



## Research Paper

**Cite this article:** Bardavid S et al. (2024)

Identifying medium- and large-sized mammal species sensitive to anthropogenic impacts for monitoring in subtropical montane forests.

*Environmental Conservation* page 1 of 8.

doi: [10.1017/S037689292400002X](https://doi.org/10.1017/S037689292400002X)

Received: 8 May 2023

Revised: 15 January 2024

Accepted: 16 January 2024

**Keywords:**

Human footprint; occupancy modelling; Southern Yungas; wilderness

**Corresponding author:**

Natalia Politi; Email: [natipoliti@fca.unju.edu.ar](mailto:natipoliti@fca.unju.edu.ar)

# Identifying medium- and large-sized mammal species sensitive to anthropogenic impacts for monitoring in subtropical montane forests

Sofía Bardavid<sup>1</sup> , Luis Rivera<sup>1</sup>, Sebastián Martinuzzi<sup>2</sup>, Anna M Pidgeon<sup>2</sup>, Volker C Radeloff<sup>2</sup> and Natalia Politi<sup>1</sup> 

<sup>1</sup>Instituto de Ecorregiones Andinas CONICET/UNJu, San Salvador de Jujuy, Jujuy, Argentina and <sup>2</sup>SILVIS Lab, Department of Forest and Wildlife Ecology, University of Wisconsin–Madison, Madison, WI, USA

## Summary

Medium- and large-sized mammals play important roles in maintaining forest ecosystem functions, and these functions often diminish when mammal species are depleted by human activities. Understanding the sensitivity or tolerance of mammal species to human pressure and detecting species changes through monitoring programmes can inform appropriate management decisions. The objective of our study was to identify medium- and large-sized mammal species that can be included in a monitoring programme in the Southern Yungas of Argentina. We used occupancy modelling to estimate the probability of habitat use ( $\psi$ ) of 13 of 25 mammal species detected by 165 camera traps placed in forests across a range of human footprint index (HFI) values. As defined by the HFI, 54% of the study area is wilderness. The probabilities of habitat use of two mammal species were significantly associated with the HFI: the lowland tapir (*Tapirus terrestris*;  $\psi = 0.33$ , range = 0.22–0.50) was inversely associated with HFI values, whereas the grey brocket deer (*Mazama gouazoubira*;  $\psi = 0.79$ , range = 0.67–0.87) was positively associated with the HFI. Monitoring the probability of habitat use of the sensitive species (lowland tapir) could help us to detect changes in areas experiencing anthropogenic impacts before they cause extirpation, whereas the high probability of the habitat use values of the tolerant species (grey brocket deer) might indicate that anthropogenic impacts are strongly influencing habitat, signalling that mitigation strategies might be warranted. The Southern Yungas retains an intact mammal fauna, and we showed that the HFI is useful for monitoring anthropogenic impacts on these mammals. There are still opportunities to develop conservation strategies to minimize threats to mammal species in the region by implementing a monitoring programme with the proposed species.

## Introduction

Forest ecosystems harbour approximately two-thirds of terrestrial biodiversity, yet few forests have escaped anthropogenic impacts (FAO 2006). Neotropical forests harbour high levels of biodiversity but are threatened by vegetation loss and degradation (Laurance et al. 2014). Cultivated areas and human settlements and the construction of roads and other infrastructure result in habitat loss and fragmentation for many species and contribute to high extinction rates globally (Barnosky et al. 2011). Protected areas are key to species conservation; however, they are insufficient for the long-term conservation of some species, especially those with large home ranges (Gardner et al. 2009).

Medium- and large-sized mammals (>1 kg body mass) play important roles in maintaining ecosystem functions; they act as landscape engineers, shaping the structure and composition of ecosystems and communities (Bakker et al. 2016, Morris & Letnic 2017). However, many of these mammals have suffered population declines or extirpation due to overhunting and habitat loss and degradation (Ceballos et al. 2017, Vynne et al. 2022). Many formerly remote areas are now accessible through roads, which can increase hunting pressure, and are affected by exotic species such as dogs and domestic livestock (Cullen et al. 2000, Laurance et al. 2006, Michalski & Peres 2007).

The human footprint index (HFI) captures anthropogenic impacts on biodiversity and has been mapped at global (Sanderson et al. 2002, Venter et al. 2016) and at regional scales (Leu et al. 2008, Woolmer et al. 2008). The HFI is defined through certain geographical indicators, such as human population density, human settlements, roads, agricultural lands and electrical infrastructure, which are summed to calculate the HFI (Sanderson et al. 2002). Where the HFI is higher, anthropogenic impact is also higher and native wildlife species experience greater threats to survival or reproduction (Martinuzzi et al. 2021). Areas with HFI values equal to 0 are defined as wilderness areas, which are likely to contain the best-conserved environments with intact or nearly intact biological communities (Sanderson et al. 2002, Vynne et al. 2022). Wilderness areas

are important for biodiversity conservation, climate stabilization and the provision of essential goods and services for human well-being (Watson et al. 2018, Grantham et al. 2020). In summary, wilderness areas maintain ecosystem functionality, in part by supporting complete medium- and large-sized mammal assemblages (Estes et al. 2011, González-Maya et al. 2017).

Although global assessments using the HFI have been conducted at 1-km scale resolution, global-scale geographical information may be insufficient in terms of accuracy, resolution and detail at finer scales (Sanderson et al. 2002), where information at a finer resolution might be needed to apply human footprint measures at regional, national or local scales. Recently, the global HFI has been improved with a higher resolution (300 m), resulting in substantial improvements to the spatial interpretation of landscape transformation (Sanderson et al. 2022). Additionally, regional HFIs developed at higher resolution (90 m) allowed for the inclusion of more anthropogenic variables and revealed a level of spatial heterogeneity in landscape transformation that was masked in the global analysis (Leu et al. 2008, Woolmer et al. 2008). Greater detail in human footprint analysis makes it particularly applicable to conservation planning at local or regional scales, at which most plans are implemented. Recently, an ecoregional-scale human footprint map was developed for the forests of Argentina at 100-m resolution to identify the most intact forest in the country (Martinuzzi et al. 2021).

The Southern Yungas are forests distributed along the eastern slopes of the Andes in north-western Argentina and southern Bolivia (Politi & Rivera 2019). The Southern Yungas are considered a global biodiversity hotspot that is under increasing anthropogenic threat (Myers et al. 2000). Approximately 30% of the original area of the Southern Yungas of Argentina has been converted to other land uses (Politi & Rivera 2019). The most widespread human activities in remnant forests are logging and cattle raising, and many rural communities use multiple forest resources (e.g., firewood, subsistence hunting), facilitated by logging or oil roads (Politi & Rivera 2019). In Argentina, the Southern Yungas harbours 157 species of mammals, of which 36 species are medium- or large-sized mammals, including several that are categorized as globally or nationally threatened (i.e., *Panthera onca*, *Tayassu pecari*, *Tapirus terrestris*, *Myrmecophaga tridactyla*) due to notable contractions of their historical distributions (SAREM 2019). Although much remains to be discovered about the anthropogenic impacts on mammals in the Southern Yungas, early work has shown that native mammal species richness might decrease with elevation (Di Bitetti et al. 2013), that tapirs persist on private land with greater probability near to than farther from national parks (Rivera et al. 2021) and that high cattle abundance is associated with low abundance of large native herbivores (Cuyckens et al. 2022).

Monitoring programmes are essential to detecting and quantifying population trends and assessing the influences of various threats on wild populations (Ficetola et al. 2018). Monitoring populations is important not only because countries contracting to the Convention on Biological Diversity are obligated to do so, but also because if they are not monitored they are often marginalized in decision-making processes (Boutin 2009, Perino et al. 2022). The sensitivity or tolerance of medium- and large-sized mammals to human pressure probably varies with species, and therefore detecting changes over time to the probability of habitat use of these species in relation to the human footprint is valuable for determining at what point it might be necessary to mitigate negative human impacts (Fisher & Burton 2018, Shackelford et al.

2018, Toews et al. 2018). In the Southern Yungas, there is no monitoring of changes in forest condition, and the establishment of an early warning programme to detect population changes of medium- and large-sized mammals in wilderness and in areas experiencing anthropogenic impacts is urgently needed (Clements et al. 2019). Here, our goals are: (1) to assess how medium- and large-sized mammals respond to anthropogenic threats as measured by the HFI; and (2) to identify mammal species that could serve to help us monitor human impacts in the Southern Yungas of Argentina.

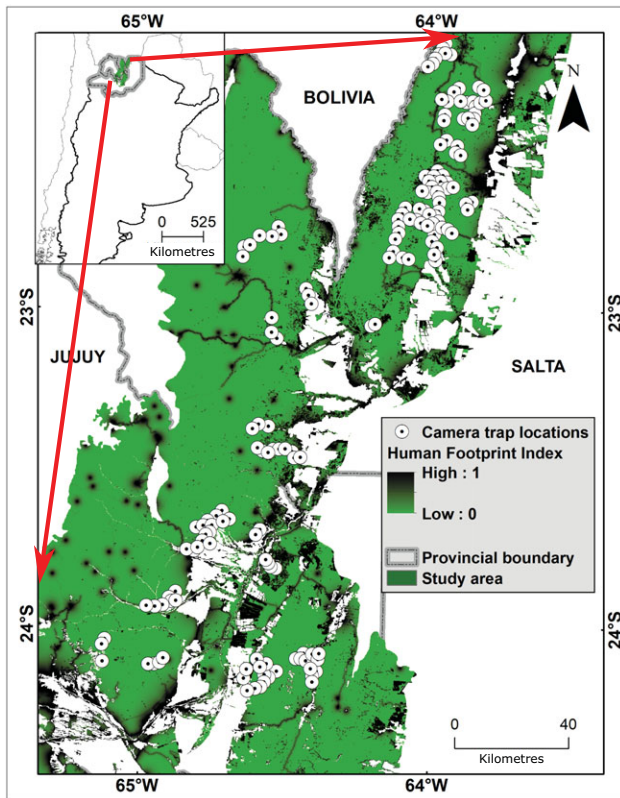
## Materials and methods

### Study area

Our study area includes the Southern Yungas of the provinces of Salta and Jujuy (Argentina; Fig. 1); it is bounded by the border with Bolivia to the north and by El Rey National Park to the south. We used the human footprint map generated for forests of Argentina at a 100-m resolution (Martinuzzi et al. 2021), which integrates human settlements (urban and rural settlements), transportation (roads and trails), energy infrastructure (oil and gas wells and pipelines) and land use (exotic tree plantations and deforestation). The human footprint map uses an influence score and a decay function to represent declining human influence with increasing distance, and it was calibrated based on local forest studies to better represent local conditions (see Martinuzzi et al. 2021). For example, data on the rural settlements locally known as *puestos* (one or a few houses clustered around an artificial water source for livestock), and *caserios* (clusters of a few rural houses plus a first-aid post and a small school) are not included in global maps but are regionally very important. The values in the human footprint map were obtained through Theobald's fuzzy algebraic sum of each variable of human influence that ranges from 0 (i.e., minimum human influence, or wilderness) to 1 (maximum human influence; Martinuzzi et al. 2021). The total study area comprises c. 3.1 million ha of forest with a mean HFI value of 0.14 (range = 0–0.88), of which 1.7 million ha (54%) are wilderness (i.e., HFI value equal to 0), and the remaining 1.4 million ha (46%) are under human influence (i.e., HFI value > 0; Fig. 1).

### Camera trapping of medium- and large-sized mammals

Camera traps are a reliable, non-invasive and low-cost sampling tool for monitoring medium- and large-sized mammals (Burton et al. 2015, Steenweg et al. 2016). We placed 165 camera traps within private properties where we obtained permits to work. Within these properties, camera traps were set in continuous forests across different levels of HFI values up to 0.6, as greater values represent areas where forests have been completely transformed to other land uses (e.g., cities) and our objective was to assess mammal species in forested areas (Fig. S1). We attached camera traps to a tree at a height of 30 cm from the ground, spaced  $1.62 \pm 0.51$  km apart and more than 100 m from crops or roads. We programmed the camera traps to take photographs during the day and night and remain active for at least 30 days. We set camera traps in groups of 10–20 camera traps at a station and then moved to another station; each station was sampled only once during May–October in 2016, 2017, 2018 or 2019, the months coinciding with the dry season in the Southern Yungas, when the properties could be accessed (TEAM Network 2011). We processed image data from camera traps using the program *Wild.ID* (TEAM Network 2011) and identified



**Figure 1.** Human footprint map for the Southern Yungas of the provinces of Salta and Jujuy (Argentina; Martinuzzi et al. 2021) and locations of camera traps (white circles). The left box shows the relative location of the main box in Argentina and the green shading shows the portion of the Southern Yungas that was included as the study area.

individuals present in the photographs to species level. We excluded records of the Dasypodidae family (armadillos) due to the complexity of taxonomic identification through photographs. In addition, we excluded records of exotic species such as cattle, dogs and horses as our objective was to determine the presence of native mammal species.

### Data analysis

We constructed detection histories to determine the encounter history for each species with the independent photographs (i.e., >60 min between photographs of the same species; Sollmann 2018). We calculated naïve occupancy as the sum of camera traps where each species was detected over the total number of cameras placed (MacKenzie et al. 2017). Occupancy models were constructed for species with a naïve occupancy  $\geq 0.07$  (14 of 25 species) because a low number of detections results in poor occupancy model output (Einoder et al. 2018).

We used single-species, single-season occupancy models and a sampling occasion defined as a 5-consecutive-day period of operation for each camera (MacKenzie et al. 2017). The occupancy models were composed of two sub-models, one for probability of habitat use ( $\Psi$ ) and one for detection ( $p$ ). The detection sub-model describes the observational process used to estimate the probability of detection for each sampling occasion and camera, conditional on the presence of the species and following a Bernoulli probability distribution (MacKenzie et al. 2017), whereas the probability of habitat use sub-model describes the ecological process of the probability of habitat use at each camera, also following a Bernoulli

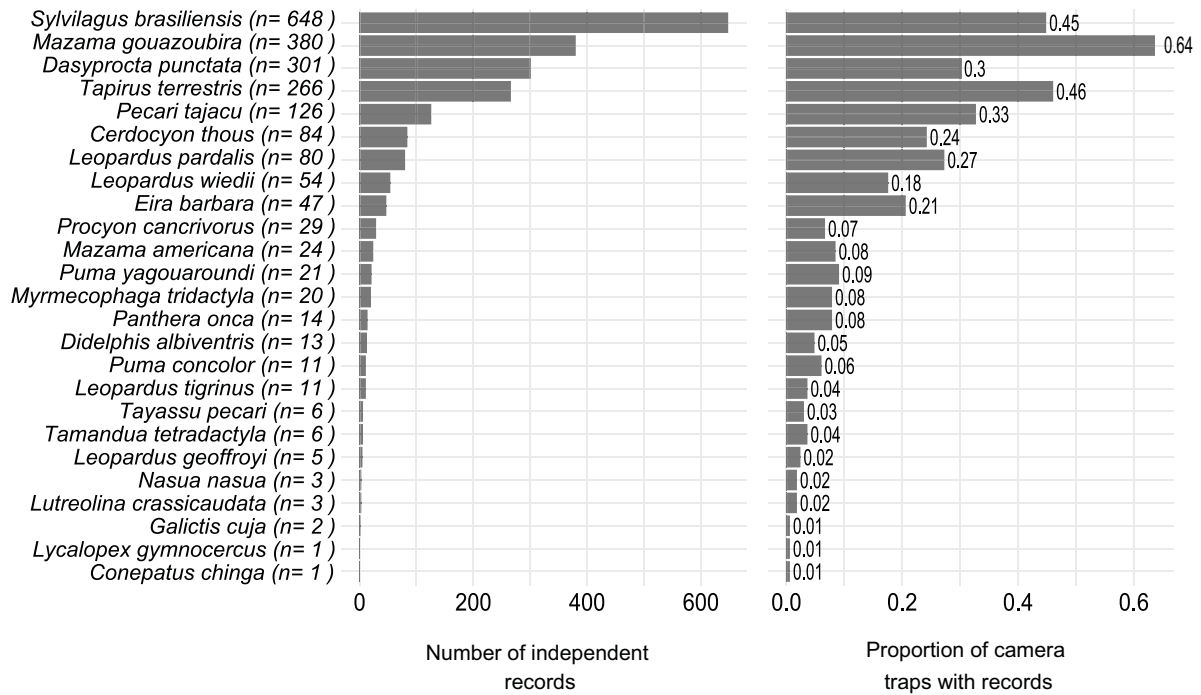
distribution. In the probability of habitat use sub-models, we used the mean value of the HFI calculated within 500 m of each camera trap as the explanatory variable to avoid overlap of values between camera traps and because this is the average home range of the medium- and large-sized mammals of interest (Maffei et al. 2002, Rovero et al. 2013). The variable ‘effort’ was included in the detection models and represents the total number of days for which each camera trap was active. Both variables (i.e., HFI and effort) were standardized by subtracting the mean and dividing by the standard deviation (Zipkin et al. 2010). To select the best occupancy models, we followed a secondary candidate model selection strategy (Morin et al. 2020), in which the Akaike information criterion corrected for small samples (AICc) was used to rank the possible candidate models. For each species, the best model was that for which the difference in AICc ( $\Delta AICc$ ) was  $< 2$ . In the case that more than one model was retained ( $\Delta AICc < 2$ ), we used the averaged model to define the best model. To run the analyses, we used the ‘camtrapR’ (Niedballa et al. 2020) and ‘unmarked’ (Fiske & Chandler 2011) packages in R version 4.3 (R Computing Team 2023). The results from this study should be interpreted as probability of habitat use and not occupancy probability as the spacing of camera traps might be smaller than the home ranges of some of the species, therefore not ensuring spatial independence (MacKenzie & Nichols 2004).

To assess the goodness of fit of the models for each species, we used the 1000 parametric bootstrap approach to compare the sampling distribution (Fiske & Chandler 2011). In addition, the dispersion parameter ( $\hat{c}$ ) was calculated as the ratio of the observed  $\chi^2$  statistic value over the mean of the simulated distribution. The entire fitting procedure of the single-species occupancy models was performed with a maximum likelihood approach using the ‘unmarked’ package (Fiske & Chandler, 2011) in R (R Computing Team 2023). We evaluated the autocorrelation of the residuals of the best models with a spatial correlogram using the ‘ncf’ package (Bjornstad 2016) because this allows for the generation of correlograms using a non-parametric significance test by means of Monte Carlo simulations (Bjornstad 2016).

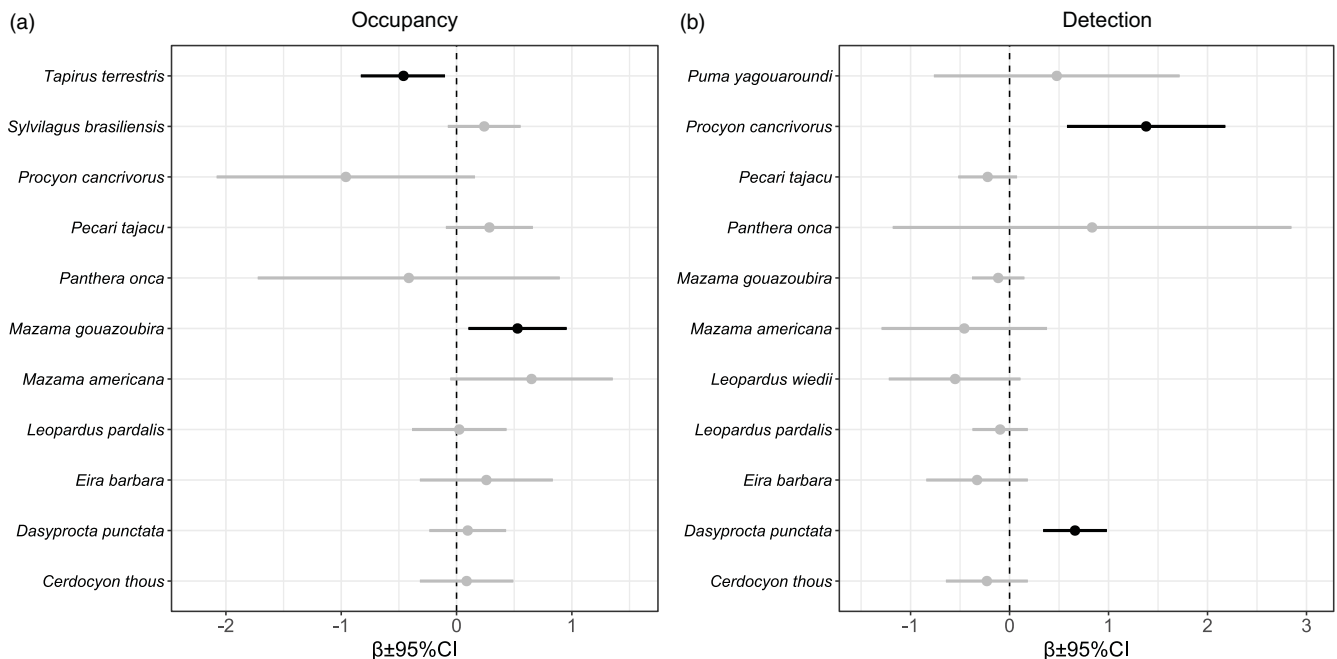
### Results

With 6043 camera trap-nights across all cameras, we obtained a total of 2156 independent records of 25 species that belong to 12 families of medium- and large-sized mammals (Fig. 2). Five species (common tapeti *Sylvilagus brasiliensis*, grey brocket deer *Mazama gouazoubira*, Central American agouti *Dasyprocta punctata*, lowland tapir *Tapirus terrestris* and collared peccary *Pecari tajacu*) accounted for 80% of the records (Fig. 2). We produced 56 single-species, single-season models for 14 medium- and large-sized mammal species (Table S1). No convergence of models was found for the giant anteater (*Myrmecophaga tridactyla*; Table S1). For all but one species (margay *Leopardus wiedii*), the selected models included the HFI as a covariate (Table S1). We found an association trend between the detection probability and sampling effort for 11 species, and this association was only significant for the crab-eating raccoon (*Procyon cancrivorus*) and the Central American agouti (Fig. 3).

We found a significant negative association between the occupancy of lowland tapir and the HFI (Figs. 3 & 4 & Table S2). The best model for lowland tapir included only the HFI as an explanatory variable (Table S1); it had a good fit (Fig. S2), and there was no evidence of autocorrelation in the residuals (Fig. S3). For



**Figure 2.** Number of independent records and proportion of camera traps with records of medium- and large-sized mammal species in the Southern Yungas of Salta and Jujuy provinces (Argentina).

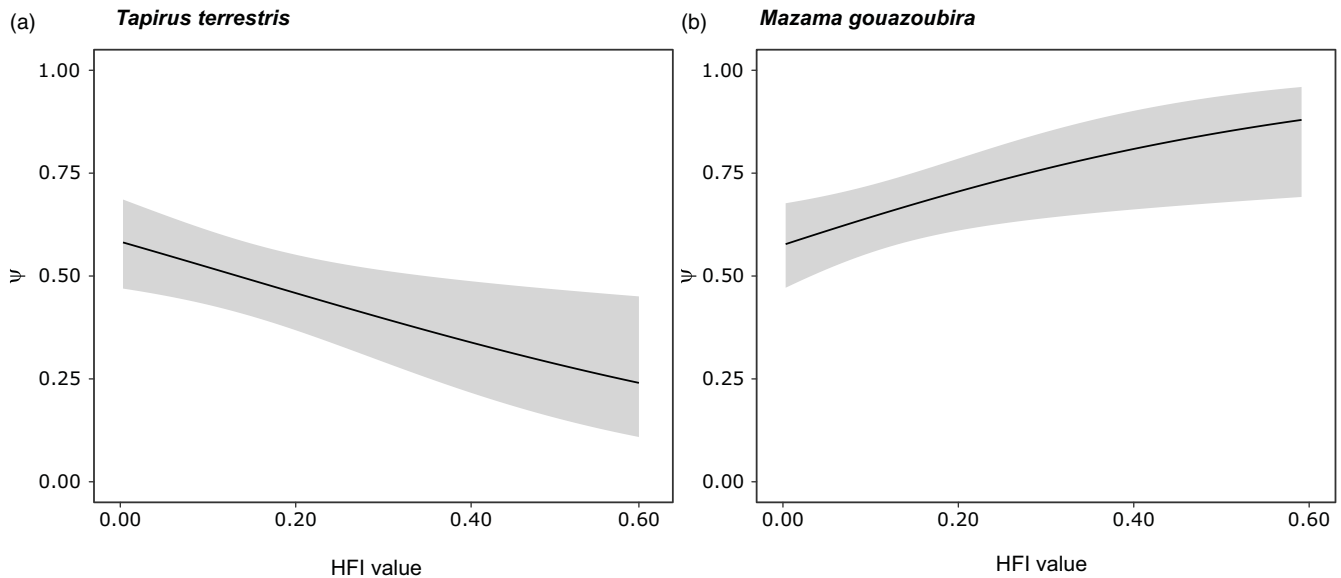


**Figure 3.**  $\beta$  parameter estimate and 95% confidence intervals (CIs) of (a) probability of habitat use (occupancy) and (b) detection models for medium- and large-sized mammal species in the Southern Yungas of Salta and Jujuy provinces (Argentina). Black lines indicate statistically significant  $\beta$  parameter estimates ( $p < 0.05$ ) and grey lines indicate non-statistically significant  $\beta$  parameter estimates ( $p > 0.05$ ). We did not include here the probability of habitat use of jaguarundi (*Puma yagouaroundi*) because the values exceeded the graph boundaries ( $\beta = 4.96$ ; 95% CI =  $-4.95$  to  $14.88$ ).

grey brocket deer, the models indicated a significant positive association of occupancy with the HFI (Figs. 3 & 4 & Table S2). For grey brocket deer, the final model was averaged between the global model and the HFI model (Table S1); this had a good fit (Fig. S2), and there was no evidence of autocorrelation in the residuals (Fig. S3).

Other species associated with the HFI that are worth highlighting yet were not statistically significant were the crab-eating raccoon, which showed a negative trend, and the common tapeti, the collared peccary and the red brocket deer (*Mazama americana*), which showed positive trends in their occupancy as the HFI increased (Fig. 3). Based on the estimates from the





**Figure 4.** Probability of habitat use ( $\Psi$ ; black line: mean; grey shading:  $\pm 95\%$  confidence intervals) related to the human footprint index (HFI) values for (a) lowland tapir (*Tapirus terrestris*) and (b) grey brocket deer (*Mazama gouazoubira*) in the Southern Yungas of Salta and Jujuy provinces (Argentina).

best-ranked models, mean occupancy ranged from  $\psi = 0.03$  (range = 0.01–0.17) for the crab-eating raccoon to  $\psi = 0.79$  (range = 0.67–0.87) for the grey brocket deer (Table 1).

### Discussion

We identified two mammal species (i.e., lowland tapir and grey brocket deer) that would be suitable for monitoring programmes in the Southern Yungas because they are easily identifiable, they are frequently detected in camera traps and their probability of habitat use shows a significant association with the HFI (MacKenzie & Nichols 2004). The lowland tapir is strongly associated with wilderness areas, and monitoring the probability of habitat use of this species through camera traps could provide an early warning system of increasing levels of human impact. An increase in human impact can negatively affect the probability of habitat use of this species, with cascading effects on the ecosystem and interactions among species of the entire mammal assemblage, as is the case for other species and ecoregions (Galetti et al. 2009). We expected to find this positive association for lowland tapir with wilderness areas due to the species' sensitivity to anthropogenic impacts (Rivera et al. 2021). Wilderness areas are more remote from roads, infrastructure, crop edges and human settlements, making access by hunters and resource extraction more difficult (Martinuzzi et al. 2023). In addition, lowland tapir has been shown to be one of the first species to disappear in landscapes with high levels of transformation and fragmentation (Boron et al. 2019). The lowland tapir is a globally and nationally threatened species, so monitoring its occupancy is further justified (Flesher & Medici 2022).

On the other hand, monitoring the probability of habitat use of the grey brocket deer could indicate changes in forest conditions due to increased human impact because we found this probability to be associated with areas of higher anthropogenic impact. This deer species has a high degree of tolerance to human disturbance and high ecological plasticity, and it is found in a wide range of environmental conditions, even on agricultural lands (Ferreguetti et al. 2015, Rodrigues et al. 2017). The grey brocket deer and the

other species that showed a similar trend (i.e., common tapeti, collared peccary and red brocket deer) are dependent on forests, and the positive association of these species with higher human impact values might lead to negative outcomes in landscapes severely depleted of forest (Bianchi et al. 2021). Therefore, we call for caution when using these results and stress that we are not stating that these species can tolerate areas with no forest (HFI > 0.6), but rather that these species have high adaptive plasticity to disturbed forests and can inhabit highly modified forest landscapes (relatively high road and settlement density; Bianchi et al. 2021). The observed association of the grey brocket deer with human impact may be related to changes in forest structure, exclusion of predators (e.g., jaguar avoidance of human presence may lead to a predator-free environment) or increases in the availability of food resources (e.g., crops; Pérez & Pacheco 2006), which should be explored in future studies.

Our work points to the HFI, developed at a finer resolution, being a useful tool for monitoring anthropogenic impacts on medium- and large-sized mammals in the Southern Yungas of Salta and Jujuy provinces. The HFI used in this analysis (Martinuzzi et al. 2021) incorporated layers of locally relevant variables not available in global-scale human footprint maps at 1-km resolution (WCS & CIESIN 2005) such as *puestos*, *caserios* and different types of energy infrastructure, allowing for a more detailed grain of analysis for the study area (100-m resolution) and calibration of the intensity scores and distance of influence that better reflect the local conditions (Leu et al. 2008, Woolmer et al. 2008). However, the global-scale human footprint map has recently been updated with a ninefold improvement in spatial resolution (300 m) over previous efforts (Sanderson et al. 2022), which allows for similar results to be obtained using the same datasets as those applied at an ecoregional scale (Table S3). In this sense, the human footprint map used in this study and the updated global human footprint (300-m resolution) provide proxies for other human activities that are widespread in the Southern Yungas, as in most Neotropical forests, but are difficult to detect and map, such as poaching, because roads, *puestos* and *caserios* provide access for hunters (Sanderson et al. 2002, Peres & Lake 2003, Peres

**Table 1.** Probability of habitat use expressed as mean, minimum (Min) and maximum (Max) ranges for medium- and large-sized mammal species in the Southern Yungas of Salta and Jujuy provinces (Argentina).

Species	Probability of habitat use		
	Mean	Minimum	Maximum
<i>Mazama gouazoubira</i>	0.79	0.67	0.87
<i>Puma yagouaroundi</i>	0.60	0.004	0.99
<i>Pecari tajacu</i>	0.48	0.27	0.67
<i>Sylvilagus brasiliensis</i>	0.48	0.32	0.64
<i>Eira barbara</i>	0.43	0.18	0.72
<i>Leopardus pardalis</i>	0.36	0.23	0.50
<i>Panthera onca</i>	0.34	0.02	0.91
<i>Tapirus terrestris</i>	0.33	0.22	0.50
<i>Dasyprocta punctata</i>	0.32	0.22	0.44
<i>Cerdocyon thous</i>	0.30	0.19	0.43
<i>Mazama americana</i>	0.28	0.05	0.60
<i>Leopardus wiedii</i>	0.25	0.16	0.37
<i>Procyon cancrivorus</i>	0.03	0.01	0.17

& Palacios 2007). Poaching affects medium- and large-sized game mammals and can lead to local extinction of prized species (Fa et al. 2002, Di Bitetti et al. 2008, Barboza et al. 2016). We did not find a negative association between the most prized game species in the Southern Yungas (e.g., red brocket deer, grey brocket deer and collared peccary) and increasing HFI values. This could either indicate that the poaching level is low or that the high proportion of wilderness areas can buffer the negative effects of poaching by acting as population sources for these species (Peres 2001, Peres & Palacios 2007).

We recorded 80% of the 32 medium- and large-sized mammal species (excluding the four species of armadillos) known to occur in the Southern Yungas (SAREM 2019). The seven species that were not recorded in this study are arboreal, semi-aquatic or associated with other types of environment (SAREM 2019). This suggests that the Southern Yungas of Argentina have not experienced the extirpation of species as has been observed for other nearby Neotropical ecoregions (e.g., Atlantic Forest; Bogoni et al. 2018). Therefore, we highlight that there are still opportunities to develop conservation strategies that minimize threats to mammal species in the Southern Yungas. However, conservation strategies should not be delayed because local extirpations have already occurred in some parts of the study area; for example, that of the jaguar (*Panthera onca*) in the Serranía de Santa Bárbara (Perovic et al. 2015).

Avoiding the defaunation that has already occurred in other Neotropical ecoregions requires that wilderness areas are preserved (Bogoni et al. 2020). Consequently, it is important to conserve an adequate amount of intact native forest and keep human impacts in these areas at low levels, especially through the creation of protected areas, sustainable land management plans and corridors to maintain connectivity between protected areas (Bogoni et al. 2018). Avoiding the expansion of anthropogenic impacts into wilderness areas is fundamental to prevent species range contractions, declining abundances and cascading effects on communities and ecosystems (Erb et al. 2012, Venier et al. 2014). The Southern Yungas forest in Argentina still contains large tracts of wilderness and provides suitable habitat for many species that elsewhere are experiencing negative population trends (Martinuzzi et al. 2018, Politi & Rivera 2019). However, anthropogenic pressures are increasing in the Southern Yungas, and some species of medium- and large-sized mammals are sensitive to human impacts, such as the lowland tapir, and can show population

declines that may make them prone to rapid extirpation (Woinarski et al. 2017). We showed here that the HFI, when applied at finer (100-m or 300-m) resolutions, is useful for monitoring anthropogenic threats to medium- and large-sized mammals. Specifically, we propose that monitoring the occupancy of the lowland tapir and the grey brocket deer could serve as an early warning system for tracking cumulative anthropogenic impacts on native forest (Toews et al. 2018).

**Supplementary material.** To view supplementary material for this article, please visit <https://doi.org/10.1017/S037689292400002X>.

**Acknowledgements.** We thank the private landowners who authorized us to place camera traps on their properties, the numerous field assistants and the provinces of Jujuy and Salta for the permits to conduct this research. We are grateful to Fundación CEBio ([www.cebio.org.ar](http://www.cebio.org.ar)), which provided the necessary support to carry out this work. The authors would like to thank the editor, Nicholas Polunin, the associate editor and two anonymous referees who reviewed an earlier version of this manuscript and provided valuable suggestions and comments.

**Financial support.** This work received financial support from University of Jujuy B/064 2018, the National Agency for the Promotion of Science and Technology PICT 2020 SERIE A-03040, PICT-2021-I-A00708, the National Research Council CONICET PIP 100954, the Ministry of Science, Technology and Innovation Interinstitutional Projects on Strategic Issues PITES 03, the National Aeronautics and Space Administration (NASA) Biodiversity and Ecological Forecasting Program 80NSSC19K0183, Rufford Small Grants and the Whitley Fund for Nature.

**Competing interests.** The authors declare none.

**Ethical standards.** None.

## References

- Bakker ES, Gill JL, Johnson CN, Vera FW, Sandom CJ, Asner GP, Svenning JC (2016) Combining paleo-data and modern enclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proceedings of the National Academy of Sciences of the United States of America* 113: 847–855.
- Barboza RRD, Lopes SF, Souto WM, Fernandes-Ferreira H, Alves RR (2016) The role of game mammals as bushmeat in the Caatinga, northeast Brazil. *Ecology and Society* 21: 2.
- Barnosky AD, Matzke N, Tomiya S, Wogan GO, Swartz B, Quental TB, et al. (2011) Has the Earth's sixth mass extinction already arrived? *Nature* 471: 51–57.
- Bianchi R, Jenkins JM, Lesmeister DB, Gouveia JA, Cesário CS, Fornitano L, Gompper ME (2021) Tayra (*Eira barbara*) landscape use as a function of cover types, forest protection, and the presence of puma and free-ranging dogs. *Biotropica* 53: 1569–1581.
- Bjornstad ON (2016) Package 'ncf'. Spatial nonparametric covariance functions. R v. 1.1-7 [www document]. URL <https://CRAN.R-project.org/package=ncf>
- Bogoni JA, Peres CA, Ferraz KM (2020) Extent, intensity, and drivers of mammal defaunation: a continental-scale analysis across the Neotropics. *Scientific Reports* 10: 1–16.
- Bogoni JA, Pires JSR, Graipel ME, Peroni N, Peres CA. (2018) Wish you were here: how defaunated is the Atlantic Forest biome of its medium- to large-bodied mammal fauna? *PLoS ONE* 13: e0204515.
- Boron V, Deere NJ, Xofis P, Link A, Quiñones-Guerrero A, Payan E, Tzanopoulos J (2019) Richness, diversity, and factors influencing occupancy of mammal communities across human-modified landscapes in Colombia. *Biological Conservation* 232: 108–116.
- Boutin S, Haughland DL, Schieck J, Herbers J, Bayne E (2009) A new approach to forest biodiversity monitoring in Canada. *Forest Ecology and Management* 258: 168–175.

- Burton AC, Neilson E, Moreira D, Ladle A, Steenweg R, Fisher JT, et al. (2015) Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology* 52: 675–685.
- Ceballos G, Ehrlich PR, Dirzo R (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences of the United States of America* 114: E6089–E6096.
- Clements HS, Kerley GIH, Cumming GS, De Vos A, Cook CN (2019) Privately protected areas provide key opportunities for the regional persistence of large- and medium-sized mammals. *Journal of Applied Ecology* 56: 537–546.
- Cullen Jr L, Bodmer RE, Pádua CV (2000) Effects of hunting in habitat fragments of the Atlantic forests, Brazil. *Biological Conservation* 95: 49–56.
- Cuyckens GAE, Gonzalez Baffa Trasci NV, Perovic PG, Malizia LR (2022) Effect of free-ranging cattle on mammalian diversity: an Austral Yungas case study. *Oryx* 56: 877–887.
- Di Bitetti MS, Albanesi SA, Foguet MJ, De Angelo C, Brown AD (2013) The effect of anthropic pressures and elevation on the large and medium-sized terrestrial mammals of the subtropical mountain forests (Yungas) of NW Argentina. *Mammalian Biology* 78: 21–27.
- Di Bitetti MS, Paviolo A, Ferrari C A, De Angelo C, Di Blanco Y (2008) Differential responses to hunting in two sympatric species of brocket deer (*Mazama americana* and *M. nana*). *Biotropica* 40: 636–645.
- Einoder L, Southwell D, Lahoz-Monfort J, Gillespie G, Wintle B (2018) Occupancy and detectability modelling of vertebrates in northern Australia using multiple sampling methods. *PLoS ONE* 13: e0203304.
- Erb PL, McShea WJ, Guralnick RP (2012) Anthropogenic influences on macro level mammal occupancy in the Appalachian Trail corridor. *PLoS ONE* 7: e42574.
- Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Wardle DA (2011) Trophic downgrading of planet Earth. *Science* 333: 301–306.
- Fa JE, Peres CA, Meeuwij J (2002) Bushmeat exploitation in tropical forests: an intercontinental comparison. *Conservation Biology* 16: 232–237.
- FAO (2006) *Global Forest Resources Assessment 2005: Progress Towards Sustainable Forest Management*. Rome, Italy: Food and Agriculture Organization (United Nations).
- Ferreguetti AC, Tomás WM, Bergallo HG (2015) Density, occupancy, and activity pattern of two sympatric deer (*Mazama*) in the Atlantic Forest, Brazil. *Journal of Mammalogy* 96: 1245–1254.
- Ficetola GF, Romano A, Salvidio S, Sindaco R (2018) Optimizing monitoring schemes to detect trends in abundance over broad scales. *Animal Conservation* 21: 221–231.
- Fisher JT, Burton AC (2018) Wildlife winners and losers in an oil sands landscape. *Frontiers in Ecology and the Environment* 16: 323–328.
- Fiske I, Chandler R (2011) unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43: 1–23.
- Flesher KM, Medici EP (2022) The distribution and conservation status of *Tapirus terrestris* in the South American Atlantic Forest. *Neotropical Biology and Conservation* 17: 1–19.
- Galetti M, Giacomini HC, Bueno RS, Bernardo CS, Marques RM, Bovendorp RS, et al. (2009) Priority areas for the conservation of Atlantic Forest large mammals. *Biological Conservation* 142: 1229–1241.
- Gardner TA, Barlow J, Chazdon R, Ewers RM, Harvey CA, Peres CA, Sodhi NS (2009) Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters* 12: 561–582.
- González-Maya JF, Martínez-Meyer E, Medellín R, Ceballos G (2017) Distribution of mammal functional diversity in the Neotropical realm: influence of land-use and extinction risk. *PLoS ONE* 12: e0175931.
- Grantham HS, Duncan A, Evans TD, Jones KR, Beyer HL, Schuster R, et al. (2020). Anthropogenic modification of forests means only 40% of remaining forests have high ecosystem integrity. *Nature Communications* 11: 1–10.
- Laurance WF, Clements GR, Sloan S, O'Connell CS, Mueller ND, Goosem M, et al. (2014) A global strategy for road building. *Nature* 513: 229–232.
- Laurance WF, Croes BM, Tchignoumba L, Lahm SA, Alonso A, Lee ME, Ondzeano C (2006) Impacts of roads and hunting on central African rainforest mammals. *Conservation Biology* 20: 1251–1261.
- Leu M, Hanser SE, Knick ST (2008) The human footprint in the west: a large-scale analysis of anthropogenic impacts. *Ecological Applications* 18: 1119–1139.
- MacKenzie DI, Nichols JD (2004) Occupancy as a surrogate for abundance estimation. *Animal Biodiversity and Conservation* 27: 461–467.
- MacKenzie DI, Nichols JD, Royle A, Pollock KH, Bailey LL, Hines J (2017). *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. London, UK: Elsevier.
- Maffei L, Cuellar E, Noss A (2002). Uso de trampas-cámara para la evaluación de mamíferos en el ecotono Chaco-Chiquitania. *Revista boliviana de ecología y conservación ambiental* 11: 55–65.
- Martinuzzi S, Olah AM, Rivera L, Politi N, Silveira EMO, Pastur GM, et al. (2023) Closing the research-implementation gap: integrating species and human footprint data into Argentina's forest planning. *Biological Conservation* 286: 110257.
- Martinuzzi S, Radeloff VC, Pastur GM, Rosas YM, Lizarraga L, Politi N, et al. (2021) Informing forest conservation planning with detailed human footprint data for Argentina. *Global Ecology and Conservation* 31: e01787.
- Martinuzzi S, Rivera L, Politi N, Bateman BL, Ruiz de los Llanos E, Lizarraga L, et al. (2018) Enhancing biodiversity conservation in existing land-use plans with widely available datasets and spatial analysis techniques. *Environmental Conservation* 45: 252–260.
- Michalski F, Peres CA (2007) Disturbance-mediated mammal persistence and abundance-area relationships in Amazonian Forest fragments. *Conservation Biology* 21: 1626–1640.
- Morin DJ, Yackulic CB, Diffendorfer JE, Lesmeister DB, Nielsen CK, Reid J, Schaub EM (2020) Is your ad hoc model selection strategy affecting your multimodel inference? *Ecosphere* 11: e02997.
- Morris T, Letnic M (2017) Removal of an apex predator initiates a trophic cascade that extends from herbivores to vegetation and the soil nutrient pool. *Proceedings of the Royal Society B: Biological Sciences* 284: 20170111.
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Niedballa J, Courtiol A, Sollmann R, Mathai J, Wong ST (2020) Package 'camtrapR' [www document]. URL <https://cran.rproject.org/web/packages/camtrapR/index.html>
- Peres CA (2001) Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conservation Biology* 15: 1490–1505.
- Peres CA, Lake IR (2003) Extent of nontimber resource extraction in tropical forests: accessibility to game vertebrates by hunters in the Amazon basin. *Conservation Biology* 17: 521–535.
- Peres CA, Palacios E (2007) Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. *Biotropica* 39: 304–315.
- Pérez E, Pacheco LF (2006) Damage by large mammals to subsistence crops within a protected area in a montane forest of Bolivia. *Crop Protection* 25: 933–939.
- Perino A, Pereira HM, Felipe-Lucia M, Kim H, Kühl H, Marselle MR, et al. (2022) Biodiversity post-2020: closing the gap between global targets and national-level implementation. *Conservation Letters* 15: e12848.
- Perovic PG, de Bustos S, Rivera L, Arguedas Mora S, Lizarraga L (2015) *Plan estratégico para la conservación del yaguararé (Panthera onca) en las yungas argentinas*. Salta, Argentina: Administración de Parques Nacionales, Secretaría de Ambiente de Salta, Secretaría de Gestión Ambiental de Jujuy y Escuela Latinoamericana de Áreas Protegidas.
- Politi N, Rivera L (2019) Limitantes y avances para alcanzar el manejo forestal sustentable en las Yungas Australes. *Ecología Austral* 29: 138–145.
- R Computing Team (2023) R Language Definition, version 4.3 [www document]. URL [www.rstudio.com](http://www.rstudio.com)
- Rivera LO, Martinuzzi S, Politi N, Bardavid S, De Bustos S, Chalukian S, Pidgeon A (2021) National parks influence habitat use of lowland tapirs in adjacent private lands in the Southern Yungas of Argentina. *Oryx* 55: 625–634.
- Rodrigues TF, Kays R, Parsons A, Versiani NF, Paolino RM, Pasqualotto N, et al. (2017) Managed forest as habitat for gray brocket deer (*Mazama gouazoubira*) in agricultural landscapes of southeastern Brazil. *Journal of Mammalogy* 98: 1301–1309.

- Rovero F, Zimmermann F, Berzi D, Meek P (2013) 'Which camera trap type and how many do I need?' A review of camera features and study designs for a range of wildlife research applications. *Hystrix, the Italian Journal of Mammalogy* 24: 148–156.
- Sanderson EW, Fisher K, Robinson N, Sampson D, Duncan A, Royte L (2022) The march of the human footprint [www document]. URL <https://ecoevorxiv.org/repository/view/3641/>
- Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The human footprint and the last of the wild. *BioScience* 52: 891–904.
- SAREM (2019) Categorización 2019 de los mamíferos de Argentina según su riesgo de extinción. Lista Roja de los mamíferos de Argentina. Eds Secretaría de Ambiente y Desarrollo Sustentable de la Nación y Sociedad Argentina para el Estudio de los Mamíferos (2019) [www document]. URL <http://cma.sarem.org.ar>
- Shackelford N, Standish RJ, Ripple W, Starzomski, BM (2018) Threats to biodiversity from cumulative human impacts in one of North America's last wildlife frontiers. *Conservation Biology* 32: 672–684.
- Sollmann R (2018) A gentle introduction to camera-trap data analysis. *African Journal of Ecology* 56: 740–749.
- Steenweg R, Whittington J, Hebblewhite M, Forshner A, Johnston B, Petersen D, et al. (2016) Camera-based occupancy monitoring at large scales: power to detect trends in grizzly bears across the Canadian Rockies. *Biological Conservation* 201: 192–200.
- TEAM Network (2011) *Terrestrial Vertebrate Protocol Implementation Manual, v. 3.1*. Arlington, VA, USA: Tropical Ecology, Assessment and Monitoring Network, Center for Applied Biodiversity Science, Conservation International.
- Toews M, Juanes F, Burton AC (2018) Mammal responses to the human footprint vary across species and stressors. *Journal of Environmental Management* 217: 690–699.
- Venier LA, Thompson ID, Fleming R, Malcolm J, Aubin I, Trofymow JA, et al. (2014) Effects of natural resource development on the terrestrial biodiversity of Canadian boreal forests. *Environmental Review* 22: 457–490.
- Venter O, Sanderson EW, Magrach A, Allan JR, Beher J, Jones KR, et al. (2016) Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications* 7: 12558.
- Vynne C, Gosling J, Maney C, Dinerstein E, Lee AT, Burgess ND, Svenning JC (2022) An ecoregion-based approach to restoring the world's intact large mammal assemblages. *Ecography* 2022: e06098.
- Watson JE, Evans T, Venter O, Williams B, Tulloch A, Stewart C, Lindenmayer D (2018) The exceptional value of intact forest ecosystems. *Nature Ecology & Evolution* 2: 599–610.
- WCS, CIESIN (2005) *Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Footprint Dataset (Geographic)*. Palisades, NY, USA: NASA Socioeconomic Data and Applications Center (SEDAC).
- Woinarski JCZ, Garnett ST, Legge SM, Lindenmayer DB (2017) The contribution of policy, law, management, research, and advocacy failings to the recent extinctions of three Australian vertebrate species. *Conservation Biology* 31: 13–23.
- Woolmer G, Trombulak SC, Ray JC, Doran PJ, Anderson MG, Baldwin RF, et al. (2008) Rescaling the human footprint: a tool for conservation planning at an ecoregional scale. *Landscape and Urban Planning* 87: 42–53.
- Zipkin EF, Andrew Royle J, Dawson DK, Bates S (2010) Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation* 143: 479–484.