Effect of free-ranging cattle on mammalian diversity: an Austral Yungas case study

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Abstract Extensive cattle ranging is an important economic activity in mountains, with diverse effects on native mammal communities. The effects of cattle *Bos taurus* can be negative, positive or neutral, mostly depending on the stocking rate. We examined the effect of cattle on the diversity and abundance of native mammalian species in the Austral Yungas region of Argentina, considering environmental variables, land protection status, and human influence. Using 12,512 trap-nights from 167 camera-trap stations over 11 years (2009–2019), we calculated a relative abundance index using camera events and used generalized linear models to estimate the effect of cattle on small mammals, large herbivores, species of conservation concern and felids. Cattle had different effects on each group of native mammals. We observed a lower abundance of large native herbivores and the absence of small mammals in areas with high cattle abundance. The tapir *Tapirus terrestris*, jaguar *Panthera onca* and white-lipped peccary *Tayassu pecari* are rare in the Yungas and therefore potentially vulnerable to extinction there. Conservation of small felids and low cattle abundance could be compatible, but felids are threatened by other anthropogenic influences. Native mammalian diversity and richness were related to land protection status. The entire ecoregion is potentially suitable for cattle, suggesting the potential for further threats, and that cattle should be excluded from strictly protected areas. To ensure extensive cattle ranging is compatible with wildlife conservation in areas where exclusion is not possible, we recommend improved management of cattle and moderate stocking rates.

Keywords *Bos taurus*, cattle, empty forest, human footprint, livestock, national parks, niche-based distribution modelling, threatened species

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Introduction

Free-ranging cattle affect native fauna, species interactions and ecological communities across geographical regions in a variety of ways (Elliott & Barrett, 1985; Moser & Witmer, 2000; Hettinger, 2001; Pia et al., 2003; Shepherd & Ditgen, 2005; Chaikina & Ruckstuhl, 2006). In forest ecosystems in Australia, the presence of free-ranging cattle negatively affects vegetation regeneration by compacting the soil through trampling and diminishing the abundance of seedlings by grazing (Eldridge et al., 2016). In South American forests, the effect of cattle *Bos taurus* is heterogeneous and studies have been restricted to a few forest ecosystems and ecological variables (Mazzini et al., 2018).

The intensive use of the forest understorey by cattle can cause a reduction in plant biomass, potentially reducing the complexity of the understorey (Loeser et al., 2005) and increasing the density of shrubs resistant to browsing (Vandenberghe et al., 2009), thus changing forest structure and composition. These changes in vegetation could have both direct and indirect effects on native mammal biodiversity. By affecting the understorey of forests and reducing refuge and food availability, cattle have the potential to affect small forest mammals negatively (Tabeni et al., 2013). Cattle may also affect large native herbivores by reducing food diversity and competing for pastures (Madhusudan, 2004). By altering small mammal abundance (i.e. prey for carnivores), cattle also cause cascading effects on higher trophic levels (Pia et al., 2003).

The influence of cattle is not straightforward (Hettinger, 2001) and is mainly determined by the stocking rate (Schieltz & Rubenstein, 2016). Mammalian species exhibit different responses linked to their specific life traits (Suraci et al., 2021). Forest specialist mammal species decline rapidly when forest cover decreases and are unlikely to be found in secondary forests, whereas non-specialists survive in human-modified habitats (Newbold et al., 2014), and some species such as the white-eared opossum *Didelphis albiventris* and Molina's hog-nosed skunk *Conepatus chinga* could benefit from cattle-modified habitat (Di Bitetti et al., 2010).

To ensure the protection of biodiversity, a total exclusion of cattle and strict controls against hunting are imposed by national parks in Argentina (IUCN category II protected areas). Other categories (VI) allow traditional cattle raising. In regions where cattle are managed extensively and with little veterinary control, the management of a site plays a fundamental role in the local stocking rate, and therefore in fauna conservation (Schieltz & Rubenstein, 2016).

Since the 1950s, the range of domestic cattle in Argentina has expanded into areas marginal for agriculture, mostly forested areas (Guevara et al., 2009) such as the Austral Yungas in the north-west. In the Argentine Yungas, cattle raising entails releasing cattle into the forests, without nutritional supplements and with little to no management (Quiroga et al., 2005). This extensive ranging of livestock, combined with selective logging and firewood extraction, has adverse effects on the structure of native forests (Campanello et al., 2007; Blundo et al., 2018). However, the effect of cattle has not been considered as an explanatory variable when examining patterns of mammalian diversity, nor is it known how cattle affect fauna in one of the most biodiverse ecosystems in Argentina.

We aimed to assess the effect of cattle on the native mammalian community of the Austral Yungas and any potential interaction with altitude, latitude and land protection status. We considered four species groups: small mammals, large herbivores, species of conservation concern and the felid community. We also examined the potential of cattle to inhabit the Yungas ecoregion on a regional scale. We expected (1) lower mammalian richness and diversity at higher altitudes, increasing latitude and in areas of lower protection status, (2) lower abundance or absence of the four species groups in areas with greater cattle abundance and anthropogenic influence, and (3) that cattle could potentially inhabit the entire Yungas ecoregion.

Study area

The study area is the Austral Yungas of Argentina (sensu Brown & Pacheco, 2006) on the eastern slope of the Andes. This ecoregion is characterized by subtropical cloudy montane forests and has an altitudinal gradient of vegetation physiognomy and species composition (Brown et al., 2001). The Yungas is considered a vulnerable ecosystem (Olson & Dinerstein, 2002) of high conservation value (Malizia et al., 2012) because of the high faunal diversity (Narosky & Yzurieta, 1987; Ojeda, 1999). Cattle were introduced into the region c. 450 years ago (Brown & Grau, 1993), but their distribution is limited by the terrain and therefore cattle density is highly variable.

Methods

We surveyed using camera traps across latitudinal and altitudinal gradients in areas with forest cover (Fig. 1). To measure the success of our method, we developed a potential species list for the Yungas forests (Table 1).

Species groups

Of the recorded species, we selected four groups that can potentially be influenced by cattle. By reducing refuge and food availability for small mammals (Tabeni et al., 2013), we expected a negative influence of cattle on the presence and relative abundance of small mammal species. In this group we included unidentified small mammals (i.e. ≤ 1 kg), the agouti *Dasyprocta* sp. and the tapeti *Sylvilagus brasiliensis*. Cattle may also affect large native herbivores by reducing food diversity and competing for pastures (Madhusudan, 2004). In the large herbivore species group we included the red brocket deer *Mazama americana* and gray brocket deer *Mazama gouazoubira*. We expected a lower relative abundance of both species with higher cattle abundance, and absence of the species at a certain, unknown, threshold of cattle abundance. We predict similar effects on these two species, and therefore we pooled data for a more robust statistical analysis. For species of conservation concern we included threatened species based on national and/or international standards (Ministerio de Ambiente y Desarrollo Sostenible & Sociedad Argentina para el Estudio de los Mamíferos, 2019; IUCN, 2021): the lowland tapir *Tapirus terrestris*, white-lipped peccary *Tayassu pecari* and jaguar *Panthera onca*. Based on the potential influence of cattle on the relative abundance of small mammals and cascading effects on higher trophic levels (Pia et al., 2003), we expect a negative influence of cattle on the presence and relative abundance of small and medium-sized felids. This group comprised the medium-sized ocelot *Leopardus pardalis,* and five small felids: jaguarundi *Herpailurus yagouaroundi,* Pampas cat *Leopardus colocolo*, Geoffroy's cat *Leopardus geoffroyi,* oncilla *Leopardus tigrinus* and margay *Leopardus wiedii* (Table 1).

Camera-trap survey

We placed 166 camera stations: 22 in national parks, 40 in provincial reserves, 30 in private protected areas, 53 in private lands without protection, 12 in state properties without management, and nine in Indigenous territories. The trapping period was 10 January 2009–5 September 2019 (12,512 effective trap-nights). We recorded geographical coordinates and altitude at each point using a GPS. Camera-trap stations consisted of one camera, generally located along a trail, road or river bank, to optimize the capture of larger mammals, which prefer to walk along linear features (Harmsen et al., 2010). In some cases, to ensure cameras were not interfered with or stolen, we placed them in the forest interior. The mean distance between nearest neighbouring cameras was 1.44 ± SD 1.25 km. Cameras were programmed to obtain a set of three photographs, with a 5-minute delay between successive sets, and were active continuously.

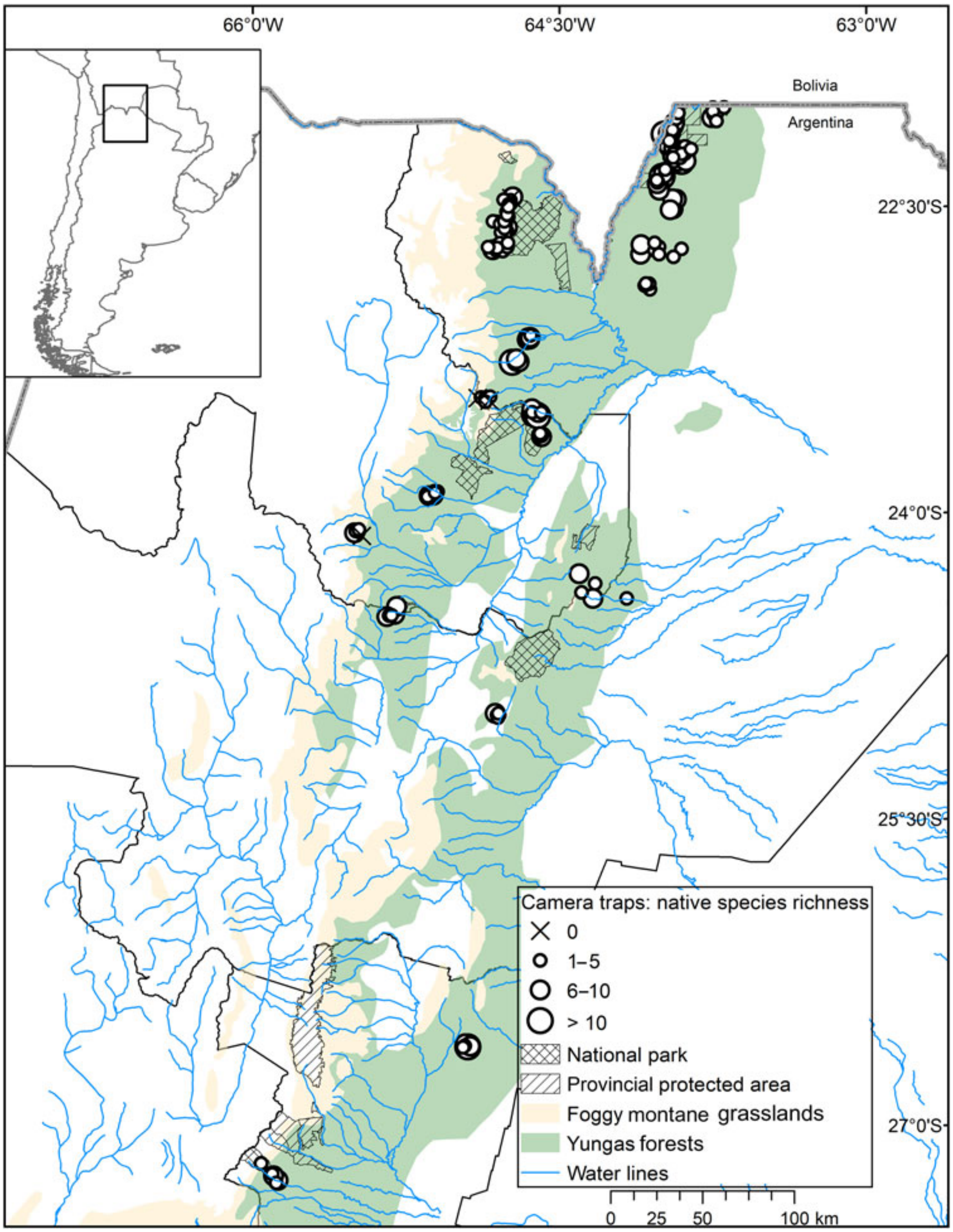

Fig. 1 Study area and location of camera traps in the Austral Yungas of Argentina. Size of circles indicates the number of native mammalian species recorded per camera trap.

Environmental variables

We used 19 bioclimatic variables (Karger et al., 2017). From altitude, we derived slope and roughness, using *QGIS 3.14.0* (QGIS, 2020), which we also used for all other geographical analyses. We obtained the human influence index from WCS & CIESIN (2005); this index incorporates human population pressure, human land use, infrastructure and human access. Values range from 0 (no influence) to 100 (maximum influence). We obtained the coupled evapotranspiration and gross primary production (hereafter referred to as primary production) from the National Tibetan Plateau Data Center (Zhang et al., 2013, 2019; Gan et al., 2018), and we generated Euclidean distances from cameras to the nearest water line (rivers, streams, brooks, rills and runnels). All 24 variables were projected to the WGS84 datum and were at a spatial resolution of 30 arc-seconds or resampled at this pixel size, equivalent to c. 1 km^2.

Mammalian diversity

We identified all large and medium-sized animals recorded by the camera traps to species level, noting whether they were native or exotic, and calculated diversity indices for the native species. Records were considered independent when they were at least 1 h apart. From the number of events and effort (i.e. the number of effective camera-trap nights of each camera), we calculated the relative abundance

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TABLE 1 Species of large and medium-sized native and exotic mammals that could potentially occur in the Austral Yungas (Ministerio de Ambiente y Desarrollo Sostenible & Sociedad Argentina para el Estudio de los Mamíferos, 2019; Fig. 1), with the species group for those species included in our analysis (i.e. small mammals, large herbivores, species of conservation concern and felids), national and IUCN Red List status for native species, and whether or not recorded in our camera-trap study during 2009–2019. The table does not include unidentified small mammal species.

Species (by family)	Species group	National status[1]	Red List status[2]	Native/ exotic	Recorded
Didelphidae					
White-eared oposum *Didelphis albiventris*		LC	LC	Native	Yes
Thick-tailed oposum *Lutreolina massoia*		NT	LC	Native	Yes
Mymercophagidae					
Southern tamandua *Tamandua tetradactyla*		NT	LC	Native	Yes
Giant anteater *Myrmecophaga tridactyla*		VU	VU	Native	Yes
Dasypodidae					
Armadillo *Dasypus mazzai*		DD	DD (as *Dasypus yepesi*)	Native	No
Nine-banded long-nosed armadillo *Dasypus novemcinctus*		LC	LC	Native	No
Six-banded armadillo *Euphractus sexcinctus*		LC	LC	Native	Yes
Cebidae					
Brown capuchin monkey *Sapajus cay*		VU	LC	Native	Yes
Canidae					
Crab-eating fox *Cerdocyon thous*		LC	LC	Native	Yes
Pampas fox *Lycalopex gymnocercus*		LC	LC	Native	Yes
Domestic dog *Canis lupus*				Exotic	Yes
Felidae					
Jaguarundi *Herpailurus yagouaroundi*	Felid	LC	LC	Native	Yes
Pampas cat *Leopardus colocolo*	Felid	VU	NT	Native	Yes
Geoffroy's cat *Leopardus geoffroyi*	Felid	LC	LC	Native	Yes
Oncilla *Leopardus tigrinus*	Felid	VU	VU	Native	Yes
Ocelot *Leopardus pardalis*	Felid	VU	LC	Native	Yes
Margay *Leopardus wiedii*	Felid	VU	NT	Native	Yes
Cougar *Puma concolor*		LC	LC	Native	Yes
Jaguar *Panthera onca*	Conservation concern	CR	NT	Native	Yes
Domestic cat *Felis catus*				Exotic	No
Mustelidae					
Molina's hog-nosed skunk *Conepatus chinga*		LC	LC	Native	Yes
Neotropical river otter *Lontra longicaudis*		NT	NT	Native	No
Tayra *Eira barbara*		NT	LC	Native	Yes
Little grison *Galictis cuja*		LC	LC	Native	Yes
Procyonidae					
Crab-eating raccoon *Procyon cancrivorus*		LC	LC	Native	Yes
South American coati *Nasua nasua*		LC	LC	Native	Yes
Tapiridae					
Lowland tapir *Tapirus terrestris*	Conservation concern	VU	VU	Native	Yes
Tayassuidae					
Collared peccary *Pecari tajacu*		VU	LC	Native	Yes
White-lipped peccary *Tayassu pecari*	Conservation concern	EN	VU	Native	Yes
Cervidae					
Red brocket deer *Mazama americana*	Herbivore	VU	DD	Native	Yes
Gray brocket deer *Mazama gouazoubira*	Herbivore	LC	LC	Native	Yes
Leporidae					
Tapeti *Sylvilagus brasiliensis*	Small mammal	LC	EN	Native	Yes
Common hare *Lepus europaeus*				Exotic	No
Sciuridae					
Yungas squirrel *Sciurus ignitus*				Native	Yes

Table 1 (*Cont.*)

Species (by family)	Species group	National status[1]	Red List status[2]	Native/ exotic	Recorded
Erithizontidae					
Bicolored-spined porcupine *Coendou bicolor*		VU	LC	Native	No
Prehensile-tailed porcupine *Coendou prehensilis*		VU	LC	Native	No
Hydrochaeridae					
Capybara *Hydrochoerus hydrochaeris*		LC	LC	Native	No
Dasyproctidae					
Yungas agouti *Dasyprocta* sp.	Small mammal	LC	LC	Native	Yes
Myocastoridae					
Coypu *Myocastor coypus*		LC	LC	Native	No
Suidae					
Pig *Sus scrofa*				Exotic	Yes
Bovidae					
Cattle *Bos taurus*				Exotic	Yes
Equidae					
Horse *Equus caballus*				Exotic	Yes
Donkey *Equus asinus*				Exotic	Yes
Ovidae					
Sheep *Ovis aries*				Exotic	Yes
Capridae					
Goat *Capra* sp.				Exotic	Yes

[1]Ministerio de Ambiente y Desarrollo Sostenible & Sociedad Argentina para el Estudio de los Mamíferos (2019).
[2]IUCN (2021).
DD, Deficient Data; LC, Least Concern; NT, Near Threatened; EN, Endangered; CR Critically Endangered.

index (RAI) as:

$$\mathrm{RAI_i} = ntot/daystot \times 100 \quad (1)$$

where *ntot* is the number of independent events of the ith species and *daystot* is the total number of effective trap-nights, using the package *camtrapR* (Bengsen et al., 2011; Mandujano & Pérez-Solano, 2019) in *R 2.15.2* (R Core Team, 2019). We calculated two measures of diversity, using the package *vegan* (Oksanen et al., 2019) in *R*: species richness (*S*) and the Shannon–Weaver index (*H*). The latter was calculated as:

$$H = -\sum_{i=1}^{S} RAI_i \times \ln(RAI_i) \quad (2)$$

The value of the relative abundance index increases with increasing richness and evenness in the abundance of species in the community.

We developed generalized linear models (GLM) to examine the effect of cattle and land protection status on *S* and *H*. As biodiversity follows global patterns, with an increase in species richness toward the tropics and a decline in species richness with increasing elevation (Pianka, 1966; Lomolino, 2001; Hillebrand, 2004), we included altitude and latitude as factors in the models. For each of the four species groups we examined the potential influence of explanatory variables on presence/absence of species and on relative abundance index; for small mammals: cattle abundance and primary production; for large herbivores: cattle abundance, primary production and the human influence index; for species of conservation concern: cattle abundance, primary production, human influence index, land protection status and distance to water lines; for the felid community: cattle relative abundance index and the human impact index. For presence/absence models, we used the negative binomial error and Gaussian distributions for abundance, using the package *MASS* (Venables & Ripley, 2007) in *R*. We checked for homogeneity by plotting residuals vs fitted values, for normality using quantile-quantile plots, and for independence by plotting residuals vs each explanatory variable. Because we had several combinations of variables and therefore multiple models, we used single-term deletions to obtain the most parsimonious model, using Akaike's information criterion (AIC; Burnham & Anderson, 2002).

A niche-based model for cattle

Species distribution models examine the potential influence of environmental variables on species presence. *MaxEnt* finds the distribution of maximum entropy (i.e. the largest spread in a geographical dataset of species presences), subject to the constraint that the projected value of each variable is close to its empirical average (Phillips et al., 2020). This information can then be extrapolated to non-sampled areas (Phillips et al., 2006).

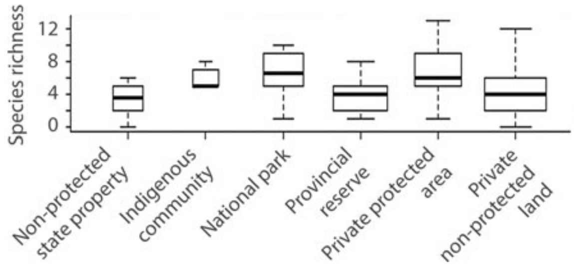

FIG. 2 Mean native species richness recorded by camera traps set in areas of varying protection status. Boxes represent the interquartile range, box widths are proportional to the square root of the sample sizes, the horizontal solid line indicates the median, and the whiskers indicate the 95% CI.

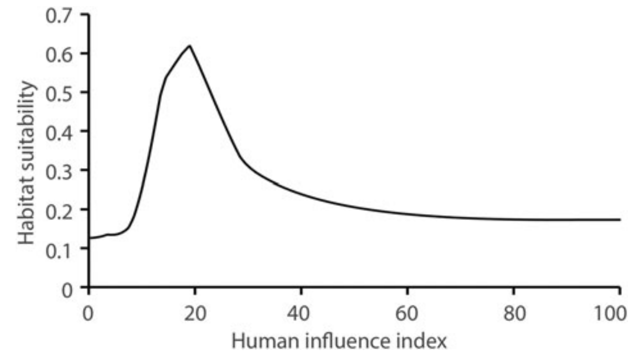

FIG. 3 Habitat suitability for cattle *Bos taurus* (from the niche-based model) in relation to the human influence index.

The study area for modelling was the Yungas ecoregion with a 50-km buffer. We generated 100,000 random points to extract values for the environmental variables, and tested for correlations with the Pearson test, selecting only those with a correlation ≤ 0.7. These were: mean diurnal temperature range, temperature seasonality, mean temperature of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, roughness, human influence index, and distance to nearest water lines.

We used 89 presence records of cattle obtained from the camera traps. We ran the species distribution model 100 times and used the average outcome. To measure the general performance, we used the area under the receiver operating characteristic curve (AUC), which measures the probability that a randomly chosen presence point will rank above a randomly chosen background point (AUC 0.5 = random; values closer to 1 indicate better discrimination power; Bellamy et al., 2013). We converted the model into a binary model by applying the minimum presence logistic threshold (0.015) and categorized habitat suitability for cattle into five classes (very low: < 0.015; low: 0.015–0.25; medium: 0.26–0.50; high: 0.51–0.75; very high: > 0.75) for visualization as a map.

Results

We recorded 29 native species, 81% of the species that could potentially occur in the region (Table 1), and seven exotic species, with 165 of 166 cameras (99%) recording at least one native species and 100 cameras (60%) at least one exotic species. The range of species richness per camera was 0–13 (mean 4.9) for native and 0–5 (mean 1.0) for exotic species. *Bos taurus* had the highest relative abundance index and was also the most frequently recorded species. Other domestic species recorded were horses, pigs, goats and dogs. Domestic cats were not recorded.

Small mammals were recorded by 99 cameras (60%). Brocket deer (i.e. *M. gouazoubira* or *M. americana*) were recorded by 101 (61%) cameras. Gray brocket deer had a relative abundance index of 0–322, and red brocket deer 0–83. Among the species of conservation concern, the lowland tapir had the highest relative abundance index (recorded by 51 cameras), the white-lipped peccary had the lowest relative abundance index (three cameras) and the jaguar was recorded by 22 cameras. The ocelot was the most abundant felid species, followed by the margay, jaguarundi, oncilla, Pampas cat and Geoffroy's cat. The maximum number of small and medium-sized felid species detected by one camera was five.

Native species richness was almost 50% higher in national parks and private protected areas than in provincial protected areas, with intermediate values for Indigenous territories and private lands (Fig. 2). Native species richness and diversity decreased with altitude, without interactions with cattle relative abundance index or latitude (Fig. 3, Table 2).

Presence, but not relative abundance, of small mammals and large native herbivores was influenced by cattle relative abundance index. For small mammals to be present, the relative abundance index of cattle had to be < 17, and large herbivores were absent at a cattle relative abundance index of 13 and present at 5. Thus, to assure the presence of large herbivores, the number of independent cattle records should not be greater than five times the number of effective trap-nights (for example, in a survey of 90 trap-nights the number of independent cattle events should be < 450). Lowland tapir relative abundance increased with distance from water lines and was not influenced by cattle relative abundance index. Jaguar relative abundance and presence were not significantly associated with any of the measured variables. Data for the white-lipped peccary could not be analysed because there were only three records. The human influence index negatively affected felid richness, but not relative abundance, with an abrupt decrease in richness at a human influence index of ≥ 22. Primary production did not influence the presence or relative abundance of small mammals or the tapir (Table 2).

TABLE 2 Generalized linear models for native species richness (number of species) and diversity (Shannon−Weaver index), small mammal presence/absence, deer *Mazama* sp. presence/absence, lowland tapir *Tapirus terrestris* relative abundance index and felid species richness in the Austral Yungas. Only significant models are presented, with *t* and P values for potentially influential variables.

	t	P
Species richness		
Latitude	0.036	0.846
Altitude	−0.002	0.0002**
Protection status	−0.850	2.75×10^{-08}**
Cattle relative abundance index	−0.005	0.415
Species diversity		
Latitude	0.060	0.197
Altitude	-4.96×10^{-04}	1.54×10^{-06}**
Land protection status	−0.123	0.001*
Cattle relative abundance index	−0.002	0.239
Small mammals		
Cattle relative abundance index	−2.100	0.041*
Primary productivity	−0.078	0.938
Deer		
Cattle relative abundance index	0.023	0.021*
Human influence index	1.859	0.067
Tapir relative abundance index		
Cattle relative abundance index	−0.039	0.781
Primary productivity	0.937	0.352
Distance to rivers	2.070	0.042*
Felid species richness		
Cattle relative abundance index	−0.814	0.418
Human influence index	−2.870	0.005*

*P < 0.05; **P < 0.001.

We obtained a habitat suitability model for cattle with AUC = 0.961. Values > 0.75 are considered to indicate models with a good general performance (Phillips & Dudík, 2008). Cattle encounter suitable habitat in most (65%) of the Yungas, with higher habitat suitability towards lower latitudes and lower suitability towards higher altitudes (Fig. 4). Habitat suitability for cattle increases with the human influence index, peaking at 20 and then decreasing abruptly (Fig. 5). Lower suitability corresponds to areas already transformed into croplands, human settlements or roads (Fig. 4).

Discussion

As far as we are aware, this is the first study to use a large camera-trap data set for the Yungas ecoregion over an extended period (11 years) and the first to examine the factors affecting the native mammalian community. In contrast to our expectation, general mammalian species richness and diversity were not directly related to the cattle relative abundance index, but the latter affected two of the four groups of species studied. Small mammals and brocket deer were absent where the cattle relative abundance index was above 17 and 13, respectively. Felids were negatively affected by the human influence index but not by cattle relative abundance, suggesting that felids are influenced not by cattle directly but by activities related to their presence. As cattle have the potential to inhabit most of the Austral Yungas and their presence is associated with hunting, exotic species (domestic dogs and cats), and selective logging (Perovic, 2002), we recommend cattle should be reduced to abundances that allow coexistence with wildlife in all areas with forest cover, and excluded from strictly protected areas. Strictly protected areas (private or state-managed) are the only management regime ensuring long-term fauna conservation in the Yungas.

We recorded 81% of the native species that could potentially occur in the Austral Yungas and therefore we consider our methodology successful. We did not record water-associated species such as the capybara *Hydrochoerus hydrochaeris*, nutria *Myocastor coypus* and neotropical otter *Lontra longicaudis*, the latter being rare in the Yungas (Albanesi et al., 2017). As we did not place cameras in trees, our methodology was not suitable for detecting arboreal species such as the bicolored-spined porcupine *Coendou bicolor* and prehensile-tailed porcupine *Coendou prehensilis*, which are also rare. We did, however, record arboreal species such as the capuchin monkey *Sapajus cay* and Bolivian squirrel *Sciurus ignitus*, but on the ground. Only two of the six cingulate species (armadillos) were recorded, suggesting they have a naturally low relative abundance or are difficult to record with camera traps. A national-scale assessment indicated the need to protect these six species (Abba et al., 2012).

The niche-based distribution model for cattle shows their potential to occupy almost the entire Yungas ecoregion except for the mountain peaks, probably because of the low winter temperatures, low carrying capacity and the difficulty of access for people. The positive association between habitat suitability for cattle and the human influence index is a result of the association of cattle with people, but areas with a human influence index > 20 are no longer suitable for cattle. The raster layer of suitable habitat for cattle could be used in areas not surveyed to estimate cattle presence locally, and could serve as a tool to analyse the effects of cattle in the Austral Yungas.

Environmental variables, which are influenced by latitude and altitude, affect the diversity and composition of native biodiversity. As predicted, we found a decrease in species richness and diversity with an increase in elevation, in accordance with global patterns (Lomolino, 2001) and with a previous study in the northern Yungas (Di Bitetti et al., 2013). We found high mountain areas in the Yungas to be naturally poorer in native and exotic species than forests at lower elevations. The northern Austral Yungas has higher species richness than the central and southern

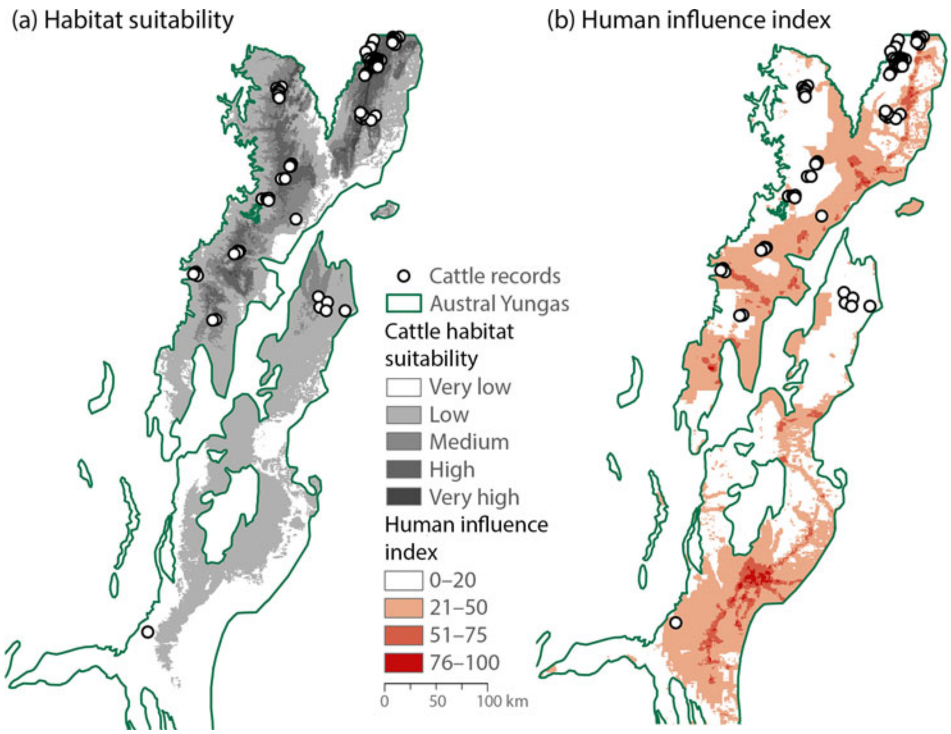

FIG. 4 Presence records of cattle with (a) predicted habitat suitability (see text for details), and (b) the human influence index (see text for details) in the Austral Yungas of Argentina.

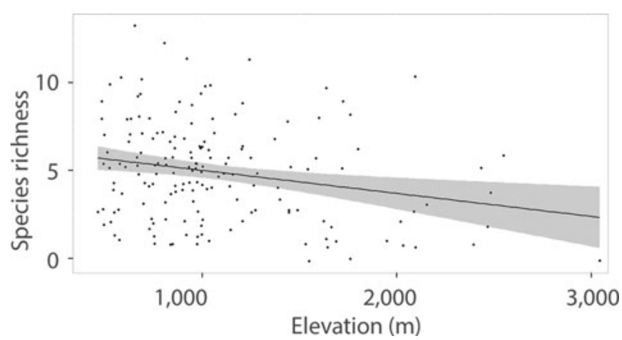

FIG. 5 Native species richness per camera trap in relation to elevation during an 11-year camera-trap study in the Austral Yungas of Argentina.

Austral Yungas and is the southern limit of the distributions of several mammal species (*Sapajus cay, Tapirus terrestris, Leopardus wiedii*), emphasizing the role of this part of the ecoregion in the conservation of these species. In contrast to general patterns (Brown & Lomolino, 1998) and to those of small forest mammals in the Yungas (Ojeda et al., 2008), we found that latitude did not influence native species richness and diversity, indicating a latitudinally homogenized native mammal community.

Land protection status was the most important variable in explaining native mammalian biodiversity. We recorded the highest values of native species richness and diversity in national parks, highlighting the importance of strictly protected areas and the complementary role of small private protected lands (Johnson & Nelson, 2004; Kamal et al., 2015), depending on their management. National Parks in Argentina are legally required to exclude cattle, although this regulation is not always implemented. They are generally larger and have stricter controls than provincial and private protected areas and have historically been established in areas with low potential for economic development (Margules & Pressey, 2000; Rodrigues et al., 2004), and hence could have a higher intrinsic value for conservation. Thus, various anthropogenic factors seem to be implicated in the persistence of native large mammals in these areas. Indigenous territories, with intermediate cattle abundance, may contribute to conservation and offer a complementary institutional model to state-run protected areas (Johnson & Nelson, 2004). Provincial protected areas, with higher cattle relative abundance index, had the lowest diversity indices, similar to unprotected areas (private or state property). In low-income countries, nature conservation is not necessarily a priority and so-called paper parks (i.e. protected areas that only exist on paper and do not achieve conservation goals), are common (Rodríguez & Rodríguez-Clark, 2001). Nevertheless, even paper parks matter (Rodríguez & Rodríguez-Clark, 2001) if they still have forest cover. To reverse the failure in the achievement of conservation objectives of such paper parks in Argentina and to achieve conservation goals, we recommend lowering cattle relative abundance index to ≤ 5 (the highest limit compatible with the presence of both deer and small mammals) and establishing adaptive management plans that include stricter controls than at present.

Our findings indicate that high cattle abundance (relative abundance > 17) is incompatible with the presence of small mammals. Trampling and browsing by cattle reduce the heterogeneity of the forest understorey for this group (Smith et al., 1996; Hayward et al., 1997). We could not identify small mammals to species level and the responses of individual species to cattle may vary (Schieltz & Rubenstein, 2016). Nevertheless, when present, small mammals had high relative abundance indices, so a prey base for medium-sized and small felids remains available.

Small felids are indirectly affected by cattle, as indicated by the human influence index. This index includes human population pressure, human land use and infrastructure and human access. Differential logging (i.e. logging of only particular tree species and individuals of a certain size, resulting in impoverished species richness and affecting forest structure) could also affect forest specialists such as the oncilla and margay. Therefore, we suggest direct hunting and associated activities, such as the presence of dogs (Perovic, 2002) and habitat transformation, are underlying explanations for the influence of humans on felids, not the presence of cattle directly. We did not record domestic cats, so these may not yet be a threat to small felids in the Yungas. We found that the Vulnerable oncilla had the lowest relative abundance and was the rarest of the felid group and therefore its conservation status should be monitored.

In agreement with Nanni (2015), we found brocket deer only in areas with low cattle relative abundance. The human influence index did not affect these large herbivores, suggesting a direct effect of cattle on these two species. In agreement with Mazzini et al. (2018), we suggest biological interactions such as competition and dietary overlap between cattle and native herbivores are the cause of this effect.

Species of conservation concern had low relative abundance indices. Lowland tapir relative abundance was negatively influenced by distance to linear watercourses. Like the Malayan tapir *Tapirus indicus* and Baird's tapir *Tapirus baardii*, which depend on proximity to water (Dudgeon, 2007; Reyna-Hurtado et al., 2019), lowland tapirs use water banks to browse and mate, and enter the water to take refuge from predators (Brooks et al., 1997). Lowland tapir relative abundance was not negatively influenced by cattle relative abundance index. Tapirs probably differ in feeding habits from cattle, browsing more on seedlings and fruits. Prey remains available for jaguars, but the abundance of wild prey is decreasing, which could provoke jaguars to start predating on cattle, with consequent escalations in human–predator conflict (Perovic, 2002; Cuyckens et al., 2014). The species of conservation concern considered here (lowland tapir, white-lipped peccary and jaguar) are large mammals, and body size is an indicator of extinction risk (Cardillo, 2005) as it determines susceptibility to hunting pressure and habitat selectivity. Our study was in areas that still have forest cover. Hence, the effects of cattle and human activities such as habitat destruction and hunting for food (peccaries) and in retaliation (jaguars), are probably having negative, synergistic effects on species of conservation concern (Romero-Muñoz et al., 2020). These species depend on protected forests with extensive cover and protection against hunting.

This is the first study based on an extensive camera-trap survey to provide evidence that cattle affect the assemblage of mammals in the Austral Yungas, both directly and indirectly. We have provided guidelines for cattle abundance that should be implemented in protected areas where cattle raising is allowed. However, we cannot provide guidelines for cattle abundance compatible with species of conservation concern (jaguar and white-lipped peccary), and their low abundances indicate their high risk of extinction in this region. Following Mazzini et al. (2018), we used directly measured cattle relative abundance at the local scale and complemented this with an indirect method at the regional scale (distribution modelling). Our work therefore provides both a method for future assessments of cattle impacts and an indicator of potential cattle abundance in unsurveyed areas in the Austral Yungas.

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Author contributions Study conception: GAEC, LRM; study design, fieldwork: GAEC, PGP; data input: GAEC, NGBT; data analysis: GAEC, writing: all authors.

Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards.

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