

Occurrence dynamics of mammals in protected tropical forests respond to human presence and activities

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Protected areas (PAs) play a vital role in wildlife conservation. Nonetheless there is concern and uncertainty regarding how and at what spatial scales anthropogenic stressors influence the occurrence dynamics of wildlife populations inside PAs. Here we assessed how anthropogenic stressors influence occurrence dynamics of 159 mammal species in 16 tropical PAs from three biogeographic regions. We quantified these relationships for species groups (habitat specialists and generalists) and individual species. We used long-term camera-trap data (1,002 sites) and fitted Bayesian dynamic multispecies occupancy models to estimate local colonization (the probability that a previously empty site is colonized) and local survival (the probability that an occupied site remains occupied). Multiple covariates at both the local scale and landscape scale influenced mammal occurrence dynamics, although responses differed among species groups. Colonization by specialists increased with local-scale forest cover when landscape-scale fragmentation was low. Survival probability of generalists was higher near the edge than in the core of the PA when landscape-scale human population density was low but the opposite occurred when population density was high. We conclude that mammal occurrence dynamics are impacted by anthropogenic stressors acting at multiple scales including outside the PA itself.

Land-use change is the primary driver of biodiversity loss, mainly through the loss, degradation and fragmentation of habitat^{1,2}. This is particularly the case with the conversion of species-rich tropical forests to anthropogenic land uses^{3,4}. With growing threats such as land-use change, hunting and fires, protected areas (PAs) provide vital refuges for many species as they can prevent biodiversity declines especially in medium- and large-sized mammals^{5,6}. For this reason, the need to increase and expand the coverage of PAs has been recognized globally

as a conservation priority (UN Biodiversity Conference, COP 15). Concurrently, there is an urgent need to assess the degree to which PAs can conserve wildlife, how different anthropogenic stressors may affect the potential of PAs in protecting wildlife populations and how this depends on the species and the location.

At least three factors hamper our ability to make robust conclusions about the effectiveness of PAs in the tropics. First, availability of biodiversity data across the tropics are scarce^{7,8}. Second, available data

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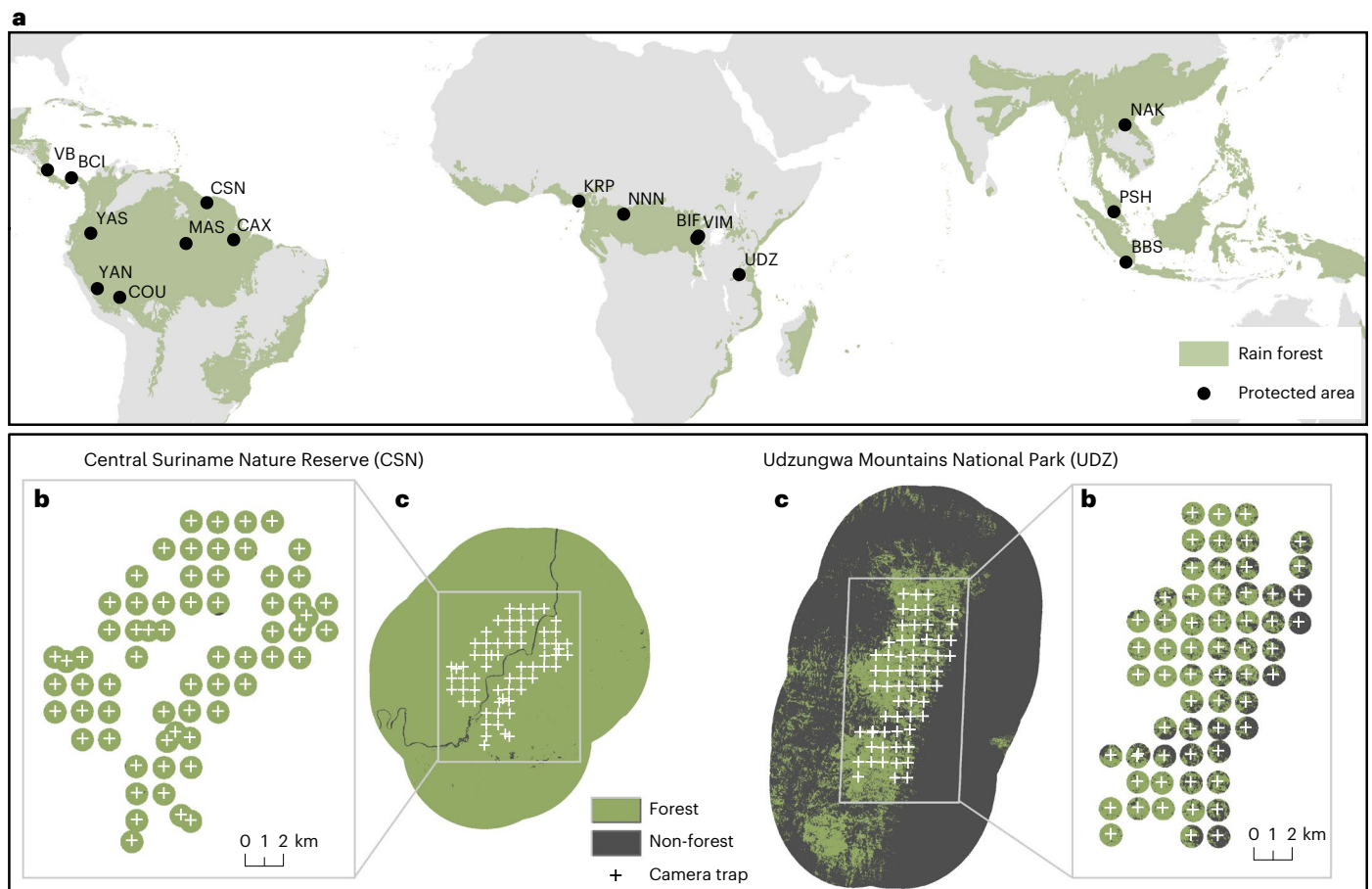


Fig. 1 | Distribution of study locations. **a**, Location of PAs ($n = 16$) in tropical and subtropical rain forests. **b, c**, Camera-trap sites and forest cover for two PAs (Central Suriname Nature Reserve (CSN) and Udzungwa Mountains National Park (UDZ)) at the local scale (600 m circular buffer around camera-trap sites) (**b**) and landscape scale (10 km buffer around camera-trap arrays) (**c**). CSN provides an example of a protected area with a high percentage of forest cover (**b** and **c**) and low forest fragmentation at the landscape scale (**c**). On the contrary, camera-trap sites from UDZ show a larger variation in forest cover at the local scale (**b**)

and high fragmentation at the landscape scale (**c**). BBS, Bukit Barisan; BCI, Barro Colorado Nature Monument–Soberania National Park; BIF, Bwindi Impenetrable National Park; CAX, Caxiuana National Forest; COU, Cocha Cashu–Manu National Park; KRP, Korup National Park; MAS, Manaus; NAK, Nam Kading; NNN, Nouabali Ndoki; PSH, Pasoh Forest Reserve; VB, Volcan Barva; VIR, Virunga Massif; YAN, Yanachaga Chimillen National Park; YAS, Yasuni National Park. Map data credits: **a**, GIS Lounge; **b, c**, ref. 3.

often register the presence or absence of a species at a single point in time rather than trends over time⁹, which precludes monitoring and assessment of changes^{10,11}. Finally, species responses to anthropogenic pressures at a given location depend on the spatial extent (hereafter scale) at which they are measured, yet biodiversity patterns often reflect multiple processes that operate at different scales^{12–14}. Pumas, for example, select certain habitat such as woodlands or grasslands at a local scale (250–530 m) but avoid agricultural and urban areas at larger scales (7.6–9.9 km)¹⁵. This is important because species may be affected by not only human presence and activities inside the PA (at the local scale) but also at larger scales that encompass areas outside the PA. Others¹⁶ investigated how forest cover at the local scale (30–120 m) related to the occurrence dynamics of tropical mammals and did not detect a significant relationship. However, such results may be confounded by larger landscape-scale conditions. For instance, a pantropical meta-analysis suggests that habitat destruction around PAs is associated with biodiversity declines inside PAs¹⁷. Empirical evidence of how anthropogenic stressors at multiple scales impact the dynamics of biodiversity within tropical PAs is sparse. In particular, the extent to which processes at the local and landscape scale interact and how such interactions affect tropical-forest mammal communities remains largely unknown.

The scale at which environmental change impacts mammal populations has implications for PA management. For instance, if forest fragmentation or human population density at the landscape scale reduces local colonization, large-scale land-use planning and protection should be prioritized (inside and outside PAs). Examples are by establishing buffer zones around PAs where only compatible land uses are permitted (such as low-intensity native polyculture instead of exotic monoculture tree plantations) or by increasing connectivity to other reserves¹⁷. Similarly, hunting restrictions or regulations within PAs (local scale) may be insufficient to halt the negative landscape-scale effects of hunting and other human impacts¹⁸. Alternatively, if habitat within the PAs is the main influence on colonization, emphasis should be placed on maintaining this protected habitat.

Anthropogenic threats do not act randomly, with some species more affected than others. Additionally, the effects of anthropogenic activities on species can differ in the direction of their effect as seen in both negative and positive responses to habitat fragmentation^{19,20}. For example, species that occupy only a few habitat types (hereafter specialists) are at greater risk of extinction than those that occupy many (hereafter generalists) and are also known to be more sensitive to human-induced environmental changes such as habitat loss^{21–24}. Furthermore, assessing species-specific responses

to multiple anthropogenic stressors offers a nuanced picture of the impacts of human activities on mammals. For instance, individual species responses to anthropogenic stressors that are not related to habitat characteristics (for example, hunting pressure) can be difficult to capture when focusing on species groups representing habitat preferences. Understanding species-specific variation can also guide conservation planning, as conservation efforts can be better focused on species recognized as vulnerable in the local context.

Assessments of biodiversity patterns often rely on static models which fail to capture the processes underlying patterns of change²⁵. Dynamic modelling approaches permit direct assessment of biodiversity changes and the factors influencing them. Dynamic occupancy analysis, for example, uses data from multiple time periods (seasons or years) to model changes in species occurrence over time—'occupancy dynamics' sensu ref. 26—as arising from the process of local extinction and (re)colonization events across multiple sites within a study area²⁶. In this framework, an occupied site within the study area can become unoccupied (local extinction) and can subsequently be recolonized. The species can remain extant in the study area even if it disappears at certain sites. Both local extinction (or its complement, survival) and colonization probabilities can be modelled as functions of environmental variables, potentially yielding a process-based understanding of human and other impacts on wild populations. Additionally, like conventional single-season occupancy models, dynamic occupancy models account for imperfect detection²⁶. Finally, Bayesian hierarchically structured multispecies frameworks permit assessment of species responses to anthropogenic processes and impacts simultaneously at the species, group and community levels.

Here, we quantified the effects of anthropogenic stressors on the occurrence dynamics of mammals. We used data from the largest standardized tropical-forest camera-trap monitoring system which included 1,002 sites from 16 PAs (Fig. 1) and a hierarchical Bayesian dynamic multispecies occupancy model. We focused on 159 medium-to-large mammal species (>1 kg) and used habitat breadth information to classify species as specialists or generalists²⁷. To model local colonization and survival probabilities we used spatial covariates extracted both at the local scale (home range) and landscape scale (10 km buffer around each camera-trap array²⁸). Local-scale covariates capture processes and impacts inside the PA, whereas landscape-scale covariates capture processes and impacts both inside and outside the PA. For two of the largest PAs, the landscape-scale covariates reflect processes mostly inside the PA (Supplementary Fig. 1). These covariates reflected anthropogenic stressors: deforestation (percentage of forest and division index as a measure of forest fragmentation) and human pressure (distance to protected area edge, distance to built-up areas and human population density). Additionally, we modelled detection probability as a function of three fixed covariates: maximum temperature, slope and species body mass. Specifically, we addressed two questions:

- (1) How do local- and landscape-scale anthropogenic stressors relate to local colonization and survival probabilities?
- (2) Do these relationships differ between habitat specialists and habitat generalists and among species of the same group?

Results

We compiled data on 159 species (388 populations) based on a total sampling effort of almost 170,000 camera-trap nights. Of these species, 90 were classified as habitat specialists occurring in four or fewer suitable International Union for Conservation of Nature (IUCN) habitat types and 69 as habitat generalists occurring in five or more habitats (Supplementary Table 1). At the local scale, percentage of forest ranged from 0 to 100, distance to PA edge from 0.02 to 25.16 km and distance to built-up areas from 0.05 to 48.78 km (Supplementary Figs. 2–5). At the landscape scale, division index ranged from 0 to 0.98 and human population density (number of people per km²) from 0 to 575.10 people per km² (Supplementary Fig. 6).

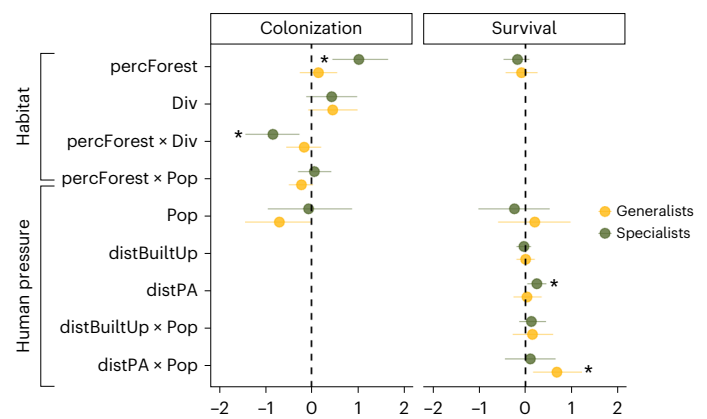


Fig. 2 | Effect of habitat- and human pressure-related covariates on colonization and survival probability for habitat specialists and generalists. Plots include mean standardized β coefficients and 95% BCI. Covariates are percentage of forest (percForest), division index (Div), human population density (Pop), distance to built-up (distBuiltUp) and distance to PA edge (distPA). The effect of a covariate was considered significant (marked with *) when the 95% BCI did not overlap zero (dashed vertical lines).

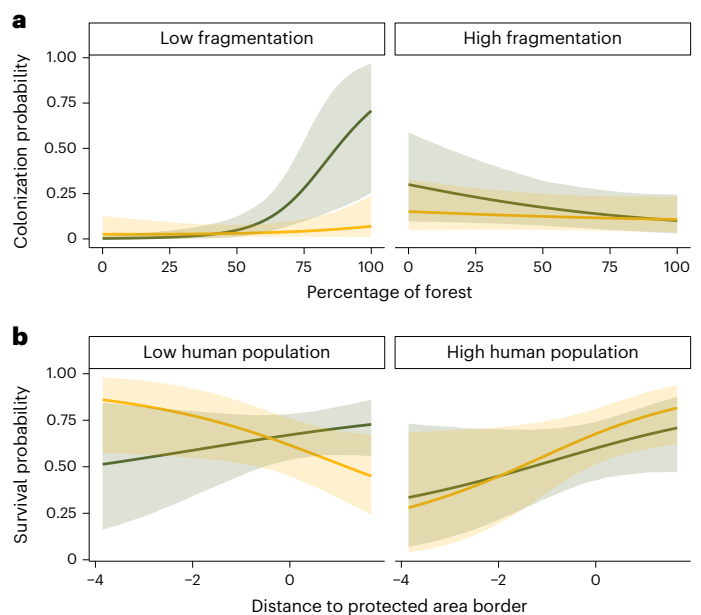


Fig. 3 | Mean predicted colonization probability for specialists and generalists in relation to habitat- and human pressure-related covariates. **a**, Colonization probability in relation to percentage of forest and division index. Low fragmentation represents the lowest large-scale division index value (0) and high fragmentation the highest division index value (0.98). **b**, Survival probability in relation to distance to PA edge and human population density. Low human population represents a human density of 4 people km⁻² (mean value of the lower 50th percentile of human population values) and high human population a density of 189 people km⁻² (mean value of the upper 50th percentile of human population values). Shaded areas indicate 95% BCI.

Overall, multiple covariates representing anthropogenic processes and impacts at the local and landscape scales (percentage of forest, division index, human population density and distance to PA edge), had significant effects on occurrence dynamics which varied between generalists and specialists (Figs. 2 and 3), as well as among species within groups (Figs. 4 and 5 and Supplementary Figs. 7 and 8). Detection probability was negatively associated with maximum

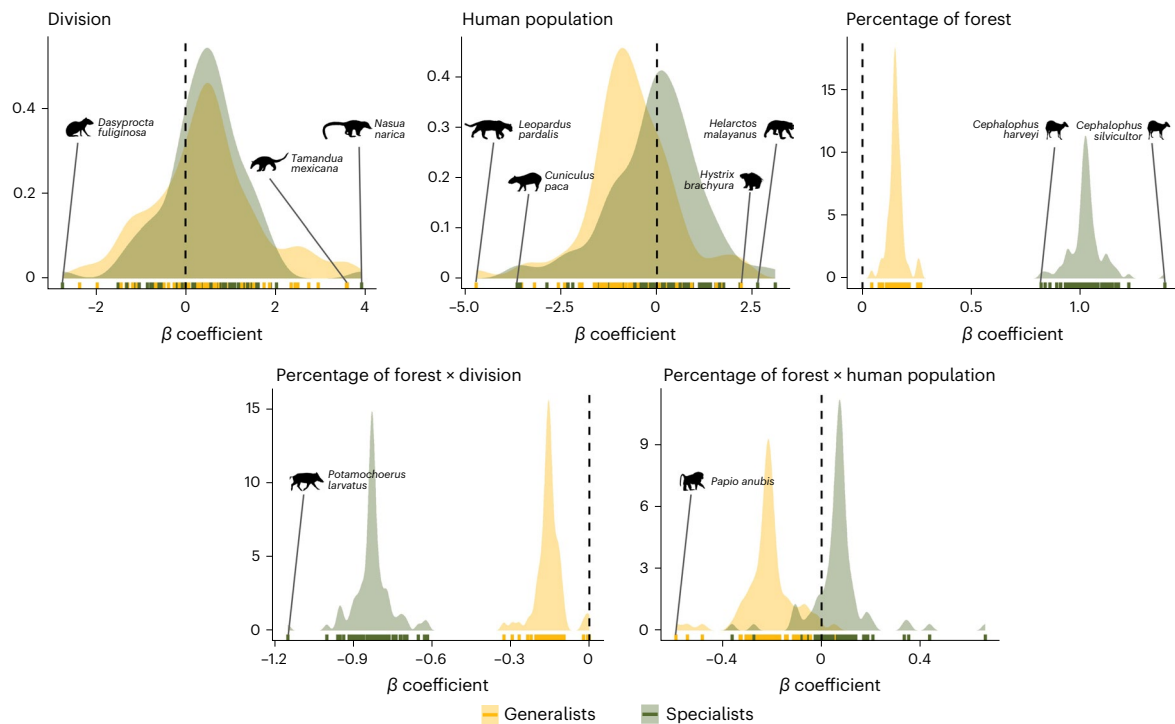


Fig. 4 | Density plot for species-specific β coefficients for colonization probability. Each coloured line on the x axis represents one distinct species, with the strongest significant effects highlighted with black silhouettes. Uncertainties associated with group-specific parameters are provided in Fig. 2 and Supplementary Fig. 9. Uncertainties associated with species-specific estimates are included in Supplementary Fig. 7. Dashed lines indicate a value of zero for the

β coefficient. Species silhouette images credit: Phylopic (*Dasyprocta fuliginosa*, *Helarctos malayanus*, *Cuniculus paca* and *Papio anubis* by Margot Michaud; *Tamandua mexicana* by Xavier A. Jenkins; *Nasua narica* by RS; *Leopardus pardalis* by Gabriela Palomo-Munoz; *Hystrix brachyura* by T. Michael Keesey; *Cephalophus harveyi* and *Cephalophus silvicultor* by Kai Caspar; *Potamochoerus larvatus* by Ferran Sayol).

temperature of the month when the camera trap was active (or months if the camera trap was active for more than one month) but positively associated with slope and body mass (Supplementary Table 2), although only slope had a significant effect on detection probability ($\beta = 0.06$; 95% Bayesian credible intervals (95% BCI) = 0 to 0.12). We note that here in the results we use the term 'effect' in its statistical sense and do not infer causation.

Colonization probability

Local colonization—the probability that an empty camera-trap site becomes occupied by the subsequent year—was associated with habitat-related covariates more strongly for specialists than for generalists; that is, percentage of forest and division index had significant effects on colonization only for specialists. However, covariates related to human pressure; that is, human population density and the interaction between human population density and percentage of forest, did not have detectable effects on either specialists or generalists (Fig. 2). Percentage of forest at the local scale had a positive effect on local colonization of specialists ($\beta = 1.03$; 95% BCI = 0.46–1.66). This positive effect was consistent for all specialist species, with only 6% of specialists ($n = 5$ of 90) revealing a non-significant effect (Fig. 4 and Supplementary Fig. 7). Division index also had a positive effect on colonization ($\beta = 0.44$; 95% BCI = -0.11 – 0.99) but the interaction between percentage of forest (measured at the local scale) and division index (landscape scale) had a negative effect on colonization ($\beta = -0.83$; 95% BCI = -1.42 to -0.26 ; Fig. 2). This means that forest cover had a strong and positive effect on colonization in PAs where large-scale fragmentation was low but a weak negative effect when large-scale fragmentation was high (Fig. 3). The effect of the interaction between percentage of forest and division index on colonization was consistent for all specialists, although 51% ($n = 46$ of 90) did not show a significant species-level effect (Fig. 4 and Supplementary Fig. 7).

Survival probability

Local survival—the probability that an occupied camera-trap site remains occupied the following year—was associated with covariates representing human pressure. Distance to PA edge had a positive effect on survival although this effect was only statistically significant for specialist species ($\beta = 0.25$; 95% BCI = 0.05–0.45). This result was consistent for all species of that group although only two species showed significant relationships (yellow-backed duiker, *Cephalophus silvicultor* and common opossum, *Didelphis marsupialis*) (Fig. 5 and Supplementary Fig. 8). Importantly, the interaction between distance to PA edge (measured at the local scale) and human population density (landscape scale) had a positive effect on survival but this effect was significant for generalists only ($\beta_{\text{generalists}} = 0.69$; 95% BCI = 0.17–1.22; $\beta_{\text{specialists}} = 0.11$; 95% BCI = -0.44 – 0.65 ; Fig. 2). This means that generalists had a higher probability of surviving near the PA edge in areas with low human population density (large scale) and further from the PA edge in areas with high human density, whereas specialist species always had higher survival probabilities further from the PA edge (Fig. 3).

Differences within species groups

Within-group variation was lowest for the effect of percentage of forest on colonization and this was particularly the case for generalists ($\sigma^2_{\text{generalists}} = 0.15$; 95% BCI = 0.01–0.38; Supplementary Fig. 9). The effect of percentage of forest on colonization was positive for all species in both groups although none of the generalist species had a significant effect. We found the strongest effect for the yellow-backed duiker ($\beta = 1.39$; 95% BCI = 0.61–2.33; Fig. 4 and Supplementary Fig. 7).

Within-group variation was highest for the effect of human population density on both colonization and survival, especially for habitat specialists ($\sigma^2_{\text{colonization specialists}} = 2.22$; 95% BCI = 1.50–3.18; Supplementary Fig. 9), which means that we observed substantial variation among

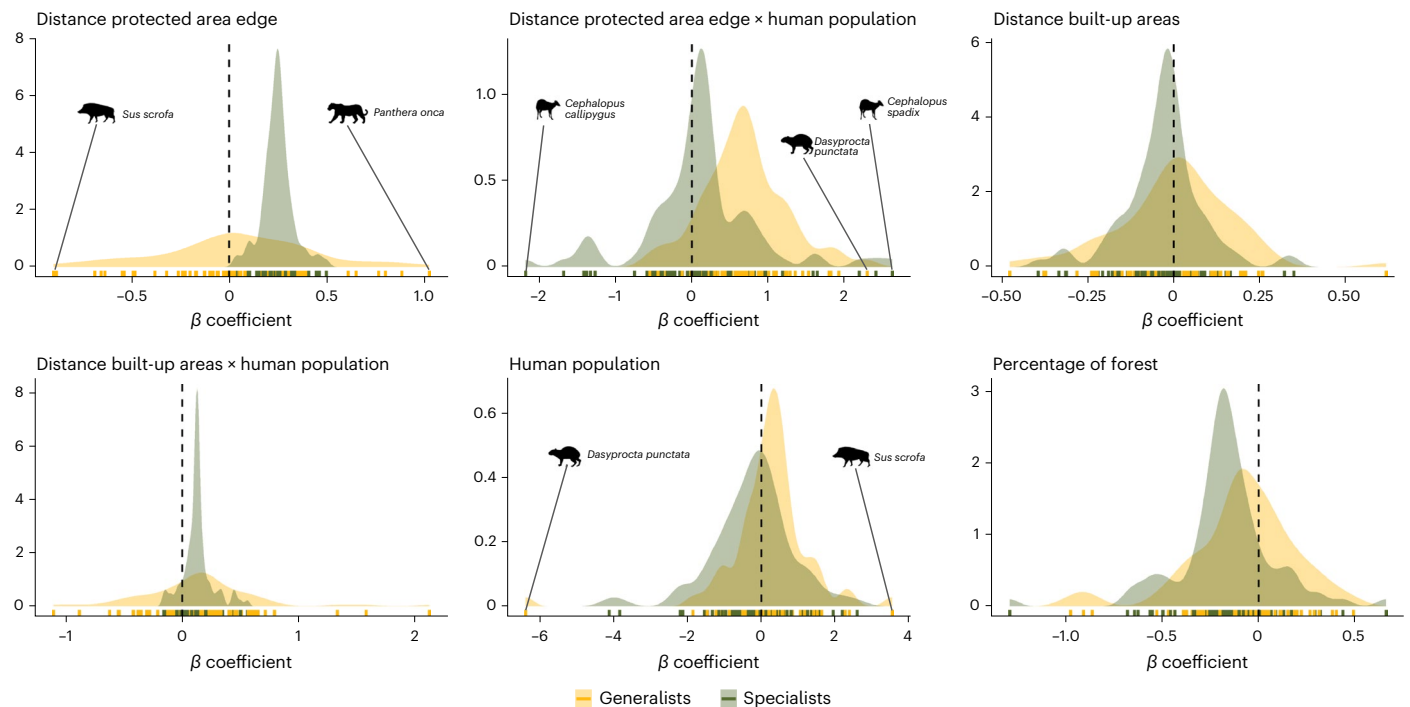


Fig. 5 | Density plot for species-specific β coefficients for survival probability. Each coloured line on the x axis represents one distinct species, with the strongest significant effects highlighted with black silhouettes. Plots for distance to built-up, distance to built-up $\times$ human population and percentage of forest do not contain examples of species because few showed significant effects (none, one and three species respectively). Uncertainties associated with group-

specific parameters are provided in Fig. 2 and Supplementary Fig. 9. Uncertainty associated with species-specific estimates is included in Supplementary Fig. 8. Dashed lines indicate a value of zero for the β coefficient. Species silhouette images credit: Phylopic (*Sus scrofa* by Steven Traver; *Panthera onca* and *Dasyprocta punctata* by Gabriela Palomo-Munoz, *Cephalopus callipygus* and *Cephalopus spadix* by Kai Caspar).

specialist species in their response to human population density. For example, we found strong negative effects of human population density on colonization for the ocelot, *Leopardus pardalis* ($\beta = -4.72$; 95% BCI = -6.81 to -2.94) and lowland paca, *Cuniculus paca* ($\beta = -3.65$; 95% BCI = -4.71 to -2.64 ; Fig. 4 and Supplementary Fig. 7), while we found strong positive effects for the sun bear, *Helarctos malayanus* ($\beta = 2.62$; 95% BCI = 0.06 – 5.55) and Malayan porcupine, *Hystrix brachyura* ($\beta = 2.19$; 95% BCI = 0.93 – 3.54 ; Fig. 4 and Supplementary Fig. 7). Regarding survival, we found for example, a strong negative effect for the wild Central American agouti, *Dasyprocta punctata* ($\beta = -6.38$; 95% BCI = -9.54 to -3.48) and a strong positive effect for the wild boar, *Sus scrofa* ($\beta = 7.23$; 95% BCI = 4.72 – 10.01 ; Fig. 5 and Supplementary Fig. 8). The effect of division index on colonization also showed high within-group variation, especially for generalists ($\sigma^2_{\text{generalists}} = 1.59$; 95% BCI = 1.18 – 2.12 ; Supplementary Fig. 9). Nevertheless, we detected the strongest significant effects among specialist species: strongest negative coefficient in the black agouti (*Dasyprocta fuliginosa*) ($\beta = -2.74$; 95% BCI = -4.78 to -0.87) and the strongest positive coefficient in the white-nosed coati (*Nasua narica*; $\beta = 3.92$; 95% BCI = 2.75 – 5.30 ; Fig. 5 and Supplementary Fig. 7).

Discussion

We assessed how anthropogenic processes and impacts covary with mammal occurrence dynamics in tropical protected forests. Three key findings emerged. First, the probability of a site being colonized by specialists depended on forest cover at the local scale (within the PA) but also on habitat fragmentation at the landscape scale (within and outside the PA). Second, generalists had higher survival near the PA edge when human population density at the landscape scale was low. Finally, habitat specialists were particularly vulnerable to habitat destruction, whereas generalists were vulnerable to other human pressures, although there was considerable variation among species within both specialist and generalist groups.

Colonization probability

Local colonization by habitat specialists was primarily associated with habitat-related covariates. Forest cover at the local scale was positively linked with colonization probability ($H1_v$, Table 1) and was the most important predictor of colonization, followed by the interaction between local-scale forest cover and landscape-scale fragmentation. This agrees with previous studies showing that responses to forest loss depend on ecological specialization^{29,30} and, reassuringly, supports the assumption that deforestation poses a greater threat to forest specialists than to generalists as the latter are more likely to persist in anthropogenic and heterogeneous habitats²¹. Similar results have been documented for birds, for which a decrease in forest cover was negatively associated with the diversity of specialist taxa²⁹. We note that our classification for habitat specialization should be understood as a relative measure, meaning that specialists are species occupying fewer habitat types than generalists and that different criteria can be used to define specialist species. Assessing how strictly specialist species (species which occur only in one type of habitat) respond to anthropogenic stressors would be interesting; however, our data did not contain sufficient species occupying a single habitat type (only 19 species) to draw robust inferences (Supplementary Fig. 10).

Landscape context modulated the effect of forest cover on colonization and, again, this was clearly detected only for habitat specialists. When landscape-scale fragmentation was low, the probability of colonizing a camera-trap site increased with increasing forest cover at the local scale. This relationship, however, disappeared when fragmentation increased. Most studies on the effects of fragmentation on extinction–colonization dynamics have focused on patch size and isolation^{31–33} and both positive and negative biodiversity responses to fragmentation have been documented^{19,20}. Our results highlight that fragmentation at the landscape scale strongly mediates the relationship between colonization and percentage of forest and confirms that, as we

Table 1 | Covariates for explaining detection, colonization and survival probability

Covariate	Description	Spatial scale	Data source	Hypothesis
Detection (p)				
maxTemp	Maximum temperature of the month(s) when the camera trap was active	Local: camera-trap site	CRU-TS 4.03 (ref. 66) downscaled with WorldClim 2.1 (ref. 67)	H1 _p : mammals may be less active when it is too hot, thus decreasing p
Slope	Slope of the camera-trap site	Local: camera-trap site	R package elevatr ⁶⁸	H2 _p : p may be lower in camera-trap sites with higher topographical irregularity as the viewshed of a camera will be more restricted
Mass	Adult body mass	Species covariate	Ref. 69	H3 _p : large species may be easy to photograph ⁷⁰ , however, they have large home range sizes and low population densities, thus, p may be lower than for small species
Colonization (γ)				
percForest	Percentage of forest pixels in the buffer	Local: 300/600/2,100 m buffer around each camera-trap site	Ref. 3	H1 _γ : forests provide habitat for many species and γ may be high in camera-trap sites with high percentage of forest cover
Div	Probability that two random pixels in the landscape are not situated in the same forest patch	Landscape: 10 km buffer around camera-trap array	Ref. 3	H2 _γ : γ may be low if the landscape is fragmented (low dispersal capacity, high probability of being killed by humans)
Pop	Number of people per km ²	Landscape: 10 km buffer around camera-trap array	2022 Global Human Settlement data ⁷¹	H3 _γ : γ may be low if landscape-scale human pressure is high (hunting pressure, road kills and so on)
percForest×Div	Interaction between percentage of forest and division index	Local and landscape	Ref. 3	H4 _γ : γ may be high if local-scale habitat availability is high and landscape-scale habitat is low
percForest×Pop	Interaction between percentage of forest and human population density	Local and landscape	Ref. 3; 2022 Global Human Settlement Layer ⁷¹	H5 _γ : γ may be high if local-scale habitat availability is high and landscape-scale human population density is low
Survival (ϕ)				
percForest	Percentage of forest pixels in the buffer	Local: camera-trap site	Ref. 3	H1 _φ : forests provide habitat for many species and ϕ may be low in camera-trap sites with low forest cover
distPA	Euclidean distance from the camera-trap site to the PA edge ^a	Local: camera-trap site	World Database on Protected Areas ⁷²	H2 _φ : ϕ may be low in camera-trap sites near the PA edge
distBuiltUp	Euclidean distance from the camera-trap site to the closest built-up area	Local: camera-trap site	2022 Global Human Settlement Layer ⁷³	H3 _φ : built-up areas include roads and settlements (human access) and thus ϕ may be low in camera-trap sites near built-up areas
Pop	Number of people per km ²	Landscape: 10 km buffer around camera-trap array	2022 Global Human Settlement Layer ⁷¹	H4 _φ : ϕ may be low if landscape-scale human pressure is high (hunting pressure, road kills and so on)
distPA×Pop	Interaction between distance to PA edge and human population density	Local and landscape	World Database on Protected Areas ⁷² ; 2022 Global Human Settlement Layer ⁷¹	H5 _φ : ϕ may be low in sites near the PA edge, especially if landscape-scale human population density is high
distBuiltUp×Pop	Interaction between distance to built-up areas and human population density	Local and landscape	2022 Global Human Settlement Layer ^{71,73}	H6 _φ : ϕ may be low in sites near built-up areas, especially if landscape-scale human population density is high

^aFor Manaus we calculated the Euclidean distance to the closest edge between forest and non-forest as a PA edge was not available.

would suspect (H4_γ, Table 1), the probability of a site being colonized is highest when local-scale forest cover is high and landscape-scale fragmentation is low.

Survival probability

We found that distance to the edge of the PA had a strong positive effect on local survival of specialists. This means that a site that was occupied in a given year was more likely to be occupied the next year if it was far from the PA edge, where forest cover is usually more continuous and where human activities, such as hunting, are lower (H2_φ, Table 1). The strongest positive effects of distance to PA edge on colonization were found for generalist species such as jaguars (*Panthera onca*) which may reflect specific factors: in the case of the jaguar, its high persecution

due to retaliatory hunting and the depletion of its main prey in areas accessible to humans^{34,35}. Generalist species had higher survival near the PA edge when human population density was low. Such species are flexible and have broad habitat preferences and may benefit from having access to forest edges and to alternative environments. For example, wild boars (*Sus scrofa*) can benefit from croplands where they find food resources³⁶. Nevertheless, the effect of distance to the PA edge on survival changed from negative to positive when human population density at the landscape scale increased thus supporting our hypothesis (H5_φ, Table 1). This indicates that generalists had a higher probability of surviving at the core rather than near the edge of PAs in regions with high human population density (mean survival probability for generalists near the PA edge decreased from 0.86 to 0.28 when comparing

PAs with low and high human population density, Fig. 3). This was for example the case for the Central American agouti or the Abbott's duiker (*Cephalophus spadix*), both heavily hunted species^{37,38}. These results suggest that, while the edges of PAs provide suitable habitat for species, human activities such as hunting may suppress these benefits. This is in line with previous research demonstrating that overhunting across the tropics reduces mammal abundances even inside PAs³⁹ and highlights that the establishment of PAs may not always reduce the negative impacts of human activities within their boundaries⁴⁰.

Differences within species groups

Aside from group level differences in how occupancy dynamics respond to anthropogenic stressors, we also found substantial variation among species. The highest within-group variation was observed in the responses to human population density and fragmentation. The effects of fragmentation on biodiversity remains unclear, with studies reporting both negative and positive effects^{19,20,41}. We therefore expected to find variation across species regarding the effect of division index on colonization probability. Generalist species showed the strongest variation, with the northern tamandua (*Tamandua mexicana*) showing a strong positive response to fragmentation, a finding that has been previously attributed to easier access to food resources such as ants or termites in fragmented landscapes⁴². Specialists, although to a lesser degree, also exhibited variation among species. For example, colonization probability in fragmented landscapes was lowest for the Central American agouti and highest for the white-nosed coati. Even though according to our classification the coati is considered as a forest-dependent species, research has demonstrated that it can use and even inhabit anthropogenic landscapes⁴³.

Some variation in species responses to human population density probably reflects hunting preferences. Hunters generally target larger species rather than species with specific habitat preferences^{44,45}. Socio-cultural beliefs or practices can also contribute to explain variation in species responses to human population density⁴⁶. We therefore suspect that body mass and other potentially desirable traits in the contexts of the neighbouring human cultures, may help to characterize differences between species when assessing the effect of human population density on occurrence dynamics. We found the strongest significant negative effect of human population density on colonization for ocelots (Fig. 4), a species that is persecuted due to human–predator conflicts and fur trade^{47,48}. By contrast, colonization in sun bear was positively related to human population density. Similar results were found in Borneo, where sun bears thrived in human-modified forests, when hunting pressure was low⁴⁹. We detected the strongest positive effect of human population density on survival in wild boars, which are less hunted in some tropical forests of Southeast Asia because of religious taboos⁵⁰, potentially explaining their high survival probability in areas with high human population density. Variation can also be explained by hunting methods, yet these patterns remain poorly investigated in tropical forests. For example, hunting with dogs is popular in some cultures and is known to selectively impact species such as armadillos (for example, *Dasypus novemcinctus*) or the common paca in Brazil⁵¹, as well as primates such as the colobus monkeys in the Udzungwa mountains of Tanzania⁵².

Other potential explanations for diverse responses include species-specific differences in resilience. For example, wild pigs (*Sus* spp.) have a high reproductive rate and are known to persist even when hunting pressure eliminates many other species that are slow to mature and reproduce^{46,53}. Other potential explanations include management activities by PA staff and species-specific conservation measures. For instance, previous research demonstrated that six national parks in Central and East Africa were effective in protecting certain species, such as forest duikers, from hunting pressure⁵⁴.

Despite differences between species groups and among species in the same group, we also found some common trends. All species

showed a positive relationship between colonization and forest cover, highlighting the importance of forest protection inside PAs. The same applied to the interaction between forest cover and forest fragmentation: all species (independent of habitat specialization) were more likely to colonize a site when forest cover was high and fragmentation at the landscape scale was low.

Conclusions

PAs are key for conserving tropical biodiversity and can slow and prevent severe biodiversity declines⁵⁵. Nonetheless, PAs comprise a fraction of the landscape and their conservation effectiveness may be affected by anthropogenic stressors acting at multiple scales including outside the PA itself. Here, we found that occurrence dynamics of medium-to-large terrestrial mammals inside protected tropical forests can be explained by the presence of humans and their activities at both the local and landscape scale. All these anthropogenic stressors are likely to increase, given growing human populations and consumption⁵⁶. Our results suggest that, where possible, PAs should be combined with wider measures aimed at decreasing large-scale forest fragmentation, for example by defending and increasing landscape connectivity through habitat restoration⁵⁷. Additionally, our findings suggest that forest protection and restoration should be especially emphasized to preserve populations of habitat specialists, while strategies aiming at diminishing the impacts of human activities (for example, enforcement of hunting regulations) should be especially prioritized to safeguard habitat generalists. While these conclusions followed expectations, it is reassuring to see them reflected in global patterns. What may be more unexpected and challenging is the variation among species in their response to anthropogenic stressors. This highlights the importance of further detailed species-level assessments to inform effective conservation strategies.

Methods

Camera-trap data

We used camera-trap data from 16 PAs in three biogeographic regions (Fig. 1 and Supplementary Table 3). Although IUCN management category is not available for all PAs included in this study, most are classified under category II (national park; Supplementary Table 3). We highlight that this classification does not capture the type or effectiveness of the management implemented in the PA but the official purpose of the protected area. Data were collected by the Tropical Ecology Assessment and Monitoring (TEAM) Network following a standardized camera-trapping protocol⁵⁸. TEAM camera-traps are deployed at 60–90 sites in each PA at a density of about one camera per 2 km², although this density was lower in two PAs (one camera per km²). Mean distance between cameras was 1.32 km (s.d. = 0.19 km). Camera-traps were active for ~30 days during the dry season although some were active for less than 30 days due to damage or failure (mean = 36.16, minimum = 0, maximum = 80). Species accumulation curves indicate that this sampling effort was enough to detect most of the species in the community at each PA (Supplementary Fig. 11). Data were collected between 2008 and 2017 although the number of years varied per PA (minimum, 2 yr; maximum, 10 yr; mean = 6.5 yr). Here, we excluded camera-trap sites with inconsistencies in the date–time stamps and thus analysed data from 1,002 camera-trap sites (mean number of sites per PA, 62.63; minimum, 60; maximum, 89). Further details on the field methods can be found in Supplementary Methods 1.

Dynamic multispecies occupancy model

We used a hierarchical Bayesian dynamic multispecies occupancy model to describe species occurrence as a result of two underlying processes, colonization and survival²⁶. We modelled colonization and survival probabilities as a function of covariates representing anthropogenic processes and impacts (see below). As in single-season occupancy models, the ecological process is related to the latent ecological

state (true occurrence, z) and the observation process to the observed data (detections/non-detections, y). In dynamic occupancy models two temporal scales are considered. Species occupancy at a given site (here each camera trap) is described for each primary period while the detection of a species is described for each secondary session within a primary period. In addition, dynamic occupancy models describe the changes in species occupancy among primary periods. Here, primary periods refer to seasons and secondary sessions to sampling occasions. A season was composed of up to five sampling occasions and we defined each sampling occasion as seven consecutive camera-trap nights^{16,41}. An important assumption of this model is that the system is closed within a season, meaning that the occupancy of a site remains unchanged among sampling occasions of the same season. The number of days during which a system is considered to be closed depends on species characteristics such as dispersal or generation time⁵⁹. Here, we conservatively used a maximum of five sampling occasions per camera-trap site (35 camera-trap days) to ensure that the closure assumption was met. Another characteristic of dynamic occupancy models is that changes in occupancy are modelled as a first-order Markov process: the probability of a camera-trap site being occupied in a given year, depends on the occupancy state of the camera-trap site in the previous year, thus accounting for temporal correlation⁶⁰. We did not account for the fact that colonization probabilities can be a function of the occupancy state at neighbouring camera-trap sites (a camera-trap site is more likely to be colonized if more of its neighbours were occupied the previous year), the distance among camera-trap sites, as well as species dispersal capabilities⁶¹.

We treated the regression parameters of each species as random effects, meaning that species-specific parameters were drawn from a group-specific distribution, with hyperparameters to be estimated (see below for the definition of our species groups). As we estimated parameters at the global level, not at the PA level, we drew parameters from two (one for each species group) global-level distributions. This allowed us to reduce uncertainty around species-specific estimates as there were more data available than if we had used a community-level distribution (PA level in our case) which is commonly done in studies from a single study area. We provide the formula for the random effects below.

We wished to compare habitat specialists versus habitat generalists thus we used habitat breadth information to classify species into specialists or generalists. Habitat breadth represents the number of IUCN suitable habitat types occupied by a species²⁷. We defined specialists as those species with habitat breadth lower than or equal to the median (species with habitat breadth values between 1 and 4) and habitat generalists as those species with habitat breadth higher than the median (habitat breadth values between 5 and 26). As a pragmatic choice we used the median to classify species into groups as this yielded sufficient species in each group (Supplementary Fig. 10). Note that in our classification, specialists are not restricted to one type of habitat but rather occupy a lower number of habitat types than the generalists. Additionally, our classification is not limited to forest habitat categories only; however, given that all PAs are located in well-preserved forests (regardless of surrounding habitat), forest is listed as an IUCN habitat category for all but two of the species (*Crocota crocuta* and *Hystrix africaeustralis*).

For the first year, true occurrence of species k at site i , year 1, protected area p and biogeographic region b (z_{i1kpb}) is drawn from a Bernoulli distribution:

$$z_{i1kpb} \approx \text{Bernoulli}(\psi_{i1kpb})$$

where ψ_{i1kpb} represents the occupancy probability.

For all subsequent years ($t > 1$), true occurrence of species k at site i , year t , protected area p and biogeographic region b (z_{itkpb}) is also represented by a Bernoulli trial and depends on whether the site

was occupied or not the previous year ($t - 1$) and on the survival and colonization probability:

$$z_{itkpb} | z_{it-1kpb} \approx \text{Bernoulli}(z_{it-1kpb} \times \phi_{ikpb} + (1 - z_{it-1kpb}) \times \gamma_{ikpb})$$

where the survival probability ϕ_{ikpb} is the probability that an occupied site i during year $t - 1$ remains occupied during year t , while the colonization probability γ_{ikpb} is the probability that an unoccupied site i during year $t - 1$ becomes occupied by species k during year t .

Finally, in the observation process, detection of species k for occasion j at site i , year t , protected area p and biogeographic region b is drawn from a Bernoulli distribution:

$$y_{ijt kpb} \approx \text{Bernoulli}(z_{itkpb} \times p_{itkpb})$$

where p_{itkpb} represents the detection probability and is conditional on the site being occupied, that is, $z_{itkpb} = 1$.

Covariates on detection

We modelled detection probability with logistic regression using maximum temperature (maxTemp), slope and species body mass (Mass) as covariates (see Table 1 for hypotheses and Supplementary Methods 2). We calculated the two spatial covariates (maxTemp and Slope) for each camera-trap site and maxTemp varied among seasons because climate data with a higher temporal resolution (variation across sampling occasions) was not available at the desired spatial scale:

$$\text{logit}(p_{itkpb}) = \alpha p_k + \beta p_{1k} \times \text{maxTemp}_{itpb} + \beta p_{2k} \times \text{Slope}_{itpb} + \beta p_{3k} \times \text{Mass}_k$$

Where the intercept (αp) is the species-specific intercept defined as $\alpha p_k \approx \text{Normal}(\mu, \sigma^2)$, μ is the mean at the global level and σ^2 the variance around that mean, also at the global level. The species-specific coefficients (βp) describe the relationship between detection probability and covariates. Values βp_1 and βp_2 were also sampled for each species from global-level normal distributions.

Covariates on colonization and survival

We modelled colonization (γ) and survival (ϕ) probability as functions of both local- and landscape-scale covariates. We included two-way interactions between covariates at different scales to assess whether the effect of local-scale covariates on colonization and survival changed, depending on landscape context. We included interactions on the basis of our hypotheses (Table 1):

$$\text{logit}(\gamma_{ikpb}) = \alpha \gamma_k + \beta \gamma_{1k} \times \text{percForest}_{itpb} + \beta \gamma_{2k} \times \text{Div}_{itpb} + \beta \gamma_{3k} \times \text{Pop}_{itpb} + \beta \gamma_{4k} \times \text{percForest}_{itpb} \times \text{Div}_{itpb} + \beta \gamma_{5k} \times \text{percForest}_{itpb} \times \text{Pop}_{itpb}$$

$$\text{logit}(\phi_{ikpb}) = \alpha \phi_k + \beta \phi_{1k} \times \text{percForest}_{itpb} + \beta \phi_{2k} \times \text{distPA}_{itpb} + \beta \phi_{3k} \times \text{Pop}_{itpb} + \beta \phi_{4k} \times \text{distBuiltUp}_{itpb} + \beta \phi_{5k} \times \text{distPA}_{itpb} \times \text{Pop}_{itpb} + \beta \phi_{6k} \times \text{distBuiltUp}_{itpb} \times \text{Pop}_{itpb}$$

where $\alpha \gamma$ and $\alpha \phi$ are species-specific intercepts and $\beta \gamma$ and $\beta \phi$ are species-specific coefficients describing the relationship between colonization/survival probability and the covariates. Species-specific parameters (intercepts and coefficients) were drawn from two group-specific normal distributions: $\alpha \gamma_k \approx \text{Normal}(\mu_g, \sigma_g^2)$, where μ_g is the group-specific mean at the global level and σ_g^2 the group-specific variance around that mean, also at the global level. Due to data limitations and an already complex model, we did not allow survival and colonization probabilities to vary over time for a given species in a given site. Nonetheless, occupancy could change over time as it emerged from vital rates and past occupancy states.

We used two habitat-related covariates reflecting forest loss and forest fragmentation: percentage of forest and division index. Division index is defined as the probability that two randomly selected pixels in the landscape are not situated in the same forest patch. Additionally, we used three covariates representing human pressure: distance to protected area edge, distance to built-up areas and human population density (Table 1 and Supplementary Methods 2). We also explored data representing management effectiveness of the PAs such as the ‘management effectiveness tracking tool’⁶² but this information was unavailable for six PAs. We calculated percentage of forest (percForest), distance to protected area edge (distPA) and distance to built-up areas (distBuiltUp) at the local scale and division index (Div) and human population density (Pop) at the landscape scale.

We defined the local scale to calculate percentage of forest as a circular area of analysis or ‘buffer’ around each camera-trap site (Fig. 1) and selected the size of the buffer based on the home range sizes of the species included in this study (Supplementary Methods 3 and Fig. 12). To avoid misunderstanding from double meanings, we use the term ‘buffer’ to represent a conceptual area considered in the analysis and it does not relate to any specific area of management. We used a 300 m radius buffer for species with a small home-range size, 600 m radius for species with a medium home-range size and 2,100 m radius for species with a large home-range size. We excluded elephant species (*Loxodonta Africana* and *Elephas maximus*) because their large body and home-range sizes would require using a large buffer to assess the effect of forest cover on colonization and survival at the appropriate local scale. We used different buffer sizes to assess the effect of local-scale covariates on occupancy dynamics to facilitate comparison between species with different area requirements and home range sizes. We note, nonetheless, that the biological interpretation of ‘occupancy’—and thus local survival and colonization driving its dynamics—may differ across species. It may also be impacted by differences in camera-trap density across PAs (as mentioned above, two PAs were sampled at a density of one camera per km²). Specifically, for species with large home ranges and high dispersal capabilities, in combination with smaller camera trap spacing, occupancy may more closely represent use rather than occurrence⁶³. For distance to protected area edge and distance to built-up areas, we calculated the Euclidean distance from the camera-trap site to the protected area edge and closest built-up area, respectively.

To define the landscape scale, we created a 10 km buffer around each camera-trap array within a protected area (Fig. 1)²⁸. This buffer included both protected and unprotected area (Supplementary Fig. 1). In one PA, camera-traps were deployed in three separate clusters, with different landscape and anthropogenic characteristics (Manaus; Supplementary Fig. 1), thus resulting in three distinct (non-overlapping) landscape-scale buffers. In this case, we averaged the landscape-scale covariates across the three landscape-scale buffers and used the mean values in our models. To ensure that averaging values across landscapes did not unduly influence our results, we additionally run the same model considering each camera-trap array in Manaus as an individual PA. The β coefficients of this model remained similar and we decided to treat Manaus as a single PA (Supplementary Fig. 13). Human population density was defined as the average number of people living per km² in the 10 km buffer surrounding each camera-trap array.

The values of time-varying covariates (percentage of forest, division index, human population density and distance to built-up areas) remained fairly stable across years. Therefore, for these covariates, we used single values instead of time-matched covariates to avoid including repeated values (Supplementary Figs. 2–6). For habitat-related covariates (percentage of forest and division index) we used the mean value over the sampling years for each PA. For human-related covariates (human population density and distance to built-up areas), we used data from the year 2010 or 2015, depending on the average sampling year of each PA (Supplementary Table 4).

For the analysis, we transformed covariates with extreme values (log transformation for slope, body mass, human population density, distance to protected area edge and distance to built-up areas) and standardized them to 0 mean and 1 standard deviation. Further details on the calculation of the spatial covariates included in the detection, colonization and survival model are provided in Supplementary Methods 2.

Model fitting

We fitted our Bayesian model using Markov chain Monte Carlo (MCMC) methods and the R package nimble⁶⁴. We used NIMBLE default samplers except for the regression coefficients for γ and ϕ where we used a block sampling approach for each pair of α and β (random-walk block sampler with multivariate normal proposal in NIMBLE) to improve MCMC efficiency (effective sample size/MCMC run time).

We used uninformative or weakly informative priors (model code in Supplementary Methods 4). We ran six chains, each of 400,000 MCMC iterations and discarded the initial 80,000 iterations as burn-in. We visually inspected trace plots to assess convergence and mixing of the chains and calculated the Gelman–Rubin statistic for each parameter (R-hat values <1.1 indicated convergence)⁶⁵. To assess the effect of covariates on colonization and survival probabilities we used the mean of the posterior distribution and the associated 95% BCI of each β coefficient. We report estimates at the global level meaning that they correspond to mean β coefficients at global level instead of coefficients for each protected area. Modifying the sampling effort (number of years or camera-trap sites in each PA) should not affect β coefficients but their uncertainty (wider or narrower 95% BCI).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Covariates included in our model are based on publicly available data and extracted values are in a Figshare repository (<https://doi.org/10.6084/m9.figshare.21947300>), as well as the R script to subset and organize the data. The detection non-detection matrix is also available from Figshare and raw camera-trap data from the TEAM Network are available on the Wildlife Insights platform (wildlifeinsights.org).

Code availability

All code to reproduce the analysis has been archived on Figshare (<https://doi.org/10.6084/m9.figshare.21947300>).

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Author contributions

D.S. and R. Bischof accessed funding. A.S.P., D.S. and R. Bischof conceptualized the study. A.S.P. developed and performed the analyses. R. Bischof, P.D. and S.D. contributed to the analyses. A.S.P. wrote the manuscript with support from R. Bischof, D.S. and L.B. Camera-trap data collection in the TEAM study areas was carried out by D.S., J.A., E.A., R. Bitariho, S.E., P.A.J., M.G.M.L., E.H.M., B.M., F.R., F.S. and E.U. The manuscript was finalized by A.S.P., with input and approval from all authors.

Competing interests

The authors declare no competing interests.

Additional information

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Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a Confirmed

- | | | |
|-------------------------------------|-------------------------------------|--|
| ☐ | ☒ | The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement |
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| ☒ | ☐ | The statistical test(s) used AND whether they are one- or two-sided
<i>Only common tests should be described solely by name; describe more complex techniques in the Methods section.</i> |
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| ☐ | ☒ | A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons |
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| ☒ | ☐ | For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
<i>Give P values as exact values whenever suitable.</i> |
| ☐ | ☒ | For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings |
| ☐ | ☒ | For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes |
| ☐ | ☒ | Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated |

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection	Raw camera-trap data from the Tropical Ecology Assessment and Monitoring (TEAM) Network are available on the Wildlife Insights platform (wildlifeinsights.org). DeskTEAM is the dynamic software package developed by the TEAM network for processing camera-trap data. We used R to extract and calculate predictor covariates.
Data analysis	We used the R package NIMBLE to run our model. The model code is provided in the Supplementary information and the entire R script code to reproduce the analysis has been archived on Figshare .

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

Data

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All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

Covariates included in our model are based on publicly available data, and extracted values are in a Figshare repository, as well as the R script to subset and

organize the data. The detection non-detection matrix is also available from Figshare and raw camera-trap data from the TEAM Network are available on the Wildlife Insights platform (wildlifeinsights.org).

Human research participants

Policy information about [studies involving human research participants and Sex and Gender in Research](#).

Reporting on sex and gender

Population characteristics

Recruitment

Ethics oversight

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We used standardized camera-trap data collected by the Tropical Ecology Assessment and Monitoring (TEAM) Network where camera-traps are deployed in protected areas across tropical forests. In each protected area, camera-trap arrays cover a minimum of ~100 km ² , and cameras are deployed at a density of one camera per 2 km ² but this density is lower (1 camera per 1 km ²) for a few sites. Within each protected area, between 60 and 90 cameras are deployed sequentially in arrays of 20–30, rather than simultaneously (i.e., all 60/90 cameras at the same time). TEAM uses Reconyx camera-traps (models: HC500, HC600, PC800, PC900, RC55, RC60, RM45) which are distributed in a regular grid, and deployed close to animal trails and without using bait. In each deployment, cameras are active for a minimum of 30 consecutive days during the dry season (i.e., months with less than 100 mm average rainfall or the driest part of the year in the absence of dry season).
Research sample	All medium-to-large terrestrial mammal species (>1 kg) detected by the camera-traps (n = 159 species).
Sampling strategy	The sampling design for the TEAM Terrestrial Vertebrate Monitoring Protocol was carefully specified to maximize the probability of photographing an adequate sample of tropical forest terrestrial mammal and bird species. It was intended to monitor changes in the community of ground-dwelling, terrestrial vertebrates, and not to monitor the abundance of individual species. This is an important distinction. As such, the sampling design represents a compromise between the level of effort required to detect species that range over large areas (>100 km ²), and the effort required to detect species with smaller home ranges (~1 km ²). The design also accounts for sampling constraints in the field, which may vary in different parts of the world, and for the logistical trade-offs of cost versus effort.
Data collection	Camera-trap data across the 16 protected areas included in this study were collected by the TEAM network and following a standardized camera-trapping protocol. In each protected area, cameras were deployed at a density of one camera per 2 km ² but this density is lower (1 camera per 1 km ²) for a few sites. Within each protected area, between 60 and 90 cameras were deployed sequentially in arrays of 20–30, rather than simultaneously. Cameras were active for a minimum of 30 consecutive days.
Timing and spatial scale	Camera-trap data was collected during the dry season (i.e., months with less than 100 mm average rainfall or the driest part of the year in the absence of dry season) between 2008 and 2017, and each protected area was surveyed for a minimum of 2 years and a maximum of 10 years (mean = 6.5 years). In each protected area, camera-trap arrays covered a minimum of ~100 km ² , and cameras were deployed at a density of one camera per 2 km ² but this density was lower (1 camera per 1 km ²) for a few sites.
Data exclusions	We excluded camera-trap sites for which inconsistencies in the date-time stamps were found (i.e., detection day was before the camera-trap deployment day). We included a total of 1002 camera-trap sites.
Reproducibility	Camera-traps were successfully deployed in all sites. The initial deployment of some cameras in Barro Colorado Nature Monument - Soberania National Park failed and those sites were re-sampled later. This did not affect the analyses/results of our study.
Randomization	We classified detected species into two groups: habitats specialists and habitat generalists. We used habitat breadth information to classify species into specialists or generalists. Habitat breadth represents the number of IUCN suitable habitat types occupied by a species. We defined specialists as those species with habitat breadth values lower or equal than the median (i.e., species with

habitat breadth values between 1 and 4), and habitat generalists as those species with habitat breadth values higher than the median (i.e., habitat breadth values between 5 and 26). We used the median to classify species into groups as this allowed us to have sufficient data in each group, and note that in our classification, specialists are not restricted to one type of habitat, but occupy a low number of habitat types.

Blinding

Not applicable. Blinding was not relevant to the collection and compilation of these data. Experts identified the images and there were various cross checks and quality controls applied to ensure consistency.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions

Fieldwork was carried out during the dry season (i.e., months with less than 100 mm average rainfall or the driest part of the year in the absence of dry season). Average minimum temperature across all sites was ~19 °C and average maximum temperature across all sites was ~29 °C (WorldClim data).

Location

Location of the 16 protected areas is shown in the manuscript (Figure 1).

Access & import/export

TEAM managers from each protected area got the necessary permits for carrying out the fieldwork inside the protected areas. Samples were not imported/exported.

Disturbance

There were not disturbances caused in the protected areas.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

- | | |
|-------------------------------------|---|
| n/a | Involved in the study |
| ☒ | ☐ Antibodies |
| ☒ | ☐ Eukaryotic cell lines |
| ☒ | ☐ Palaeontology and archaeology |
| ☐ | ☒ Animals and other organisms |
| ☒ | ☐ Clinical data |
| ☒ | ☐ Dual use research of concern |

Methods

- | | |
|-------------------------------------|---|
| n/a | Involved in the study |
| ☒ | ☐ ChIP-seq |
| ☒ | ☐ Flow cytometry |
| ☒ | ☐ MRI-based neuroimaging |

Animals and other research organisms

Policy information about [studies involving animals; ARRIVE guidelines](#) recommended for reporting animal research, and [Sex and Gender in Research](#)

Laboratory animals

The study did not involve laboratory animals.

Wild animals

The study did not capture wild animals. We used camera-traps which is a non-invasive technique to monitor mammals.

Reporting on sex

Sex data was not collected in this study.

Field-collected samples

The study did not involve samples collected from the field.

Ethics oversight

Tropical Ecology Assessment and Monitoring (TEAM) Network, a collaboration between Conservation International, the Smithsonian Tropical Research Institute and the Wildlife Conservation Society.

Note that full information on the approval of the study protocol must also be provided in the manuscript.