and percentages of the total co-inertia from RLQ axes 1 and 2; the covariance and correlation between the sample scores, which are constrained by the environmental variables in R, and the species scores, which are constrained by the traits in Q; the projected inertia of the R, L and Q tables on the first 2 RLQ axes; and the percentage of the inertia from separate analyses of the R and Q tables along the same axes (Table 3).

a.	Variance axis 1	Variance axis 2
R/PCA	3.15 (35%)	2.26 (25.2%)
L/CA	0.80 (4.5%)	0.76 (4.2%)
Q/ACM	0.82 (10.7%)	0.65 (8.40%)
b.	RLQ axis 1	RLQ axis 2
Eigenvalue	0.38 (71.8%)	0.09 (18%)
Covariance	0.6	0.3
Correlation	0.5	0.3
R/RLQ	2.9 (90.7%)	4.42 (81.7%)
L/RLQ	0.48 (54.5%)	0.30 (35.1%)
Q/RLQ	0.55 (67.3%)	1.19 (81.6%)



**Fig. 2.** First and second components in the RLQ analysis, where RLQ axis 1 shows the human impact gradient for mammals with (a) environmental variables and (b) traits. See Tables 1 and 2 for code identifications.

and maximum of 29 species (Table A.1). Only 3 (4.4%) localities showed completeness below 100% and above 80%, while the others showed 100% completeness (Fig. 1(b)). The most dominant trait groups are Granivores (23.6%) and Insectivore Arboreal (20.8%) in the trophic group; Volants (37.3%) in the locomotion group; and mammals that were less than 20 g (76.9%) in the body size group (Table 1). Although myrmecophages, sanguinivores, carnivores–omnivores and herbivores–browsers appeared for three or less species, all these traits showed a good representation at the sites (10 sites or more) except for myrmecophages, which were excluded from the statistical analyses because they were only present in three sites (Table A.3).

The Monte Carlo permutation test indicated a significant association between environmental variables and functional traits ( $p < 0.001$ ). First, two RLQ axes explained 89.9% of the variance in the analysis. The eigenvalue of the first axis of the RLQ analysis was 0.38, which explained 71.8% of the total variance in the data set (Fig. 2). Negative scores in the structure of the first main gradient seemed to be associated with non-human impacts (i.e., high ecological integrity). The ecological traits that were characteristic of these areas were highly correlated with See (eigenvector =  $-0.48$ ), Plr (eigenvector =  $-0.42$ ) and Ucp (eigenvector =  $-0.27$ ). The traits that were associated with these conditions were carnivores (eigenvector =  $-5.84.0$ ), frugivores–herbivores (eigenvector =  $-4.38$ ), large mammals above 17.8 kg (eigenvector =  $-3.44$ ) and arboreal (eigenvector =  $-2.68$ ) for the first axis of ordination (Fig. 2(b)). Proportions of the variance that were attributed to each table were compared to those from their separate analyses (Table 3). The first axis of the RLQ (with a covariance of 0.61 and correlation of 0.49) accounted for 90.7% of the variance in the separate analyses of R, 54.5% in the separate analyses of L and 67.32% in the separate analyses of Q (Table 3). Similarly, the second RLQ axis accounted for 81.7%, 35.15% and 81.63%, respectively.

**Table 4**

Species and traits from non-impact sites in Mexico in the HIGB. The numbers in parenthesis indicate the first (1) and second (2) percentiles in trait ordination (RLQ Axis 1). All of the species belong to the first percentile (RLQ Axis 1). Trophic habit traits: Carnivores (C), Frugivores–Herbivores (FH), and Frugivores–Granivores (FrG); Locomotion traits: Arboreal (A); and Body mass: > 1.78 kg (B) and above > 17.8 kg (L). The 24 species represent 11.4% of all the mammal species that were analyzed in Mexico.

Species	Body mass		Trophic group		Locomotion		Number of more sensitive traits by species
	L(1 <sup>b</sup> )	B(2 <sup>b</sup> )	C(1 <sup>b</sup> )	FrG(2 <sup>b</sup> )	FrH(1 <sup>b</sup> )	A(2 <sup>a</sup> )	
<i>Agouti paca</i>				×			1
<i>Alouatta pigra</i>					×	×	2
<i>Ateles geoffroyi</i>					×	×	2
<i>Bassariscus sumichrasti</i>						×	1
<i>Coendou mexicanus</i>					×	×	2
<i>Dasyprocta punctata</i>				×			1
<i>Didelphis marsupialis</i>		×					1
<i>Didelphis virginiana</i>		×					1
<i>Herpailurus yagouaroundi</i>			×				1
<i>Heteromys desmarestianus</i>				×			1
<i>Heteromys gaumeri</i>				×			1
<i>Leopardus pardalis</i>			×				1
<i>Mazama americana</i>	×				×		2
<i>Nasua narica</i>		×					1
<i>Odocoileus virginianus</i>	×						1
<i>Otonyctomys hattii</i>				×		×	2
<i>Ototylomys phyllotis</i>					×		1
<i>Pecari tajacu</i>	×				×		2
<i>Potos flavus</i>						×	1
<i>Puma concolor</i>	×		×				2
<i>Sciurus alleni</i>				×			1
<i>Sciurus aureogaster</i>				×			1
<i>Sciurus deppei</i>				×			1
<i>Sciurus yucatanensis</i>				×			1
<i>Tayassu pecari</i>	×				×		2

<sup>a</sup> Traits significant with See in fourth-corner analyses.

<sup>b</sup> Traits significant with See and Plr in fourth-corner analyses.

We compared the taxonomic and functional approaches by using statistics from the CA and ACM. The taxa had low relative variance that was explained by the 1st CA axis (4.5%), while the functional traits had high relative variance that was explained by the 1st ACM axis (10.7%) (Table 3). This structure reflected a gradient in the traits' distributions along the 1st axis of the RLQ from human impact-sensitive (Table 4) to human impact-tolerant traits (Fig. 2). When the 1st and 2nd CA and ACM axes were compared, the functional approach had greater variability than the taxonomic approach. The relative variances of the first two ACM and CA axes were 19.1% and 8.7%, respectively (Table 3). Therefore, functional traits should be more appropriate for biomonitoring than taxon presence in the form of a 2-dimensional diagram. The relationship between functional traits and taxonomic grouping (Fig. A.3) could be determined by the left part of the ordination (negative) in the first axis for both variables (Table 4). Additionally, sensitive taxa in the left part (first and second percentile, Fig. 2) of the ordination mainly consisted of large predators (e.g., *Puma concolor*), FrH and FrG habits, and A locomotion. Indeed, some taxa showed more than one of those traits (Table 4). For example, *Alouatta pigra*, *Ateles geoffroyi* and *Coendou mexicanus* showed both A and FrH habits.

Our approach showed that the traits were correlated and distributed according to environmental filters that were associated with an impact gradient (Fig. 2). We detected the best combination of environmental variables (Fig. 2(a)) that were associated with the impact gradient, in addition to those traits that were related to this gradient (Fig. 2(b)). The first component showed (according to the eigenvectors) that a main environmental variable determined positive gradient scores, which are interpreted here as high human-impact values. These values are the Hsi (eigenvector = 0.42). These values were mainly associated with two trophic groups, namely, HP (eigenvector = 1.65) and G (eigenvector = 1.37), and two locomotion groups, namely, F (eigenvector = 1.36) and SF (eigenvector = 1.07). The second component showed another way in which Hc (eigenvector = 0.44) interacts with the Plr to determine an independent factor (orthogonal), which occurs mainly in highland regions (Te eigenvector = 0.36), and is also correlated with the Fdi and the Hsi (Fdi eigenvector = 0.31, Hsi eigenvector = 0.30). In contrast, Slp (eigenvector = -0.31) and Ucp (eigenvector = -0.29) were in the negative ordination (Fig. 2(a)).

The fourth-corner analysis extracted 49 significant relationships between the 11 environmental variables and the 26 trait categories at  $\alpha = 0.05$  (Table 5). The environmental variables that were most significantly related to the trait structure included See (with 10 significant relationships), Plr (9), Te (9) and His (6). Conversely, Hc (1), Fdi (2), and Slp (3) were less significantly related to the trait structures of mammals. Inversely, the traits that were most significantly related to the environmental variables were the G trophic group and SF locomotion (with 5 significant relationships among 49



**Table 5**

Results of fourth-corner analysis that was performed with taxa, functional traits, and environmental variables in Mexico. Blank cells means a non significant ( $p > 0.05$ ) relationship, minus sign means a negatively significant relationship ( $p < 0.05$ ), and plus sign means a positively significant relationship ( $p < 0.05$ ). See the traits and environmental codes in Tables 1 and 2.

Traits groups		Environmental variables								
		See	Ucp	Hc	Plr	Slp	Te	Hsi	Had	Fdi
Locomotion	A	+								
	F									+
	SC	+			+	–			+	
	SF	–	–		–		+	+		
	SQ									
	T						+	+		
Throphic	V		+				–	–		
	C	+			+				+	
	CO									
	Fr	+		–			–	–		
	FrG	+			+		–		+	
	FrH	+			+	–	–			
	FrO									
	G	–	–		–		+	+		
	HP						+			
	HR									
	IA									
	IO									
	IS									
	N									
	S									
Body mass	B	+			+		–	–		
	L	+	+		+	–				
	M									
	S				–				–	
	SM		–							+

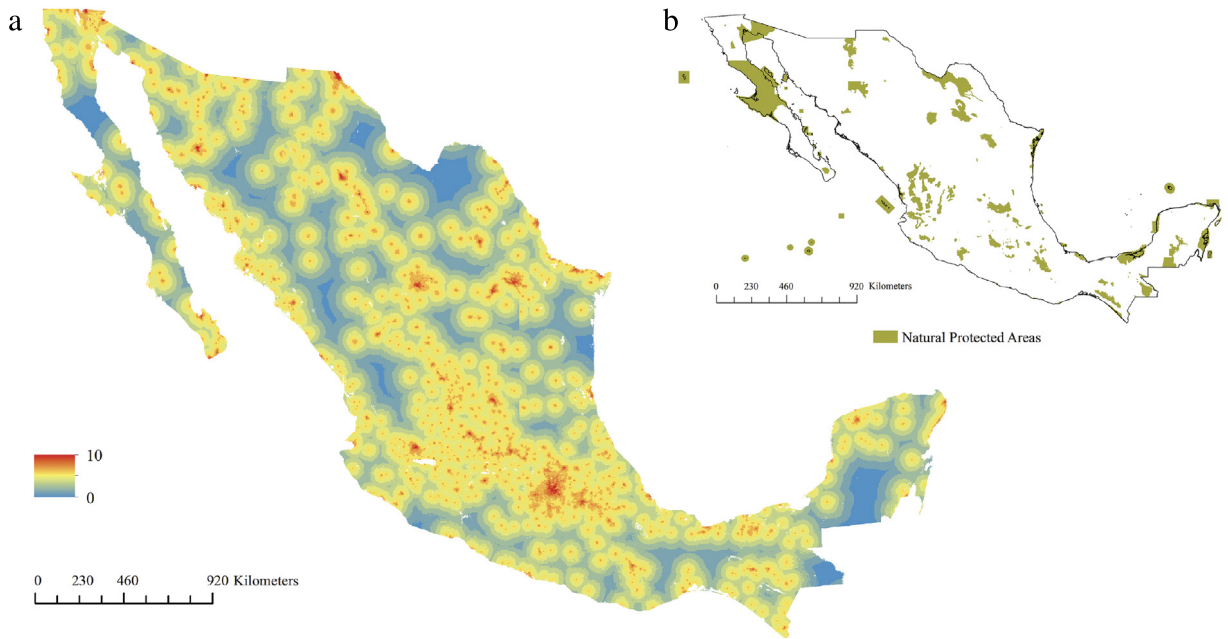
relationships). However, the CO, FrO, HP, HR, IA, IO, IS, N, and S trophic groups and the S, M size and SQ locomotion groups (46.15% of all traits) showed no significant correlations with any environmental variables.

Significantly positive relationships exist among C, FrG and SC with Had, See, Ucp and Plr. The FrG (e.g., *Agouti paca*, *Ammospermophilus leucurus*, *Dasyprocta punctata*), FrH (e.g., *Alouatta pigra*, *Ateles geoffroyi*, *Coendou mexicanus*) and Fr (e.g., *Potos flavus*, *Uroderma bilobatum*, *Chiroderma salvini*, *Carollia brevicauda*, *Artibeus hirsutus*) showed a significant relationship with the environmental variables See and a negative relationship with Hsi. Meanwhile, Fr and FrH had a significantly positive relationship with See and Plr. These results were in accordance with the results of the RLQ analysis (Fig. 2).

The human impact variables (Hsi, Had, Fdi) showed an association with some traits. Hsi showed a negative relationship with the V locomotion group, Fr trophic group and B size group. On the other hand, positive relationships were found for SF, T and G. The F and SF locomotion traits were positively associated with the two main impact groups Hsi and Fdi. SF and G had a negative relationship with See, Ucp and Plr. Only two (7.4%) traits (F and SM) out of 26 traits were related to Fdi. In particular, the SM size group was also negatively related to Ucp. L mammals were positively related to vegetation elements (See, Ucp and Plr). The L and B size groups and the Fr, FrG, FrH and V locomotion groups were negatively related to Te, and SF and T were positively associated with Te. We decide to exclude Rd, As and Hep from the final analyses because they did not show significant relationships with any trait according to the fourth-corner analyses. Excluding each of these variables increases the percentage of the variability that is explained by RLQ axis 1 (from 69.3% to 71.8%).

### 3.1. Mapping weighted environmental variables with RLQ analysis

The spatial co-occurrence of different human impacts in a specific site means a different degree of risk to mammals. Thus, a spatial index that incorporates the presence of all significant human impact variables in the HIGB. We identified areas with a higher risk because of human influence by mapping high RIB values. Conversely, low values indicated sites with more intact conditions (Fig. 3(a)). The spatial patterns of the RIB was represented by ten classes, which were identified by the natural breaks method (Jenks, 1967). This method minimizes each class's average deviation from the class mean (Class 1 = –11.5 to –5.8, Class 2 = –5.8 to –3.2, Class 3 = –3.2 to –1.38, Class 4 = –1.38 to 0.03, Class 5 = 0.03 to 1.3, Class 6 = 1.3 to 2.5, Class 7 = 2.5 to 4.37.3, Class 8 = 4.37.3 to 7.3, Class 9 = 7.3 to 12.2, Class 10 = 12.2 to 40.3). The RIB map showed that 13% of Mexico belongs to the lowest values (from 1 to 2), 40% of the surface to intermediate-low risk (classes 3 and 4), 39% to intermediate-high risk (class 5 and 6), 3.5% to high values (7–8) and 1.1% to the highest values (10) (Fig. 3).



**Fig. 3.** Map of the (a) Risk Index for Biodiversity and (b) Natural Protected Areas in Mexico (CONANP, 2015).

#### 4. Discussion

The Human Impact Gradient for Biodiversity (HIGB) was identified through environmental variables along the first component, reflecting both human impacts, which are mainly explained by human settlement index (Hsi), and close natural sites, which are mainly explained by natural regeneration of forests (See) and tree richness (Plr). The transformation of areas is complex and scale-dependent (Blair, 2004), which renders the generalization of particular findings difficult (Clergeau et al., 2006), and the identification of ecological mechanisms that are involved in natural communities that face such large scale perturbations remains unclear. However, this process can profoundly influence the fates of species' communities. One example is urbanization, which is considered one of the most severe impacts (Vitousek et al., 2008; Pauchard et al., 2006) because it is accompanied by many activities that dramatically affect the abundance and diversity of species (Chace and Walsh, 2006). Increasing urban patches over time alters the ability of species to disperse because of the loss of habitat connectivity (Devictor et al., 2007). However, other human impacts such as forest damage index (Fdi) were not relevant for the HIGB for mammals probably because the Fdi range in Mexico is not widely represented in localities (Table 2). Therefore, conservation decisions must be made carefully because the habitat degradation factors that are evaluated in Fdi inside forests, such as mining activities, small human settlements, forest management, and local land transformation, are associated with defaunation (Dirzo et al., 2014). Consequently, the loss of species interactions, which alter functional ecosystem processes such as pollination, will affect the phylogenetic community structure and phylogenetic diversity (Cavender-Bares et al., 2009). Therefore, future analyses should represent a wider gradient on this type of variable to increase the amount of localities and reduce their size. On the other hand, See and Plr were the biophysical variables in the non-impacted section of the HIGB that were highly connected by their crucial role in tree regeneration and the maintenance of biodiversity (Moore and Allen, 1999). Meanwhile, disturbances can greatly influence the community composition, tree population structure and regeneration ability of forest ecosystems (Lalfakawa, 2010; Gebreselasse, 2011). Seedling recruitment is a critical bottleneck in the population dynamics of many plant species (Horvitz and Schemske, 1994; Wenny, 2000). Successful seedling regeneration is determined by the presence of a sufficient number of seedlings, saplings and young trees in a given population. However, this process is affected by the availability of seeds for germination and favorable site conditions. Therefore, both non-impact and impact extremes of the gradient were well recognized because they are associated with ecosystem processes that are known through the ordination analyses.

Although the second component explained 18% of the variation, it is not clearly associated with an impact gradient. The second component was associated for example with habitat connectivity (Hc). Apparently, this variable is associated with natural areas, but human impact variables such as Fdi is correlated with this biophysical variable. Therefore, the positive section of the second principal component represents both natural and impacted areas where well-conserved sites are close to human settlements. These conditions are typical in the central region of Mexico throughout the Neovolcanic Belt (Fig. 1), where nearly 40% of Mexican people live. This region experiences high deforestation (INEGI, 2000; Velázquez et al., 2001) but several small Natural Protected Areas have been decreed (Fuller et al., 2006). Because we could not identify a second human impact gradient on the second axis, we focus our attention on discussing the relevance of the ordination score through

the first component, which summarized the joint structure among the three tables over an important percentage (71%). Furthermore, 16 of 27 traits showed significant relationships with the environment.

We developed a decision criteria framework by using the HIGB to identify species that are sensitive to degradation based on ecological function information through the traits that are constrained to non-impact sites. This decision criteria framework considered (1) traits that belong to the first and second percentiles in the trait ordination (RLQ, PC1) and (2) species that belong to the first percentile (RLQ, PC1) of the non-impacted gradient. The significant correlation among all of the sensitive traits and the variables through the gradient allows us to validate their utility in the criteria (Table 4). Criterion 1 is useful because it detects biological traits that are mainly associated with natural areas with important (see below) ecological functions (e.g., FrG and their seed dispersal role). Additionally, Criterion 2 identifies target species with implications for conservation planning because these species have low tolerance to human disturbance.

Our results showed that species belong to specific trophic groups Carnivore (C), Frugivore–Granivore (FrG) and Frugivore–Herbivore (FrH), few body size categories (> 17.78 kg (L) and 17.78–1.78 kg (B)) and locomotion groups (Arboreal (A)) that are sensitive to degradation (Fig. 2(b)). See and Plr show a significant correlation with these traits. We also observed that the same traits that are significant for Plr (6 traits) are the same traits that are significant for See (7 traits) because there is a theoretical correlation between See and Plr (Moore and Allen, 1999).

Carnivores are important regulators of ecosystem structure that help to preserve the biodiversity of terrestrial communities (Soulé and Terborgh, 1980). Here, C are represented by *Herpailurus yaguarundi*, *Leopardis pardalis* and *Puma concolor*, which are top predators in Mexico. Top predators around the world are now restricted to tiny fractions of their historical ranges, so the integrity of biological communities over large portions of the Earth is threatened by grossly distorted predator regimes (Estes et al., 2011; Erlinge et al., 1984; Ripple et al., 2014). Even where C are present, the population densities tend to be low and predators' behavior is so secretive that sightings are infrequent, so their role in ecosystems remains contentious (Soulé and Terborgh, 1980). Furthermore, many of the demographical risk factors are characteristic of animals at the top of the food web; therefore, top predators are especially vulnerable to habitat degradation or loss (Lawton, 1995). In addition, some experiments in the field confirm that top predators are differentially lost under habitat alteration or fragmentation (Didham et al., 1998; Petchey et al., 1999) along with the persecution, utilization and depletion of prey (Ripple et al., 2014). The loss of local species (particularly animals) is likely to have important effects on ecosystem functions (Dirzo et al., 2014; Hooper et al., 2012). Losses at high trophic levels (i.e., consumers) would probably have much greater impacts on ecosystem functions than the loss of producers (Reiss et al., 2009; Cardinale et al., 2006).

The frugivore group (except Frugivore–Omnivore, FrO) showed a consistently significant relationship with environmental variables such as See to the natural gradient and a negative relationship to human impact gradient such as Hsi; moreover, Frugivore (Fr) and FrH had a positive significant relationship with Plr. Frugivores improve seed survival by removing seeds from the parent tree (Janzen, 1970; Connell, 1971), escaping from seed predators, improving germination through gut treatment (Traveset et al., 2008), increasing gene flow, and playing a recolonization and restoration role in disturbed ecosystems (Sekerciöglu et al., 2004). These functional trophic groups are relevant in ecosystems because they are associated with seed dispersal and forest regeneration (Gallegos et al., 2014). Frugivores are especially associated with forest integrity because they eat large volumes of fruit and greatly depend on the abundance and nutritional composition of fruits. Additionally, they may disperse plants to new habitats (Howe and Smallwood, 1982); therefore, the loss of frugivory functions could change plant communities and lead to local losses in particular plant species. Food specialization makes species more sensible because of the restricted availability of resources (Devictor et al., 2010), therefore by this reason frugivores as fruits specialist eater could be sensitive to degradation.

Although body size was a group that showed less association with the environmental impact gradient than the trophic groups (but see Farneda et al., 2015), interesting results occurred. L size mammals were positively related with See, understory coverage percentage (Ucp) and Plr and did not show a negative association with impacts (only with slope, Slp). However, we believe that they are sensitive to degradation because they are highly associated with the biotic gradient section. The L size mammals are prone to extinction and have been historically threatened by hunting (Koch and Barnosky, 2006). Currently, human activities such as habitat transformation create an additional threat. Over all when landscape change is not random and disproportionate changes typically occur in flatter areas, at lower elevations and on more productive soils. Interestingly, L mammals showed a negative relationship with Slp (Table 5), which may be because the slope indicates an unnecessary waste of energy given their size (Table 5), therefore they apparently prefer flat areas. In summary the most consistent correlation of animal vulnerability to both habitat destruction and hunting appears to be a large body size (Dirzo et al., 2014; González-Suárez et al., 2013). Unfortunately, human hunting does not show national reports of these activities and thus was not measured here. The vulnerability of larger animals and higher trophic levels has been documented repeatedly in a wide range of terrestrial ecosystems (Diamond, 1982; Redford, 1992; Didham et al., 1998; Purvis et al., 2000; Alroy, 2001; Cardillo and Bromham, 2001). The local extinction of many carnivores and herbivores large-bodied mammals has direct consequences on plant regeneration (Duffy, 2003; Svenning et al., 2015). Therefore, their main role in trophic cascades has been recognized because humans have truncated it, with strong effects on ecosystems and often negative consequences on biodiversity (Estes et al., 2011; Ripple et al., 2013).

In this analysis, a low number of mammalian species (Table 1) represented most of the traits that occurred at non-impact sites. Consequently, these species have low redundancy and compensation potential to ecosystems (Cumming and Child, 2009) and the functions that they perform. For example, the trophic habits traits covered FrH (7 species, 3.3%) and C (4 species, 1.89%); the locomotion traits covered A (9 species, 4.3%) and the body mass traits covered B (18 species, 8.5%) and

L (5 species, 2.4%). These 43 species (Table A.4) represent only 11.9% of all of the mammal species that were analyzed in Mexico. This apparently low compensation could increase the fragility of ecosystems (Cumming and Child, 2009). In this sense, our results indicate that the traits that are more sensitive to human impacts are also more vulnerable as a group because of their low species representation. Therefore, special attention should be paid to maintaining a high functional diversity in remnant natural areas.

Given that many key functional aspects of ecosystems closely depend on biotic interactions, such as the trophic relationships among species, (e.g. predation or seed dispersal), their loss may have pervasive effects and accelerate local species extinction and the decay of ecosystem functions (Estes et al., 2011), eventually collapsing the derived services that are provided to humans (Díaz et al., 2013). Therefore identifying sensitive functions that are associated with the traits in the most conserved areas is critical to provide an early diagnosis of environmental problems.

Mapping the Risk Index for Biodiversity (RIB) helps to identify spatial threats at the country level in order to support the environmental early diagnosis. This national assessment is an approach that identifies sites where main human stressors threatening mammal species are located. RIB suggests that around 15% of Mexico's surface is not at risk, highlighting its spatial coincidence with the Natural Protected Areas (CONANP, 2015; Fig. 3). Regions under highest risk are mainly located in Mexico's central region, which is highly populated (Fig. 1(a)). Conservation strategies such as mammalian-habitat restoration are more likely to succeed in sites under lower risk values.

HIGB was identified for a variety of ecosystems and data types (e.g. field-based, remote sense data) but also can be used under multiple spatial scales. Given the degradation trend of natural systems at the global scale (Steffen et al., 2011), this approach aims to be useful for the identification of ecological integrity indicators by detecting sensitive biodiversity components. Thus, we identified traits, species and sites that should receive special attention for decision-making processes on conservation. This is particularly important for specific traits which are not only sensitive to human impacts, but are also more vulnerable as a group, due to their low species representation and functional relevance. In order to recognize certain biodiversity indicators (functional or taxonomic), it is necessary to generate further information of current species distributions in order to refine the analyses scale and be able to test differences among scales, ecosystems and other vertebrates in the resulting impact gradients.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2016.01.004>.

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