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ORIGINAL RESEARCH

Landscape-scale drivers of tayra abundance in the Ecuadorian Andes

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Abstract
Habitat conversion to agriculture and overexploitation of wildlife are the two largest drivers of biodiversity loss globally. Biodiversity loss is especially prevalent in areas undergoing rapid economic development at the expense of natural land cover as is the case across much of South America. Despite expected declines in wildlife populations associated with ongoing large-scale land conversions, for many species we lack sufficient data on key threats and drivers of abundance in order to inform appropriate management and conservation. Collecting data to estimate critical state variables such as abundance can be expensive, logistically challenging, and even implausible on spatial scales relevant to species management, especially for carnivores which are elusive and difficult to monitor. Here, we use detection-non-detection data collected using a structured camera trap survey repeated over two years in the Ecuadorian Andes to produce insights into the habitat associations and potential threats faced by the tayra, a medium-sized carnivore that despite being perceived to be relatively common in South America, remains largely understudied. We use hierarchical modelling to estimate an index of abundance for the tayra while accounting for imperfect detection. We demonstrate the tayra to be a lowland habitat generalist, with conversion of land to agriculture potentially benefitting this species in the short term, with increasing proportion of core agricultural land being associated with higher indices of abundance. However, we highlight that this state could potentially serve as an ecological trap in the long term. We provide evidence for negative impacts of human population density on tayra abundance. We hypothesize this relationship could be underpinned by conflict and subsequent persecution by humans, which is likely to be exacerbated in agricultural landscapes. These findings suggest that like many carnivores, the tayra may be able to adapt and even thrive in human modified landscapes given societal acceptance, thus, conservation strategies for the tayra that focus on fostering co-existence between humans and this medium-sized carnivore may contribute to its future.

keywords Population monitoring · Hierachical modeling · Human-wildlife conflict · Carnivore conservation · Eira barbara

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Introduction

Human encroachment on habitats is one of the most important drivers of biodiversity loss and on-going extinctions globally (Sala et al. 2000; Cardinale et al. 2012; Maxwell et al. 2016). The pressures on biodiversity are expected to be particularly severe throughout much of South America due to ongoing economic development underpinned by large-scale land conversion to agriculture. For example, natural land modification in South America expanded by 268 million ha between 1985 and 2018, impacting over 40% of the country's landmass (Zalles et al. 2021). The ability of carnivores to recolonize and survive in landscapes greatly modified by and shared with humans has challenged long standing edicts about the habitat requirements of such species, demonstrating many carnivores to be habitat generalists and able to adapt well to anthropogenically altered landscapes (Chapron et al. 2014; Morales-Gonzalez et al. 2020; Twining et al. 2020). Despite recent success stories, the population trajectories of many carnivore species across the globe are less certain, and likely, less positive (i.e. Ripple et al. 2014). Given ongoing widespread habitat loss and land conversion in the global south, many species are suspected to be threatened by severe declines (e.g. Powers and Jetz 2019), but there is a paucity of data to inform confident conclusions (Conde et al. 2019). Data deficiency remains a key obstacle in enacting appropriate conservation and management actions that could otherwise act to halt, mitigate, or even reverse such biodiversity declines.

Carnivore populations generally are thought to be experiencing declines across the globe both in their population sizes and geographic ranges (Ripple et al. 2014). Population size is a critical state variable helping conservationists and wildlife managers describe biodiversity losses, with many shared objectives revolving around managing population sizes to protect imperilled species or to mitigate conflicts in problematic species (Williams et al. 2002). Declines in carnivore populations are primarily driven by habitat loss and conflict with, and subsequent persecution by, humans (Ripple et al. 2014). Thus, understanding the ecology, habitat associations, and population trends of species in areas undergoing rapid anthropogenic change can inform evidence-based conservation strategies aimed at mitigating the most severe of these impacts.

It is notoriously difficult to produce accurate and precise population estimates of carnivore species due to their typically wide-ranging behaviour, occurrence at low densities, and elusive nature, which hinders the collection of robust data on population trends (Gese 2001; Wilson and Delahay 2001). Many methods used to estimate abundance and density (e.g. spatial capture–recapture [SCR] applied to live-trapping, non-invasive genetic sampling) require a significant investment of time and money (Royle et al. 2013; Fuller et al. 2016; Twining et al. 2020). Such methods therefore can be challenging or impossible to conduct when interest is on landscape-level spatial scales relevant to the management of highly mobile, low density, and elusive species such as carnivores. Instead, detection-non-detection data can be collected from repeated surveys and modelled using a hierarchical framework to estimate occurrence of a species while accounting for imperfect detection (MacKenzie et al. 2002). One of the main applications of occupancy modelling is large-scale monitoring for the purposes of studying species distributions, estimating trends, and identifying habitats that are critical to the species (MacKenzie 2005; Bailey et al. 2007). Detection–non-detection data can be used in a similar way to estimate an index of abundance by modelling and exploiting the link between heterogeneity in abundance and heterogeneity in detection probability to estimate the underlying distribution of abundances (Royle and Nichols 2003). While not estimates of true abundance as provided by more

intensive methods (e.g. SCR), this approach provides a relatively inexpensive method to inform trends and drivers of species that are otherwise difficult to monitor over relevant spatial scales.

Tayras (*Eira barbara*) are medium-sized carnivores (~2.7–7 kg) with generalist tendencies that occur across Latin America from southern Mexico to northern Argentina (Hall 1981; Presley 2000). Despite being one of the most common mammals within their geographical range, tayras are relatively unstudied compared to other neotropical mammal species (Konecny 1989; Oliveira 2009). Tayras are one of the least known members of the Guloninae which contains the extensively studied, temperately occurring martens (*Martes* sp.), fishers (*Pekania pennanti)*, and wolverines (*Gulo gulo*, Koepfli et al. 2008). What knowledge that does exist on tayras is largely based on field studies with highly limited sample sizes (e.g. n = 1, Sunquist et al. 1989; n = 1, Michalski et al. 2006). The data on the habitat requirements and associations of the species that do exist are highly contradictory (Goulart et al. 2009; Bogoni et al. 2013; Cove et al. 2014; Tobler et al. 2015; Bianchi et al. 2021), and little to no information is available on the trends of the species. Furthermore, data are entirely absent regarding how the species may be impacted by ongoing land conversion and increased overlap with humans in newly modified landscapes. As a key predator in neotropical systems (Bianchi et al. 2021), understanding the drivers of tayra abundance on scales meaningful to species management is becoming increasingly urgent as large areas of the species range undergoes rapid anthropogenic change.

The ability of tayras to coexist with humans is likely the greatest contributor to their broad geographic distribution and ability to persist in a variety of different habitat types (Sunquist et al. 1989; Presley 2000). Tayras have been reported to be associated with forested habitats with intermediate levels of disturbance, such as secondary forest and edge habitats (Presley 2000; Cove et al. 2014). However, the threshold of disturbance where the direction of this association may change is unclear. Many generalist carnivores with a variable diet and a capacity for prey switching like tayras have been reported to be able to survive in human modified landscapes (Chapron et al. 2014). As a consequence of tayras' propensity to inhabit anthropogenically altered habitats, conflicts with humans can arise due to the depredation of poultry, livestock, and beehives (Naughton-Treves et al. 2003; Flores-Armillas et al. 2020; Desbiez et al. 2020; dos Santos et al. 2020; Salom et al. 2021). Human-wildlife conflict and subsequent persecution by humans with which they share the landscape could pose a threat to tayra populations. The conflation of low reproductive rates and low densities of tayras that is typical of many carnivores makes them particularly vulnerable to the impacts of persecution and may inhibit their ability to inhabit human modified landscapes in the future, given their apparent reputation among farmers who consider the animal a pest species (Rocha et al. 2006; Oliveira 2009).

We use a hierarchical modelling framework to produce an index of abundance and examine the habitat associations of tayras in the Chocó-Andean region of Ecuador. In contrast to most of the existing literature on tayras, the sampled area is within a multi-use landscape. The region is highly fragmented by agricultural expansion both in the form of pasture for cattle grazing as well as crop lands for subsistence farming. The area has historically been used for these purposes by local communities and, more recently, is also being impacted by urban development and ecotourism. We hypothesise that tayra abundance will be positively associated with native forest cover (Goulart et al. 2009; Bogoni et al. 2013; Bianchi et al. 2021), scrub cover (e.g. Matos et al. 2009), and agricultural land (Cove et al. 2014; Pardo Vargas et al. 2016), and negatively associated with human density (Naughton-Treves et al. 2003; Flores-Armillas et al. 2020; Desbiez et al. 2020; dos Santos et al. 2020; Salom et al. 2021). This study provides the unique opportunity to estimate an index of

abundance for tayra in an area where fragmentation and human influence on the landscape are expanding and enables predictions for how the species might be impacted by anthropogenic change more broadly in the future.

Methods

Study area

Our study area lies within the Chocó-Andean region of the Ecuadorian Andes northwest of Quito, Ecuador (approximately − 78.586 longitude, 0.205 latitude), which is located at the convergence of two of the world's biodiversity hotspots—the forests of Chocó and the Tropical Andes (Myers et al. 2000). The study area is composed mainly of montane cloud forest, where average annual precipitation totals 236.8 cm with an average temperature of 17.76 °C (Jarvis and Mulligan 2011). Elevation within the study area ranges from 1300 to 3800 m. Native and old growth forests represent approximately 66% of the study area, but this landscape also supports multiple human uses. At least 13% of the landscape has been partially or fully deforested and converted to pasture that is used for cattle grazing, as well as for growing crops that support the livelihoods of local communities. Less than 3% of the area is protected within the Pululahua Geobotanical Reserve, and parts of the remaining forest are privately owned and have been developed for ecotourism.

Camera trap surveys

We monitored remotely activated trail cameras (Bushnell® Trophy Cam™ HD) from August 21, 2016–November 22, 2016, and 21 April, 2017–31 August, 2017. We used a stratified random sampling design to select 103, 1 km^2 sample units across the study area. The survey was initially conducted at 70 sites in 2016 and repeated at 103 sites in 2017 using the same method. Trail cameras were deployed on trees approximately 50 cm off the ground and placed facing either north or south to avoid direct sunlight during sunrise and sunset. A one-meter-tall stick was positioned approximately five meters in front of each camera with a vanilla scent lure applied to the top of the stick. Where possible, two cameras were used at each site in order to increase the probability of detection. A subset of 64 sites had two cameras, while the remaining 109 sites had one camera (44% of the 70 sites sampled in 2016, and 32% of the 103 sites sampled in 2017 had two cameras). At sites with two cameras, both cameras were pointed at the bait stick so that their zones of detection overlapped but the cameras were not directly facing each other. Camera sensitivity was set to "Normal", and cameras were programmed to take a burst of three photos with each trigger, and a one second interval between triggers. Cameras were deployed at each site for an average of 11.7 weeks (range = 6–13 weeks), with visits to check cameras approximately every 2 weeks when we switched memory cards, batteries, and replaced scent lure. Detection histories were created for tayra over a maximum of 10 weeks at each site. Only one detection was allowed for each occasion, with an occasion length of 1 week to ensure independence of detections. Any variability in survey effort (number of cameras and length of camera deployments at each site) was recorded and accounted for during analysis. A map of the sampling sites and study area can be seen in Fig. 1.

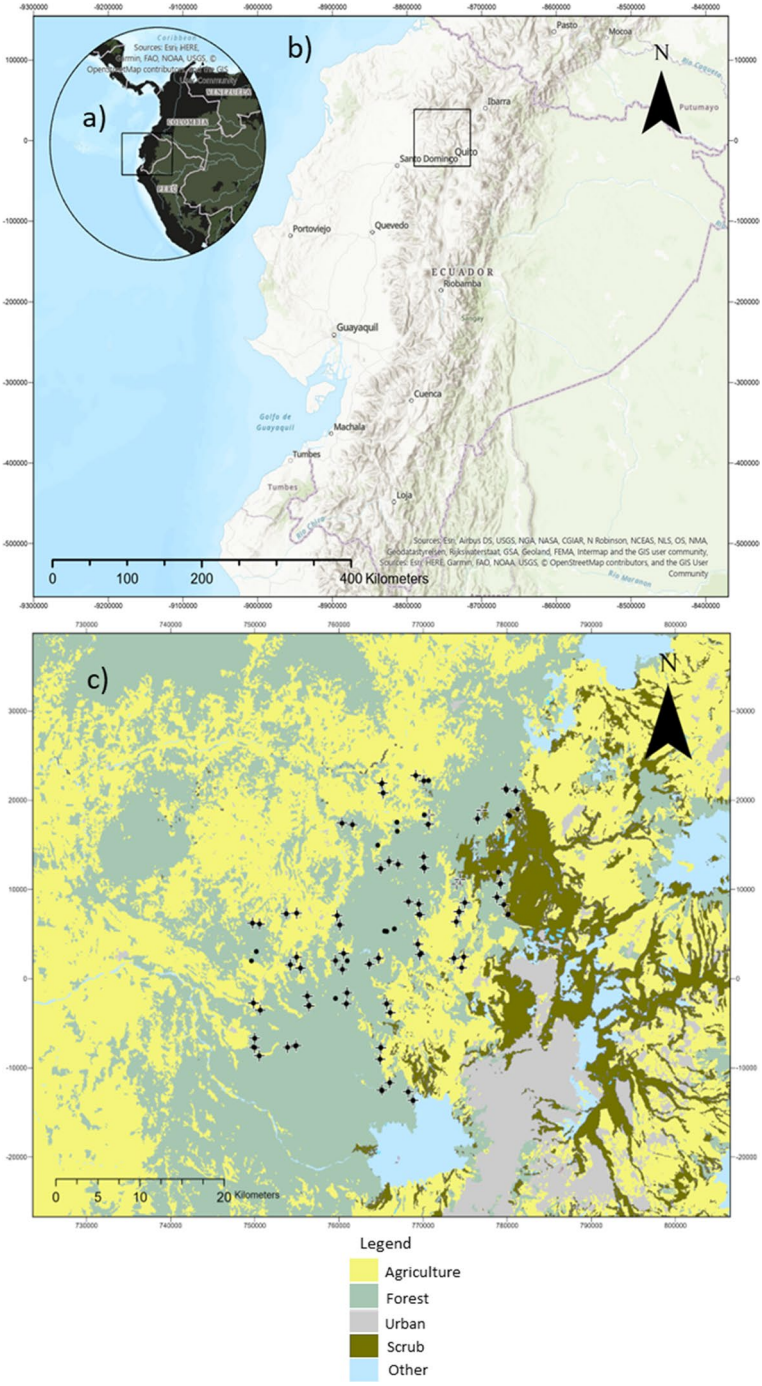

Fig. 1 **a)** Map of Ecuador in the context of Central and South America, **b)** location of Chocó-Andean region study area in the Ecuadorian Andes, and **c)** the sites sampled for tayra (*Eira barbara*) using camera traps across the 2 years of sampling (n = 173). Crosses denote the 70 sites sampled in 2016, black dots represent the 103 sites sampled in 2017

Abundance modelling

Our focus is on calculating an index of abundance for the tayra to infer habitat associations across the landscape. We achieved this by using a hierarchical modelling framework, specifically, the Royle-Nichols (RN) model (Royle and Nichols 2003). The approach is a variation on the standard occupancy model (Mackenzie et al. 2002) that uses a repeat visit sampling design to account for imperfect detection. The RN model includes a component for how variation in abundance induces variation in detection probability. The model exploits the link between heterogeneity in abundance and heterogeneity in detection probability to estimate the underlying distribution of abundances, and account for site level heterogeneity in detection. We do not attempt to estimate true abundance, but rather we assess site level variation through an index of abundance, in order to infer habitat associations across the landscape. The RN model assumes that the population level probability of detection is a function of individual detection probability and the number of individuals at the site, calculated as:

$$p_{ij} = 1 - \left(1 - r_j\right)^{N_i}$$

where p is the population level detection probability at site i on occasion j, r is individual level detection probability, N is the number of individuals (or alternatively it can be considered a random effect on heterogeneity in detection). Individual detection probability r_j is modelled as a function of observation covariates, and thus while constant for the population, r_j can vary across time and space. The observed detection non-detection data (y) at site i on occasion j are modelled as a Bernoulli trial with population level detection probability (p_{ij}):

$$y_{ij} \sim Bernoulli\left(p_{ij}\right)$$

In the state model, the number of individuals exposed to sampling at a site, N_i, are modelled as being drawn from a Poisson distribution with parameter λ_i, where $\log(\lambda_i)$ is modelled as a function of site covariates:

$$N_i \sim Poisson\left(\lambda_i\right)$$

The RN model assumes that at each survey occasion j at site i, $\mathrm{N_i}$ individuals are available to be detected. N_i is assumed to be constant over the sampling occasions, but can vary through space, with highly mobile animals and independent detectors, the abundance index derived from the λ_i parameter should be interpreted as the average number of individuals at site i. There are two critical assumptions of RN models; (1) the independence assumption that animal detections are independent and (2) the closure assumption that the number of animals at a site is assumed to be constant throughout sampling. We use a Poisson model, which despite its simplicity, is the natural distribution for modelling an index of abundance; the most obvious approach to constructing statistical models that explain variation in *N's* is a Poisson generalised model with a log-linear link for explaining variation in the mean of N (Royle and Nichols 2003). To explain variation in marginal abundance rates (the abundance of a species at a site given variation in a specific covariate with all others kept at their mean), we considered five landscape variables that had previously been observed to influence the species (Cove et al. 2014; Pardo Vargas et al. 2016; Bianchi et al. 2021). These variables were related to forest composition (% native forest), human disturbance (population

density -number of people per km^2), and core agricultural area (km^2), non-forested habitat (% scrub), and topography (elevation (m)). See Table S1 for definitions, range of values sampled, and sources of each covariate used in the analysis. We produced 5 km^2 buffers around each site and each covariate was summarized at the 5 km^2 scale. A 5 km^2 resolution was selected as it approximates the home range size of a tayra (Michalski et al. 2006). To explain variation in detectability, we considered six observation covariates. These covariates included time since scent was applied (averaged across each occasion), a learned behavioural response (1 if the focal species had been detected previously at a site, 0 if not), the date (ordinal day, both linear and quadratic terms), the number of operational camera days per occasion (to account for variation in number of cameras and deployment lengths), and the number of sampling occasions (ranging from 4 to 10, where a sampling occasion is 1 week). All continuous covariates were scaled and standardized to have unit variance and a mean of zero, and, based on variance inflation factors, there was no evidence of strong collinearity between any covariates (e.g. Zuur et al. 2009).

We considered all additive combinations of the five landscape covariates to describe variation in the index of abundance (see above), and all additive combinations of the six observation covariates to explain variation in detection probability (see above). We highlight that these data were collected across two primary survey periods (2016 and 2017). As our focus was not on colonization-extinction dynamics (which would not be advisable with just two years of data), we used a "stacked" design whereby each site-year combination was treated as a distinct site. As such, we include a year effect on both parameters in all models to account for any non-independence. Using a two-stage approach (Karanth et al. 2011), we first used model selection to find the most parsimonious covariate combination for detection probability while keeping lambda constant (i.e., $\lambda(.)$), and then, taking the top ranked detection model (i.e., p(top)), used model selection to determine the most parsimonious covariate combination for lambda. We used parametric bootstrapping to assess goodness of fit of the global model and calculate an overdispersion parameter ($\hat{c}$) for model selection and adjustment of standard errors (Mackenzie and Bailey 2004). Temporal dependence across years may result in artificially reduced standard errors lowering the uncertainty in parameter estimates, thus the $\hat{c}$ adjustment accounts for overdispersion using error inflation. We calculated quasi-Akaike's Information Criterion (QAIC) for model selection and used QAIC weights for model averaging which is the recommended practice for tackling lack-of-fit or overdispersion (Kéry and Royle 2016). Additionally, we calculated relative variable importance (w+) as the sum of the QAIC weights of all models that include a given covariate (Burnham and Anderson 2002). To avoid variable-selection ambivalence resultant from using 95% confidence intervals with an information theoretic approach, and for consistency between AIC-based model selection and reporting paradigms, we report 85% confidence intervals for each parameter (Arnold 2010). To increase clarity in model selection tables we removed parameter covariates with 85% confidence intervals that included zero, though all model sets were retained for model averaging and calculation of relative variable importance (Arnold 2010). The analysis was conducted using statistical software (in R version 4.2 [R Core Team, 2020] using the package "*unmarked*" for model fitting [function *occuRN()]*, Fiske & Chandler 2011). The goodness of fit testing, model averaging and QAIC-based ranking also were conducted using statistical packages ("AICcmodavg" [functions *gof.mb()* and *model_avg*()], Mazerolle 2020) and "*MuMIn*" (Barton 2022).

Results

Total effort for the two surveys across the 2 years of sampling was 16,226 sampling days (24-h periods) across 173 sites (6840 days at 70 sites in 2016 and 9386 days at 103 sites in 2017). Over the duration of the study there were 122 independent detections of tayras (maximum of one per weekly occasion, 55 in 2016, and 67 in 2017). The goodness-of-fit test indicated overdispersion with $\hat{c} = 1.31$ for the global model. Thus, QAIC scores using this $\hat{c}$ adjustment were used for subsequent model selection.

Model selection results from the first stage of our fitting process indicated that detection was influenced strongly by a single observation covariate: operational camera days. This represented an increase in detection of tayras with an increasing number of camera days in an occasion ($\beta_{\text{camdays}} = 0.40 \pm 0.13$, see Fig. 2). The top detection model had strong support (see Table 1) with all other parameters apart from time since scent application, showing evidence of redundancy (see Table S2 for full model selection results with uninformative parameters left in). Average individual detection probabilities (r) ranged from 0.07 to 0.16 depending on the year and number of operational camera days in the occasion.

At the 5 km^2 scale, model selection results from the second stage of the model fitting process were indicative of model uncertainty (Table 2). Relative variable importance

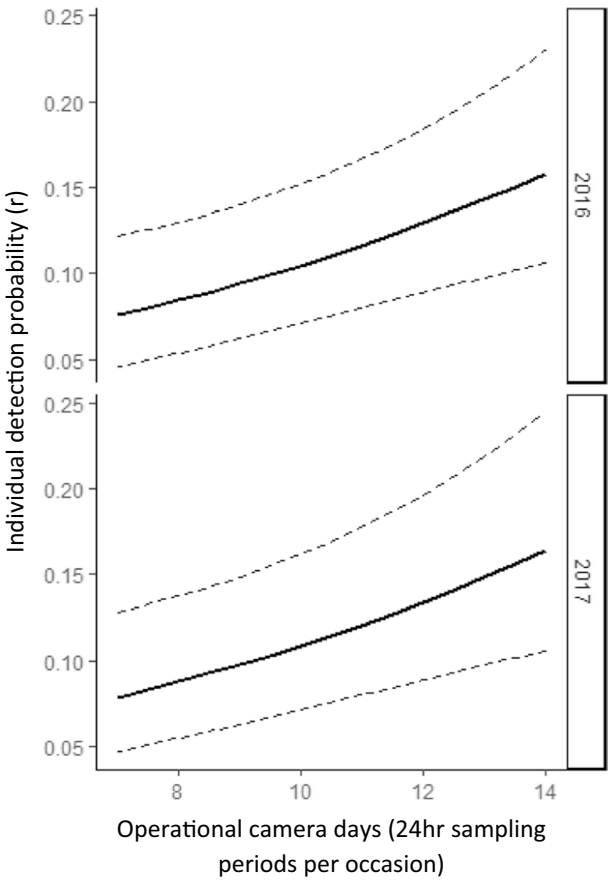

Fig 2 Variation in individual detection probability across the observed range of number of operational camera days per weekly sampling occasion during sampling for tayras in the Choco-Andean region of Ecuador in 2016 (top) and 2017 (bottom). Dashed lines are 85% confidence intervals

Table 1 Model selection results for covariates influencing the detection probability of tayras (*Eira barbara*) at a site using 173 camera trap stations throughout the Choco-Andean region of Ecuador between 2016 and 2017, with redundant parameters removed

Model	K	− 2logL	QAIC	Δ_{QAIC}	ω_{QAIC}
r(camdays)	4	− 387.93	602.25	0.00	0.68
r(camdays + scent)	5	− 387.88	604.18	1.93	0.26

Only models with $\Delta_{QAIC} < 2$ are displayed. Camdays is the number of operational camera days per occasion at a site, and scent is the average time since the application of scent at a site

Table 2 Model selection results for covariates influencing the index of abundance (λ) of tayras using 173 camera trap stations throughout the Choco-Andean region of Ecuador between 2016 and 2017

Model	K	− 2logL	QAIC	Δ_{QAIC}	ω_{QAIC}
λ (core agricultural + elevation + human)	8	− 379.37	597.19	0.00	0.18
λ (core agricultural + elevation + human + forest)	9	− 378.39	597.69	0.51	0.14
λ (core agricultural + elevation + human + forest + scrub)	10	− 377.47	598.29	1.10	0.10
λ (core agricultural + elevation + forest + scrub)	9	− 378.90	598.48	1.29	0.09
λ (core agricultural + elevation + human + scrub)	8	− 380.36	598.70	1.52	0.08
λ (core agricultural + elevation + forest)	9	− 379.27	599.04	1.86	0.07

The top detection model (operational camera days) is fixed for all models and not shown. Only models with $\Delta_{QAIC} < 2$ are displayed. K is the number of parameters in the model, − 2logL is the log-likelihood, QAIC is quasi-Akaike's Information Criterion (QAIC) value and ωQAIC is the QAIC weight

Table 3 Relative variable importance (ω+) for index of tayra abundance covariates at a 5 km^2 scale, calculated as the cumulative quasi-Akaike's Information Criterion (QAIC) weight of models that include each covariate. Each covariate was represented in an equal number of models

Lambda covariate	ω+
Elevation	0.95
Agriculture	0.83
Human population	0.64
Native forest	0.50
Scrub	0.36

values (Table 3) indicate that elevation (ω+ = 0.95) and core agricultural area (ω+ = 0.83) were the key predictors. Human population density (ω+ = 0.64) and native forest cover (ω+ = 0.50) were also important but less so than the former. Finally, scrub was the least important of the covariates (ω+ = 0.36).

We report model averaged estimates along with 95% confidence intervals (95% CIs), unless otherwise stated. Model averaged estimates of the index of abundance (λ) across sites in each year were 0.48 (95% CI 0.34–0.62) in 2016 and 0.34 (95% CI 0.24–0.45) in 2017. The model averaged parameter estimates suggest that higher elevations were related to lower tayra abundances ($\beta_{elevation} = -0.47$, CI 85% = − 0.70 to − 0.24). Human population density also had a negative relationship with the index of abundance for tayras ($\beta_{human} = -0.31$, CI 85% = -0.56 to − 0.07). Conversely, native forest had a positive association with tayra abundance ($\beta_{forest} = 0.35$, CI 85% = 0.02–0.67),

and higher proportions of core agricultural area were also related to higher indices of abundance ($\beta_{agriculture} = 0.39$, CI 85% = 0.16–0.63). Tayra index of abundance was independent from scrub cover ($\beta_{scrub} = 0.17$, CI 85% = − 0.07 - 0.41), with high uncertainty and 85% confidence intervals that overlapped zero (see Figs 3, 4). The model averaged predictions of lambda in 2017 across the entire 1332 grid cell landscape (6660 km^2) demonstrate how variation in elevation, core agricultural area, native forest, human population density, and scrub throughout the Ecuadorian Andes interact to jointly influence the index of abundance of tayras (see Fig. 5). Landscape predictions indicated a mean index of abundance (λ) of 0.25 (95% CI 0.13–0.61) at the landscape level.

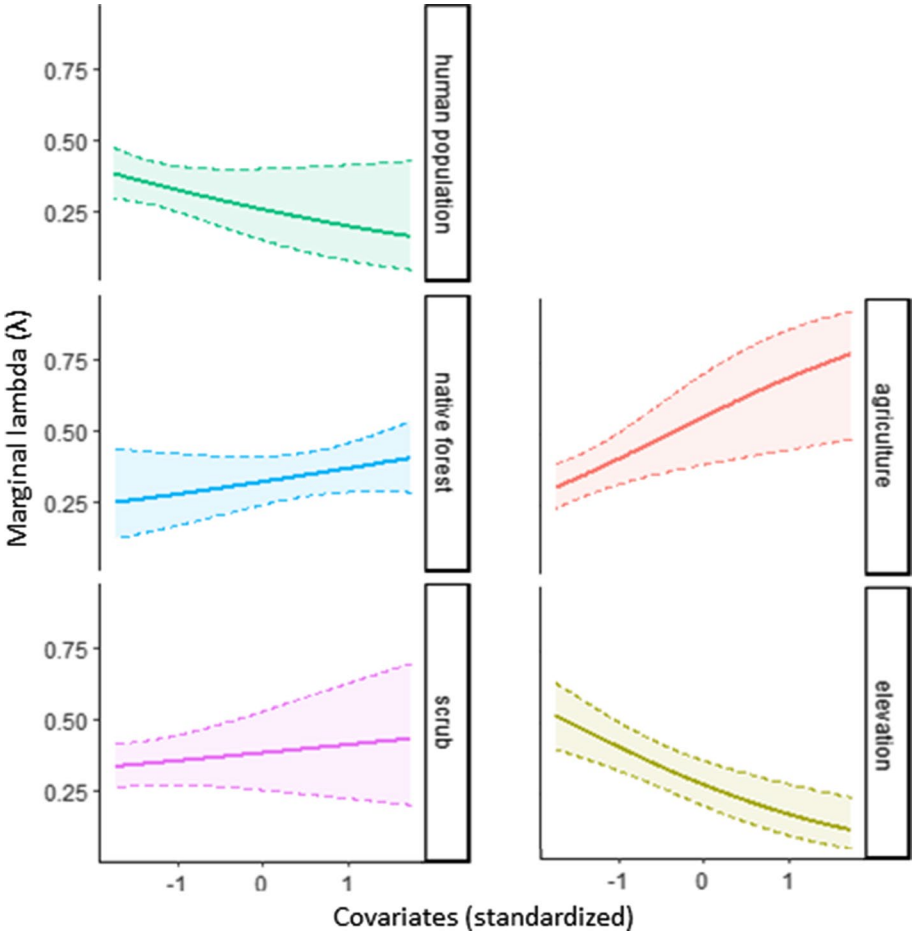

Fig. 3 Marginal model averaged predicted index of abundance (λ) for the tayra as a function of sampled parameter space for elevation, native forest, human population density, scrub cover, and core agricultural area (see Table S1 for total range of sampled values for each covariate). Dashed lines are 85% confidence intervals

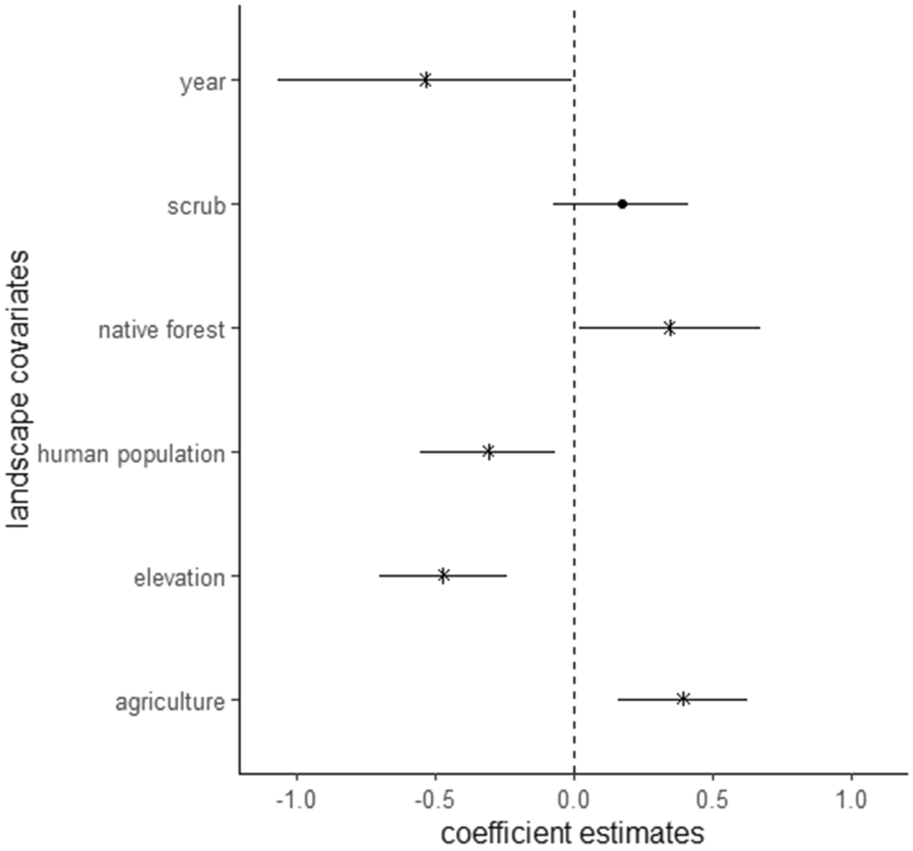

Fig. 4 Model averaged Royle–Nichols model coefficient estimates on the logs-odd scale with 85% confidence intervals showing associations between tayra index of abundance and model covariates from a camera trapping study of tayras in the Choco-Andean region of Ecuador from 2016 to 2017. Asterisks represent coefficients with strong relationships to tayra abundance (i.e., confidence intervals do not overlap 0)

Discussion

Our study suggests that tayras, while associated with native forest, are habitat generalists that are tolerant of and may even benefit from habitat conversion to agriculture. The index of abundance was positively correlated with the proportion of core agriculture albeit with high uncertainty at the upper limits of parameter space. The index of abundance for tayra was negatively associated with human density throughout the landscape; given the positive impact of human modified land uses (i.e., agriculture) on tayra abundance, human-tayra conflicts involving the depredation of poultry, livestock, and bees (e.g. Naughton-Treves et al. 2003; Flores-Armillas et al. 2020; Desbiez et al. 2020;dos Santos et al. 2020; Salom et al. 2021) could potentially lead to retaliatory killings of tayra and drive this negative association. However, it is also possible that tayra may avoid areas with high human activity and disturbance. In this multi-use landscape, scrub, an expected key habitat of the species, was independent from the index of abundance. This result supports the hypothesis that tayras are generalists with minimal habitat requirements, however, it is critical to note

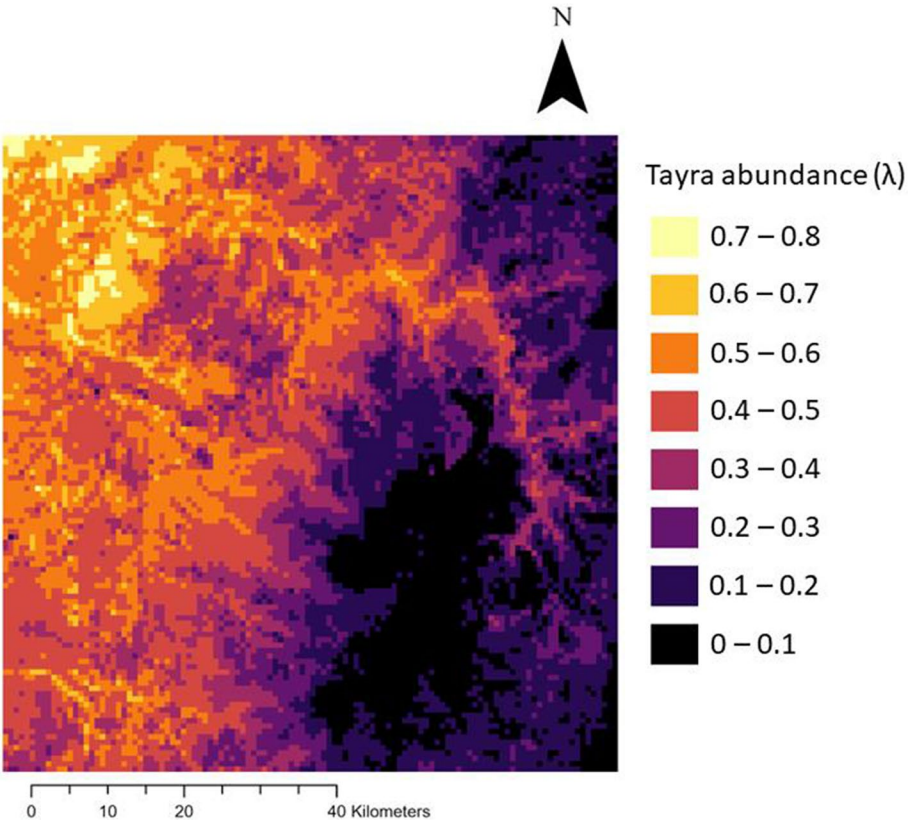

Fig. 5 Model averaged predictions of tayra index of abundance (λ) across approximately 6726 km^2 landscape in the Ecuadorian Andes based on single-species Royle-Nichols models applied to a camera trapping dataset collected from the Choco-Andean region between 2016 and 2017

the importance of elevation on tayra abundance observed here. Elevation had a strong negative relationship with the index of abundance for tayra. This negative relationship suggests the tayra is a lowland species that is limited in the less productive higher elevation habitats of the Ecuadorian Andes. Combined, these results suggest that for tayra populations inhabiting neotropical landscapes undergoing rapid anthropogenic change and growth, conservation efforts focused on the human dimensions of coexistence and conflict mitigation/reduction are likely to be critical to the species future. Indeed, increased understanding of human attitudes and behaviours towards tayras and other carnivores in the region could be important for tayra conservation. As opposed to the requirement of pristine reserves and protected areas that may be considered key to species conservation, our study results suggest that tayras are disturbance-tolerant and able to adapt and survive in modified landscapes, given social acceptance. This is a critical finding when prescribing effective conservation strategies for the species given the expected increases in human presence in neotropical landscapes in the near future.

In consensus with a growing body of literature focused on the ongoing carnivore declines and recoveries globally, we suggest that tayras, a medium sized generalist predator in the neotropics, are able to adapt to and exploit human modified landscapes (Chapron

et al. 2014; Twining et al. 2020). Previous research has observed tayras occurring in close proximity to agricultural fields, orchards, and other human-altered landscapes retaining some forest cover, with the suggestion that the species may be benefitting from the abundance of small mammals, birds, and insects associated with edge habitats, as well as the human trophic resources (e.g. crops) present in these habitats (Presley 2000; Dotta and Vedade 2011; Timo et al. 2014; Cove et al. 2014). It has also been hypothesized that tayras observed associations with agricultural lands may be linked to reduced competition and predation from larger predators that do not occur in such matrix habitats (Massara et al. 2018), however, given growing evidence of habitat tolerance of many large carnivores in a range of systems globally, this seems a less likely explanation.

Global declines of carnivores have primarily been attributed to habitat loss and human persecution (Ripple et al. 2014). We provide another example of a carnivore that is tolerant of land-use change but is sensitive to human presence, with potential population-level impacts that could be driven by conflict with humans as has been observed with other carnivores (Liberg et al. 2011; Nowak and Myslajek 2016). As with large carnivores globally, it appears co-adaptation and managing public perception and human interactions with tayra may be important for the species ability to co-exist with humans in expanding human modified landscapes (Sharpe et al. 2001; Clark and Rutherford 2014; Carter and Linnell 2016). We infer this from the fact that human population density was associated with lower abundances of the tayra despite human land-uses (core agriculture) being positively associated with tayra abundance. The potential for conflict with tayra and negative human response is supported by the fact that tayras are increasingly mentioned as a problem species in research on human-wildlife conflict across a range of localities in Central and South America (e.g. Flores-Armillas et al. 2020; Desbiez et al. 2020; dos Santos et al. 2020; Salom et al. 2021). Additional evidence stems from a study that showed tayras to cause the second highest amount of damage to crops per season after tapirs (*Tapiridae* sp.) in a multi-use landscape in nearby Peru and, where they were also cited as key wild predators of livestock losses, namely poultry and pigs (Naughton-Treves et al. 2003). This previous work suggested that carnivores such as the tayra are unlikely to be able to persist in multi-use zones in Amazonian forests without restriction of hunting or legal protection. However, the efficacy of legal protection alone remains unclear, with illegal cryptic killings still sufficient to halt recovery or even drive declines of carnivores in certain localities (e.g. Musto et al. 2021).

The tayra is generally considered to be a forest specialist (Goulart et al. 2009; Bogoni et al. 2013; Bianchi et al. 2021). However, apparently conflicting evidence exists from Costa Rica where tayra occupancy was negatively associated with forest cover (Cove et al. 2014) and Peru where no relationship was exhibited (Tobler et al. 2015). We see in our study that forest cover was positively correlated with our index of tayra abundance. While it is possible that these observed habitat associations represent the true states and associations of tayra which vary across these different localities, it is also possible they are facets of different study designs and the extents of parameter space explored. For example, in Cove et al. 2014, while the parameter space explored was relatively broad (17–100% forest cover), all the cameras themselves were deployed in forested sites. Thus, the study design used results in a bias that must be recognized, and a negative relationship between forest and occurrence does not suggest that tayras are not forest dependent, it may simply reflect the species propensity to thrive in edge and matrix habitats when forest is present and they have opportunities to exploit additional resources such as crops and livestock, as we see here. Additionally, as a habitat generalist tayra abundance may peak at intermediate values of parameter space (displaying a quadratic, as opposed to linear relationship). We were

unable to explore this relationship here due to limitations of sample size. Nonetheless, the myriad of responses observed by the tayra across its range (Goulart et al. 2009; Bogoni et al. 2013; Cove et al. 2014; Tobler et al. 2015; Bianchi et al. 2021) provide additional support for the species status as a generalist that may be relatively robust to the rapidly occurring land-use changes being witnessed in the neotropics.

While 2 years of monitoring is not sufficient to describe a population trend, with any variation more likely due to natural stochasticity than an actual trend, we did observe that the mean estimated index of abundance on a landscape-level appeared to decline in the second year of sampling. Tayras are dietary generalists with reported dietary items varying from fruits, invertebrates, small mammals, birds, and reptiles, to larger mammals including primates and South American brown brocket (*Mazama gouazoubira,* Calouro, 2000; Campos and Mourão 2015; Sobroza et al. 2016; Sáenz-Bolaños et al. 2019). Thus, it would be unexpected for the species population dynamics to vary significantly interannually as is observed in specialist predators in predator–prey limit cycles where predator population dynamics are coupled with specific prey that undergo pronounced interannual cycles (Hanski et al. 1991). It is possible that the changes in the index of abundance in our study may be due to unmodelled factors that are affecting heterogeneity in detection, not linked to abundance. Nonetheless, the decrease in our index of abundance at the landscape level between the years, while potentially a red herring, raises the importance of further monitoring. The small number of repeated surveys conducted here can provide insights into the drivers of species occurrence and abundance, but they are not sufficient to provide reliable inference on population trends which is only attainable through the establishment of long-term monitoring programs.

The models used herein (RN models) are sensitive to violations of the implicit model assumptions (outlined in the methods; namely, assumptions of independence and closure). Given the site spacing, the occasion length, and home range size estimates for tayras (5 km^2, Michalski et al. 2006), the independence assumption appears to hold. As a territorial mustelid, and member of the *Martes* complex, one can assume somewhat similar movement patterns and stability of territories as their more extensively studied cousins: martens and fishers (Powell 1979, 1994; Facka and Powell 2021). Thus, assumptions of closure initially appear to be unbroken also, however, an outstanding issue remains: it is unclear whether tayras have a discrete breeding season, with natural history observations suggesting the species may breed continuously throughout the year. Given this unknown about tayras breeding habits, we recognize that it is possible for closure assumptions to be violated, but to an unspecified magnitude. Due to all sampling being conducted over a 3-month period in each year, we assume that any violations of closure assumptions due to breeding are minimal. Our evidence is correlative as opposed to being experimental, but it is derived from a repeated structured survey, and couples probabilistic methods that explicitly account for imperfect detection of the target species with a large and representative sample. Central to the design of this study was its placement in a multi-use landscape with sampling encompassing a broad range of parameter space for each of the key covariates (see Table S1). Our study therefore is valuable in being able to help inform conservation and management in this region.

We provide support for the tayra as a habitat generalist, and while the species may require forest cover in some form, it is likely to be able to survive in human modified landscapes. We highlight the potential for agricultural lands and other human land uses that provide exploitable human trophic subsidies to potentially benefit the species. However, we caution overoptimism, and suggest potential for human-wildlife conflicts to pose a threat to tayra abundance in the future. Tayras may be increasingly sharing their

landscapes with humans as human impacts on natural lands across the region increase. Thus, conservation efforts may benefit by anticipating and mitigating future human-wildlife conflict through additional research focused on understanding the attitudes, behaviours, and motivations of humans in conflict with tayras.

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Data availability The data are available on request to corresponding author.

Declarations

Competing interests The authors declare they have no competing interests.

Ethical approval This project was entirely non-invasive, using remote cameras to record detections of animals, and thus did not require ethics approval.

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